Eco-phenotypic physiologies: a new kind of modeling for unifying evolution, ecology and cultural transmission

Fabrizio Panebianco[*] *Emanuele Serrelli*[†]

Prepared for:
International Conference on Evolutionary Patterns
Calouste Gulbenkian Foundation, Lisbon
May 27-29, 2013
http://evolutionarypatterns.fc.ul.pt/

Abstract

Mathematical modeling can ground communication and reciprocal enrichment among fields of knowledge whose domains are very different. We propose a new mathematical Framework applicable in biology, specified into ecology and evolutionary biology, and in cultural transmission studies, considered as a branch of economics. Main inspiration for the model are some biological concepts we call "eco-phenotypic" such as development, plasticity, reaction norm, phenotypic heritability, epigenetics, and niche construction. "Physiology" is a core concept we introduce and translate differently in the biological and cultural domains. The model is ecological in that it aims at describing and studying organisms and populations that perform living, intended as a thermodynamic, matter-energy process concerning resources gathering, usage, and depletion in a spatiotemporal context with given characteristics, as well as with multiplication and space occupation. The model also supports evolution, in-

---

[*] Economics Dept., and CISEPS Center for Interdisciplinary Studies in Economics, Psychology and Social Sciences, University of Milano-Bicocca, fabrizio.panebianco@unimib.it.

[†] AppEEL - Applied Evolutionary Epistemology Lab, Faculdade da Ciencias, Universidade de Lisboa; "Riccardo Massa" Dept. of Human Sciences, and CISEPS Center for Interdisciplinary Studies in Economics, Psychology and Social Sciences, University of Milano-Bicocca, emanuele.serrelli@unimib.it.

tended as a dynamics including cumulative change in the features of unique organisms that are connected into breeding populations. The model is then applicable to the economics of cultural transmission in which individuals form their attitudes and patterns of behavior under a complex system of influences derived from their "cultural parents", other members of the society, and the environment. On the side of biology, an innovative goal is to integrate in a single model all the eco-phenotypic concepts as well as both evolution and ecology. On the side of cultural transmission, eco-phenotypic modeling seems more appropriate in capturing some aspects of cultural systems which are modeled away in the earlier framework based on Mendelian population genetics.

1 Introduction

Mathematical modeling can ground communication and reciprocal enrichment among fields of knowledge whose domains are very different. We propose a **Framework of formal relations** general enough to be applicable in *biology* and in *cultural transmission* studies, where the former is further specified into *ecology* and *evolutionary biology*, and the latter is considered as a branch of *economics*. The idea of connecting biology and economics is, of course, not new. On the contrary, cultural transmission studies stemmed from the idea of applying the mathematics of population genetics to cultural traits treated as genetic alleles: Cavalli-Sforza and Feldman [Cavalli-Sforza 81] inaugurated a way of building unified models of the genetics and culture of ancient human populations, and familiarity between economics and biology has been consolidated by decades of this kind of modeling [Bisin 10]. While acknowledging such debt, our Framework lies outside the fundamental tradition of cultural transmission studies inspired to population genetics. We are indeed interested in modeling some biological concepts we will call "eco-phenotypic concepts"[1] such as development, plasticity, reaction norm, phenotypic heritability, epigenetics, and niche construction.

In evolutionary biology, after a period of marginalization [Pigliucci 07], eco-phenotypic concepts are now fully integrated in theory, and central both in empirical research and modeling, but available modeling frameworks are either too complicated or too reductive for our purpose. On the complicated side, we have quantitative genetics [Via 85] which, despite some criticisms [Pigliucci 06], contains the most advanced mathematical tools to specify a

---

[1] We adopt here a term that was in use since the 1980s, in particular in aquatic invertebrate paleontology [Loden 80, Miller 82, Reyment 88, Scrutton 96, Burton 07, Harper 07, Werderlin 07, Zieritz 09, Wilk 09, Dynowski 10, Schneider 10, Whelan 12], but also more recently in mammals [Piras 10, Colangelo 12]. It will become clear in the Framework that, differently from this literature, we do not oppose eco-phenotypic variation and evolution.

phenotype as a multidimensional set of traits, and to study their co-variance, their heritability and plasticity, and their dynamics, releasing transmission (inheritance) from the necessity of a detailed allelic/particulate mechanism [Borenstein 06, Chevin 10, Engen 11]. Quantitative genetics models, devised for elaborating empirical data, are a promising ground for modeling, but our Framework doesn't build on them. On the reductive side, we have population genetics models that do not allow a proper consideration of eco-phenotypic concepts. This is true (and more puzzling) also in the population genetics literature on niche construction [Laland 01] that, despite many manifestos about organisms that are active in the ecological world, treat phenotypes as nothing but combinations of alleles, and model evolution as a dynamics of changing shares of alleles in the population [Donohue 05].

Eco-phenotypic concepts are familiar in ecological modeling [Miner 05], where, in our view, these concepts seem very promising for an integration with evolution. Interpreted as *ecological*, our Framework aims at describing and studying organisms and populations that perform living, where life is intended as a thermodynamic, matter-energy process. Life concerns resource gathering, usage, and depletion in a spatiotemporal context with given characteristics, as well as multiplication and space occupation. The conjunction of ecology and evolution into the same model cannot be taken for granted. In the literature, evolutionary ecological models are not easily built and do not have a consolidated tradition [Pelletier 09, Smallegange 12]. Our Framework also supports *evolution*, intended as a dynamics which has to do not only with multiplication and space occupation, nor only with the fluctuation of frequencies of basic types of organisms, but also with the cumulative change in the features of unique organisms that are connected into inbreeding populations.

The Framework also applies in the economics of *cultural transmission*, in which individuals form their attitudes and patterns of behavior under a complex system of influences derived from their “cultural parents” and from other members of the society, as well as from the environment. Eco-phenotypic concepts seem to capture some aspects of cultural transmission and economics that are modeled away by a population genetic approach. Some ideas similar to eco-phenotypic concepts have already been developed, without full consciousness of their links with biological issues. In particular, in part of the economic literature, cultural traits have ecological relevance, thereby modifying the environment through some economic or production activity, with a biological counterpart in niche construction; traits may change depending on environmental stimuli and the possible choices of the individuals, creating a link with the ideas of phenotypic plasticity, reaction norms and rationality; and traits reproduction crucially depends on the environmental feedback received. An *ad hoc* kind of modelization is necessary and, at the same time, complementary to the established one based on population genetics.

2 The Framework

The various elements of the Framework are connected to each other and can be differently interpreted in biology and in economics or cultural transmission. The Framework is *agent-based.* If the model is interpreted biologically, agents will be organisms in an ecological world, and they will be constrained to each other by means of ecological interactions as well as genetic sharing. Within a cultural transmission interpretation, instead, agents will be inhabitants of a cultural context, producers of culture, and they will be under each others' influence through cultural contact as well as the sharing of cultural rules. We first present the key concept of physiology and its role; we then define the environment and how resources are extracted by each individual. We then move to the dynamic part by showing how resources regenerate and can be subject to niche construction, and we define how agents reproduce and how physiologies evolve.

Physiology

Consider a population that, at each point in time, is composed of a number N_t of agents, located in a world endowed with a quantity $R_t \in \Re^+$ of resources. Each agent is characterized by a *physiology* $\bar{P}_t^i$: an algorithm that defines the resource management behavior of the agent. In particular, a physiology determines how an agent would get resources and how many resources it would extract from the environment. Each physiology, thus, provides information about the resources needed by the agent for the basic survival $\tilde{M}^i$; about the efficiency is the resource extraction α^i and the efficiency of their use β^i; given these information a physiology also defines the agent's *resource intake target* G_t^i, that defines the maximal amount of resources the agent is willing to extract and use for its survival and for offspring production. We can then define

$$\bar{P}_t^i = (\tilde{M}_t^i, \alpha^i, \beta^i, G_t^i) \tag{1}$$

We want our agents to be ecological: an agent will be a living process consisting in an organized circulation of resources. Conversely, resources are such with respect to the living process. Resources circulate in a particular pattern we call the agent's physiology [Thurman 10]. An agent in ecology – an organism – consists in an organized circulation of matter, energy, chemical compounds. The existence of an organism commits a part of the matter and energy that would otherwise be 'free' in the environment, or better, committed into other processes.

Ecological modelers like Kylafis and Loreau [Kylafis 08] treat plants in an ecosystem as a "compartment", whose environment is the "soil nutrient pool", i.e. the stocks of a nutrient in inorganic form in the soil. Although the plants compartment does not have an endogenous target similar to our G, the realized uptake can have an exogenous limit in the competition for other factors (e.g., water, light, space), being not exclusively dependent on the plants' nutrient uptake *ability*. Kylafis and Loreau's uptake ability can be compared to our α. Our β concerns the effect upon the agent of extracted resources, therefore quantities, such as health and size, that the ecologists subsume as limiting factors to the growth of the compartment. The soil can be fertile or infertile compared with plants requirements, and the study of the plant-soil dynamical system allows for the discovery of the conditions of plant persistence or extinction.

Cultural studies are much less familiar with seeing an agent as an organized circulation of resources. Interpreting the concept of a physiology-endowed ecological agent in a cultural environment, we are forced to think to cases where the agent's existence consumes resources and commits them in a particular pattern. One example of cultural physiology could be working cultures.

Environment

We define environment as all the elements of the world and of the population that are not part of the agent. In this sense the environment is not objectively determined but has to be defined with respect to each agent. We then call the environment E_t^i. Using this definition, the environment is composed of different elements. First of all, the environment consists of the resources R_t that are available to the population. Note that these resources are a common quantity among all individuals if we assume that all agents have access to the same pool of resources. However, for each agent, the environment is also composed of all the other components of the population, and their features. Thus the environment consists also of N_t and of the vector of all the other agents' physiologies $\bar{P}_t^{-i}$. We can then define

$$\bar{E}_t^i = (R_t, N_t, \bar{P}_t^{-i}) \tag{2}$$

As we shall see, we want our agents to be developmentally plastic: they achieve their life-long identity (i.e., in the Framework, their physiology) through a maturation stage or function in which multiple cues bias the final, 'grownup' outcome. An agent doesn't develop by facing a private environment in complete isolation from all the other agents in the population. On the contrary, its physiology will be influenced by the abundance of other agents (density-dependent) and by the physiologies they exhibit. This looks like a good way to model cultural agents, who learn fundamentally from parents, authoritative figures, and peers [Sinha 05, Taborsky 12], and we shall see that our Framework doesn't impose that the agents-to-agent influence be in terms of copying others' physiologies. But also in biology conspecifics' physiologies are fundamental developmental cues. As an example, in a recent study [Sadeh 11], fire salamander larvae have been shown to respond early in ontogeny to dried conspecifics as a cue for future desiccation of the ephemeral pools where they live.[2] More straightforward influence may take place in plants, where, for example, a plant's physiology will be biased in a crowded environment and/or in a population where many plants have very demanding physiologies.[3]

Resource extraction

At each period, each individual in the population is supposed to extract resources in order to survive and to produce offspring. The way in which each individual determines the amount of resources is clearly constrained by the total amount of resources available to the population so that $\sum_i R_t^i \leq R_t$. Moreover, the amount of resources each agent finally gets, R_t^i, crucially depends on its own resource intake target G_t^i, but also on the others' resource intake targets G_t^{-i} and on the population-wide vector of all extraction efficiencies $\bar{\alpha}$. We can then define

$$\bar{R}_t^i = (R_t, G_t^i, G_t^{-i}, \bar{\alpha}) \tag{3}$$

Notice that the way in which the final resource extraction is determined can be simple, in the case in which each individual extracts resources individually with no interaction with other members of the society, or it can be very complex, as for complex societies (ants or humans) in which resources are extracted through a division of labour and rules for resource distribution hold. Notice that if $R_t^i < \tilde{M}^i$, then the agent dies.

This is the agent-centered version of a phenomenon which is well represented in ecological modeling. Kylafis and Loreau's plants compartment shrinks and eventually gets extinct in presence of an infertile soil, but in nature, population reduction seems to be a plausible and straightforward way for a population to cope with a resource-poor environment. More generally, in some ecological models there is a "carrying capacity" of the ecosystem that sets

---

[2] The response is a costly acceleration of the developmental process towards metamorphosis. The modification thus concerns the timing of development itself, not the final physiology, and this makes things more complicated. Moreover, later in ontogeny, developing salamanders can fully compensate for this response in case of contradictory more reliable cues. Finally, this example is not appropriate because actually larvae respond to chemicals released in the decomposition of **dead** conspecifics (!).

[3] Kylafis and Loreau, as we have seen, do not treat individual plants as agents, but they model their reciprocal regulation in growth through the k parameter, i.e. "competition for other resources".

a limit to the population size. However, it is already evident from what we presented so far, that our Framework allows for a multiplicity of solutions. Instead of a change in population size, scarcity of resources might be matched with different physiologies, less demanding or more efficient, as well as with different patterns of labour division and resource distribution in the population. Changes may also concern reproduction strategies that, in our Framework, are formalized as follows.

Matching function and reproduction

Once each individual gets R_t^i, sexual reproduction takes place in order to produce a new generation of individuals. In order to set up the mating process, we need to assume the presence of a *matching function* that matches each male of the community with one female. This matching function can be totally random, individuals being blind in the search process, or can be very complex. It may take into account some phenotypic features we do not have in the model or, more interestingly, it can consider the resources extracted. Then we can observe assortative matching, with agents extracting many resources being mated with similar agents, or the reverse, depending on the specific problem we study.

Assume that each male with physiology i, who extracted R_t^i, is matched with a female of physiology j who extracted R_t^j. Given the matching, each agent decides how many resources to take for its own subsistence, and how much to devote to offspring production. Call

$$\gamma_t^{ij}(R_t^i, R_t^j)$$

the share of R_t^i that an agent of physiology i in a ij matching devotes to own subsistence and $(1-\gamma_t^{ij})$ the share devoted for offspring production. Notice that γ_t^{ji} is the same quantity of i's partner: γ_t^{ji} is then couple-specific, and it may be referred to as allocation coefficient. Since γ_t^{ji} depends on the partners' physiologies, and since these may in turn depend on resources as will be clear in (6), the Framework allows for a change in allocation strategies when resources in the environment change. Wing-dimorphic insects, for example, exhibit a migration dimorphism with a volant morph and a flightless, sedentary morph. The volant morph enjoys the obvious benefits of long-range migration, while the sedentary morph has a higher reproductive output. The trade-off in the allocation of resources between migratory ability and reproduction depends on ecological conditions [King 10]. Call

$$O_t^i = (1-\gamma_t^{ij})R_t^i$$

The same happens for the partner so that $O_t^j = (1-\gamma_t^{ji})R_t^j$.[4] Given the total resources devoted to offspring, an offspring production function can be identified assessing N_{t+1}^{ij}, being

---

[4] In some cases the resources for own subsistence and for offspring are determined inside the couple taking

the number of new generation individuals that are born from the couple ij. Then

$$N^{ij}_{t+1}(O^i_t, O^j_t) \tag{4}$$

Matching and offspring production functions are necessary because agents are specially exposed to their parents, not only by experiencing the family environment, i.e. a subset of the environment populated by the parents' physiologies, but also by inheritance. As we shall see, parents transmit to offspring a "reaction norm", i.e. a rule for achieving a physiology, and a mixture of cues to which the reaction norm can be sensitive. This is vertical transmission, and does not exclude oblique influences (from other adults of the population), to which the reaction norm can be sensitive as well. If the population starts with different physiologies, even in presence of a single population-wide reaction norm, the "rule and cues" vertical inheritance system allows for evolutionary processes like natural selection and drift.

The possibility for evolution through sorting among the agents is an innovation with respect to ecological models, that usually don't chase vertical streams of inheritance. In Kylafis and Loreau's ecological model, evolution is a series of point events that happen at ecological equilibria and that consist in the horizontal replacement of a perfectly homogeneous population with another, slightly different, perfectly homogeneous population.[5] Inter-individual diversity within the population is, instead, the fuel of population genetics models, which are the standard evolutionary models: here we have genetic variants that are vertically transmitted, and compete, and reach equilibria throughout generations of mating and reproduction. Evolutionary and ecological models carry the same idea of inheritance: phenotypic traits are inherited, and evolution is cumulative change in what is inherited.[6] In our Framework, evolution still is a change in what is inherited, inheritance is a more complex matter, and phenotypic traits are not inherited but produced.

It is important to notice here that the Framework can be used to build either analytic

---

into account the aggregate resources extracted by the couple.

[5] Evolution is a process of successive invasions of the population by mutants. At any time, the population is homogeneous for traits like nutrient uptake ability (u) or an environment-modifying trait (c), and the assumption (from the theory of adaptive dynamics [Geritz 97]) is that evolution takes place when the plant-nutrient system is at an ecological equilibrium. The mutant is an individual with a combination of traits (u, c) not much different from the majority. A dynamic model calculates which mutant may break the ecological equilibrium and push the system towards a new one, taking also into account the costs of the new traits compared to the standing ones.

[6] Evolutionary models have finer resolution on traits than ecological ones, and they allow for continuous change whereas ecological models are "invasional" (although the mutants are forcefully kept not too different from the others). Evolutionary models formalize in terms of differentially inherited genes the relationship between generations, and in particular between parents and offspring. Ecological models need not to.

or probabilistic models. Probabilistic models don't trace individual agents, but rather they calculate the whole new generation from the whole previous generation by deriving probability distributions. Therefore, in probabilistic models, agents will be disconnected from their parents. However, probabilities in a probabilistic model will incorporate knowledge of the configuration of vertical and oblique influences on an agent's physiology we just described.

Niche construction and resource regeneration

After the resources are extracted at time t, left resources have time to regenerate so that $R_{t+1} = (R_t - \sum_i R_t^i)(1+\lambda)$. The regeneration rate λ, however, can be exogenous or endogenous. In particular, if individuals resource extraction and physiologies are *niche constructing* then $\lambda_t(\bar{R}_t)$ so that

$$R_{t+1} = (R_t - \sum_i R_t^i)(1 + \lambda_t(\bar{R}_t)) \tag{5}$$

In Kylafis and Loreau's model, the soil nutrient pool is replenished by a constant input of inorganic nutrient through precipitation or dry deposit. While plants take up quantities of nutrient from the soil, plant litter decomposes, being in part recycled to the soil nutrient pool and, in another part, lost from the ecosystem or made unavailable to plants. Kylafis and Loreau then incorporate the ability of plants to add an amount of nutrient to the system through their niche constructing activities. In terrestrial ecosystems, plants can alter various soil properties (e.g. humidity, temperature, fertility), and thus influence nutrient cycling. In particular, plants can modify nutrient mineralization, either through their litter quality or even by creating favourable abiotic conditions for decomposers under their canopy. They can also modify nutrient inputs in their local soil environment. For example, they can enrich the soil with nitrogen via symbiotic or non-symbiotic nitrogen fixation, or with other nutrients via uplift from previously inaccessible soil resources using deep roots. Some tree species are very efficient at retaining dry atmospheric inputs due to their large surface area and aerodynamic resistance. Some shrub species alter airflow dynamics, and thereby accumulate mineral-rich clay materials under their canopy. Only a fraction of the nutrient made available by niche construction directly benefits plants and is incorporated into their biomass. The remaining fraction of the nutrient coming from niche construction is added to the soil inorganic nutrient pool. In Kylafis and Loreau's model, as niche construction increases plants' biomass, the ability to perform further niche construction becomes limited, also in order to avoid the possibility of a boundless autocatalytic process leading to unlimited growth of nutrient stocks.

Reaction norms and the new generation's physiology

Once the new generation is born, newborn agents have to achieve their own physiology through maturation. This is done according to a *reaction norm* that dictates how to use or not use information from the environment and from parental physiologies as cues to form a new physiology. The reaction norm X^i_{t+1} thus may accept, as an input, the resources faced by the new generation R_{t+1}, the parental physiologies P^i_t and P^j_t, and the physiologies agents in new generation meet during their formation process $\bar{P}_t$. We can then state that:

$$P^i_{t+1} = X^i_{t+1}(R_t, P^i_t, P^j_t, \bar{P}_t) \tag{6}$$

If we think again to Kylafis and Loreau's model of plants in an ecosystem, we will find a single and rather autarchic reaction norm: P is fixed by X, i.e., each individual plant develops a physiology without taking into account the available resources, nor any existing physiology. And since the achieved physiologies have no intake target, relation (3) becomes: $\bar{R}^i_t = (R_t, \bar{\alpha})$: the competition for resources affects directly population size, and, in determining which physiologies survive, any supposed difference in efficiency α will matter, or – in case of evenness – it will just be a matter of chance. In fire salamander larvae, instead, we have a reaction norm that takes into account the physiologies in the population $\bar{P}_t$, although with no special importance of parents, and uses them as a proxy for water resources: $P^i_{t+1} = X^i_{t+1}(\bar{P}_t)$. A reaction norm that specifically accepts parental physiologies (P^i_t, P^j_t) may be used to model not only phenomena that have to do with direct copy, such as learning from parents, but also many others. For example, parents may bias offspring's physiologies by passing to them some extra-genes that do not determine the reaction norm, but *to which* the reaction norm is sensitive, genes that have perhaps biased their physiologies in the past. Through generations, there can be evolution in these extra-genes – an aspect very important to those authors who identify evolution with genetic change. In our Framework, such evolution of the extra-genes appears as a shifting parental bias on offsprings' physiologies. Other known parental biases on offsprings' phenotypes pass through epigenetics, i.e. inheritable non-genetic modifications of gene expressions, and through parental care and active phenotype determination.

All imaginable kinds of reaction norms are possible in the Framework. The reaction norm comes from one parent. In particular, the new individual born from matching ij will take i's reaction norm with probability p^{ij}_t:

$$X^i_{t+1} = X^i_t$$

With probability $1 - p^{ij}_t$, the agent will instead take j's reaction norm:

$$X^i_{t+1} = X^j_t$$

Developmentally plastic agents differ from agent-copying agents that are found in the majority of models in the literature [Bisin 10]: developmentally plastic agents do not copy how other agents are, or look like; they copy, or somehow receive, the rule that drives other agents to become what they are. Motivations to modeling rule-copying instead of agent-copying come both from evolutionary biology and economics.

Biology distinguishes between genotype and phenotype. Biologists talk about a reaction norm to indicate how, in presence of a constant genotype, the phenotype (dependent variable) changes as a function of the environment. The phenotype is thus conceptualized as a reaction of a genotype to the environment. The genotype – what is transmitted, inherited – does not have a phenotype 'attached' to it, but rather it features a reaction norm that governs the making of the phenotype. In evolutionary biology, several theorists are arguing that developmental plasticity is non-negligible, not only because it is widespread, but also because it contributes to evolutionary outcomes, e.g. by buffering or facilitating genetic change [West-Eberhard 89, Pigliucci 01, West-Eberhard 03, Crispo 08, Pigliucci 10].

In the established field of cultural transmission modeling, cultural transmission is formalized as a passing of preferences or behaviors, thus analog to genetic transmission with no plasticity. But intergenerational studies show that cultural transmission concerns the rationale behind preferences rather than preferences themselves (refs.). Modeling developmentally plastic agents has several advantages. First, it allows environmental conditions to intervene in the agent's maturation. Other agents are obviously important – they are both reaction norm transmitters and phenotype exhibitors – but they are not the only source of the individual agent's phenotype. Second, and partly as a consequence, this modeling allows for the appearance of unobserved and unprecedented agents. That is very important for researching innovation that goes beyond the recombination of a limited number of already existing traits [West-Eberhard 08, Müller 10].

Evolution

Eco-phenotypic concepts require, in our view, an explicit modelization of phenotypes and their evolution. Simple population-genetic-style models cannot do the job, and the multivariate approach of quantitative genetics is very promising but also very complicated. We then proposed a Framework as a fresh start.

To summarize, evolution in our Framework minimally consists in the cumulative change of the physiologies of the agents that compose the population, as well as in fluctuations in their number. At each generation, physiologies develop according to a reaction norm that may or may not take into account resources in the environment and the physiologies of all the agents in the previous generation, with possible specific importance of parental physiologies. Parents are part of a generation that, like any generation, features differential matings and reproductive outputs, and they bias their offspring's physiologies in a particular way that includes extra-genes, epigenetic modifications, parental care and phenotypic induction. Additionally, evolution may simultaneously consist in the differential diffusion of alternative reaction norms in the population. In any case, the population extracts and uses resources from the environment, and it can also niche-construct, i.e. top-up onto the automatic regeneration of resources so that an additional, positive feedback is established between resources in the environment and the evolving population that exploits them and react to them in a plastic way.[7]

3 Discussion

In perspective, we should build specified models inspired to problems in evolution, ecology, and cultural transmission, with the aim of analyzing general features of the models built in our Framework. The models will be be either probabilistic or agent-based. One difference we have seen above is that in probabilistic models agents are disconnected from their parents. In both cases, however, the patterns of heritability (i.e. the difference in influence between parents and other agents) will have to be specified in detail.

It will surely be interesting to study the outcomes of different characteristic reaction norms. Our Framework does not force reaction norms to be "adaptive", i.e., norms that tune physiologies for a longer survival of the population over environmental change. In case of adaptive reaction norms, how much forward-looking do we expect them to be? For example, will they economize resource consumption with a 1-, 2-, 3- generations foresight? What are the short- and long-term effects of different reaction norms on the population's environment? How much plasticity is present in successful populations? What are the features of reaction norms that have more effect on the dynamics? And are there mandatory characteristics any

---

[7] There are many things our Framework doesn't allow to model. For example, in evolutionary biology, phenotypic plasticity is important for its biogeographical implications. Fiddler crab species [Thurman 10] whose osmoregulation is more plastic are more able to tolerate different salt concentrations: the osmotic toleration of individuals varies as a result of habitat acclimation. This affects geographical range, and ultimately evolution: in presence of global warming and sea level rise, the plastic species is less likely to run out extinct. Our model cannot account for these dynamics, since it is not spatially explicit and does not introduce changes in the environment. Under these respects, we see the spatiotemporal scale of our model as more circumscribed. The model also neglects spatial environmental heterogeneity, so all individuals in the population are assumed to experience the same physical environment at any given time.

reaction norm should have?

In every model, not all the elements of the Framework will be equally in focus: some of them will be set as parameters with trivial values (e.g., matching function or niche construction effect). One of the simplifications that can surely be made is to perform studies of a population that is homogeneous with respect to reaction norm, and see what are their performances and outcomes in terms of survival/extinction, population size fluctuations, stable or unstable dynamics of recurring physiologies, and similar issues. The Framework allows for a much more complex dynamics, where multiple reaction norms are present and differentially transmitted in the population, so that their fate can be followed together with that of the population and its environment. While, in a situation of reaction norm homogeneity, probabilistic models are largely sufficient, in presence of different RN agent-based models can provide additional information such as variance and clustering whose relationship with different trajectories and outcomes can be studied.

References

[Bisin 10] Alberto Bisin & Thierry Verdier. *The economics of cultural transmission and socialization.* In Jess Benhabib, Alberto Bisin & Matt Jackson, editeurs, Handbook of Social Economics, chapitre 9. Elsevier Science, 2010.

[Borenstein 06] E Borenstein, I Meilijson & E Ruppin. *The effect of phenotypic plasticity on evolution in multipeaked fitness landscapes.* Journal of Evolutionary Biology, vol. 19, pages 1555–1570, 2006.

[Burton 07] T. Burton, B. Knott, P. Vercoe & a. Brearley. *Eco-phenotypic growth in juvenile smooth marron, Cherax cainii (Decapoda: Parastacidae).* Fisheries Management and Ecology, vol. 14, no. 5, pages 309–317, October 2007.

[Cavalli-Sforza 81] Luigi Luca Cavalli-Sforza & Marcus W. Feldman. Cultural transmission and evolution: A quantitative approach. Princeton: Princeton University Press, 1981.

[Chevin 10] Luis-Miguel Chevin & Russell Lande. *When do adaptive plasticity and genetic evolution prevent extinction of a density-regulated population?*

Evolution; international journal of organic evolution, vol. 64, no. 4, pages 1143–50, April 2010.

[Colangelo 12] Paolo Colangelo & Anna Loy. *Cranial distinctiveness in the Apennine brown bear: genetic drift effect or ecophenotypic adaptation?* Biological Journal of . . . , vol. 107, pages 15–26, 2012.

[Crispo 08] Erika Crispo. *Modifying effects of phenotypic plasticity on interactions among natural selection, adaptation and gene flow.* Journal of evolutionary biology, vol. 21, no. 6, pages 1460–9, November 2008.

[Donohue 05] Kathleen Donohue. *Niche construction through phenological plasticity: life history dynamics and ecological consequences.* The New phytologist, vol. 166, no. 1, pages 83–92, April 2005.

[Dynowski 10] Janina F. Dynowski & James H. Nebelsick. *Ecophenotypic variations of Encrinus liliiformis (Echinodermata: Crinoidea) from the middle Triassic Muschelkalk of Southwest Germany.* Swiss Journal of Palaeontology, vol. 130, no. 1, pages 53–67, December 2010.

[Engen 11] Steinar Engen, Russell Lande & Bernt-Erik Saether. *Evolution of a plastic quantitative trait in an age-structured population in a fluctuating environment.* Evolution; international journal of organic evolution, vol. 65, no. 10, pages 2893–906, October 2011.

[Geritz 97] Stefan A H Geritz, J A J Metz, Éva Kisdi & Géza Meszéna. *Dynamics of Adaptation and Evolutionary Branching.* Physical Review Letters, vol. 78, no. 10, pages 2024–2027, 1997.

[Harper 07] Charles W. Harper, John C. Tipper & Victor G. Walmsley. *Ecophenotypic strategies of dalmanellid brachiopods.* Lethaia, vol. 15, no. 1, pages 31–40, October 2007.

[King 10] Elizabeth G King & Derek a Roff. *Modeling the evolution of phenotypic plasticity in resource allocation in wing-dimorphic insects.* The American naturalist, vol. 175, no. 6, pages 702–16, June 2010.

[Kylafis 08] Grigoris Kylafis & Michel Loreau. *Ecological and evolutionary consequences of niche construction for its agent.* Ecology letters, vol. 11, no. 10, pages 1072–81, October 2008.

[Laland 01] Kevin N. Laland, J. Odling-Smee & M.W. Feldman. *Niche construction, biological evolution, and cultural change.* Behavioral and brain sciences, vol. 23, no. 01, pages 131–146, 2001.

[Loden 80] M.S. Loden & W.J. Harman. *Ecophenotypic Variation in Setae of Naididae (Oligochaeta).* Aquatic Oligochaete Biology, pages 33–39, 1980.

[Miller 82] A. A. L. Miller, D. B. Scott & F. S. Medioli. *Elphidium excavatum (Terquem); ecophenotypic versus subspecific variation.* The Journal of Foraminiferal Research, vol. 12, no. 2, pages 116–144, April 1982.

[Miner 05] Benjamin G Miner, Sonia E Sultan, Steven G Morgan, Dianna K Padilla & Rick a Relyea. *Ecological consequences of phenotypic plasticity.* Trends in ecology & evolution, vol. 20, no. 12, pages 685–92, December 2005.

[Müller 10] Gerd B. Müller. *Epigenetic Innovation.* In Massimo Pigliucci & Gerd B. Müller, editeurs, Evolution: The Extended Synthesis, pages 307–332. Cambridge, MA: MIT Press, 2010.

[Pelletier 09] F Pelletier, D Garant & a P Hendry. *Eco-evolutionary dynamics.* Philosophical transactions of the Royal Society of London. Series B, Biological sciences, vol. 364, no. 1523, pages 1483–9, June 2009.

[Pigliucci 01] Massimo Pigliucci. Phenotypic plasticity: Beyond nature and nurture. Baltimore: Johns Hopkins University Press, 2001.

[Pigliucci 06] Massimo Pigliucci. *Genetic Variance–covariance Matrices: A Critique of the Evolutionary Quantitative Genetics Research Program.* Biology & Philosophy, vol. 21, no. 1, pages 1–23, January 2006.

[Pigliucci 07] Massimo Pigliucci. *Do we need an extended evolutionary synthesis?* Evolution; international journal of organic evolution, vol. 61, no. 12, pages 2743–9, December 2007.

[Pigliucci 10] Massimo Pigliucci. *Phenotypic plasticity.* In Massimo Pigliucci & Gerd B. Müller, editeurs, Evolution: The Extended Synthesis, pages 355–378. Cambridge, MA: MIT Press, 2010.

[Piras 10] Paolo Piras, Federica Marcolini, Pasquale Raia, Mariateresa Curcio & Tassos Kotsakis. *Ecophenotypic variation and phylogenetic inheritance in first lower molar shape of extant Italian populations of Microtus (Terricola) savii (Rodentia).* Biological Journal of the Linnean Society, vol. 99, no. 3, pages 632–647, February 2010.

[Reyment 88] R. a. Reyment, F. L. Bookstein, K. G. McKENZIE & S. Majoran. *Ecophenotypic variation in Mutilus pumilus (Ostracoda) from Australia, studied by canonical variate analysis and tensor biometrics.* Journal of Micropalaeontology, vol. 7, no. 1, pages 11–20, May 1988.

[Sadeh 11] Asaf Sadeh, Noa Truskanov, Marc Mangel & Leon Blaustein. *Compensatory development and costs of plasticity: larval responses to desiccated conspecifics.* PloS one, vol. 6, no. 1, page e15602, January 2011.

[Schneider 10] Simon Schneider, Franz T. Fürsich, Tanja Schulz-Mirbach & Winfried Werner. *Ecophenotypic Plasticity Versus Evolutionary Trends—Morphological Variability in Upper Jurassic Bivalve Shells from Portugal.* Acta Palaeontologica Polonica, vol. 55, no. 4, pages 701–732, December 2010.

[Scrutton 96] C. T. Scrutton. *Ecophenotypic variation in the early Silurian rugose coral Palaeocyclus porpita.* Proceedings of the Yorkshire Geological Society, vol. 51, no. 1, pages 1–8, June 1996.

[Sinha 05] Anindya Sinha. *Not in their genes: phenotypic flexibility, behavioural traditions and cultural evolution in wild bonnet macaques.* Journal of biosciences, vol. 30, no. 1, pages 51–64, February 2005.

[Smallegange 12] Isabel M Smallegange & Tim Coulson. *Towards a general, population-level understanding of eco-evolutionary change.* Trends in ecology & evolution, pages 1–6, August 2012.

[Taborsky 12] Barbara Taborsky & Rui F Oliveira. *Social competence: an evolutionary approach.* Trends in ecology & evolution, vol. 27, no. 12, pages 679–688, October 2012.

[Thurman 10] Carl Thurman, Joshua Hanna & Chad Bennett. *Ecophenotypic physiology: osmoregulation by fiddler crabs (Uca spp.) from the northern*

Caribbean in relation to ecological distribution. Marine and Freshwater Behaviour and Physiology, vol. 43, no. 5, pages 339–356, October 2010.

[Via 85] Sara Via & Russell Lande. *Genotype-environment interaction and the evolution of phenotypic plasticity.* Evolution, vol. 39, pages 505–22, 1985.

[Werderlin 07] Lars Werderlin & J. Otto R. Hermelin. *Testing for ecophenotypic variation in a benthic foraminifer.* Lethaia, vol. 16, no. 4, pages 303–307, October 2007.

[West-Eberhard 89] Mary Jane West-Eberhard. *Phenotypic plasticity and the origins of diversity.* Annual Review of Ecology and Systematics, vol. 20, no. 249-278, 1989.

[West-Eberhard 03] Mary Jane West-Eberhard. Developmental plasticity and evolution. Oxford: Oxford University Press, 2003.

[West-Eberhard 08] Mary Jane West-Eberhard. *Toward a Modern Revival of Darwin's Theory of Evolutionary Novelty.* Philosophy of Science, vol. 75, no. 5, pages 899–908, December 2008.

[Whelan 12] N. V. Whelan, P. D. Johnson & P. M. Harris. *Presence or absence of carinae in closely related populations of Leptoxis ampla (Anthony, 1855) (Gastropoda: Cerithioidea: Pleuroceridae) is not the result of ecophenotypic plasticity.* Journal of Molluscan Studies, vol. 78, no. 2, pages 231–233, February 2012.

[Wilk 09] John Wilk & Rüdiger Bieler. *Ecophenotypic variation in the Flat Tree Oyster, Isognomon alatus (Bivalvia: Isognomonidae), across a tidal microhabitat gradient.* Marine Biology Research, vol. 5, no. 2, pages 155–163, March 2009.

[Zieritz 09] Alexandra Zieritz & David C. Aldridge. *Identification of ecophenotypic trends within three European freshwater mussel species (Bivalvia: Unionoida) using traditional and modern morphometric techniques.* Biological Journal of the Linnean Society, vol. 98, pages 814–825, 2009.