The time of populations: Viability and Dynamics
in History, Population Economics, Population Biology,
and Population Genetics

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1 The Time of Populations

The unexpected Part of population studies concern stable population models, convergence toward equilibria, cycles, asymptotic distributions. Yet, human populations, because of history, call for a different view of time. For example, fertility time-series display sudden changes, breaks, jumps from one regime to another, temporary stagnation, unexpected. . . This variability of time signals raises the question of the viability of underlying systems: how, in our advanced economies, do we manage the fits and starts of the age structure, such as the massive arrival of schooled children then students than job seekers, then now pensioners? How, in traditional populations, can a society pass through epochs of wars, plagues, and dearth? How does family limitation appear and diffuse in territory and society, as it was the case in France from mid-eighteenth century throughout the nineteenth century?

Re-founding concepts linked to the time of humans The time of populations covers the non linearity of processes, where small effects can bring about large changes, a context of uncertainty, and the possibility of action and human agency. The concepts of trajectory and equilibrium are no longer adequate to tell on causality. This is why they ought to be superseded respectively by the concepts of attainable set and by the maximal set of states from which there exists at least one solution allowing the system to perpetuate itself, and, as a complement, the set of states from which the system is doomed to failure. The concept of optimal strategy familiar to economists or biologists is replaced by the concept of viable strategy, and optimal gain or utility by capture-viability of achievements ex ante or ex post. Forecasting is replaced by how to obtain the maintenance within a set of constraints or by the capturability of a target set. Priority is given to transient dynamics, allying temporary permanence and changes in social forms, instead of asymptotic considerations
(among which stable population models, ergodic theorems, demo-economic or biological cycles).

When I was introduced to viability theory in 1992, this theory was a pure abstraction. Its “illustrations” were pure school exercises. I was longing at mathematics of time adapted to my own idea of time in historical social situations. Viability theory helps us answer questions outside the frame of probability theory, help us deal with the time of populations outside equilibria and without the constructed concept of trajectory. Typically, when I was invited to comment on anthropologist Fredrik Barth’s work, I was supposed to talk about game theory. However, reading it made it clear that, behind the metaphor of this static theory, Fredrik Barth was talking on the maintenance of nomadic populations or on the dynamic game among fishermen, that he had well understood the themes at stake in viability theory.

Mathematical innovations  The importation of this mathematics new into social sciences was not a simple application. By addressing realistic situations, I contributed to the theory: with Katharina Müllers, I introduced the concept of cascade in controlled dynamics; in economics, I faced return functions that are no longer Lipschitz; I explored the differential of viability kernels with respect to the set of admissible controls; I identified solutions of the Lotka-McKendrick system to a noteworthy dynamical set, the invariance envelope; I brought a decisive contribution to the construction of viability kernels in large state dimension, and with dynamics with delay;\(^1\)

I also situated the viable maximum of \( \int_0^T L(x(t), u(t)) \, dt \) of a continuous function \( L \in L^1(\mathbb{R}^{2m+1}, \mathbb{R}^+) \) under a dynamic \( x'(t) \in F(x(t)) \) under constraint \( x(t) \in K \) where \( K \)

is closed. Cannarsa and Frankowska solved the problem for minimal value, but passing from the minimum to the maximum is not straightforward. I showed that the viable optimum is obtained not on the boundary of an absorption basin or of an hypograph, as Aubin claimed without proof, but on the boundary of the capture-viability kernel in direction of high \( y \) of the target \( K \times \{0\} \) viable in \( K \times IR^+ \) under the extended dynamic \( (x'(t), y'(t)) \in (F(x(t)), -L(x(t), u(t))). \) I extended the result to discrete-continuous-time measurable controls. I computed the viable optimum in the case of the economic theory of the life cycle.

1.1 Controlling Economic Systems

1.1.1 The Baby-boom/Baby-bust in the twentieth Century: Human Time and Viability

The history of fertility fluctuations in the twentieth century has been thought in terms of cycles notably since the scenario suggested by economist Richard Easterlin, who conjectured the existence of cycles. Ronald Lee and Kenneth Wachter have suggested models in terms of integro-differential equations, which, in the neighborhood of a certain equilibrium and with certain parameters, produces self-sustained oscillations, which would guarantee a perfect prediction of fertility. However, only a long stagnation has been observed after a single ‘cycle’, the after-war baby-boom and baby-bust. Historical records provide no evidence to cycles in population matters. Moreover, the mathematics of time allows us to study temporal signals without a priori periodic scenarios in mind, at least since Poincaré at the beginning of the twentieth century. Phase-space analysis is highlighting: it shows that fertility time series travel between attractors, identifying fertility regimes. The phase

portrait of fertility since 1930 and its first-return map reveal the rapid rise of fertility from a low regime to a higher regime, a temporary stagnation, a slow return to the pre-war level. Instead of a linear succession in a formal chronology, phenomena jump from one regime to another one. Where typologies of time series were listed, I showed that a certain unity of temporal forms characterizes the history of European trajectories.³

This work opened the road to re-reading the past in terms of dynamical systems. Where Easterlin suggested a mechanistic relationship between economic well-being and reproduction, we know myopic agents in an uncertain environment. It is then necessary, contrary to certain popularized ideas in physics according to which simple equations generate complexity, to highlight simple dynamics in the complexity of the social world. I have supported the phase-space analysis of fertility 1930-1989 by an explanatory scheme based on inertia constraints of economic variables and maintenance or collapse of lifestyles. The trade-off between consumption and parity delineates a line of states beyond which families will be impoverished unless reproduction is reduced. This boundary is attained when one increases her consumption more quickly than her wealth for a given family size. This model allows discontinuous and unpredictable trajectories, which fit observed data.⁴

1.1.2 Fertility Fluctuations in the Old Demographic Regime

Territorial Regulation in Pays de Caux, 1588-1700  The French seventieth century constitutes an exceptional field to observe populations experiencing drastic conditions of mortality and subsistence. The plague occurred frequently, let alone war, dysentery, or dearth. Parish series (baptisms, marriages, burials) look very irregular. To exploit these

data, certain historians emphasize the peaks of deaths, which they call “mortality crises.” Others focus on the study of short-term fluctuations with econometric models.5

It is more difficult to reconstruct populations of the past, to highlight the processes of mortality and fertility. I considered the case study of the population of Pays de Caux, 1588-1700. Censuses do not exist for such traditional populations, and I suggested an original method based on the sole time series of parish registers to obtain fertility and life expectancy time series over these 113 years of old demographic regime.

Their very irregular appearance forbids one to understand the underlying dynamics in sticking to traditional econometrics. Yet, replacing these trajectories in state space restores the discontinuities, the accelerations or the slowing down movements. This operation delivers the anatomy of crises in a clinical manner or the contextual shocks. A model weaving together constraints of ground exploitation, nuptiality, and fertility of the couples to the ups and downs of mortality turns out to be a good explanatory candidate, able not only to mimic all reconstructed series, but also to retrace the series of observed numbers of marriages, a series independent so far of the reconstruction and the simulation.

The fertility of this population goes back and forth between two levels, appearing as two attractors in the phase space. After a long enough period without mortality crisis, married women are old enough, and the mean fertility is low. Brides are also old enough, and do not raise the mean fertility. Most young women must wait before marrying for a farm to be freed by the decease of its landowners. When a mortality crisis occurs, as in 1639-40, marriable people are numerous enough to replace the deceased landowners, and already old enough to maintain the fertility level still at a low level. When mortality crises repeat themselves, then the population of marriable people is depleted, and brides are chosen younger and younger, contributing to raise fertility to a high level, where it

is maintained by the high frequency of mortality peaks and its subsequent renewal of
landowners and their wives. When mortality crises calm down, fertility decreases and
returns to the low level at the same rhythm that married women age and their fertility
decreases.

At last, a model adapted to the empirical data of the Pays de Caux allows us to deepen
the consequences of such a relationship between populations and resources. Simulating
this population model and varying the probability of occurrence of mortality crises, I
showed that there exists a bifurcation value, or a value beyond and below which the sys-
tem works in different regimes: beyond eight crises per century, fertility always remains
high, maintained by high mortality, and the population, although fertile, is threatened
to be annihilated if mortality eventually goes out of reach of fertility; between 1 and 8
mortality crises per century, we observe a two-level regime, and we find again the empirical
case of Pays de Caux; in the absence of crisis, fertility is confined in the low level regime,
corresponding to late age at marriage. This case study for the first time allowed the vali-
dation of the territoriality model with genuine historical data. It highlights the topological
properties associated with the historical fluctuations of mortality and the responses of the
age-pyramid.6

Viability in Population and Environment (Malthus-Boserup)  This case study
raises the question of the interactions between population and environment. After Malthus
denounced population growth as a cause of impoverishment, Boserup sustained that a
large population has a positive effect on technological innovation. Yet, certain empirical
observations go in the direction of Boserup, others do not.

6Bonneuil N. (1990) Turbulent Dynamics in a 17th century population, Mathematical Population Stud-
ies 2, 289-311.
I suggested to revise the theoretical framework of this debate in giving a central place to inertia inherent in technological change, and in considering innovation no longer as a mechanistic process, but as a set-valued function encompassing possible futures.\(^7\) This allows us to find the ideas of Boserup without postulating them, and to re-establish contingency and indeterminacy in agents' behavior, instead of thinking them as submitted to mechanistic forces.

In representing the state space of the Malthus-Boserup system under constraints, I showed how the Boserupian hypothesis enters into a larger view, where myriad Boserupian dynamics coexist with other non-Boserupian ones. With time passing and population growing, the Malthusian equilibrium, characterized by low income, gets every day closer, with the space of attainable states shrinking, constituting an ever pressing incentive to do something, to innovate and rescue the situation. But this is not compulsory, as it is observed empirically and as it is retraced by the qualitative properties of the dynamical system.\(^8\)

**Viability among Nomads and Fishermen (from anthropologist Fredrik Barth)**

Anthropologist Fredrik Barth (1981) described another traditional society, that of Basseri nomads. He showed how this society was organized so as to perpetuate itself, and he identified the processes with which the unity of the camp was maintained. When Barth resorts to the concept of equilibrium and static games to explain the history of the group, I showed\(^9\) that he actually talked of dynamical games and viability out of equilibria.

\(^7\)writing a differential inclusion \(x' \in F(x)\).


Equilibrium on the contrary means starvation, and the problem of nomads is specifically to maintain themselves far from this equilibrium as long as their resources and their demography allow them to do so. To manage this, the group uses 'strategies' (in the sense of game theory): successively the choice of the site where to settle temporarily (when to leave the camp and where to go?), the reduction of individual consumption in situation of food shortage, and finally the sedentarization of the poorer, going to sell their work force in farms, so as to relieve livestock from human demand. If these regulations fail, mortality increases until population is adjusted to resources. In this story, nomads take decisions under the pressure of present and future constraints, they restlessly alter their own history, their 'trajectory' in the space of possible states. They cannot contemplate their future in terms of trajectory, but rather in terms of sets of attainable states, and the head of the group is specifically the one in charge of taking viable decisions, doing his best less to find the optimal choice of which he has no knowledge than to simply avoid failure; technically speaking, these decisions are those which lead the group in the interior of the set of survival constraints of the group (with the additional difficulty that the interactions between humans and livestock are not linear). In this concrete example, decision-making in uncertainty (stemming from unpredictability inherent in availability of land, in weather forecast, in natural misfortunes, . . . ) is mandatory. Instead of a chronological time, we have a social time, where a finite number of controls makes possible a myriad different stories.

This traditional population has then invented original preventive checks, exempting couples to resort to delay at marriage or to family limitation. It perpetually invents its own history, according to its resources and its development.

In another study of Norwegian fishermen, Barth showed that skippers must continually choose between following the other vessels or striking out on their own, searching for new
herring shoals. The strategy changes then all the time with respect to the movements of other vessels. I showed that it was in fact a dynamical problem, in delineating the capture domain in the phase space constituted by the capital (ship and crew) in time \( t \), by the volume of catch, and by the probability at \( t \) to find the best catch in taking risk. This is no longer a question of what other actors will do, but to determine the set of states from which a skipper has the possibility to avoid ruin, and which strategies, with respect to the system, will allow him to do so. How will a skipper effectively react, in a more or less clever manner, produces a story; the capture domain and its associated states of viable strategies discriminate successes and failures among all possible stories. As in this concrete case, the modern theory of dynamic games extends the theory of games, and allows us to overcome the limitations inherent in the static case of game theory.

1.1.3 Diffusion of Behaviors in the Demographic Transition

The French transition 1806-1906 Between fertility fluctuations at low levels since the beginning of the twentieth century and those at high levels in the seventeenth century, the demographic transition raises the question of the change of fertility behaviors in time and space. I explored this question through the data of the Statistique Générale de la France from 1806 to 1906 by départements, the French administrative subdivisions counting up to 90 for the metropolis in the nineteenth century.

The frequent censuses (every five years) are detailed at the level of département, and the statistics of deaths by age were yearly from 1851 onward. These sources are, as many other statistics, flawed with counting errors, under-recording, or declaration defects. The question of the quality of the data is often neglected, but it is inherent to demographic statistics, and this is a difficulty which I addressed. The taking into account of under-recording wiped up the myth of the baby-boom of the 1870's, and situated the French
fertility decline, which, although still pioneer in Europe, was not as marginal as it was claimed (with data not corrected of under-registration).

I suggested an original reconstruction,\textsuperscript{10} capable of correcting the SGF data from, notably, the data of deaths by age. I obtained a new panorama of demographic forces (fertility, mortality, net migration by age). Incorporating explanatory variables such as urbanization or female education, the transition appears as a dynamic system in space and time. Appropriate econometric techniques (cluster analysis, factor analysis, simultaneous regressions, co-integration) allow its study. Notably, urban hierarchy, which was concealed in the absence of reconstruction of urban data in the book by van de Walle (1974), reveals itself as a key feature of the transition. The process is double-sided: at the beginning of the transition, fertility behavior adjusts to a varying harsh environment, then, once launched, the decline goes on, through an innovation wave travelling through the territory from diffusing centers.

A problem, often encountered in the analysis of historical data, is the difficulty in overcoming missing or flawed data. Lotka-McKendrick discrete demographic model, including migration, is combined with stochastic optimization to fit available censuses and vital statistics series to reconstruct missing population data, in the presence of one or two censuses. Simulations help to calibrate the method and determine error weights associated with each data series. An empirical case study is made using data from an administrative subdivision in southern Russia for the period 1863-1916.\textsuperscript{11}

The reconstruction of the population by marital status from imperfect statistics is obtained as solution of another minimization program in large dimension. The correspon-

idence of ages between brides and grooms at each month of the year between 1867 and 1916 also results from a stochastic optimization, avoiding the introduction of ad hoc marriage functions.\textsuperscript{12}

The influence of economics in the demographic transition From the theoretical point of view, I examined the relationship between fertility, mortality, and husband-wife productivity ratio through the unilateral gift equilibrium.\textsuperscript{13} Bergstrom (AER, 2007) showed why fertility during the demographic transition has no reason to be correlated with productivity, but that it should be so with the husband-wife productivity ratio. He used a static framework at equilibrium. I showed firstly that re-introducing mortality in the unilateral gift equilibrium gives mortality the leading role of the transition, as observed everywhere. Secondly, I showed that introducing learning and inertia changes the view of a shifting equilibrium to a view of a system pursuing a moving target. The demographic transition appears then as driven by mortality and economics although correlations of observed fertility with productivity and with husband-wife productivity ratio is null, a result common to acutely documented studies of the transition.

1.1.4 The Life Cycle

Viability in the economic life cycle I resumed the question of the life cycle in a critical perspective of the economic life cycle according to Friedman, Modigliani, or Carroll, from the 1997 patrimony survey and with the modern viability theory, where I suggested


\textsuperscript{13}Bonneuil N. (2010) Family Regulation as a Moving Target in the Demographic Transition, Mathematical Social Sciences (Elsevier) 59, 239-248.
an alternative to inter-temporal utility optimization.\textsuperscript{14} Having children, guaranteeing a certain way of life, and retiring with a certain capital leaves room for many trajectories, where couples are torn between prudence for old days and for children, and impatience to consume, under the threat of unemployment or of bad returns of their saving. Agents’ heterogeneity is rendered both by the whole state space where each state corresponds to a different situation, and by the set of attainable states, which reflects uncertainty inherent both in decision-making and in external shocks. The delineation of all states from which this program in consumption, reproduction, and saving, against the battling of age, is manageable, identifies in return the timely decisions of when have children, when and how much to consume and save. The discontinuous aspect of consumption when a child is born is fully taken into account through the continuous-discrete differential inclusions. Empirical insight from the 1997 patrimony survey validates the theory; international comparison shows that lower fertility is associated with smaller sets of timely decisions. Instead of looking at the determinants of fertility as usual, I suggest to delineate the set of states from which a given parity is attainable, then to determine how this set varies with explanatory variables.

Viability-Optimality in the economic life cycle I resumed the problem of the economic life cycle to compute the viable states from which the optimal trajectories with respect to an inter-temporal utility start\textsuperscript{15}. Households starting from high wealth also start from high consumption; households starting with low wealth must consume rela-


\textsuperscript{15}ibid: Bonneuil, N. (2011), Maximum...
tively little at the beginning. The household can increase both wealth and consumption, with jumps in consumption, associated with drops or slowing down of wealth accumulation. At mid-life, the maximal-viable path consists of consuming regularly more until the end of life span, with the associated decrease of wealth. The maintenance of the trajectory within constraints is of major interest. What is the use indeed of an optimal trajectory which would leave households ruined or starving? This is the motivation for searching for viable-optimal solutions.

**Pay-as-you-go** Pensions are threatened by the arrival of numerous age classes born during the baby-boom, and followed by less numerous age classes. The numerical unbalance between payers and pensioners is emphasized by the regular lengthening of life expectancy. The usual procedure is to simulate scenarios a priori, in exploring a (necessarily small) set of plausible dates and values on the change of important variables, in deleting those which drive the pay-as-you-go system bankrupt, and with fingers crossed, that at least one attempted scenario works. However, the dimension of the space of possible changes is the number of the state variables: for example five when one considers the duration and the amount of spending, the interest rate, the rate of unemployment, and the ratio of the number of pensioners over the number of payers. This ratio varies in time with mortality, migrations, and the entry into activity of younger age classes. In a two-dimensional space, it is already very long to try all scenarios of changing these variables. The other procedure I developed\(^\text{16}\) consists in determining all states from which there exists at least one solution allowing the maintenance for long enough for pensioners and active, while respecting a certain equity between generations, without understating the resistance of social agents.

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to change. The actions necessary to maintain the system within specified constraints are notably the lengthening of paying duration and the increase of payment, for fixed unemployment and interest rates. One result of the algorithm is to indicate which are the viable decisions, when to put them in action, and with which magnitude. The difference with classical optimization procedures is the taking into account of constraints, the opening of the answer to all viable constraints, and the inclusion of constraints in the search for an optimum.

**Generational Equity** Similarly, preserving equity between generations consists in regulating the transfers between generations so that no generation spends more than it receives: I resumed this problem in avoiding to optimize an inter-generational utility over an infinite future, but in expressing the bare maintenance of inter-generational equity. I showed the existence of an optimal return rate of human capital: for low values (between 4 and 11% in the French case), a net present value for each generation increases with the rate of return of human capital and with the viability kernel; but too high a rate of return (beyond 11%) brings about a shift between pensioners and active and leads trajectories out of the equity constraint.\(^{17}\)

**Vintage models** I revisited the vintage model of economic growth from the point of view of viability compared with optimality.\(^{18}\) The viability kernel shrinks with scrapping time as the technological rate increases, showing that machines must be renewed in line with this rate in order to maintain consumption. The viable and optimal solution in

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the sense of inter-temporal consumption is obtained on the viability boundary under an auxiliary system.

Thanks to my viability algorithm (2006), I could address the question of the viability and optimality in vintage models, which have the technical difficulty of the presence of a lagged effect.

The Origin of Preferences The origin of preferences was viewed as related to the dominant eigenvalue of a Leslie matrix modelling reproductive strategies. However, in a variable environment, the coexistence of varying preferences no longer requires optimality, but is identified to the mathematical property of viability.\textsuperscript{19}

The coexistence kernel of two competitors with varying preferences is computed in the case of scalar and $2 \times 2$ Leslie matrices, with either measurable or differentiable preferences. The homologue of indifference curves is the regulation map, which is the correspondence associating the set of viable preferences to a given state of the population.

Among these viable trajectories, some are also optimal in the sense of dominance discounted in time. These viable optimal solutions are obtained as specific trajectories in an auxiliary dynamic system, and the associated maximal values constitute one boundary of the viability kernel of this auxiliary system.

Hence, the perpetuation of varying preferences allows the economic diversity of preferences, as the comparative history of fertility in nineteenth century France and England taken as an example shows.

The Ramsey model I re-visited\textsuperscript{20} the Ramsey model of economic growth is revisited from the point of view of viability compared to optimality. A viable state is a state from which there exists at least one trajectory in capital, consumption, and reproduction that remains in the set of constraints of minimal consumption and positive wealth. Viability is first presented with a constraint of minimal consumption, then with an additional criterion of economic sustainability in the sense of the Brundtland commission, which amounts to requiring a non-decreasing social welfare. The comparison of viability kernels with or without sustainability shows how much consumption should be reduced and when. One strong mathematical result is that the viable-optimal solution in the sense of inter-temporal consumption is obtained on the viability boundary of an auxiliary system. I could compute the optimal paths in a 5-dimensional problem including sustainability criteria in the sense of the Brundtland commission. Varying preference, technological, and demographic parameters randomly over simulated viability kernels with and without the Brundtland criterion help identify the determinants of the non-emptiness of the viability kernel and of its volume: technological progress works against population growth to favor the possibility for a given state of being viable or viable-sustainable.

Economic sustainability as defined by the Brundtland commission adds the restrictive criterion of non-decreasing social welfare. The viability kernel of sustainable solutions shows the necessity of limiting one's consumption, by how much, and when. The viable, optimal, and sustainable solution is computed on the viability boundary under an auxiliary system that combines optimality and constraints.

\textsuperscript{20}Bonneuil, N, and Boucekkine, R. (accepted) Viable Ramsey Economies.
1.2 Viability in Dynamical Social Networks

Regulations can also be connection matrices. The success of network analysis in social sciences relies on the statement that certain social events which are poorly explained from socio-economic explanations become clearer when they are linked to networks of relationships. The now classical procedure is to estimate connection matrices. Some authors have suggested to include socio-economic variables, and to make out dominance or substitution relationships in the construction of networks. This amounts to considering social networks as variables in spaces of networks. I have suggested a different view\(^{21}\) on dynamical networks, showing that they appear less as state variables than as controls in controlled systems. In Sampson’s benchmark study of monks, I showed that the state variable is the willingness to stay in the monastery. When a crisis occurs, the network of friendships or antagonisms rules the order of departure of the monks. The social crisis is then a viability crisis of the system. Thanks to viability conditions, I reconstituted the underlying processes leading to the observation of the event. I reconsidered a second famous example showing that the political control of the Medici in 15th century Florence ("everyone knew that the Medici wanted, as bankers, to make money; as families, to increase prestige; as neighborhood patrons, to amass power") resulted from a network of business and matrimonial network. Padgett and Ansell (1993) showed that the Medici drew their power from the central place they occupied in the network. I showed that the network actually used satisfies the viability conditions of the domination of the Medici. These conditions determine all networks which would have made possible the same success: the networks are then strategies in the struggle for power, and the state variable is political power. The challenge is then to use the viable networks, thanks to which the temporal

trajectory will bring the political control to the Medici: these networks satisfy the viability conditions. I also showed that the centrality of the Medici implies the viability of the network in the framework of political domination.

At each time, a whole set of networks is possible for the Medici, not only the one retained by chronicle: the Medici could have established new links, cease others, a whole set of change was possible, but only those viable were beneficial to the Medici. Their skill was in their ability to establish and select the right links.

1.3 Spatial Diffusion under Control (Mutational Equations)

In social sciences, diffusion has been used to describe the spread of a disease, acquisition of a skill, or social changes resulting from innovations in customs, beliefs, tools, techniques, adopted by one people from another. In natural or social sciences however, processes may draw shapes which are not necessarily regular sets (as they can be in diffusion processes). For example, schooling does not “spread” in the sense of a disease, or in the sense of a custom from one ear to another. The process requires investment in money, in organization, in humans; it is tuned by the demography of pupils. The quality of teaching or total number of children per class also stems from decision-making and resource constraints. Moreover, the differentiation of schooling between girls and boys covers political and societal will; the competition between confessional and secular systems also obeys to the law.

I developed on the concept of derivative of a shape function to study sets and set-valued maps (or correspondences). The concept of graphic derivatives of set-valued maps, and the mutation of a map (Gore, 1997) allowed me to define the velocity of a set and kinds of differential equations governing the variation of sets, in the general framework of metric spaces.22

1.4 Controlling Population Biological Systems

1.4.1 Population Genetics

Population Paths of the Distant Past from Genetic Data  Insight into the time of populations in the distant past is now made possible by the exploitation of molecular genetic data. The demographic fluctuations of the distant past are involved in the resulting heterogeneity of the genome, in particular that of mitochondrial DNA with a mutation rate higher than nuclear DNA. Does the distribution of pairs of nucleotides conceal the track of a “bottleneck” which would have occurred thousands years ago, as it was claimed? Monty Slatkin showed that the samples are all compatible with the assumption of a constant population, as with the assumption of an exponentially growing population.

I suggested to find \(^{23}\) the whole set of temporal paths capable of producing the observed genetic heterogeneity (polymorphism). This is a problem of viability: I looked for the largest set of states from which there exists a solution leading to the observed result, which here is the confidence interval of the total number of genetic differences within a sample of individuals (nucleotide differences in a pair of genes drawn at random). The solution I am mentioning is the one of the “coalescent” process: knowing the mitochondrial DNA of individuals, one can compute the probability that two of them have a common ancestor a certain number of generations ago. This probability depends on the history of the population size. Moreover, the genetic differences of two individuals come from the sole mutations occurred since the common ancestor. Hence the relationship between genetic differences and demographic fluctuations in the past, which however remains hard to handle when the population varies in time.

Instead of validating a plausible or appealing scenario such as the famous demographic "bottleneck," I computed the domain of possible histories reflected by the data.

**Protected Polymorphism: Two Loci Two Alleles** In population genetics, one important question is how to protect polymorphism in time-varying environments. Density-dependent or stochastic selection has been suggested to be present at the molecular level. In many natural bio-populations, selection coefficients are not constant but fluctuate from one generation to the next because of changing environment and genetic transmission.

In an unpredictable environment, maximum adaptability is no longer at stake, while the concept of viability kernel truthfully reflects the question of protected polymorphism. It allows us to take into account transient change, which is the rule in population biology, and to obtain results without imposing laws to fitness variations. The viability kernel plays then a central role in understanding natural selection, because the trajectories leaving this set enter into a rarity crisis, while those still within the kernel have a chance to keep the system in a sufficiently polymorphic state. The systems do not "select" the fitness. The viability kernel simply reveals that, if alleles leave the kernel, then there no longer exists any possibility to avoid impoverishment of polymorphism.\(^\text{24}\)

**Return to Polymorphism in Minimal Time** Protected genetic diversity raises the subsequent question of the advent or the return of a rare allele, a key feature in conservation genetics. The concept of minimal number of generations in impoverished polymorphism brings an answer. It allows us to assess the existence of a path toward polymorphism, and to determine which fertilities associated to allele combinations must be selected at

each generation. Depicting the level curves of the minimal number of generations out of polymorphism reveals the importance of heterozygote mating.

**Protected Polymorphism in Multiple Habitats** I re-formulated protected polymorphism under time-dependent selection and migration as a viability problem. I identified the viability kernel in the case of migration and soft selection, from two demes and two alleles and up to four demes and four alleles. I highlighted the determinants of the maintenance of polymorphism in this situation of unpredictable fitness and migration values. The viability kernel combines the trade-off between openness and closing to migrations and the interplay of the relative fitness values of both alleles in each deme. These determinants are set-valued: along the trajectory which remains in $K$, fitness values and migration rates are not fixed by a rule (e.g. constant, endogenous, frequency-dependent, cyclic, at random) but simply belong to the range of admissible values. Certain values will be taken repeatedly: the repetition of sufficiently low values or sufficiently high values of fitness and migration rates has no fixed rule of occurrence; it depends on where the system travels in the viability kernel. I then suggest that the search for regular patterns in empirical systems could be completed by the search of mere repetitions. In the interior of $K$, the trajectories remaining in $K$ are myriad, and the sequence of viable controls depends on the trajectory taken. This contributes to the uncertainty of the dynamic, without resorting to any probability law or any endogenous mechanism or to sensitivity to initial conditions.

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1.4.2 Population Biology

Prey-Predator: two-trophic and three-trophic Food Chains  The other fundamental historical model of population dynamics is the model of interactions between biological species. In dynamic game theory, each player can change her strategies at each time, taking into account the actions of the other players. Her goal is first to stay in the game, and if possible to find herself in her victory domain, the set of states from which there exists a winning solution while taking into account the strategies adopted by the other players.

The prey-predator model can be considered as such a dynamical game. First considered constant, the interactions between prey and predator actually are subjected to restless fluctuations, because of stress, of changing environment, of genetic mutations, or of phenotypic heterogeneity in populations of prey and predator. These interactions were imagined as functions “endogenizing” the densities, or as stochastic functions,... Here, as we ignore their mode of variation, the only thing we can assess is that they vary within closed sets, which cover our uncertainties and our ignorance. The challenge for the prey consists of surviving, while the predator or the super-predator must spare its prey to secure its long-term survival. These considerations of constraints on states and strategies are sufficient to delineate the largest viability domains for each protagonist, as well as the coexistence domain. I could also determine which are the strategies guaranteeing the viability of one or the other (sometimes there exists a single pair, sometimes a larger set –the regulation of the system is set-valued).27,28

Making Systems Viable  
At last, most population models, even the one where interactions are not specified and viable interactions result from constraints, rely on a conjecture which cannot be vindicated from a phenomenological viewpoint. The non-linearities which have fuelled the fortune of population models produce interesting trajectories, but are neither necessary nor sufficient for the maintenance of populations. I showed that the viability conditions are inherent in the maintenance of populations. These conditions extend the method of Lagrange multipliers to non-smooth sets of state constraints. They allow the selection of models whose solutions satisfy state constraints. I notably showed how historical experiences of Gause, Luckinbill, and Pimentel, who start from prey-predator systems doomed to extinction and alter them so as to perpetuate them, amounts to building viability multipliers (respectively by migration, alteration of the milieu, or genetic adaptations).

1.4.3 Demography Inferred from Cemeteries ('Paleodemography')

Another case study comes from paleo-demography: it was attempted to deduce fertility and mortality from the age distribution (whose very determination is matter of controversy) of skeletons found in old cemeteries. The simplest scenarios, such as the stationary or the stable population models fit poorly to data. Demographic paths as simple as these are unlikely to have existed, for example if we keep in mind the very irregular fluctuations of reconstructed fertility and mortality in 17th century France. On the contrary, my position was to notice that the age distribution of skeletons gives a mere hint at the set of demographic trajectories, those passing through the demographic states of the capture domain of this distribution, which now appears as a target in an appropriate state space, under Lotka-McKendrick dynamic. Among these demographic paths producing the observed distribution of deaths by age, one of them is the most parsimonious in terms

of fertility and mortality fluctuations, and of deviation with respect to the stable age structure. Finding this solution requires to leave the stable framework, at the price of a dramatic augmentation of the number of degrees of freedom (from 2 in the stable case to 25 in the empirical case of Belleville).

This is what I did with modern techniques of stochastic optimization.\(^{30}\) I showed that the mean life expectancy and the mean fertility are reconstructed correctly, and I could estimate these measures in the case studies of St. Thomas Anglican Church (1821-74) (Belleville, Ontario) and Dallas Freedman’s Cemeteries (1869-1907) (Dallas, Texas).

Set-valued analysis, which I pioneered in demo-economy and population genetics, allows me to reorganize the concept of trajectory, to contribute in rehabilitating the connection between mathematics, historical time, and narrative, to extend the paradigm of historical discourse out of the categories of “probability-improbability” (White, 1973) to those of “viability-non viability” in a context of uncertainty.

1.5 Theorems and Algorithms

1.5.1 Existence and Uniqueness of Solutions to Lotka-Volterra integro-differential System

Webb (1981) showed the existence and the uniqueness of the solutions of the system constituted of the McKendrick differential equation and Lotka integral equation, at the heart of the mathematics of populations,\(^{31}\) in the framework of integrable solutions in the \(L_1\) sense. Suggesting a set-valued perspective of social time, I ought to revisit the

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foundations of demography. With Jean-Pierre Aubin and Franck Maurin, I extended the theorem of existence and uniqueness of solutions to the case of functions with closed graph.\textsuperscript{32} Notably, the solutions appear now as the attainable sets issued from the initial pyramid and births. The set of these attainable sets is the invariance envelope (which is also the capture domain in reverse time of the initial pyramid and births), whose existence and uniqueness result from purely topological properties. The respect of constraints by the system throughout time comes from the very construction of the invariance envelope. The mortality, migration, and fertility forces are very general.

1.5.2 The Viability Algorithm in large State Dimension

I addressed the computation of viable states and of the viability kernel in large state dimension, based on stochastic optimization. The idea is to minimize the distance to the set of constraints of solutions starting from a given state, and to assess the viability status of this state whether or not the minimization of the distance leads to at least one trajectory remaining in the set of constraints. The search for viable states is also achieved by the minimization of a distance to the set of constraints, so that the procedure relies on a double stochastic optimization: one where the initial state under examination is fixed, so as to decide whether it is viable or not, and one where this initial state is varied.

1.5.3 The Maximum under Viability Constraints in discrete-continuous (hybrid) time

In the problem

$$\int_0^T L(x(t), u(t)) \, dt$$

$$x'(t) \in F(x(t)) \quad \text{a.e. in } [0, T], \quad x(0) = x$$

(1)

I first\textsuperscript{33} contested the unproven claim by Aubin extrapolating Cannarsa and Frankowska’s result on the viable minimum that the maximum is achieved on the boundary in the direction of low \( y \) of the “absorption-viability kernel” of \( K \) in \( K \times \mathbb{R}^+ \) under the extended dynamic \((x'(t), y'(t)) \in (F(x(t)), -L(x(t), u(t)))\). My counter-example has an empty absorption-viability kernel; yet, the viable maximum exists and is easy to compute.

Second, I showed that the viable maximum of \( \int_0^T L(x(t), u(t)) \, dt \) of a continuous function \( L \in \mathcal{L}^1(\mathbb{R}^{2m+1}, \mathbb{R}^+) \) under a dynamic \( x'(t) \in F(x(t)) \) under constraint \( x(t) \in K \) where \( K \) is closed is obtained on the boundary of the capture-viability kernel in direction of high \( y \) of the target \( K \times \{0\} \) viable in \( K \times \mathbb{R}^+ \) under the extended dynamic \((x'(t), y'(t)) \in (F(x(t)), -L(x(t), u(t)))\). The result holds true with discrete-continuous-time measurable controls.

1.6 The Time of Populations and the Viability Principle

I commented upon this perspective of time,\textsuperscript{34} in situating it with respect to chaos theory imported from physics and with respect to the narrative mode claimed by micro-history.

Instead of viewing history as unfolding along a trajectory, I pleaded for set-valued anal-

\textsuperscript{33}Bonneuil N. (2011) Maximum under continuous-discrete-time dynamic with target and viability constraints, Optimization.

ysis and differential inclusions in social sciences, as being more adequate to human time, because the direction the system can take at each time is enlarged to the set of all admissible directions. These directions do not all lead to a desirable future, and the challenge is often to go to an objective (survival, conquer or keep power, avoid poverty, succeed in a fishing campaign, maintain the diversity, . . .) in spite of uncontrolled perturbations. I also discussed the contribution of probability theory and dynamical games to History.\textsuperscript{35} I suggested the themes of continuity and connectivity as a red thread in the foundations of narrative in history, and examine various conceptions of dynamics in history telling.\textsuperscript{36}

Data of the past conceal an additional difficulty. As each time contains a myriad various trajectories, remains no longer reflect a single past. Historical data can be insufficient to reconstitute a single history, and although this history has actually existed and has been unique, we ought to acknowledge our ignorance and associate to it not the most pleasant or the easier-to-imagine scenario to past data, but the capture domain, the set of all states from which there exists at least one trajectory producing the observed data. This is what I developed in population genetics and in paleo-demography.\textsuperscript{37}


1.7 Mathematics for Social and Bio-Sciences?

I then contributed to introduce modern mathematics of time into population dynamics. The stiff framework of stable populations or Markov processes which prevail in demography tells us about kinematics, but not on the time of populations. Simulations, although very popular, are ineffectual to let us know about state space, even in two dimensions. Many models rely on conjectures, where specifying interactions tell a specific story, but seldom result from phenomenological considerations. The survival or the failure of a system constitute interesting principles in social and natural sciences. The mathematics of viability allows us to translate these principles faithfully, and to confront them to constraints so as to infer what these interactions should be in order that the system perpetuates itself or should have been in order to take the shape it has today. Rather than prediction, these set-valued maps or correspondences give the “map of the future”: how should actors react in such or such situation if the system is to perpetuate itself. I then suggest a shift in our traditional concepts of stable population, simulation, predictions, probabilities, equilibria, which, besides, I contributed to make alive in demography, toward a conceptual and mathematical framework capable of letting us think on and handle uncertainty, human agency, and transient dynamics, putting history and mathematics of time at the heart of the understanding of demographic transformations.