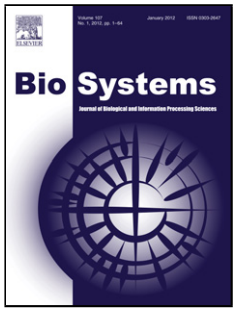

Title: A Systemic Approach for Modeling Biological Evolution using Parallel DEVS

Author: Daniel Heredia Victorino Sanz Alfonso Urquia Máximo Sandín

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Research highlights for the manuscript **A Systemic Approach for Modeling Biological Evolution using Parallel DEVS:**

- A non-neodarwinian systemic approach for modeling evolution is introduced
- Model aims to integrate new insights in modern biology and explore controversies
- A mathematical description of the model is used in computer simulation studies
- Two scenarios are used to constrast simulation results with the expected behavior
- Simulation results resemble the behavior expected from biological systems

A Systemic Approach for Modeling Biological Evolution using Parallel DEVS

Daniel Heredia[a,1], Victorino Sanz[b,*], Alfonso Urquia[b], Máximo Sandín[c,2]

[a] *Biocore S. Coop., Biological Cooperative Research, Zurbarán, 16, 28450, Collado Mediano, Madrid, Spain*
[b] *Department of Computer Science and Automatic Control, UNED, Juan del Rosal, 16, 28040, Madrid, Spain*
[c] *Department of Biology, UAM, Darwin, 2, Campus Cantoblanco, 28049, Madrid, Spain*

Abstract

A new model for studying the evolution of living organisms is proposed in this manuscript. The proposed model is based on a non-neodarwinian systemic approach. The model is focused on considering several controversies and open discussions about modern evolutionary biology. Additionally, a simplification of the proposed model, named EvoDEVS, has been mathematically described using the Parallel DEVS formalism and implemented as a computer program using the DEVSLib Modelica library. EvoDEVS serves as an experimental platform to study different condition and scenarios by means of computer simulations. Two preliminary case studies are presented to illustrate the behavior of the model and validate its results. EvoDEVS is freely available at `http://www.euclides.dia.uned.es`.

Keywords: Evolution, Simulation, Modelica, Punctuated Equilibria, Evolutionary Potentiation.

*Corresponding author. Tel: +34 91 398 9469.
Email addresses: `daniel.heredia@biocore.es` (Daniel Heredia), `vsanz@dia.uned.es` (Victorino Sanz), `aurquia@dia.uned.es` (Alfonso Urquia), `maximo.sandin@uam.es` (Máximo Sandín)
[1] Also with Laboratorio de Poblaciones del Pasado, Department of Biology, UAM
[2] Retired Professor.

1. Introduction: Current Questions in Evolutionary Biology

Evolution is a central topic for life sciences. Evolutionary biology provides a general framework for the understating of biodiversity through time, from remote past to the present day. It roots into the actual bases of every biological discipline and tries to interconnect thereof coherently.

Along the last half of the past century, evolutionary biology has been consolidated on the bases of the modern neodarwinian synthesis. Perhaps the most essential and widespread notion in the classical neodarwinian synthesis is that the evolutionary process can be explained by the main action of natural selection over populations, which contain a high degree of genetic variation due to random mutations occurring in individuals. This variation spectrum can be defined as mainly continuous, conspicuous, heritable and not unbalanced nor directed by environmental factors. As competition for limited resources (i.e., food or mates) compromises the survival of individuals, natural selection favors the reproduction of the fittest. As genes determine fitness, genetic frequencies change gradually over time as the population continuously adapt to present conditions. So, almost all evolutionary transitions, with the exceptions of genetic drift and sexual selection processes, can be explained in those terms according to the synthesis proposals.

Many extensions and complementary approaches have been proposed to classical neodarwinian synthesis in the last decades (for example, (Koonin, 2009; Eldredge, 1997; Kutschera and Niklas, 2004)). At the same time, an increasing number of phenomena have introduced several controversies and open discussions when observed from the point of view of classical neodarwinian synthesis and, consequently, new directions in evolutionary biology are being explored. A summary of these topics is presented next:

- Reticulated phylogenies are now the norm rather than the exception in the main branches of life; including lateral gene and transposon transfer (Dagan et al., 2008; Schaack et al., 2010; Crisp et al., 2015), hybridization (Arnold, 2008; Amaral et al., 2014), phyletic introgression (Baack and Rieseberg,

2007; Carrión García and Cabezudo, 2003), incomplete lineage sorting (Lönnig and Saedler, 2002; Shedlock et al., 2004), symbiosis (Sapp, 2010; Margulis, 2000; Brucker and Bordenstein, 2012) and viral genomes acquisition (Oliver and Greene, 2012; Mindell et al., 2004; Villarreal, 1999; Hunter, 2010). In a broad scale, the validity of the darwinian tree of life metaphor is being questioned (Raoult, 2010; O'Malley, 2012; Bapteste et al., 2009; Koonin, 2009).

- Fossil record is non-continuous in nature and hardly harmonizes with classical neodarwinian speciation models, but it is well defined by the punctuated equilibrium theory (Gould and Eldredge, 1993; Eldredge and Gould, 1972). That is to say, paleospecies remain unchanged along several, one to ten, millions of years and are suddenly replaced by new ones (Gould, 2004).

- Relevant macroevolutive changes for several groups can be more parsimoniously explained by macromutations than by gradual microevolutive accumulation (Theissen (2009)Rieppel (2001),Erwin (2000a)). Although macromutation is neglected by classical neodarwinism (the infamous hopeful monsters of Richard Goldschmidt), some authors have appel to recognize its importance in the evolutionary discussion (Dittrich-Reed and Fitzpatrick, 2013; Brucker and Bordenstein, 2012; Erwin, 2000a; Jablonka and Lamb, 2008; Muller and Newman, 2005; Theissen, 2009, 2006).

- Comparative genomics and cytogenetics strongly suggest that macromutational events (regulatory top-hierarchic mutations, symbiosis, chromosome rearrangements, genome duplications, etc.) have had relevant impact in macroevolutionary trajectories of some groups (Dittrich-Reed and Fitzpatrick, 2013; Sapp, 2010; Theissen, 2009; Erwin, 2000b; Ronshaugen et al., 2002; Davidson and Erwin, 2006).

- There is a reasonable coupling between major extinction events and biodiversity radiations, that modern synthesis reduces to niche availability liberation, although mutational acceleration is tenable but not broadly ac-

cepted (Erwin, 2000a; Oliver and Greene, 2011, 2012; Rando et al., 2007). Radiations (including true explosions as Cambrian, Devonian or Ordovician ones) show fast diversification of closely related organizations but complicated taxonomic resolution, including early reticulation and nearly simultaneous divergence, that do not harmonize with classical slow dichotomic models (Nishihara et al., 2009; Carrión García and Cabezudo, 2003; Droser and Finnegan, 2003; Schmitz et al., 2007).

- The contemporary advances in the knowledge of biological systems information networks demand a revisitation of classical population genetics. Genomes are now seen as complex, non-linear, systems with several control levels of regulation and expression, including alternative splicing and promoters, epigenetic signals, etc (Maher, 2012; Ecker, 2012; Blencowe, 2006; Jablonka and Raz, 2009a). Organism information is now, by definition, contextual. It depends of the genetic and epigenetic background in an ongoing dialogue with the surrounding environment (Heredia, 2012; Laland et al., 2008; Gilbert and Epel, 2009).

- Biological networks, both cellular and ecological, have complex structural properties that confronts linear causality and determinism for single gene traits inheritance, species interactions and selection (Brown et al., 2001; Petanidou et al., 2008; Gerke et al., 2010; Davidson, 2010; Goldenfeld and Woese, 2011).

- Biological systems are robust in extreme due to internal molecular mechanisms, epigenetic canalization, modularity and network structure (Gilbert and Epel, 2009; Kitano, 2004, 2002). Much of the mutational variation in organisms never manifest in the phenotype, so there is not a conspicuous continuum of variation that is available for natural selection. This situation is refereed as the *robustness paradox* (Gilbert and Epel, 2009). To stress, although robustness is pervasive, it can be punctually broken under environmental and cytological perturbation (Kitano, 2004; Gilbert and Epel, 2009; Shapiro, 2010).

- Several variation phenomena are neolamarckian-like, that is to say, not purely random but triggered by environmental and/or inner signals (Feil, 2006; Gissis and Jablonka, 2011; Koonin and Wolf, 2009; Por, 2006; Sano, 2010). For example, some methylation marks on chromatin are selectively added and removed as a systemic response to environment signalling (e.g., nutrition, light exposure and toxins), setting up genetic expression patterns that can be inherited across few to several generations (Whitelaw and Whitelaw, 2008; Henderson, 2007; Jablonka and Raz, 2009b). Moreover, the epigenetic deregulation and activation of mobile elements and endogenous retroviruses under stressful conditions (i.e., chemical, physical or biological), induces transposition bursts in genomes by means of amplification and targeted integration. These responses are more or less specifically located (Casacuberta and González, 2013; Zeh et al., 2009; Oliver and Greene, 2011; Tsukahara et al., 2009; Shapiro, 2010; Sandmeyer, 1998; Bushman, 2003). To stress, mobile elements compromise for a major part of the eukaryotes genomes and have largely configured its evolution (Kazazian, 2004; Fedoroff, 2012; Böhne et al., 2008; Bergman et al., 2006; Lynch et al., 2011; Oliver and Greene, 2011). Lastly, other phenomena as mutational capacitors, targeted mutation, prion infections and, specially, viral transfections and lateral genetic transfers (these ones with an enormous role in, at least, prokaryote evolution), are highly responsive to stress and environmental signals (Erwin, 2000b; Jarosz and Lindquist, 2010; Halfmann and Lindquist, 2010; Frost et al., 2005).

- As the previous biological mechanisms are relevant for evolution and are environmentally triggered or facilitated, new traits do not strictly arise as individual (isolated) innovations, as predicted by neodarwinism, but can recurrently occur or be acquired by several individuals along time and population size (Cho et al., 2008; Cullis, 2005; Bergman et al., 2006).

- Non adaptive processes and tendencies, relevant to explain organization and evolution of life, including self-organization and complexity growth, do

not need to be causally explained by selection, but despite of it (Karsenti, 2008; Lansing, 2003).

- Finally, neodarwinian theoretical apparatus drags some important semantic, mathematical and epistemological issues to be considered (Abdalla, 2006; Lewontin, 1972; Bosco et al., 2012). As some authors have recurrently proposed, darwinism terminology is anthropocentric, unbalanced and many terms still need to be conveniently defined (Carrión, 2003; Abdalla et al., 2010; Margulis, 2002; Sandín, 2005). The selection argument that is central to many hypothesis is considered as not veritable itself, and it must support speculative narrations impossible to prove or to false (Gould and Lewontin, 1979; Lewontin, 1972). According to Karl Popper, Darwinism would be considered not as a scientific theory but a metaphysical research program (Popper, 1982) and, according to Von Bertalanffy and others, its success in society and life sciences must be understood regarding to its sociological background (Gould, 1978). Moreover, as suggested by Bosco and colleagues using simulation models, the use of the Hardy-Wienberg equilibrium as nule hypothesis for classical population genetics does not contemplate long term oscillations and could have introduced false results in many studies, and the literature must be revisited (Bosco et al., 2012).

  To give an unifying answer to many of the previous controversies it has been strongly suggested the necessity to adopt an integrative and systemic focus for a new evolutionary approach. "Evolutionary Systems Biology" (ESB) is an emerging field within evolutionary biology that looks at the properties of complex biological systems from a classical evolutionary biology perspective (Loewe, 2009; Soyer, 2012).

In agreement with this systemic approach but in distance with the classical notions and concepts of the neodarwinian synthesis, a new formalized model is introduced in this manuscript. With this model we attempt to create a versatile tool for the study of evolutionary scenarios under conditional mutation

and survival rules, and specially, to explore how the model behaves in reference to some of the previous issues (radiation-extinction coupling, evolutionary potentiation, macromutation) and if this behavior coincides with the expected theoretical scheme, providing logical validation.

The formalized mathematical model, named EvoDEVS, constitutes a coherent simplification of biological systems and its evolutionary dynamics in consequence to the main topics of the theoretical model, for experimentation across different conditions and scenarios by means of computer simulation. This study attempts to improve the development and validate the inner logic of the theoretical model. EvoDEVS represents a two-dimensional space that contains a population of living organisms. The space, the organisms, their life cycle and their relationships are described using the Parallel DEVS formalism (Chow, 1996). Parallel DEVS allows a hierarchical and modular description of systems whose components are represented by describing their behavior or their structure (i.e., relationships between components). Thus, the use of Parallel DEVS facilitates the description of the organisms, their behavior and evolution, and the relationships among them and their environment. EvoDEVS has been implemented using the DEVSLib library (Sanz et al., 2010), that supports the description of Parallel DEVS models in Modelica (Modelica Association, 2014).

The structure of the manuscript is as follows. The theoretical model and its components are introduced in Section 2. A short introduction to the Parallel DEVS formalism is included in Section 3, in order to facilitate the comprehension of the EvoDEVS model. The EvoDEVS model is detailed in Section 4 and the experiments performed with the model are described in Section 5. Finally, some conclusions and future work ideas are given in Section 6.

2. Systemic Approach to Evolutionary Biology

Several authors have already proposed relevant hypothesis trying to complete, update or extend the modern synthesis using complementary approaches dealing with the previous controversies (Shapiro, 2011, 2010; Jablonka and Raz,

2009b; Oliver and Greene, 2011; Zeh et al., 2009; Sagan and Margulis, 2003), but currently there is not an integrated proposal trying to conciliate those facts as an ensemble. In this scenario, and based in previously proposed theoretical framework (Evolution by Complex Systems Integration (Sandín, 1995, 1997, 2002; Sandín et al., 2003; Sandín, 2006)) a new model is proposed in this manuscript to try to face the complex problems in the evolutionary biology and integrate complementary views to coherently reincorporate and conciliate saltative and neolamarkian evolution with the current state of biological knowledge.

This theoretical model uses a systemic approach, and aims for biological systems evolution. The main components, propositions and definitions of this model can be summarized in the following points (for an extended argument, see (Heredia, 2014)):

1. **Biological systems (not genes nor species) are the main subjects and objects of study.** These are described as complex adaptive[3], hierarchical, dissipative systems[4] defined by a *biological organization* (see below) which exhibit thermodynamic meta-stability[5] through entropy importation; establish material, energetic and informational exchange with the surrounding environment; and accomplish with the following properties: robustness, modularity, self-organization, self-reproduction, canalization and networked structure. Moreover, *biological systems* is a scalable and hierarchical category that ranges from biochemical networks to global ecosystems.
2. **Biological organization defines any biological system and compromises its evolution.** Biological organization is defined as the sum of

[3]Complex adaptive systems are interactive sets of elements working as a unit, that establishes exchange fluxes of matter, energy and information with the surrounding environment and adapts to ongoing changes and exhibit emergent properties.

[4]Dissipative systems are open systems that self-organize itself into structures that enhances the dissipation of thermodinamical gradients.

[5]Meta-stability is the maintenance of a dynamical but stable state through a continuous compensating process, i.e, as the flame of a lighter feed by combustion.

structure (biological network topologies and system properties), *functions* (information expression algorithms) and an *emerging program* (ecological succession or life cycle). Biological organizations can be ideally seen as attractors in a representation space, stable states rounded by an attraction field (robustness), and the trajectory from an attractor to another one can be understood as an evolutionary transformation.

3. **Biological information workflows are mainly non-linear and follow a bidirectional scheme named *organism-environment feedback*.** Biological information circulates trough three related channels: genetic, epigenetic and environmental information field (Heredia, 2012), as described in Fig. 1. So, biological systems are informationally open and can decode information inputs from the environment. The biological systems organization can change actively in response to stimulus, by means of genetic and epigenetic modification, but also by establishing symbiosis, lateral transfer and viral integration (understood as organic environment assimilation).

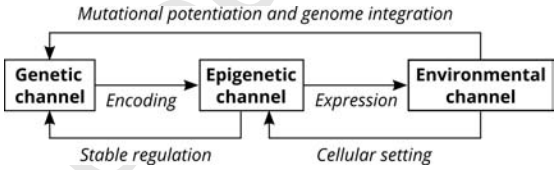


Figure 1: Biological information workflows scheme.

4. **Evolutionary epigenesis, or novelties production, are not purely random and its occurrence is defined by several mechanisms summarized in three vectors .** These vectors are named: *restrictions* (internal: constructional constrains, external: niche accessibility and suitability); *historical contingency and inheritance*; and *promotions* (probabilistic imbalances in time or/and loci, due to epigenetic and genetic potentiation). Consequently, not all changes are equally possible nor viable, and evolutionary solutions are not a continuum but constrained to limited putative stable states.

5. **There are three possible demographical processes for homogenization and stabilization of new traits and organizations, that depend on initial dimensions in phenotypic degree and evolutionary active population size.** Vectorial epigenesis defines a continuum for phenotypic degree (potentially, from slight modifications to deep macromutational leaps) but a punctuated phenotypic space (with just a limited number of solutions defined by the promotion, restriction and contingency vectors); and allows reiteration of changes in several similar systems, with an homologous history and organization when exposed to the same stimulus. Consequently, the stabilization of new organizations or traits can succeed different patterns according to the initial conditions: *isolated* (one event, just slight changes permitted in sexual organisms), *coordinated* (several concurring compatible events, no leaps restriction), and *reticulated* (one or more infective or hybridization events, selectively leaps restrictions). See Fig 2.

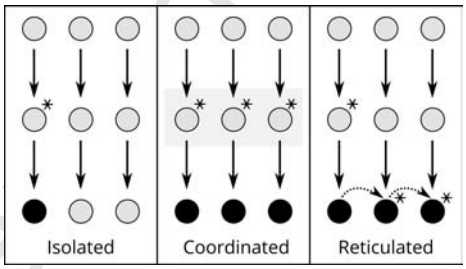


Figure 2: Patterns for new organizations. Arrows shows inheritance and stars points novelties arising.

6. **Evolutionary epigenesis (4) and demographical processes (5) can be included in an evolutionary dynamic, that harmonizes with both palaeontological and neontological data.** According to the punctuated nature of the fossil record and the robustness paradox, it is proposed that the evolution of biological systems switch from a *dynamical stability regime* (stable states protected by robustness in which systems

explore and accommodate its limits in resonance to environment); to an *evolutionary pulse regime* (highly creative and unstable states defined by lost of robustness and boosted mutational change) under stressful conditions or stimulus (including starvation, physiological shock, cytogenetic unbalances as hybridization, viral or transposon integration, etc.). As a result of these pulses, previous organizations can diversify, by nearly simultaneous bifurcation, into new stable related ones, that can persist due to demographic processes of stabilization (specially under coordinated and reticulated patterns), or perish in a masked extinction (increased infertility and abortive states due to a overlap of the promotion and restriction vectors). See now Fig. 3.

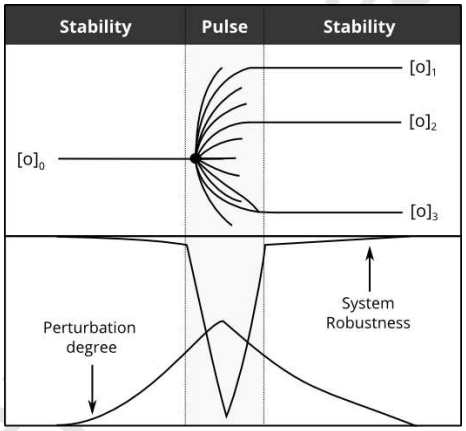


Figure 3: Regimes for evolution of biological systems.

7. **This evolutionary dynamic is highly homeomorphic to dissipative systems dynamics and predicts an escalated increase in complexity across the evolutionary trajectories.** Dissipative systems, including biological systems, can qualitatively evolve, self-organize and increase its complexity when pushed into a bifurcation point, due to the switch from a nearly dominant negative feedback regime to a positive one. That statement will be valid for inorganic systems (i.e., Bénard cells) and biological systems (according to the previous propositions). So, with some

organizational leaps, organizations can increase its complexity acquiring more information and minimizing its entropy, adding differentiated nodes, links, functions, hierarchical levels and modules to its structures, as predicted by the mechanisms underlying the vectorial epigenesis. Consequently, the increase in complexity is not linear but episodic, and tends to explore new freedom degrees for each canonical type of organization.

In order to study the behavior and logical consistency of the proposed theoretical model a coherently simplified computer simulation model has been developed. The formal specification of such model, according to the Parallel DEVS formalism, and the preliminary results obtained are presented in the following sections.

3. Introduction to the Parallel DEVS Formalism

Parallel DEVS is a discrete-event system modelling formalism (Chow, 1996; Zeigler et al., 2000; Wainer, 2009). Models in Parallel DEVS can be described behaviorally (named *atomic*) or structurally (named *coupled*). Atomic models are the smallest component that can be used to describe the behavior of a system. Their behavior is described by means of functions used to modify the state of the model after receiving external events (i.e., received as inputs through the ports of the interface) or internal events (i.e., self-triggered). Coupled models are composed of a combination of interconnected atomic or coupled models. Thus, Parallel DEVS allows a hierarchical and modular description of models.

Parallel DEVS constitutes a general purpose discrete-event modeling formalism that can be used to describe models in multiple domains or using multiple methodologies. Other formalisms can be described in terms of Parallel DEVS (Vangheluwe, 2000).

Formally an atomic Parallel DEVS model is described by a tuple of eight elements:

$$M = (X_M, S, Y_M, \delta_{int}, \delta_{ext}, \delta_{con}, \lambda, ta)$$

where:

$X_M = \{(p, v)|p \in IPorts, v \in X_p\}$ is the set of *input ports and values*.

S is the set of *sequential states*.

$Y_M = \{(p, v)|p \in OPorts, v \in Y_p\}$ is the set of *output ports and values*.

$\delta_{int} : S \longrightarrow S$ is the *Internal transition* function.

$\delta_{ext} : Q \times X_M^b \longrightarrow S$ is the *External transition* function, where $Q = \{(s, e)|s \in S, 0 \leq e \leq ta(s)\}$ is the *total state* set and e is the *time elapsed* since the last transition.

$\delta_{con} : Q \times X_M^b \longrightarrow S$ is the *Confluent transition* function.

$\lambda : S \longrightarrow Y_M^b$ is the *Output* function.

$ta : S \longrightarrow \Re_{0,\infty}^+$ is the *Time advance* function.

A detailed description of the behavior of an atomic Parallel DEVS model can be found in Chow (1996) and Zeigler et al. (2000). An informal description of its behavior is presented here.

An atomic model remains in the state $s \in S$, for a duration $t_s = ta(s)$, if no input events are received during this interval. After t_s is elapsed, an *internal event* is triggered. The actions associated with the internal event are: 1) an output can be generated using the output function and the state previous to the event; and 2) an internal transition is performed, by changing the state to $s_{new1} = \delta_{int}(s)$.

Multiple input events can be received simultaneously through one or several ports:

- If any input event is received at time instant t_{ext} where $t_{ext} < t_{last} + t_s$, an *external event* is triggered. t_{last} indicates the time instant when the last event occurred, and so the input events are received before the time instant for the next scheduled internal event. As a consequence of the external event, the state is changed to $s_{new2} = \delta_{ext}(s, e, bag)$ (i.e., an external transition is performed), where s is the current state, e is the elapsed time since the last transition ($t_{ext} - t_{last}$), and $bag \subseteq X_M^b$ is the set of received input events.

– If the external input event is received at time t_{ext} with $t_{ext} = t_{last} + t_s$, the conditions for the external and the internal events are simultaneously satisfied. This situation triggers a *confluent event* that substitutes the external and internal events. The actions associated with the confluent event are: 1) an output can be generated as $output = \lambda(s)$ (similarly to the management of internal events); and 2) a confluent transition is performed by changing the state to $s_{new3} = \delta_{con}(s, e, bag)$, being s the current state, e the elapsed time, and $bag \subseteq X_M^b$ the set of received input events (similarly to the δ_{ext} function).

A new internal event is scheduled after each internal, external, and confluent event. This new internal event will occur at time instant $t_{new} = ta(s_{new}) + time$, where $time$ is the current time, i.e., the time instant of the current event, and $ta(s_{new})$ is the duration until the next internal event scheduled as a consequence of the current event. The duration $ta(s_{new})$ is a function of the new state $s_{new} \in \{s_{new1}, s_{new2}, s_{new3}\}$ (changed by the execution of the transition function). Note that the time advance function can also return a zero or an infinite value. If $ta(s_{new}) = \infty$, s_{new} is called a passive state in which the model will remain until an external input event is received. If $0 < ta(s_{new}) < \infty$, s_{new} is called an active state, and $ta(s_{new})$ indicates the time interval before the next internal event. If $ta(s_{new}) = 0$, s_{new} is called a transitory state, which generates an immediate internal event.

4. The EvoDEVS Model

The EvoDEVS model is a coherent simplification of organismic biological systems evolving and adapting to a changing environment. EvoDEVS accomplishes with essential features and biological rules for life cycles, reproduction, genetic regulation and expression, conditioned mutation, epigenetic modification or transposition and organic architecture, as well as the central propositions of the theoretical model presented in Section 2.

EvoDEVS describes a group of individual organisms that live in a two-dimensional space. It has been formally specified using Parallel DEVS and implemented in Modelica using the DEVSLib library. The model is quite abstract due to the necessities for simulating not an specific mechanism but the essential behavior of a highly complex dynamic.

4.1. Features, Objectives and Biological Implications of the Model

EvoDEVS have some remarkable features according to the theoretical proposition modelled. A complete list of transferences between the EvoDEVS and the theoretical model statements is presented in Table 1. The most striking features can be resumed as follows:

Theoretical propositions	**EvoDEVS specifications**
Biological systems, scalable subject	Genome to population hierarchy
Structure + Functions + Program	Matrices + Values + Life Cicle
Organism-Environment feedback	Mutational potentiation under stress
Vectorial epigenesis mechanics	Restriction, mutation, transition rule
Phenotypic degree for novelties	All range allowed, but not prescribed
Novelties homogeneization *ab initio*	All range allowed, but not prescribed
Pulses/Dynamical Stability regimes	Both allowed and prescribed by rules
Macroevolutive bifurcation patterns	Allowed, but not prescribed
Scalate complexity growth	Not referred in this study

Table 1: Transferences between theoretical propositions and EvoDEVS specifications. Features not prescribed but allowed are subjects of the study, pointing for the consistency of the proposed model.

1. It introduces the main proposition of the organism - environment feedback scheme, through evolutionary conditional potentiation, that is to say, organisms are informationally open, react to disturbance and are active players in its own evolution.
2. It allows organization leaps (or macromutations) and its stabilization, when the restriction rules are satisfied.

3. The model does not represent populations nor species, but individual biological systems at organism scale. Organizations (network structures and functional, phenotype expressed, features), its evolutionary trajectories and dynamics are the main subject to study.
4. The model is hierarchically scaled. It is possible to go from population to molecular level in order to study the actual processes configuring the evolutionary trajectories.
5. There is not computed fitness values nor explicit competence. Survival is just ruled by external and internal restrictions, and differential reproduction is not preset as a condition for evolution.

This model introduces a set of rules that harmonizes with the main propositions for vectorial epigenesis, but do not define the subsequent population processes and evolutionary dynamics. With this approach, we aim for the study of diverse evolutionary scenarios and for several questions about the theoretical framework and its adequacy to real evolutionary issues, to name:

- The extinction-radiation coupling due to evolutionary pulse regime.
- The processes underlying the punctuated equilibria and organizational leaps.
- Non-linearity and causality interactions between genotype and phenotype.
- Role and weight of each vector in the population assimilation processes.
- Population demographical responses to inner and outer parameters.
- The reproduction of the expected dynamic and its logical validation.

For the last point, we have to emphasize that we talk about logical (not empirical) validation, understating that if the pattern predicted for the evolutionary dynamic is reproduced it will imply that there is not gaps in the proposed sequence of events, and so the proposal is not illogical formulated.

4.2. Description of the Model

The basic component of the EvoDEVS model is the *organism*. Roughly, an *organism* describes an organismic biological system, an idealized individual with asexual reproduction and a pre-defined maximum live span. Organisms can age, along the simulation time, reproduce and die. The description of the *organism* includes the biological system internal organization (structure, functions and live program) and the set of rules for its conditional mutation and survival (promotion and restriction vectors) and self-reproduction, including rules for inheritance of structure between the organism and its offspring. Additionally, the *organism* internal organization can evolve, due to mutation and inheritance set of rules according to the theoretical framework. The space where these organisms live, named the *world*, is represented by a two-dimensional grid of cells similar to a cellular automata model. Each cell can be empty or occupied by a single organism, both represented using the *organism* model, and are connected to its eight nearest neighbor cells.

The *organism* model has been described as an atomic Parallel DEVS model. The *world* model has been described as a coupled Parallel DEVS model, composed of interconnected *organism* models. A detailed description of these models is presented next.

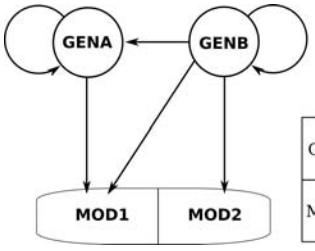
4.3. Description of the Organism *Model*

The *organism* model is composed of: the state, the interface, transition functions, output function and time advance function. Each of these components is described next.

4.3.1. Internal Organization and State

The biological system internal organization is provided by a morphogenetic network, or directed graph, used to represent genetic regulation and expression relationships. The nodes of this network are *genetic units* (GEN) or *module units* (MOD), and the edges express the relations between them. This network can be represented using two boolean matrices: GENREL is the incidence matrix

between genetic units and; MODREL represents the relations between module units and genetic units. Thus, the element $(i, j) = 1$, being i the row and j the column, if the node i receives an edge from node j, and 0 otherwise. The described network and matrices are shown in Fig. 4.



		GENA	GENB
GENREL	GENA	1	1
	GENB	0	1
MODREL	MOD1	1	1
	MOD2	0	1

Figure 4: Relationship between GENREL and MODREL matrices.

Modules represent space-temporal domains of expression that are fixed and predefined. Moreover, each genetic unit has also associated a real expression value (GENVAL), which are used to calculate final expression values for each module (EMOD = (GENVAL · GENREL^T)·MODREL^T).

For example, using the matrices from Fig. 4, and being GENVAL the expression values for the genetic units GENA and GENB, the values for EMOD are calculated as follows:

$$GENREL = [1, 1; 0, 1]$$
$$MODREL = [1, 1; 0, 1]$$
$$GENVAL = [A, B]$$
$$EMOD = \left(\begin{bmatrix} A & B \end{bmatrix} \begin{bmatrix} 1 & 0 \\ 1 & 1 \end{bmatrix} \right) \begin{bmatrix} 1 & 0 \\ 1 & 1 \end{bmatrix} = \begin{bmatrix} A+2B & B \end{bmatrix}$$

EMOD values will be considered as the phenotype of each organism. Indeed, genetic and module expression values are presented as functional abstractions nested on the network structure that interact with the environment.

The state of the *organism* model is defined as:

$S = \{\text{“}empty\text{”}, \text{“}incubation\text{”}, \text{“}infant\text{”}, \text{“}adult\text{”}, \text{“}dead\text{”}\} \times \mathbb{R}^{+}_{0,\infty} \times \{\text{“}askp\text{”}, \text{“}sendp\text{”},$

"*reproduction*", "*cicle*"$\} \times \mathbb{Z} \times \mathbb{Z}^{ng \times ng} \times \mathbb{Z}^{nm} \times \mathbb{Z}^{ng \times nm} \times \mathbb{Z}^{nm} \times \mathbb{Z}^8 \times \mathbb{Z}^8 \times \mathbb{R} \times \mathbb{R}$ and includes the following state variables:

- `phase`, used to describe the phase of the cell/organism (i.e., empty, incubation, infant, adult, dead).
- `sigma`, used to store the time interval until the next internal event.
- `action`, used to control the actions to be performed by the organism.
- `age`, represents the current age of the organism.
- `genrel[ng,ng]`, matrix of inter-genetic relations (GENREL).
- `genval[nm]`, vector of genetic values (GENVAL).
- `modrel[ng,nm]`, matrix for relation between genes and modules (MODREL).
- `eMOD[nm]`, vector of values for modules (EMOD).
- `neighbors[8]`, phase of neighbors.
- `updatep[8]`, vector of neighbors that asked for a phase update.
- `env`, current value for environment input.
- `stress`, current value for stress input.

Additionally, `ng` $\in \mathbb{Z}$ (number of genetic units), `nm` $\in \mathbb{Z}$ (number of module units), `pchangegen` $\in \mathbb{R}^{ng \times ng}$ (probabilities for changes in GENREL), `pchangemod` $\in \mathbb{R}^{ng \times nm}$ (probabilities for changes in MODREL) and `stth` $\in \mathbb{R}$ (stress threshold) are parameters of the model.

4.3.2. Model Interface and External Transition Function

The interface is composed of eight pairs of ports, $(x \in X_M, y \in Y_M)$. $X_M = \{(p, v) \ | p \in \{$"$in_1$", "$in_2$", "$in_3$", "$in_4$" "$in_5$", "$in_6$", "$in_7$", "$in_8$"$\}, v \in \mathbb{Z} \times \mathbb{Z}\}$ is the set of input ports. $Y_M = \{(p, v) | p \in \{$"$out_1$", "$out_2$", "$out_3$", "$out_4$", "$out_5$",

"out_6", "out_7", "out_8"$\}, v \in \mathbb{Z} \times \mathbb{Z})\}$ is the set of output ports. The value of each port $v = (c, t)$ corresponds to its content c (i.e., the information transported by the message) and its type t. Each pair is used to connect with a neighbor, by receiving and sending messages through the input and output port of the pair, respectively.

The external transition function is used to describe the actions performed by the model when an external input event is received. The pseudocode for this function is shown in Algorithm 1. Eight types of events are used to communicate information between cells in the model:

1. Is received when a neighbor has changed its `phase`, and thus the corresponding value of the `neighbors` vector has to be updated with the new phase received as the value of the event.
2. Is received as a signal to create a new organism in an empty cell, due to the reproduction of a neighbor. The internal organization of the new organism is initialized with its default values. The value of GENREL is transported in the event and is used for the new organism, which inherits the biological organization of its predecessor.
3. Is received together with event 2, and transports the value of GENVAL from the predecessor to be used in the new organism.
4. Also received with event 2, and transports the value of MODREL to be used in the new organism.
5. Is received when a neighbor needs to know the current phase of the cell. The current phase is sent to the demanding neighbor using the output function.
6. Is used as initial message at the beginning of the simulation. An organism that receives this message will start its life cycle.
7. Is received when the environmental restriction has changed and thus the `env` state variable has to be updated with the new value, transported with the event.
8. Is received when the stress restriction has changed and thus the `stress`

Algorithm 1: EvoDEVS δ_{ext} function algorithm.

```
input  : Current state S, time elapsed e, bag of input events
output: New state S_new
S_new = S;
for each event x in bag do
    switch x.t do // type of event
        case 1 // neighbor changed phase
            S_new.neighbors[x.p] = x.c;
            S_new.sigma = S.sigma-e;
        case 2 // reproduction 1
            S_new = create new organism;
            S_new.genrel = x.c;
            S_new.action = askp;
            S_new.sigma = 0;
        case 3 // reproduction 2
            S_new.genval = x.c;
        case 4 // reproduction 3
            S_new.modrel = x.c;
        case 5 // send phase to neighbor
            S_new.action = sendp;
            S_new.updatep[x.p] = 1;
            S_new.neighbors[x.p] = 1;
            S_new.sigma = 0;
        case 6 // initial event
            S_new.phase = infant;
            S_new.action = askp;
            S_new.sigma = 0;
        case 7 // change environment
            S_new.env = x.c;
            S_new.sigma = S.sigma-e;
        case 8 // change stress
            S_new.stress = x.c;
            S_new.sigma = S.sigma-e;
```

state variable has to be updated with the new value, transported with the event.

4.3.3. Model Behavior and Internal Transition Function

EMOD values are evaluated in order to set the state of the organism under some restriction rules. These rules state that every organization must ensure a minimal coherence with its surrounding environment (external/ecological restrictions) and to avoid constructional inviable states of the potential variation space (internal/ontogenetic restrictions).

The external restriction rule states that, in order to survive, EMOD values must fall inside a real interval, defined by a pre-defined function, which is dependent of an environmental restriction parameter (named `env`). Each module is separately evaluated, using different restriction rules to study modularity dependence. For example (having `nm=2`):

$$\text{If:} \left| \begin{array}{l} \texttt{env} < \texttt{eMOD[1]} < 3 * \texttt{env} \\ \textit{or} \\ \frac{1}{2} * \texttt{env} < \texttt{eMOD[2]} < 2 * \texttt{env} \end{array} \right. \rightarrow \text{Lives}$$

Otherwise: → Dead by external restriction.

In the other hand, internal restriction rules introduce inviable intervals for EMOD, simulating inner architectural issues and abortive states. For example (also having `nm=2`):

$$\text{If:} \left| \begin{array}{l} 2 < \texttt{eMOD[1]} < 5 \\ 10 < \texttt{eMOD[1]} < 15 \\ 25 < \texttt{eMOD[1]} < 30 \\ \textit{or} \\ 8 < \texttt{eMOD[2]} < 10 \\ 23 < \texttt{eMOD[2]} < 25 \\ 33 < \texttt{eMOD[2]} < 38 \end{array} \right. \rightarrow \text{Lives}$$

Otherwise: $\rightarrow$ Dead by internal restriction.

Other relevant rules are mutation rules, which define how and when the genetic expression values and the network structure changes (promotion). These rules depend on the level of environmental stress or perturbation (named `stress`) received by the organism, according to evolutive potentiation.

When there is no, or low, perturbation (i.e., `stress < stth`) the biological organization of the organism is subject to a basal mutation rate with a probability in the order of 10^{-3}, change according to a random modification (Drake et al., 1998). In the case of GENVAL, the i-th value (v_i) will be substituted with a random variate following a discrete uniform distribution, with values distributed in the$[v_i - 3, v_i + 3]$ interval. For the matrices GENREL and MODREL, values are substituted with its opposite boolean value (i.e., $\neg$ operation). All mutations occur independently of each other.

When the environmental perturbation reaches the preset threshold (i.e., `stress >= stth`), the mutation rate for GENVAL increases in two orders of magnitude, simulating the hypermutation and mutation capacitors effects. GENREL and MODREL change following two likelihood matrices (named `pchangegen` and `pchangemod`), that define an independent probability of mutation for each element in each matrix. Moreover, these unbalanced probabilities are not applied uniformly when the stress exceeds the threshold (unlike for the GENVAL potentiation). When the difference between the stress and the threshold increases, additional values of these matrices are used as probabilities for mutations. That is to say, higher stress values over the preset threshold trigger more active elements in both matrices, and allows higher structure mutational activity. For example, having `ng = 2`, `nm = 2` and `stth = 0.8`, when `stress` reaches 0.8, the element $(1, 1)$ of GENREL and MODREL mutates with a probability of `pchangegen[1,1]` and `pchangemod[1,1]`, respectively, while the rest of the elements follow the basal mutation rate. If `stress` reaches 0.85, then the elements $(1, 1)$ and $(1, 2)$ of GENREL and MODREL mutate

with probabilities `pchangegen[1,1]`, `pchangegen[1,2]`, `pchangemod[1,1]` and `pchangemod[1,2]`, respectively. If `stress` reaches 0.9, elements $(1, 1)$, $(1, 2)$ and $(2, 1)$ are used for mutations. And, if `stress` reaches 0.95, all the elements of the matrices are involved in the mutations.

Finally, the *organism* model has a set of internal rules that describe an elemental life cycle for ontogeny and reproduction (program). There are four possible phases that change along time depending on the age of the organism, during a maximum life span of 10 cycles:

1. incubation ($age = 0$) is an inactivity cycle when the system functions are settled, counting for space/niche occupation and program issues;
2. infancy ($age = 1$), when the restriction and mutation rules start but no reproduction is possible;
3. maturity ($1 < age < 10$), when all the rules are applied and reproduction is possible;
4. senescence ($age = 10$), when the organism consumes it maximum life span and dies.

The reproduction is asexual and occurs once per cycle since the organism reaches the mature phase and there is a surrounding empty niche to occupy (i.e., an empty cell in the neighborhood).

The internal transition function performs the actions shown in Algorithm 2 in order to define the described life cycle of the organism.

In the case of a confluent event, the internal transition is executed after the external transition. Thus, in EvoDEVS $\delta_{con}(S, e, bag) = \delta_{int}(\delta_{ext}(S, e, bag))$.

4.3.4. Output and Time Advance Functions

As described above, Parallel DEVS models can generate an output before executing the internal or confluent transition functions. The *organism* model generates outputs in order to communicate with its neighbors to know their phases or reproduce. The pseudocode that describes the behavior of the output function is shown in Algorithm 3. The `action` state variable is used to control the generation of outputs:

- When a mature *organism* reproduces sends its current biological organization (GENREL, MODREL and GENVAL) to the empty niche that will be occupied by the new organism. This represents the inheritance of bi-

Algorithm 2: EvoDEVS δ_{int} function algorithm.

```
input  : Current state S
output: New state S_new
S_new = S;
S_new.updatep = zeros;
if S.action = cycle then
    Apply mutation rules;
    if dead by restriction rule or life span reached then // die
        Set S_new to the default (empty) state;
        S_new.sigma = sendp;
        S_new.sigma = 0;
    else // maybe reproduce and age
        Find empty neighbor;
        if adult and empty neighbor exists then
            S_new.action = reproduce;
            S_new.sigma = 0;
        else
            S_new.sigma = 1;
        S_new.age = S.age+1;
else // re-set cycle action
    S_new.action = cycle;
    if S.phase == empty then
        S_new.sigma = 1;
    else
        S_new.sigma = ∞;
```

Algorithm 3: EvoDEVS λ function algorithm.

```
input  : Current state S
output: Output events
Data: msg
switch S.action do // action to perform
    case reproduction
        msg.t = 2;
        msg.c = S.genrel;
        send msg to emtpy neighbor;
        msg.t = 3;
        msg.c = S.genval;
        send msg to emtpy neighbor;
        msg.t = 4;
        msg.c = S.modrel;
        send msg to emtpy neighbor;
    case sendp // send phase
        msg.t = 1;
        msg.c = S.phase;
        send msg to neighbors in S.updatep;
    case askp // ask phase
        msg.t = 5;
        send msg to all neighbors;
```

ological structure between the predecesor and its offspring. Thus, three messages are sent with types 2, 3 and 4 and the values of `genrel`, `genval` and `modrel`, respectively.

- When the `phase` of the organism changes a message of type 1 and the new `phase` value is sent to the neighbors in order to update their current information about the phase of the organism.

- A message of type 5 is sent when the organism needs to update the local information about the phases of its neighbors. The neighbors will answer with messages containing their phases.

The time advance function is used to schedule the time for the next internal event of the organism. In EvoDEVS $ta(S) = S.sigma$. The state variable `sigma` is set during the execution of the transition functions.

4.4. Description of the World *Model*

The *world* is a coupled model that is composed of a number of *organism* models interconnected following a two-dimensional lattice structure. A *world* of size N is composed of N^2 *organism* models, where N is size of each dimension of the space. As mentioned above, each *organism* model is connected with its eight closest neighbors using the ports of its interface. Initially each *organism* model behaves as a spatial niche that can be potentially occupied by an organism when reproduction succeeds, or receives an initialization event (i.e., event type 6). The *world* model also includes one `World`, one `Fixed` and N^2 `FixedShape` components from the Modelica Standard Library that are used to automatically generate a graphical animation of the simulation (MSL). The phase of each organism is graphically represented in its corresponding position of a two-dimensional square matrix.

Also, each organism is connected, using one of its input ports, to two source models that define the values for `stress` and `env`, and generate the required input events. The value of `stress` and `env` may vary through the simulation time, and a specific pattern or regime can be preset for different experimental scenarios.

4.5. Model Implementation and Simulation

The implementation of both models has been performed using the DEVS-Lib Modelica library (Sanz et al., 2010). Modelica is a general purpose object-oriented modeling language mainly designed for describing mathematical models using acausal differential and algebraic equations (Modelica Association, 2014).

Modelica also includes functionality to manage discrete-events, which were used to develop the DEVSLib library in order to support the Parallel DEVS formalism. DEVSLib facilitates the description of DEVS models in Modelica, and its combination with other continuous-time Modelica models.

The *organism* model extends the `AtomicDEVS` model from DEVSLib (i.e., the model that implements an atomic DEVS model) and its behavior (i.e., the algorihtms above) is described using Modelica functions that replace the standard functions defined in `AtomicDEVS`. The state variables of the *organism* are defined using a Modelica `record` that replaces the standard state of `AtomicDEVS`. The *world* model includes N^2 instances of the organism model, defined using a two dimensional array. The relationships between each organism and its neighbors are defined using `connect` statements between input and output ports. The boundary conditions of the space are not wrapped, and so the organisms situated in the borders have five neighbors while the ones situated in the corners have only three. The developed models have been simulated using Dymola (Dynasim AB, 2006).

5. Simulation Experiments: Results and Discussion

Two different scenarios, named *control* and *pulses*, are presented. The simulation results obtained from these scenarios serve as a validation of the modeling premises, described in Sections 2 and 4, in comparison with the behavior of biological systems. The former scenario reproduces the conditions of a simple *in-vitro* experiment. The latter scenario is designed to study the evolution of the population of organisms in response to variations of the stress.

The initial conditions are equal in both scenarios and are shown in Table 2. They constitute arbitrary values for parameters and initial values for variables that make the initial organization viable for the initial restriction conditions. The restriction and mutation rules used are the ones described in Section 4.3.3. Both scenarios are simulated during 50 cycles. The difference between both scenarios is the variation in the stress, however it is constant during the first 12

Variable	Value
Number of genetic units (`ng`)	2
Number of modules (`nm`)	2
Environment (`env`)	10
Stress (`stress`)	0
Threshold (`stth`)	0.8
Max. age	10 cycles
Maturity	2 cycles
Sim. time	50 cycles
Reproduction	1/cycle
World size	10 x 10
Initial population size	1 org.
Genetic relations (`genrel`)	[1,0;0,1]
Module relations (`modrel`)	[1,1;1,0]
Genetic values (`genval`)	{6,15}
Module expresion values (`eMOD`)	{21,6}
GENVAL basal mut. prob.	0.003
GENVAL stressed mut. prob.	0.3
`genval[i]` mut. distrib. func.	DU(`genval[i]`-3,`genval[i]`+3)
GENREL/MODREL basal mut. prob.	0.001
GENREL mut. prob. matrix (`pchangerel`)	[0.2, 0.8;0.5;0.2]
MODREL mut. prob. matrix (`pchangemod`)	[0.5,0.2;0.2,0.8]

Table 2: Initial conditions for state variables and parameters.

cycles in order to ensure a minimal population size for experimentation.

5.1. Control Scenario

The *control* scenario establishes a uniform balanced situation with no environmental change. Both restrictive and disruptive parameters, `stress` and `env`, remain constant. Consequently, the original (preset) organization is viable along the whole the experiment, and external restriction can only occur when mutations push it to an inviable new state. Since the initial perturbation level is below the robustness threshold (`stth`), the whole the experiment develops out of the phase of evolutionary pulse (i.e., only basal mutations will be triggered). With this scenario we attempt to study the population behavior under

stability and the evolutionary trajectories of the new and initial organizations. Moreover, it allows to compare future, more complex, scenarios with variable regimes for environmental variables.

Demographical evolution: the population size grows exponentially until the 20^{th} cycle, when it starts to fluctuate around value 80 (individuals). This fluctuation highly resembles the ecosystem's carrying capacity, that is to say, space limitation (free cells surrounding in reproduction) and natural deaths (due to reaching the maximum life-span) dynamically stabilizes the population size in absence of any other factors. In fact, three variables (number of individuals, newborns and natural deaths) seem asynchronically coupled, and, as life-span is uniform for all individuals, periodical fluctuations arise. The evolution of these variables is shown in Fig. 5 This behavior (exponential growth and population size stabilization around carrying capacities) is well known in both natural and experimental biological populations, pointing for the model coherence.

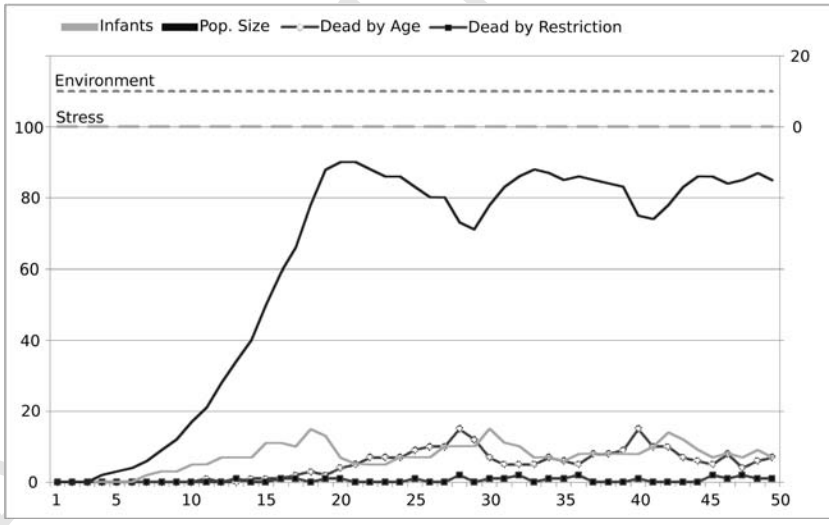


Figure 5: Demographical evolution in the *control* scenario.

Organization evolution: low phenotype and genotype evolution is observed, remaining the initial organization values as the most frequent along the simulation time. Nevertheless, a new stable value arise for each expression

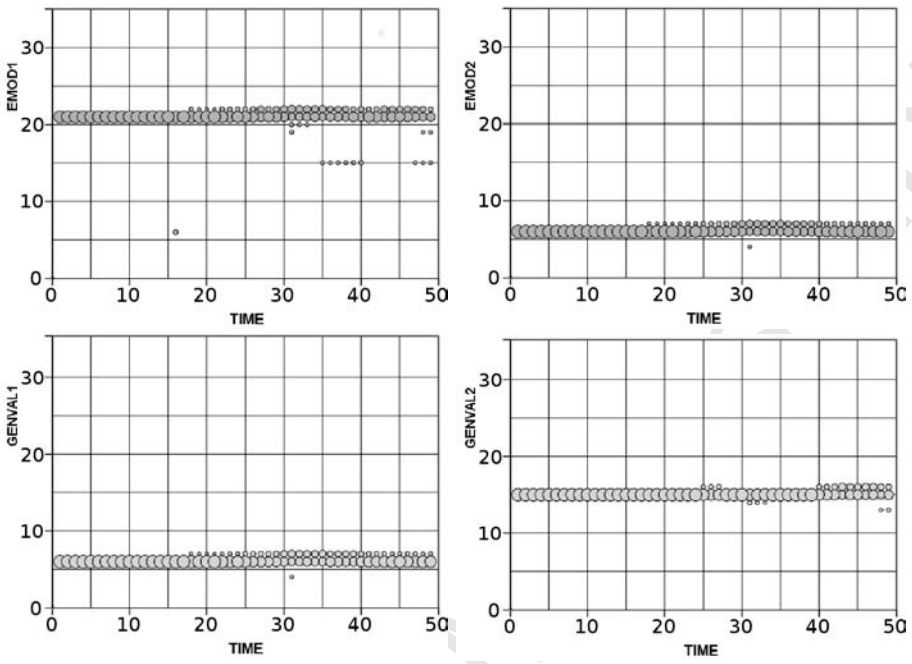


Figure 6: Morphogenic evolution. From top left to bottom right: trajectories for EMOD1 and EMOD2 (fenotypic evolution), GENVAL1 and GENVAL2 (genic evolution). The size of the dots shows its relative frequencies in the population at that moment.

module (phenotype) at the 16^{th} cycle in coincidence with just one GENVAL mutation. Moreover, several non stable states arise and decay independently on each other, but temporal recurrence is observed for both allelic and phenotypical trajectories (cf. Fig. 6). That is to say, some unstable states appear more than one time, as predicted by the proposed vectorial mechanics. Furthermore, leaps in phenotypical degree are observed for two of those unstable states. As the modelled system reproduces asexually, there is not reproductive restriction for high degree variation stabilization under an isolated innovation regime.

Mutational rates and variability: gross variability for each module, matrix, and genetic unit has been compared. All variability slightly increases along the simulation and the interaction thereof is not lineal as both structure and expression values interact for the module phenotypes. Functional mutations (GENVAL) slightly dominates over structural mutations (GENREL and MOD-

REL). The total mutation count is 34, and so, much of the genetic changes do not affect variability.

This can be explained due to four situations:

1. Mutations are neutral and do not modify the previous genetic or phenotypic values.
2. Reversion or recurrence to existent states occur, so just frequencies (not variation) change.
3. Mutated organisms die before mutations can be expressed and/or reproduced.
4. Internal and external restrictions reduce variability to viability, causing most mutated organisms to die.

Although all these causes have been observed in the model, the last one is the most prevalent. One more time, these results have not been programmed but harmonize with actual genetic phenomena and enhances the coherence of the model.

5.2. Pulses Scenario

The *pulses* scenario establishes a situation with no environmental change for restrictions, but punctually disturbed above the system robustness threshold. As for the *control* scenario, restrictive parameter (`env`) remains constant during the simulation and the initial (preset) organization is viable along the whole the experiment. Again, external restriction can only occur when basal mutations push it to an inviable new state.

On the other hand, the disturbance parameter (`stress`) changes along time, punctually outpointing the robustness threshold (`stth`). With this scenario we attempt to study the effects of an evolutionary pulse regime in the population, that resembles a potential actual scenario where biological systems are subjected to environmental or cytgenetic perturbation (hybridization, trasfection and mobile elements colonization).

Demographical evolution: the population grows exponentially until the 20^{th} cycle. Compared with the previous experiment, the most evident observation is the devastating effect of perturbation in the population size. When the stress reaches the threshold perturbation occurs, the population enters in a highly unstable state that enhances mutation and introduces new inviable organizations. Consequently, the total account for deaths by restriction greatly increases when that happens. The evolution of the population in this experiment is shown in Fig. 7. As predicted by the presented theoretical proposal, evolutionary potentiation enhances population decay.

Organization evolution: in the other hand, high innovation is observed in phenotype and genotype evolution in this experiment. When the population is subject to over threshold perturbation pulses, coordinated (synchronic) radiations are observed. This organizational bursts include recurrent and stable phenotypical leaps, as well as clustering, due to the limitations introduced by the restriction and promotion vectors. These results (cf. Fig. 8) resembles the patterns predicted by the evolutionary pulses dynamics (see again Fig. 3), and it completes the proposal for a plausible extinction-radiation coupling under punctual highly perturbed conditions.

Mutational rates and variability: gross variability for each module, matrix, and genetic unit has been studied. A comparison between both scenarios for total variability shown in Fig. 9. All kinds of variability greatly increases along the simulation, but not linearly as both structure and expression values interact for the module phenotypes. Structural mutations (GENREL and MODREL) dominate over structural mutations (GENVAL). Total mutation account scores 787 events, far exceeding the results obtained in the *control* scenario. As previously pointed, the total variability and mutational rate is greatly enhanced during pulses.

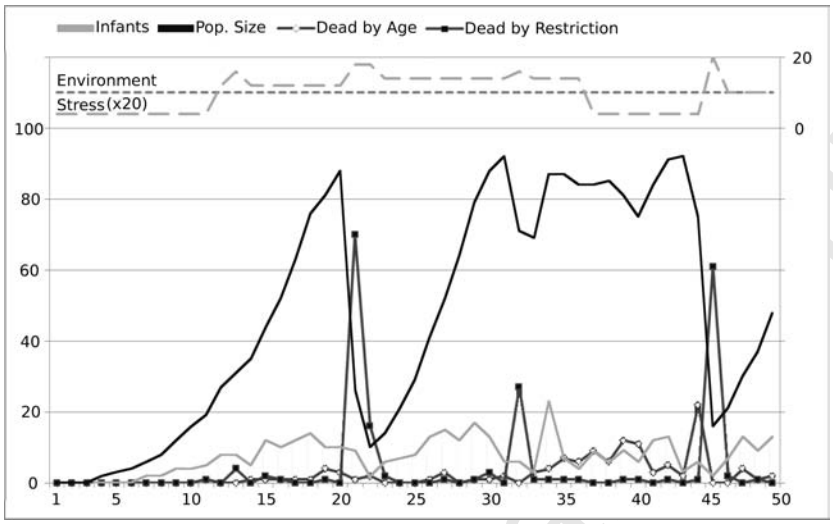


Figure 7: Demographical evolution in the *pulses* scenario.

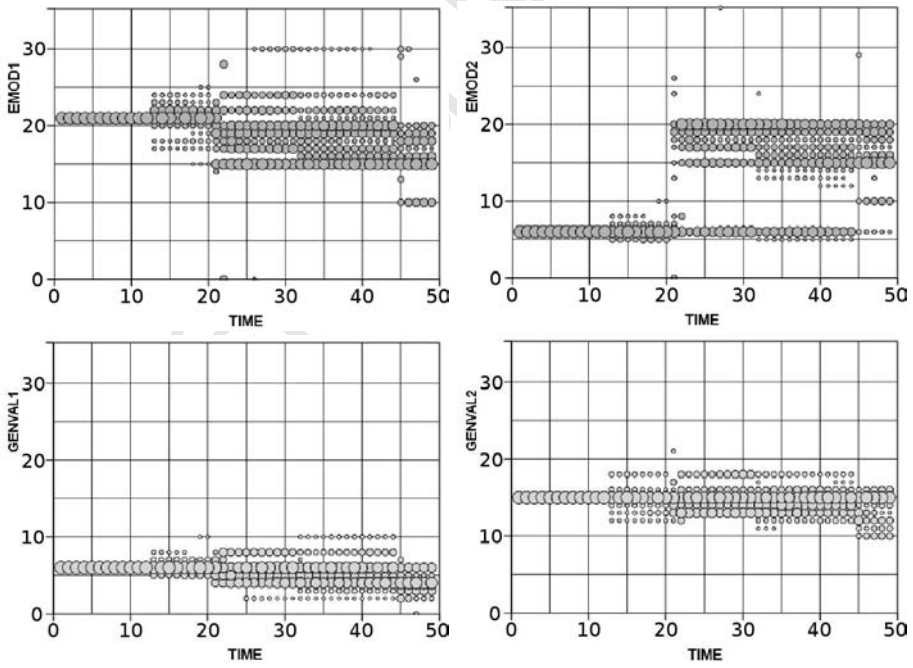


Figure 8: Morphogenic evolution. From top left to bottom right: trajectories for EMOD1 and EMOD2 (fenotypic evolution), GENVAL1 and GENVAL2 (genic evolution). The size of the dots shows its relative frequencies in the population at that moment.

6. Final Conclusions and Future Directions

In this manuscript, a model for a novel framework in ESB has been introduced. This model seems to be a versatile tool for theoretical experimentation in this field and it has provided insight about the logical coherence of the proposed framework, reproducing patterns that strongly resembles the biodiversity explosions predicted by the evolutionary pulses dynamics, and the radiation-extinction coupling hypothesis. The model also constitutes a simulation tool for exploring evolutionary scenarios, connecting individual, population and genome scales. Moreover, the results obtained in the simulations harmonize with actual biological phenomena in both ecological (demographic oscillation) and genetic (neutralism, non-linearity) dimensions; and reinforces an alternative explanation for complex macroevolutionary transitions (including mobile elements transposition, viral transfection and heritable epigenetic modification) in coherence with abundant palaeontological and genomic evidences, conciliating with the hypothesis stated by several authors (Oliver and Greene, 2011; Zeh et al., 2009; Shapiro, 2011; Sandín, 1997; Erwin, 2000b) and the presented

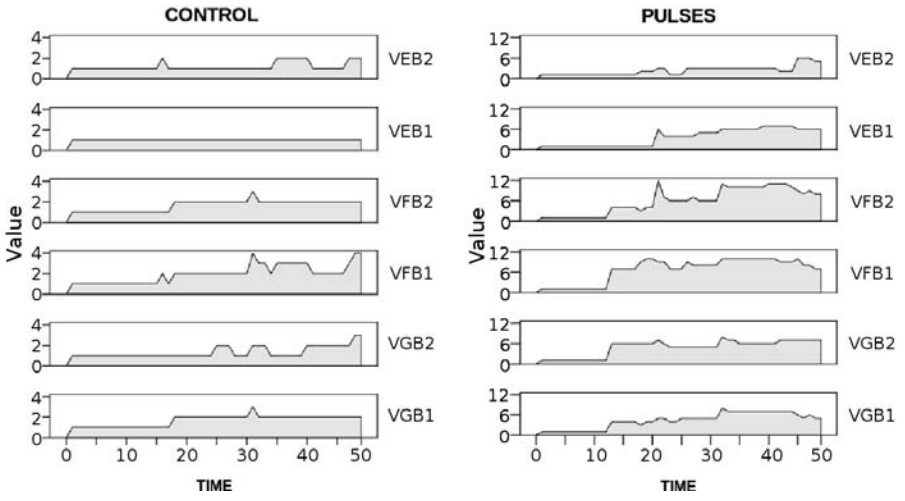


Figure 9: Variability evolution comparison between experiments. VEB2: MODREL variabiliy; VEB1: GENREL variabiliy; VFB2: GENVAL2 variabiliy; VFB1: GENVAL1 variabiliy; VGB2: EMOD2 variabiliy; VGB: EMOD1 variability.

framework.

Nevertheless, although the results obtained are interesting enough for the initial considerations of this research, this model drags several assumed simplifications that would be minimized in the future, in order to consider new and more complex scenarios:

- The size and complexity of the biological organization network of the organism are strongly limited, since no nodes (genes or modules) can be added or lost.
- Informational "organism-environment" loop is restricted just to potentiation under stress conditions.
- Life program is constant and homogeneous in all individuals, and it can not evolve.
- Only asexual reproduction is considered and it occurs just once per mature cycle.
- Environmental conditions are uniform across the represented world.
- Main environmental parameters are limited to just one restrictive and perturbing factors.
- Simulation time, world size and and experiment replication must be increased in future experiments.

Acknowledgements

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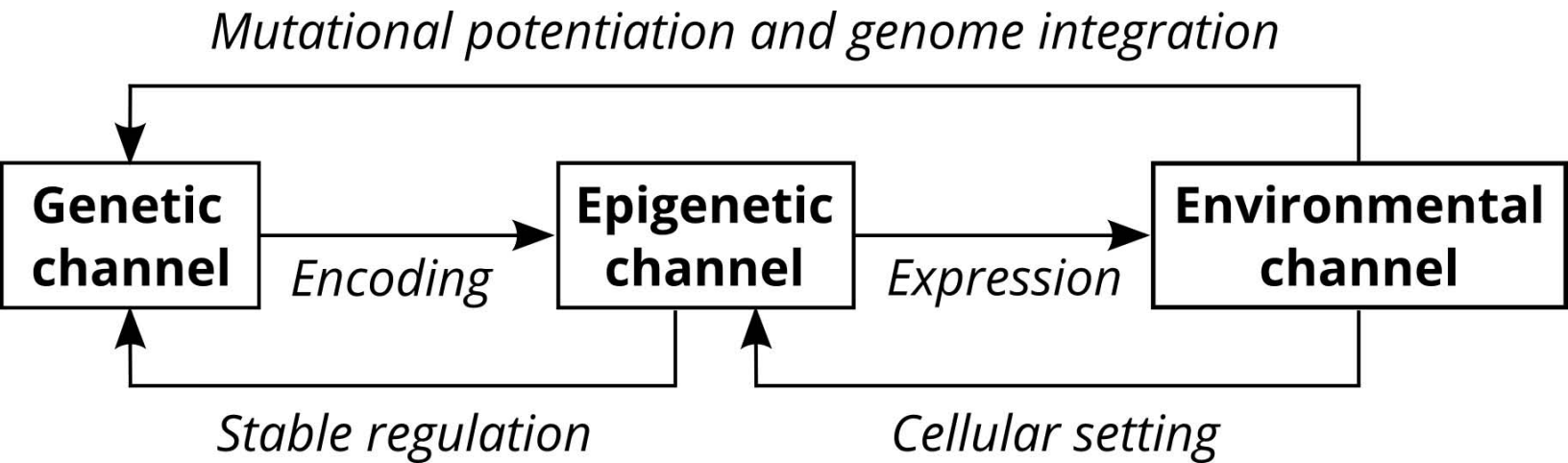

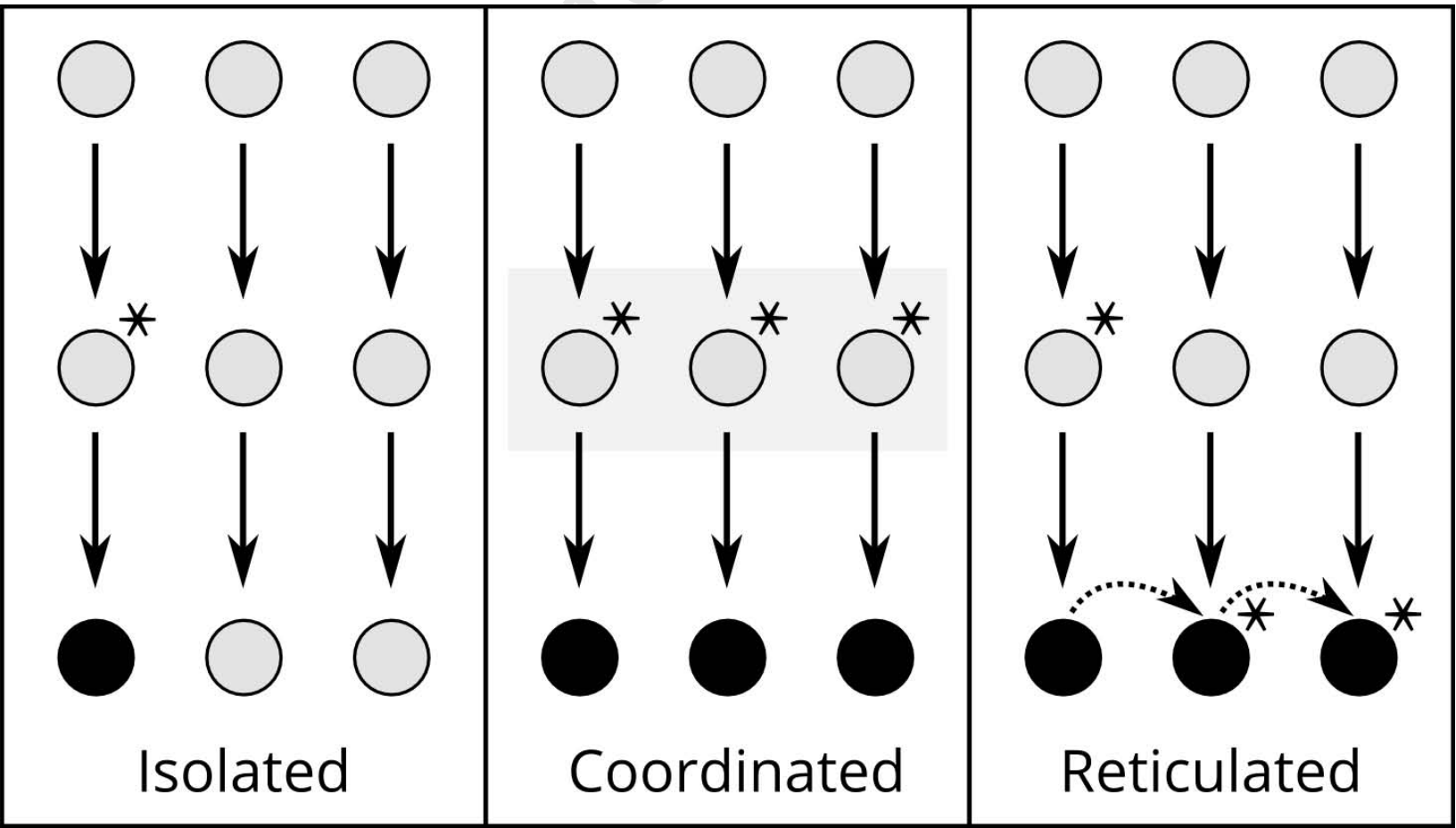

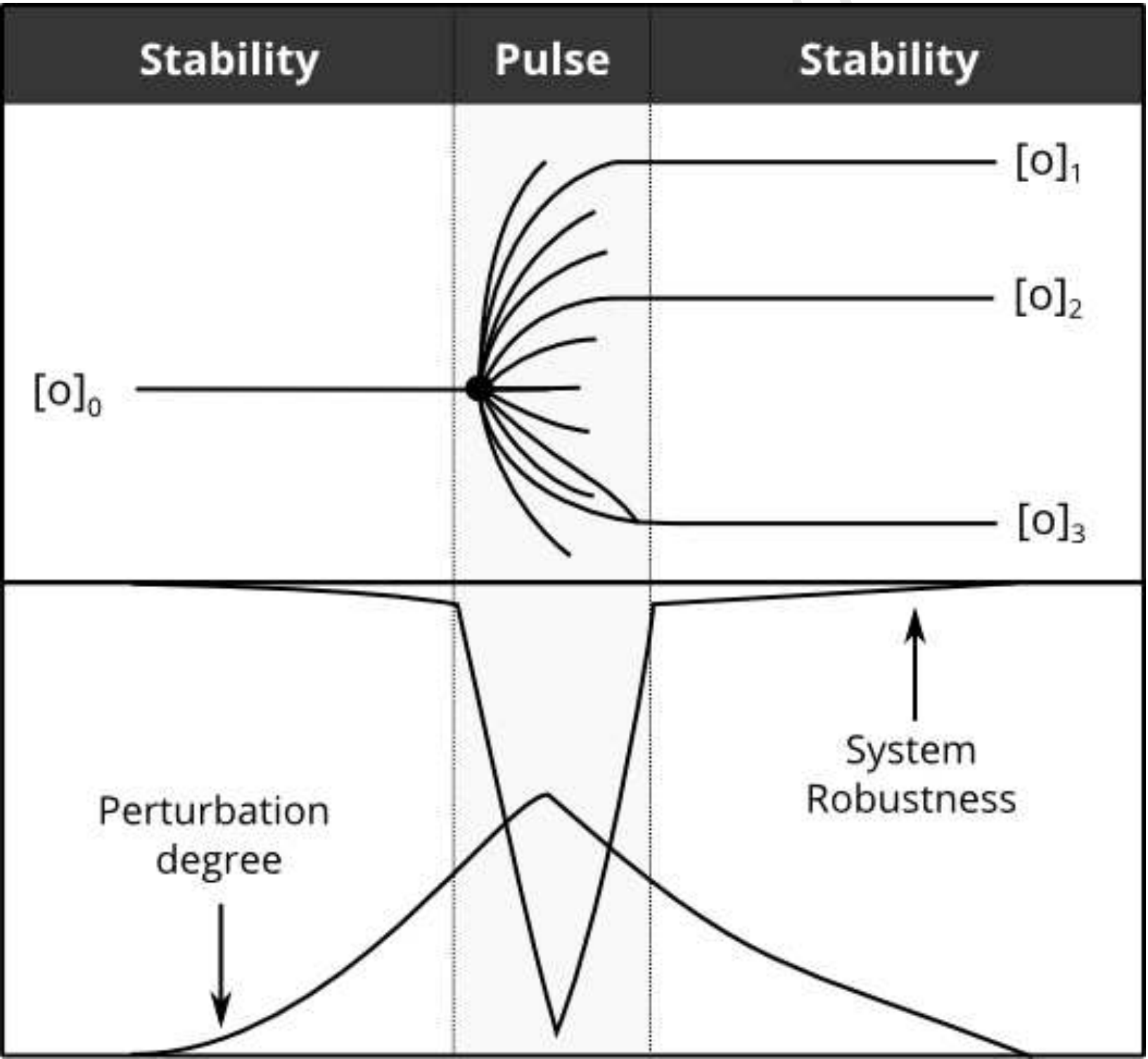

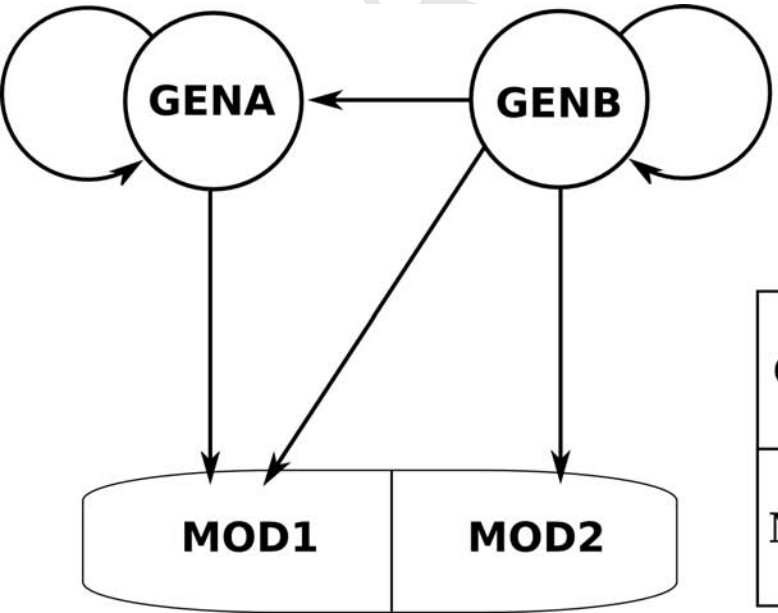

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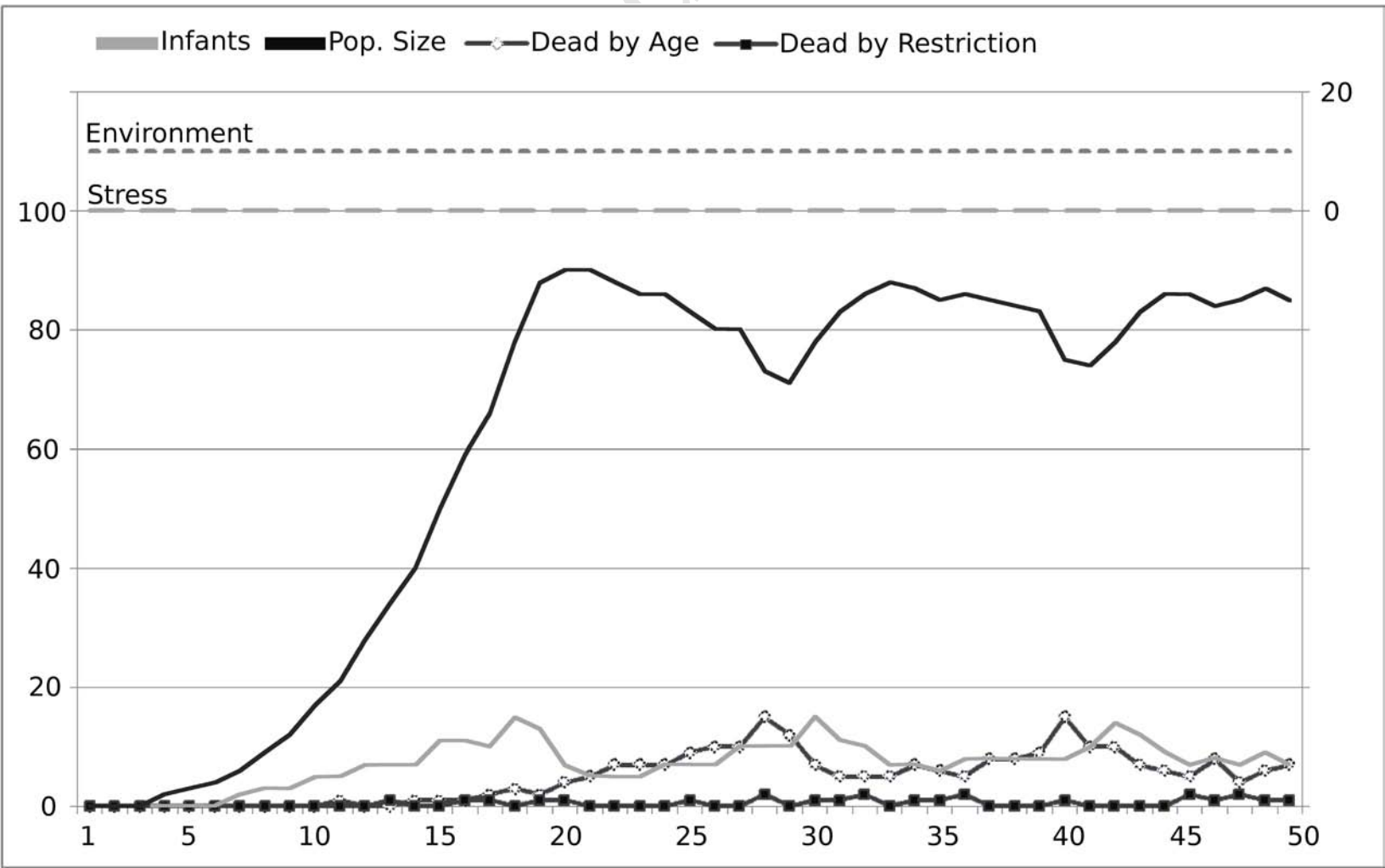
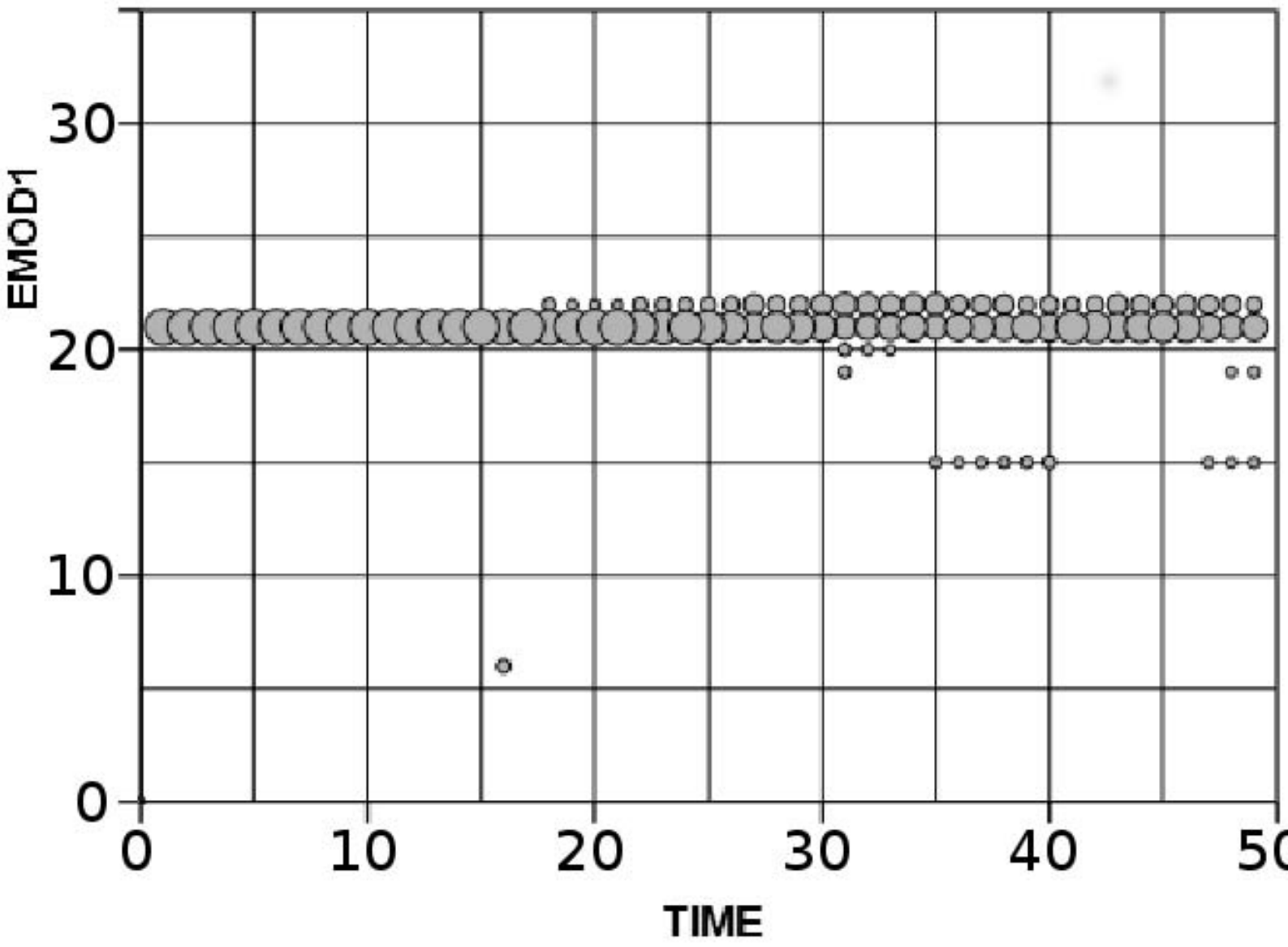
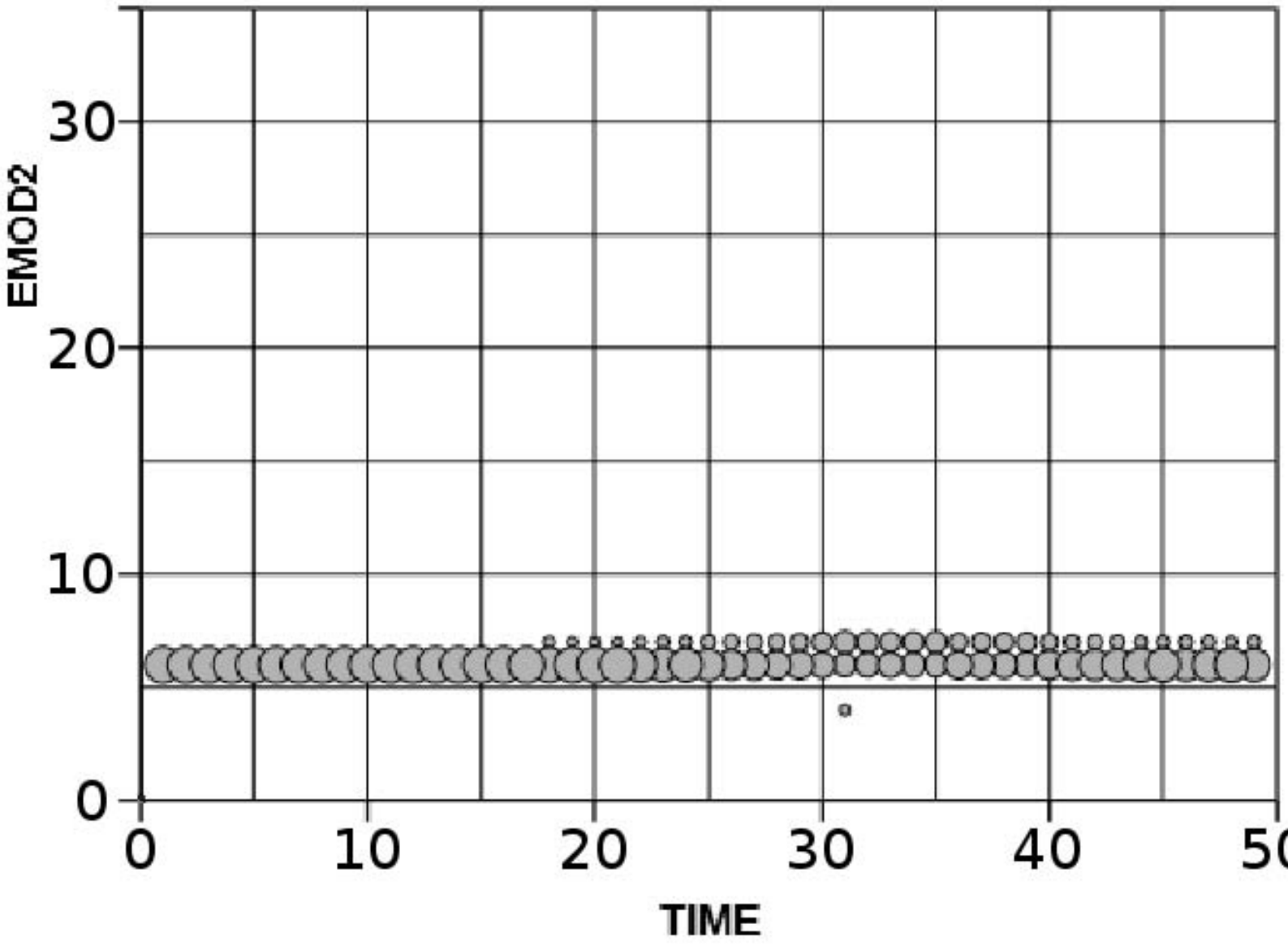
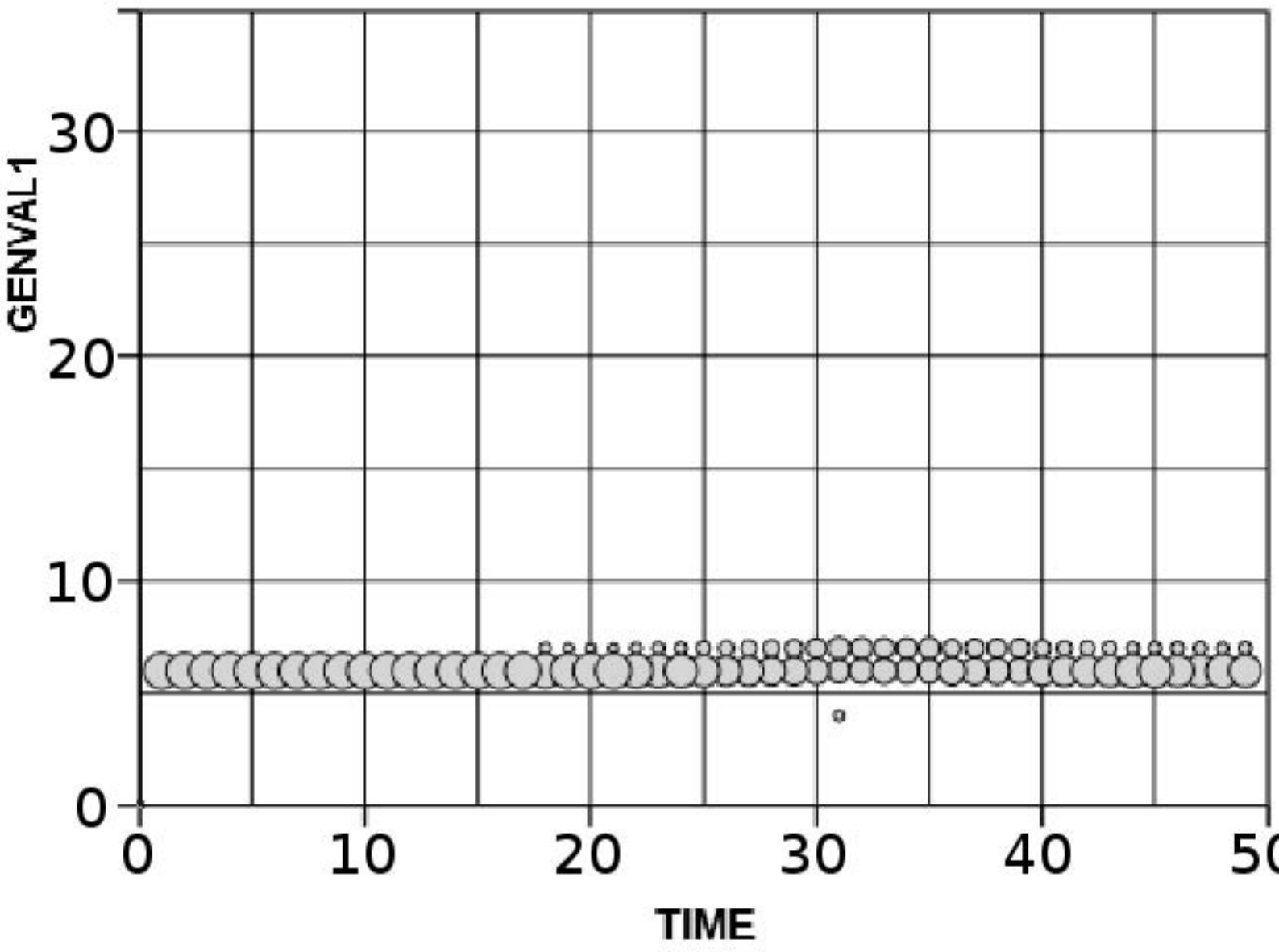
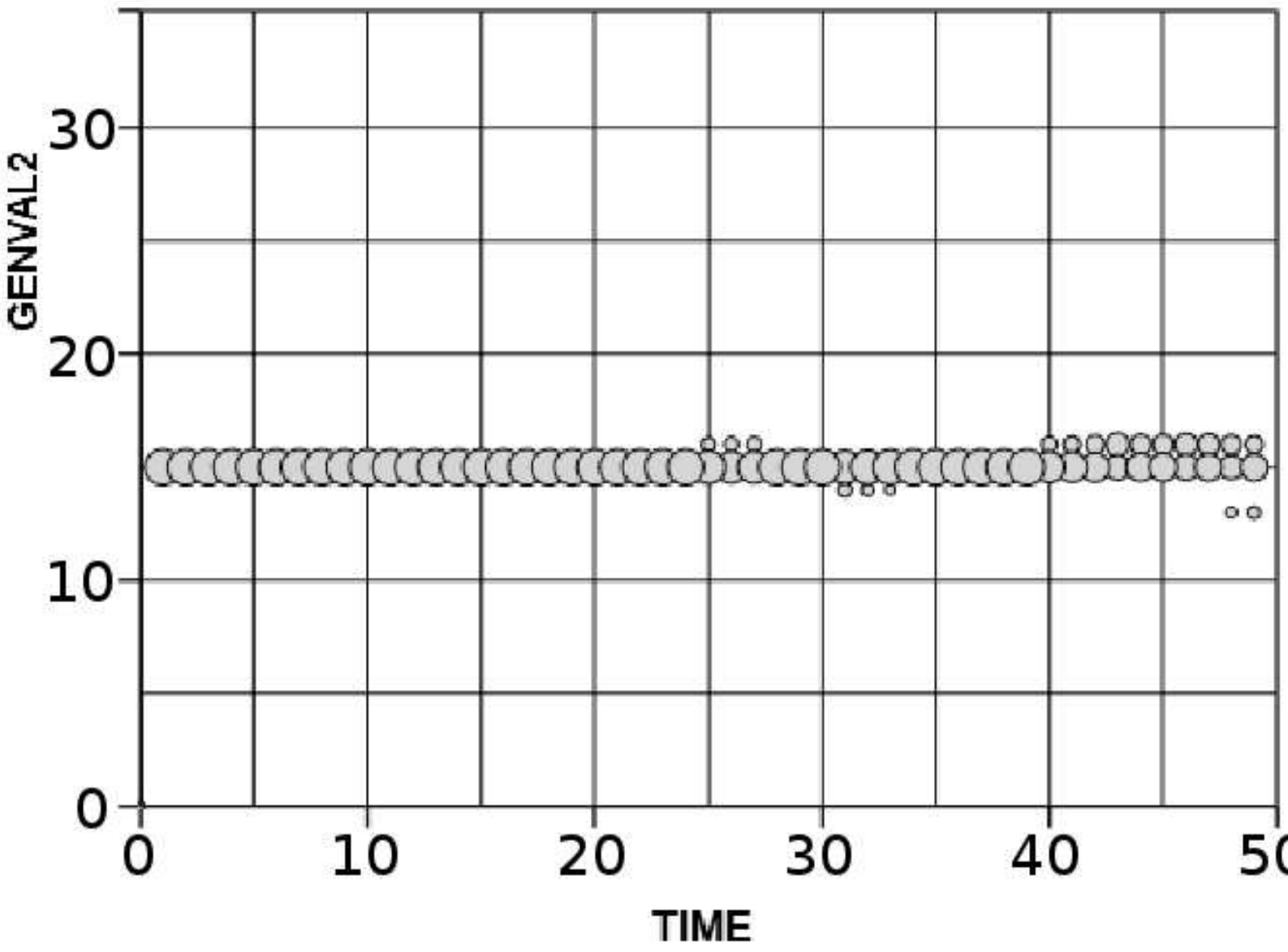
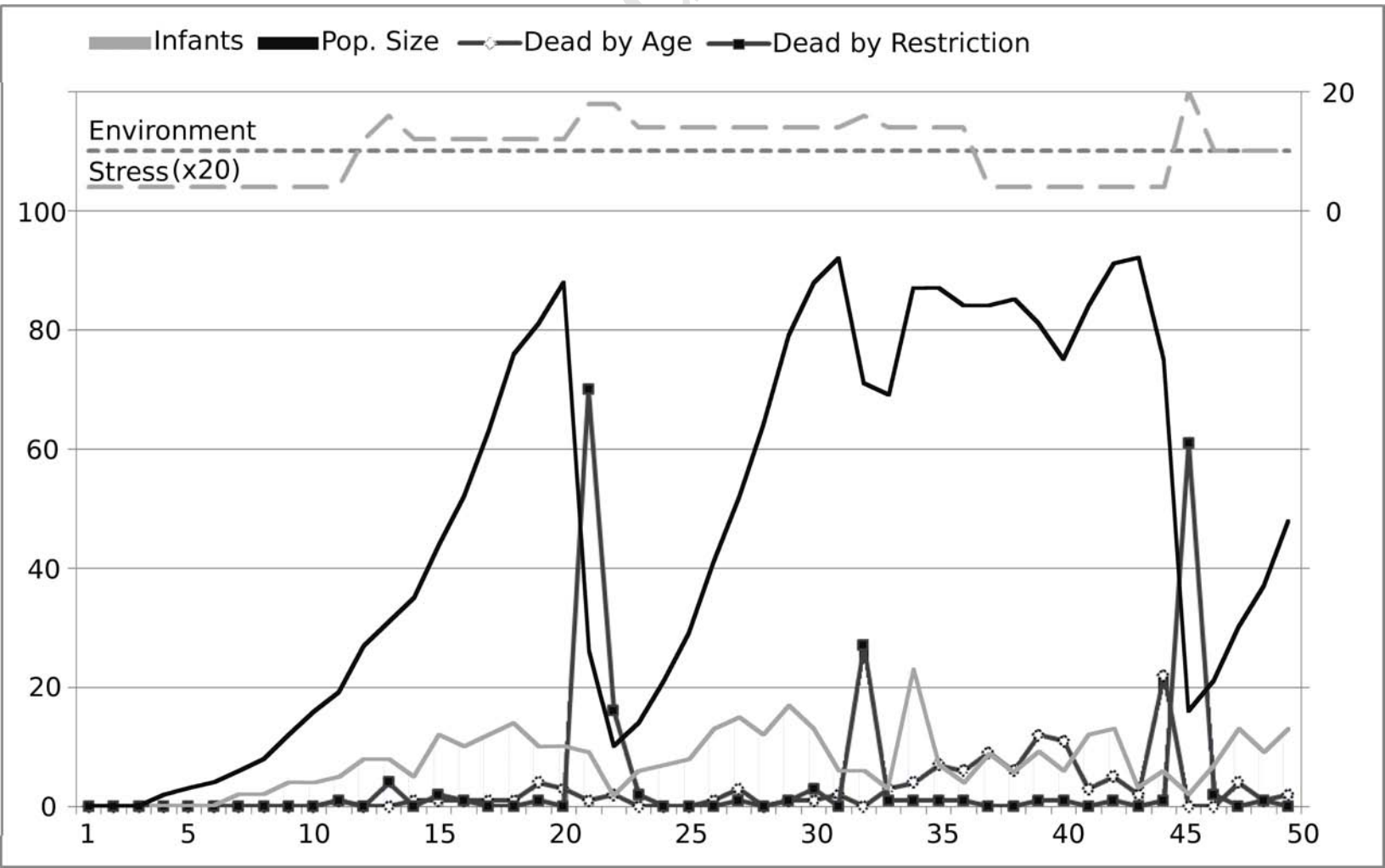


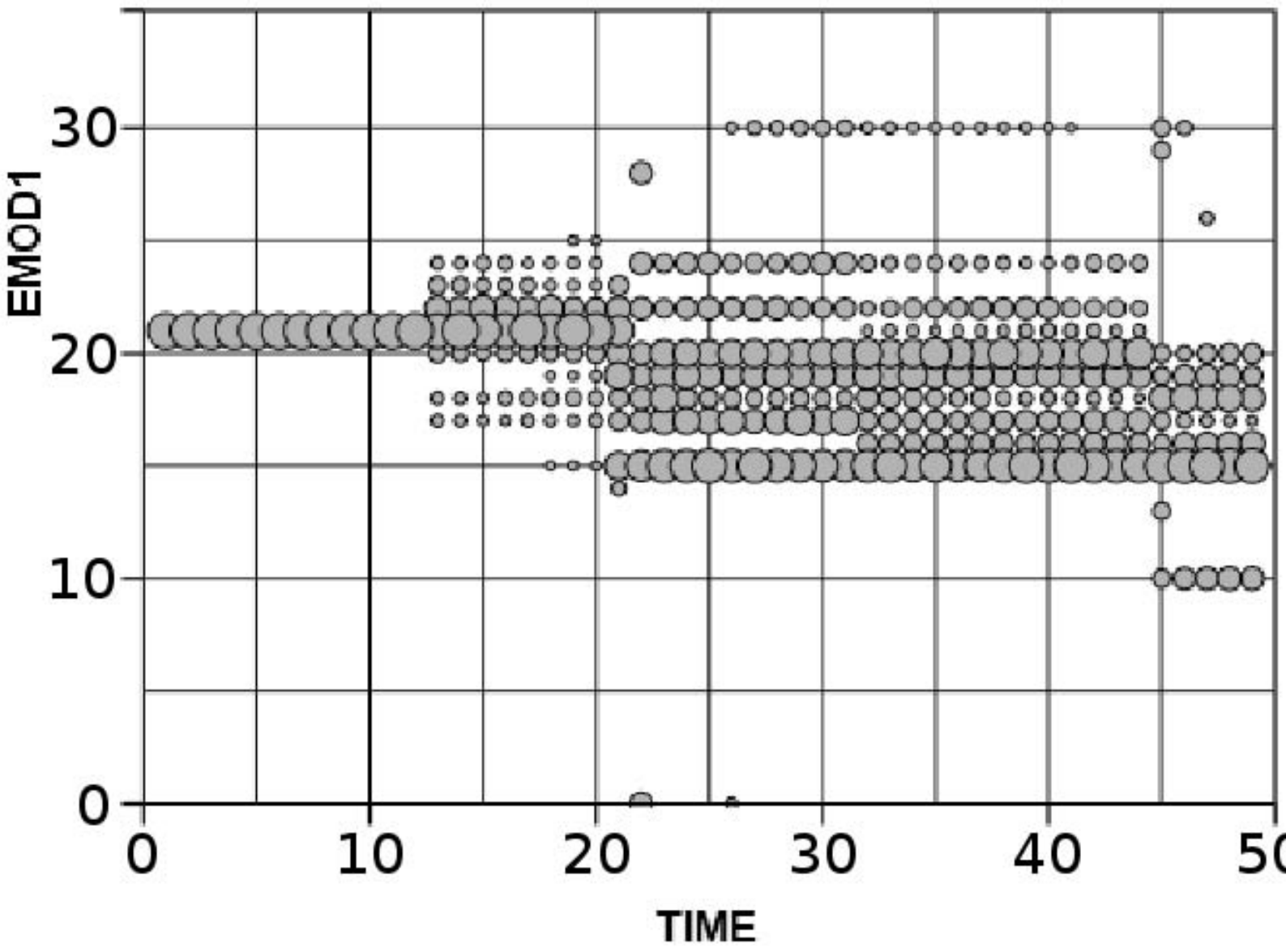


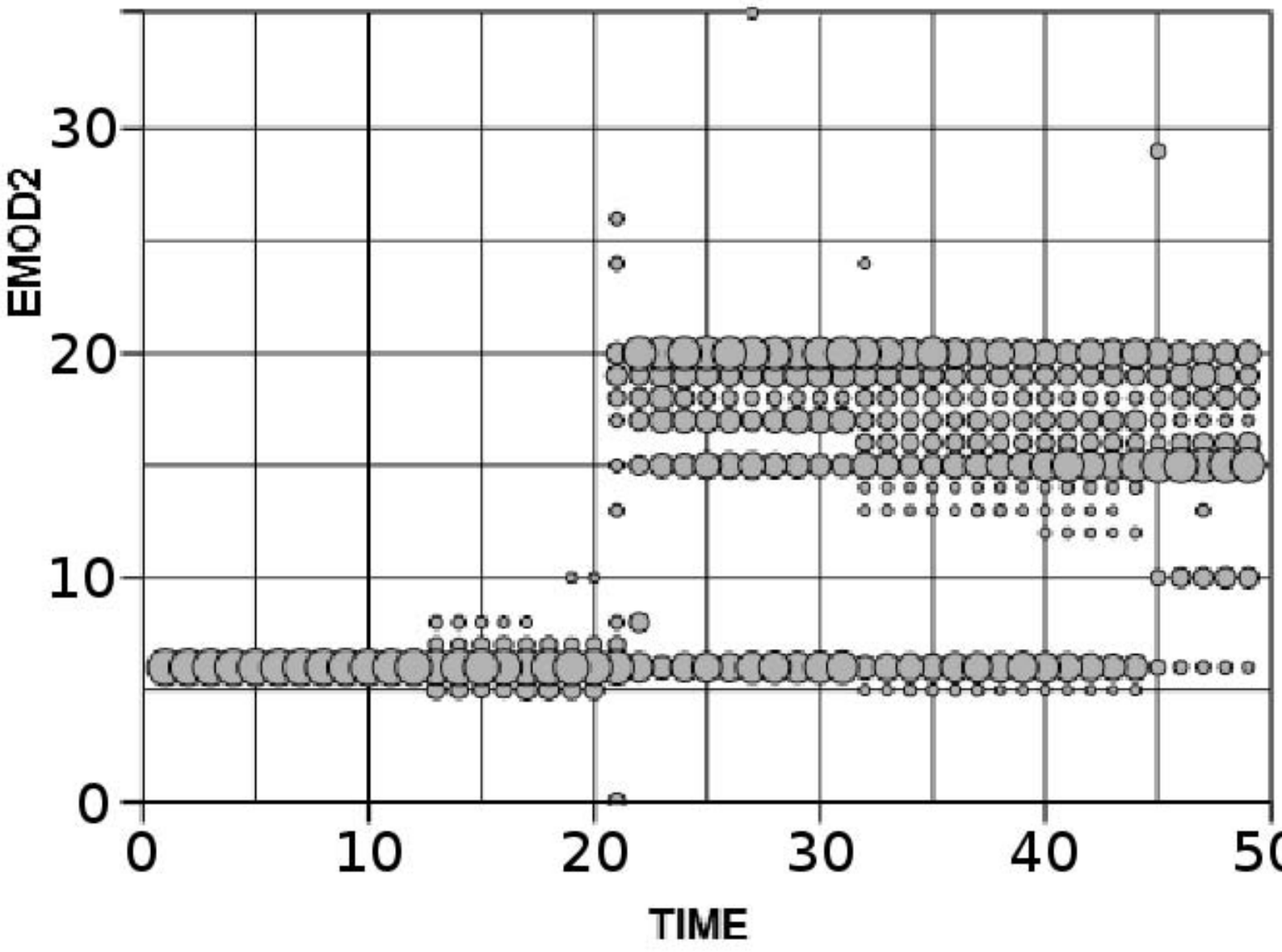


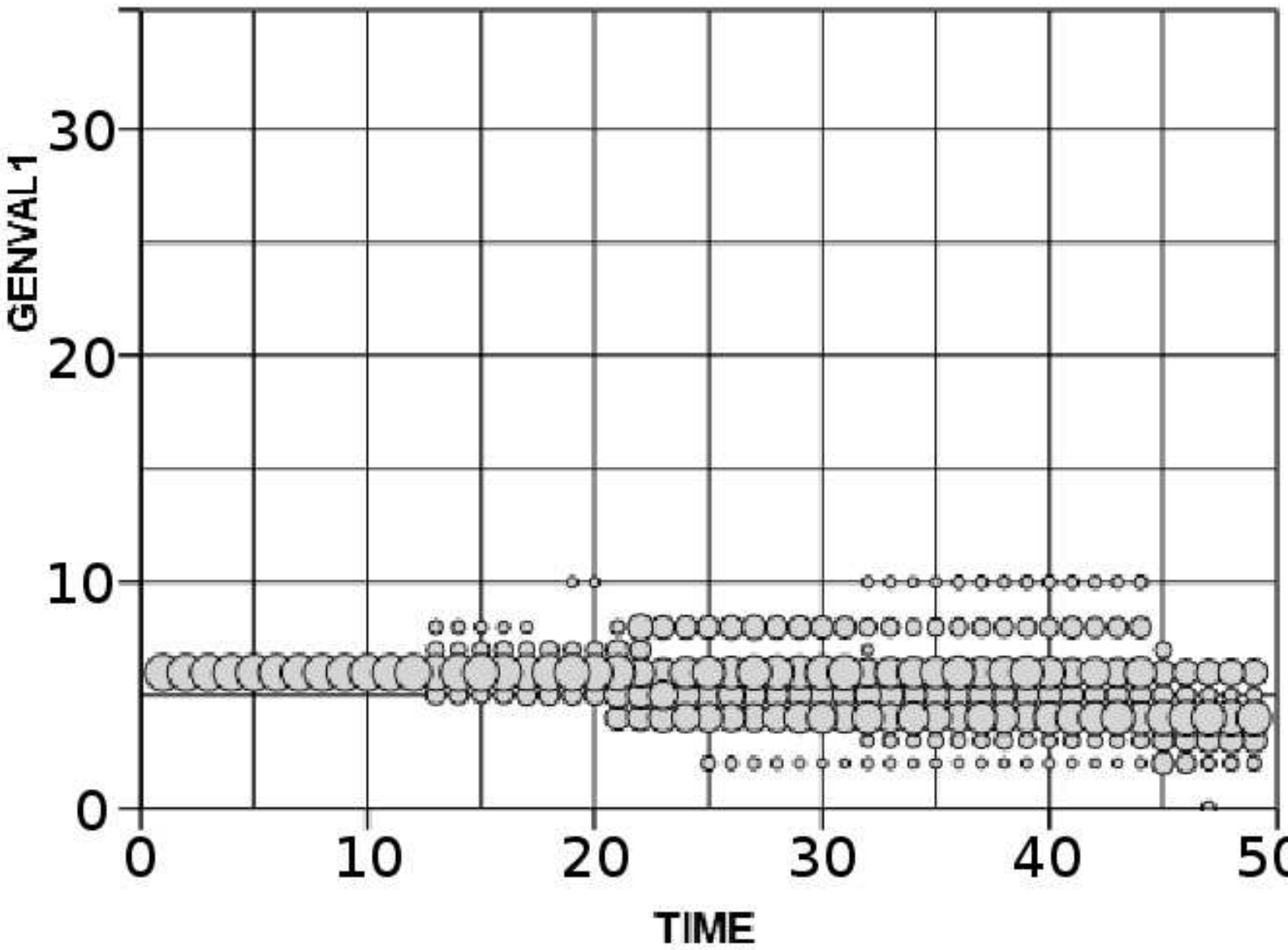


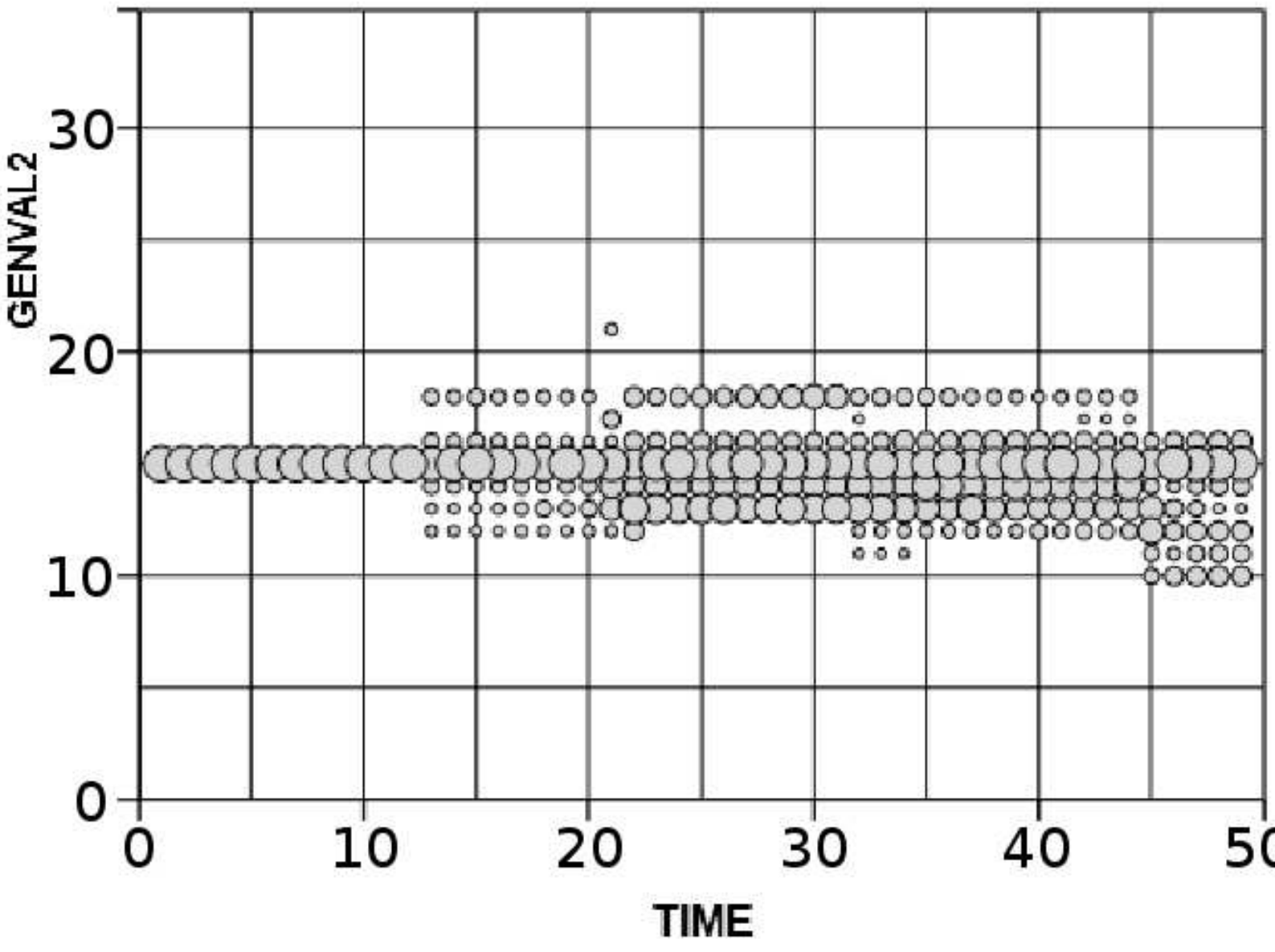


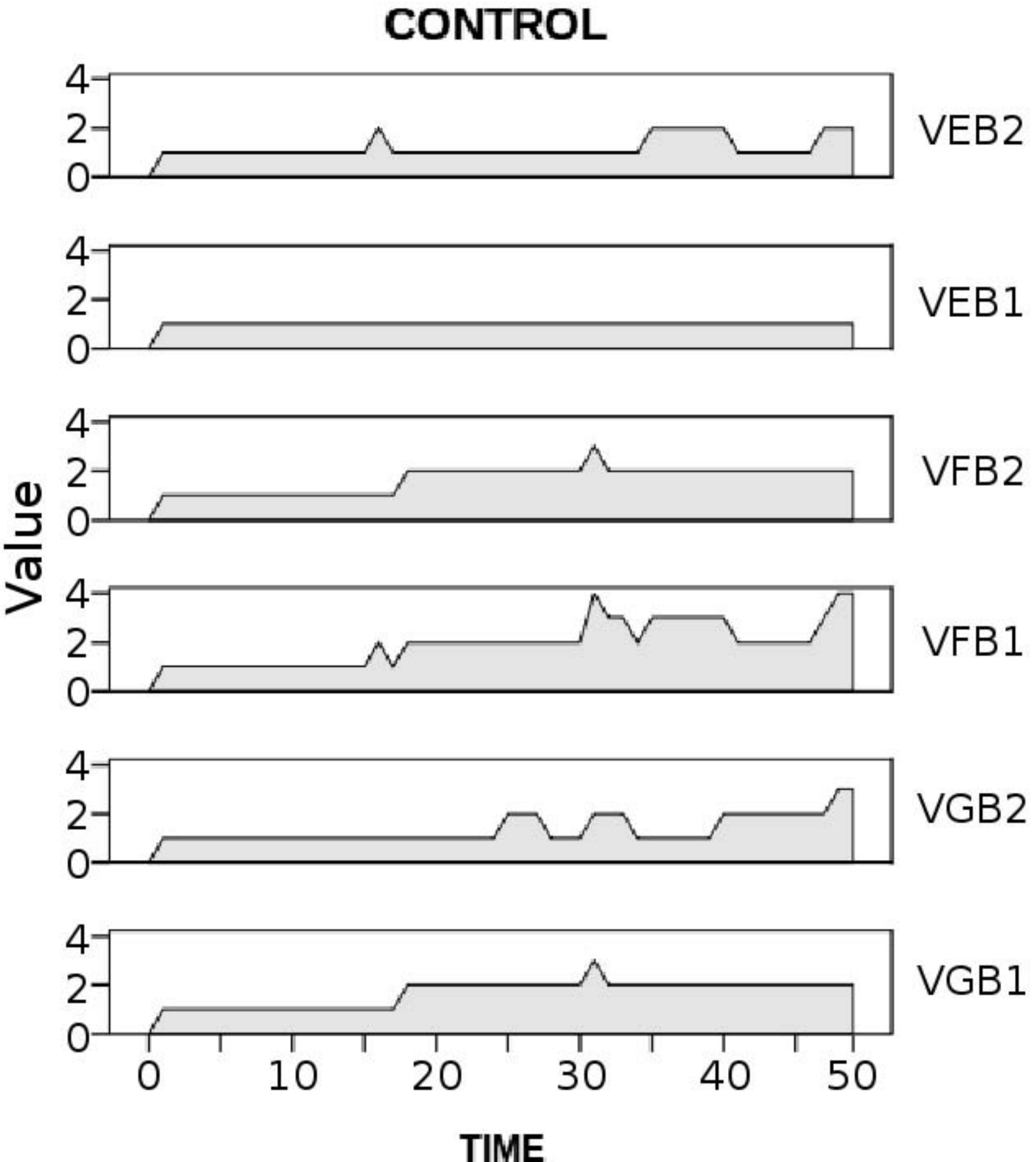


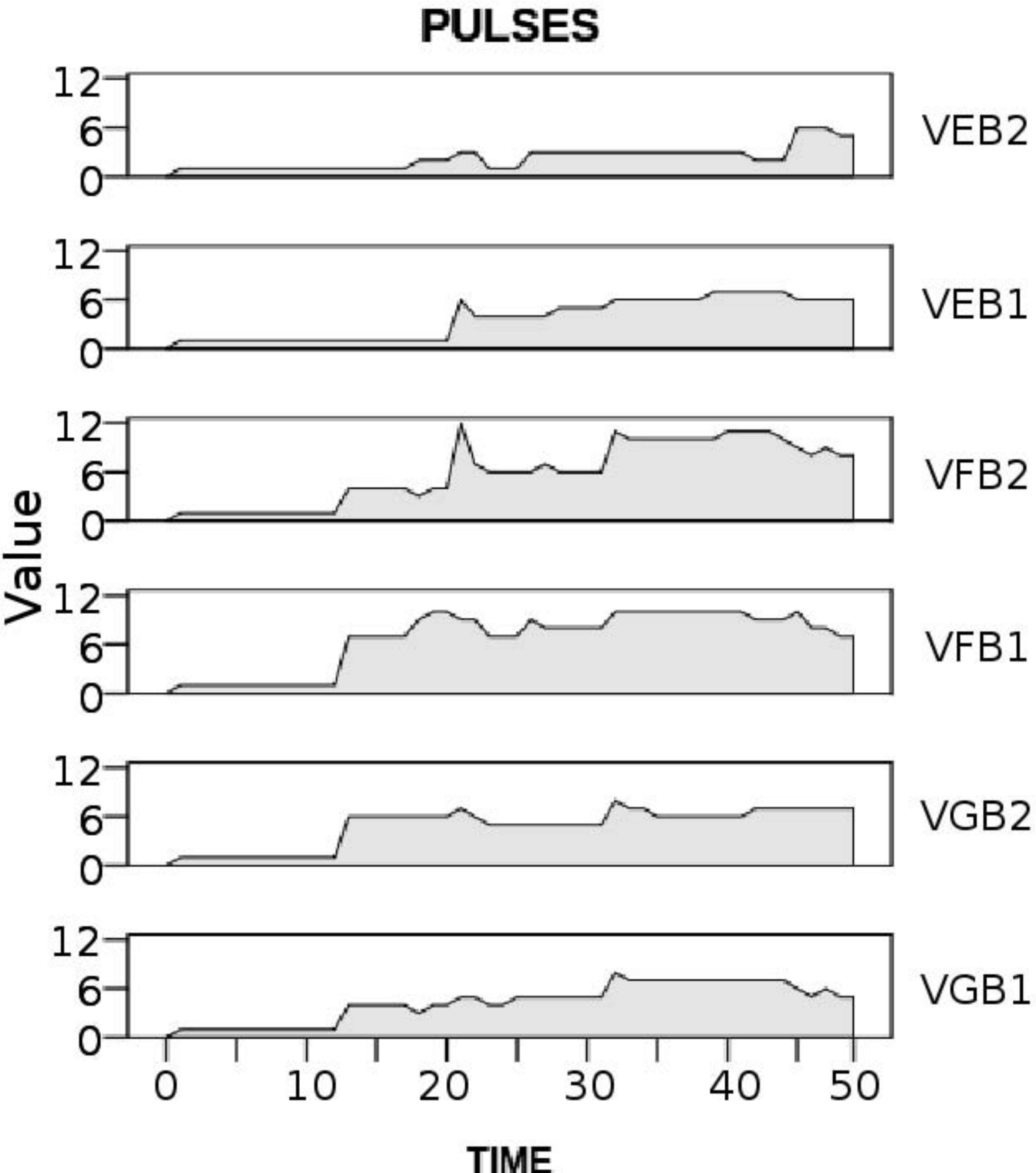




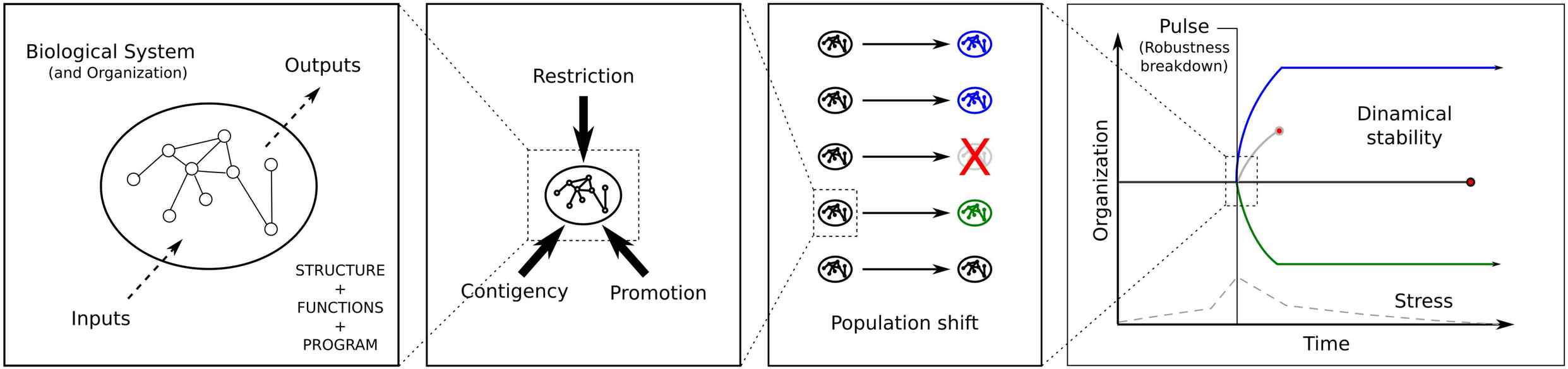








THEORETICAL PROPOSAL



SIMULATION MODEL