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The cultural implications of growth: Modeling nonlinear interaction of trait selection and population dynamics

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In this paper, we study a nonlinear model of the interaction between trait selection and population dynamics, building on previous work of Ghirlanda *et al.* [Theor. Popul. Biol. **77**, 181–188 (2010)] and Antoci *et al.* [Commun. Nonlinear Sci. Numer. Simul. **58**, 92–106 (2018)]. We establish some basic properties of the model dynamics and present some simulations of the fine-grained structure of alternative dynamic regimes for chosen combinations of parameters. The role of the parameters that govern the reinforcement/corruption of maladaptive vs. adaptive traits is of special importance in determining the model's dynamic evolution. The main implication of this result is the need to pay special attention to the structural forces that may favor the emergence and consolidation of maladaptive traits in contemporary socio-economies, as it is the case, for example, for the stimulation of dysfunctional consumption habits and lifestyles in the pursuit of short-term profits.

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Cumulative culture is a key feature of human civilization. However, both adaptive and maladaptive traits may be part of human cultural assets, and their relative shares depend on a constellation of factors. Population dynamics clearly reflect trait selection, in that adaptive traits tend to favor human reproduction, whereas maladaptive ones play against it. The interaction between trait selection and population dynamics is more complex than might be expected though, and in this paper, we study a nonlinear model that builds on previous work of Ghirlanda *et al.* (2010) and of Antoci *et al.* (2018). We find in particular that in a realistically nonlinear social environment, there is no necessary tradeoff between adaptive and maladaptive traits: it can happen that both thrive and the population gradually goes extinct or on the contrary that it grows without bound. Of course, it can also happen that one type of trait prevails at the expense of the other, with more intuitive impact over population dynamics. A crucial aspect relates to the mechanisms through which adaptive traits turn maladaptive and vice versa. The relative strength of these effects is very important in determining which dynamic regime prevails. Gaining a better understanding of such mechanisms may be of great interest for several research fields in the social sciences and, in particular, for economics where cultural transmission issues are becoming increasingly relevant in the research agenda, but where nonetheless there is still a poor understanding of the link between the social selection of maladaptive traits and the diffusion of welfare-destroying dysfunctional habits and behaviors, whose promotion is linked

to short-term profitability motives and may have serious implications for the long-term social dynamics.

I. INTRODUCTION

The explosion of human adaptive evolution in the past 50 000 years is the product of the interaction between the genetic selection effects of a large increase in the population size and the size and pace of cultural and environmental changes that are characteristics of the Anthropocene era (Hawks *et al.*, 2007). An especially important role in this regard is played by the cumulative nature of human culture, which allows the successful inter-generational transmission of increasing volumes of adaptive knowledge, paving the way for further accumulation (Hidalgo, 2015). However, modeling the reciprocal influences of population dynamics and cumulative trait selection is no easy task, and this issue is of major relevance in many different fields of research. In particular, if a large human population provides opportunity for more systematic exploration of the fitness landscape and for higher chances to reach global optima (Kobayashi and Aoki, 2012), it also increases the risk of hitting the limits of environmental carrying capacity (Nekola *et al.*, 2013) and makes space for a possible improved selection of maladaptive traits (Nesse, 2007) and for the development of behavioral disorders as a consequence of increasing social pressure to adapt (Nesse, 2004). Moreover, a large, rapidly evolving population calls for a careful fine-tuning of ecological trade-offs in the domestication of the natural environment (Kareiva *et al.*, 2007), with threatening prospects for human survival (Bostrom, 2013). Furthermore, the very adaptive success of the human species, e.g., in terms of availability of food resources much beyond survival needs, makes room for

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the development of success-specific maladaptive traits such as compulsive voracity leading to pathological obesity and resulting in a socially driven global pandemic (Swinburn *et al.*, 2011).

Economics is a field of study that has, until recently, paid little attention to cultural selection issues and has considered cumulative culture and its effects on human welfare mostly through the relatively restricted lens of its direct impacts on economic growth, that is, in its essentially instrumental dimension (Berkes and Folke, 1992). This has brought about paradoxical social consequences, in that self-interested norms of economic rationality have made it entirely legitimate and have even prescribed the pursuit of individual short-term advantages at the expense of large social costs in terms of adaptive response to social and environmental challenges (Sen, 1977). This has, for instance, prompted private companies to manufacture and aggressively promote dysfunctional foods (such as high-glucose snacks) that clearly play a major role in the diffusion and consolidation of the obesity pandemic (Candib, 2007). More generally, there has been, until recently, no major public concern about the massive provision and promotion of goods and services with a clearly negative adaptive value for humanity as a whole, such as cigarettes, alcoholic beverages, gambling, and so on (Moodie *et al.*, 2013), and likewise, there has been little concern about the global adaptive impact of the diffusion of consumerist lifestyles based upon an unconstrained deployment of non-reproducible natural resources (Frantz and Mayer, 2009). On the other hand, the cultural implications of growth in terms of the social selection and diffusion of adaptive vs. maladaptive cultural traits should be seriously taken into account to successfully address the formidable challenges of a massively anthropized planet and should be paid major attention in the analysis of the welfare consequences of individual and collective choices.

In perspective, in order to address these issues in relevant and appropriate terms, economic theory should be able to integrate a proper treatment of the social selection of cultural traits into growth models and to fully consider the cultural implications of certain types of policy measures. The existing literature that has paid attention to the cultural dimension has been more focused upon the impact of cultural differences on economic outcomes than upon the cultural consequences of economic choices (Guiso *et al.*, 2006; 2009) or has reinterpreted cultural transmission itself as the product of optimizing choices driven by paternalistic altruism (Bisin and Verdier, 2001). We think instead that a proper economic treatment of cultural transmission issues calls for a consilient integration of research from other social science domains such as human ecology, evolutionary anthropology, and social psychology, which have studied these issues from a broader perspective, are supported by a much stronger basis of field research, and are not prompted by a reductionist intent. In this spirit, we study here a human ecology-motivated mathematical model of the interaction between trait selection and population dynamics as a logical premise to a full-fledged growth model in a consilient perspective, in order to be eventually able to discuss not only the conditions for the achievement of growth targets but also their cultural

implications in terms of adaptive value and therefore their welfare consequences in a richer sense.

Taking as a reference the “macro” model of Enquist and Ghirlanda (2007) which studies the social selection of adaptive vs. maladaptive traits for a constant population, Antoci *et al.* (2018) relax the simple linear hypotheses of the original model to assess the importance of nonlinear effects. They find that in a relatively simple nonlinear model, a complex modulating role is played by the switching of traits from adaptive to maladaptive and vice versa. Therefore, as expected, the cultural change dimension has a major impact upon the stability and adaptive consequences of the social dynamics. In this paper, we extend this analysis by taking into account the dynamic interaction of trait selection and population change, thus switching from a constant population to a full ecological model. Once again, we take as a reference an analogous model by Ghirlanda *et al.* (2010) and relax again its linear structural components to explore a first, essentially nonlinear model of the trait selection-population dynamics interaction. We find that in an essentially nonlinear environment, the dynamic behavior of the model becomes rather complex and that regime switching bifurcations can occur, once again confirming the modulating role of the bi-directional transition between adaptivity and mal-adaptivity of traits. As a consequence of growth, therefore, traits that once were socially beneficial may now become dysfunctional and vice versa. Cultural change may have challenging social implications that may be difficult to anticipate. This calls for a very careful modeling and analysis of the incidence of cultural factors in determining the fine-grained structure of the social dynamics and its population effects and for an even more careful consideration of their role in policy design and evaluation.

II. BASIC FEATURES OF THE MODEL

To model the interaction between trait selection and population dynamics, we consider the following effects. Denote by u the level of adaptive cultural traits, by v the level of maladaptive ones, and by n the population level.

A. Trait (net) decay

Traits, both adaptive and maladaptive, may display different levels of persistence and tend to decay when they are not socially reinforced. In this model, as in Antoci *et al.* (2018), we consider a quadratic decay pattern: the decay of a certain type of trait is size-dependent, so that the larger the level of the type of trait (adaptive vs. maladaptive), the stronger the decay. Specifically, for u , we have a decay factor βu so that total decay is equal to βu^2 . There is moreover a linear effect αu which may take any sign (i.e., may further reinforce decay or generate new traits), so that net decay is equal to $-\alpha u - \beta u^2$, and likewise for v . Let us focus on adaptive traits to fix ideas. The sign of α will determine what happens to net decay when the level of a certain type of trait is relatively low. If α is positive, i.e., if there is a linear effect that recovers adaptive traits at risk of extinction and counteracts the quadratic decay effect in terms of generation of adaptive traits, for a low enough u , the net effect will be positive, i.e., there will be a net generation of new traits, and not a decay.

This is due to the fact that under certain conditions, when the level of adaptive traits is relatively low, there may be a strong social focus on them so that they tend to be socially reinforced to the point of bringing back on stage previously disregarded traits. However, this need not be the case necessarily; if α is negative, even when adaptive traits are scarce, such a component prompts the extinction of more traits. $\alpha > 0$ then parametrizes cases of adaptive resilience, whereas $\alpha < 0$ denotes adaptive decadence. We can reason accordingly for maladaptive traits.

B. Trait corruption/filtering

Traits, both adaptive and maladaptive, may change their nature in certain circumstances, turning from adaptive to maladaptive or the other way round. If the level of maladaptive traits is high, it may be relatively easy that adaptive traits will corrupt into maladaptive. Moreover, the larger the level of adaptive traits, the larger the absolute number of traits at risk of corruption. However, by the same token, a high level of maladaptive traits might cause a strong filtering of such traits and their transformation into adaptive traits, the higher the level of existing adaptive traits, thus causing the reverse effect. Corruption/filtering of adaptive traits will therefore be equal to γuv , where again the sign of γ will depend on the net effect of the corruption/filtering social mechanisms at work. We can again reason accordingly for maladaptive traits.

C. Generation of new traits

As in Antoci *et al.* (2018), the generation of new traits depends on the ratio of the levels of adaptive vs. maladaptive traits, on the (constant) proportions of creation of new adaptive vs. maladaptive traits (q and $1 - q$, respectively), on the population level n , and on the effect factor δ .

D. Population dynamics

The population dynamics is ruled by a logistic equation that depends on the ratio of the levels of adaptive vs. maladaptive traits and whose first-order term is linearly dependent on the net level of adaptive vs. maladaptive traits. If adaptive traits prevail over maladaptive ones, population growth is further reinforced (i.e., adaptive traits in this model are also growth-enhancing traits). Vice versa, if maladaptive traits prevail, this may cause a further contractionary effect on the population level in addition to the second-order effect typical of the logistic dynamics.

With respect to the model studied by Antoci *et al.* (2018), the present one introduces a varying population size n , considers a first-order effect with no sign restriction in addition to the second-order decay effect for both adaptive and maladaptive traits, and makes the generation of new traits explicitly dependent on the population size. Moreover, it introduces, in the spirit of Ghirlanda *et al.* (2010), a logistic-type modeling of the population dynamics. With respect to the Ghirlanda *et al.* (2010) model, the present one considers the possibility of second-order (and not only first-order) decay of traits, two-sided trait corruption vs. filtering,

and dependency of both the generation of new traits and the population logistic dynamics on the ratio of adaptive vs. maladaptive traits.

Our model therefore provides a significant generalization of previous research while at the same time encompasses it as special cases.

III. ANALYSIS OF THE MODEL

On the basis of the discussion presented in Sec. II, we can formally write our model as

$$\dot{u} = u \left[-\alpha - \beta u + \gamma v + q\delta \frac{n}{1+v} \right], \quad (1)$$

$$\dot{v} = v \left[\epsilon - \zeta v + \eta u + (1-q)\delta \frac{n}{1+u} \right], \quad (2)$$

$$\dot{n} = rn \frac{u}{1+v} [1 + \theta(u-v) - n], \quad (3)$$

defined in the prism $\bar{\Pi} = \{u, v, n \geq 0\}$. We will denote by Π the open prism, i.e., $\Pi = \{u, v, n > 0\}$. The parameters of system (1)–(3) satisfy the following conditions: $\beta, \delta, \zeta, \theta, r > 0$; $0 < q < 1$; $\alpha, \gamma, \epsilon, \eta \geq 0$.

We will specifically address two types of issues:

1. Finding the possible equilibrium points in Π and determining their stability.
2. Finding the necessary and sufficient conditions for the existence of diverging trajectories (i.e., of trajectories along which some of the variables $u, v, n \rightarrow +\infty$) and describing some region where this occurs.

A. Local analysis

We start from the existence and stability of equilibrium points, by proving the following theorem.

Theorem 1. *System (1)–(3) can have at most four equilibrium points in Π . Such points correspond to the zeros of a fourth degree polynomial $P(u)$ in u , satisfying further inequalities in u, v, n . At an equilibrium point $(\bar{u}, \bar{v}, \bar{n})$, the Jacobian determinant has the sign of $P'(\bar{u})$. Such an equilibrium point is either a sink or a saddle with one-dimensional stable manifold if $P'(\bar{u}) < 0$ or else a saddle with two-dimensional stable manifold if $P'(\bar{u}) > 0$.*

Proof. Let us look for the equilibrium points of system (1)–(3) in Π . Thus, we pose $n = 1 + \theta(u - v)$ and replace it in the expressions for \dot{u} and \dot{v} . Setting the latter equal to zero, we obtain

$$v = v(u) := \frac{\epsilon(1+u) + \eta u(1+u) + (1-q)\delta\theta u}{\zeta u + (1-q)\delta\theta + \zeta}, \quad (4)$$

where $u > 0$. Hence, in equation $\dot{u} = 0$, we can replace both n and v as functions of u , and eventually, we get an equality–inequality system, that is,

$$\begin{aligned} P(u) &= 0 \\ u &> 0 \\ \epsilon(1+u) + \eta u(1+u) + (1-q)\delta\theta u &> 0 \\ 1 + \theta(u - v(u)) &> 0, \end{aligned}$$

where $P(u)$ is a fourth degree polynomial in u , and $v(u)$ is given by (4).

Assume, now, that $(\bar{u}, \bar{v}, \bar{n})$ is an equilibrium point in Π and write the Jacobian matrix $J(\bar{u}, \bar{v}, \bar{n})$. After straightforward computation, we get $sign(detJ(\bar{u}, \bar{v}, \bar{n})) = sign(detJ'(\bar{u}, \bar{v}))$, where $J'(\bar{u}, \bar{v})$ is the Jacobian matrix of the equilibrium point (\bar{u}, \bar{v}) of the following system:

$$\dot{u} = \frac{q\delta\theta}{1+v} - \beta u + \left(\gamma - \frac{q\delta\theta}{1+v}\right)v + \frac{q\delta}{1+v}, \tag{5}$$

$$\dot{v} = \frac{(1-q)\delta\theta}{1+u} - \eta u + \left(\xi + \frac{(1-q)\delta\theta}{1+u}\right)v - \frac{(1-q)\delta}{1+u}. \tag{6}$$

Thus, calling $F(u, v)$ and $G(u, v)$ the expressions of \dot{u} and \dot{v} in (5) and (6), respectively, we get

$$detJ'(\bar{u}, \bar{v}) = \frac{\partial F}{\partial u} \frac{\partial G}{\partial v} - \frac{\partial F}{\partial v} \frac{\partial G}{\partial u}(\bar{u}, \bar{v}).$$

Moreover, $G(u, v) = 0$ is equivalent to $v = g(u)$, $g'(u) = -\frac{\partial G}{\partial u} / \frac{\partial G}{\partial v}$, where $\frac{\partial G}{\partial v} = \xi + \frac{(1-q)\delta\theta}{1+u} > 0$. Then, the stationary points of system (5) and (6), with $u, v > 0$, are given by $F(u, g(u)) = 0$. Through straightforward steps, we get $F(u, g(u)) = H(u)P(u)$, where $H(u) > 0$ when $u > 0$ and $P(u)$ is the previous fourth-degree polynomial. Then, $F(u, g(u)) = 0$ as $u > 0$ corresponds to $P(u) = 0$.

Suppose \bar{u} is one of these roots. Then

$$\frac{d}{du}(F(\bar{u}, g(\bar{u}))) = \frac{\partial F}{\partial u} - \frac{\partial F}{\partial v} \frac{\partial u}{\partial G}(\bar{u}) = H(\bar{u})P'(\bar{u}),$$

and being $\frac{\partial G}{\partial v}(\bar{u}, \bar{v}) > 0$, it follows that $sign(detJ'(\bar{u}, \bar{v})) = sign(P'(\bar{u}))$, when $\bar{u}, \bar{v} > 0$ and $P(\bar{u}) = 0$. Hence

$$sign(detJ(\bar{u}, \bar{v}, \bar{n})) = sign(P'(\bar{u})),$$

where, moreover, we require $\bar{n} = 1 + \theta(\bar{u} - \bar{v}) > 0$. Therefore, as it is easily observed that $traceJ(\bar{u}, \bar{v}, \bar{n}) < 0$, the theorem's statements follow. In particular, if $P'(\bar{u}) < 0$, Hopf bifurcations may occur for suitable values of the parameters. ■

Theorem 1 tells us that, under certain parameter configurations, there may be a locally stable stationary point for the trait selection-population dynamics. When such conditions are not met, the stationary point is a saddle whose stable manifold has positive codimension, i.e., it can only be reached along very specific trajectories.

B. Diverging trajectories

We provide necessary and sufficient conditions for the existence of diverging trajectories of system (1)–(3) in the open prism $\Pi = \{u, v, n > 0\}$ (i.e., of trajectories along which some variables tend to $+\infty$ as $t \rightarrow \bar{t} \leq +\infty$) and describe some regions where this occurs. To this end, we start by proving the following theorem.

Theorem 2. *Necessary conditions for the existence of trajectories of system (1)–(3) along which $v(t) \rightarrow +\infty$ as $t \rightarrow \bar{t} \leq +\infty$ are that recalling $\beta, \xi > 0$*

$$\gamma, \eta > 0 \quad \text{and} \quad \beta\xi \leq \gamma\eta. \tag{7}$$

If $\beta\xi < \gamma\eta$, such conditions are also sufficient.

If $v(t) \rightarrow +\infty$, then $u(t) \rightarrow +\infty$ as well, and asymptotically (that is, for a sufficiently high value of $v(t)$) $u = av + b + o(1/v)$ holds, where a and b are the rational functions of the system parameters and $o(1/v)$ denotes a quantity tending to zero as $v(t) \rightarrow +\infty$. Moreover, $n(t)$ can tend to zero or to $+\infty$ as v , i.e., $n(t)/v(t) \rightarrow c > 0$, or to $+\infty$ as v^λ , $0 < \lambda < 1$, depending on the parameters of the system.

Proof. Assume that along a trajectory starting from some $P_0 \in \Pi$, $(u(t, P_0), v(t, P_0), n(t, P_0))$, $v(t) \rightarrow +\infty$ holds. Then, $\dot{v} > 0$, for any $t_0 > 0$, in intervals $I \subset (t_0, \bar{t})$, where $\bar{t} \leq +\infty$. It follows that in I either $\eta u \geq \xi v$ or $(1-q)\delta n / (1+u) \geq \xi v$. But the latter inequality implies that $n(t) \rightarrow +\infty$ as well, and thus, $\dot{n} > 0$, i.e., $n < 1 + \theta(u - v)$, so that, being $\theta > 0$, $u(t) \rightarrow +\infty$ and $(1-q)\delta n / (1+u)$ is bounded. It follows that $u(t) \rightarrow +\infty$ and $\eta u(t) \geq \xi v(t)$ in each of the I above. Thus, $\eta > 0$ and $\frac{u(t)}{v(t)} \geq \frac{\xi}{\eta}$. Conversely, as $u(t) \rightarrow +\infty$, it is easily checked that $\gamma > 0$ and $\frac{u(t)}{v(t)} \leq \frac{\gamma}{\beta}$. Hence, $\gamma, \eta > 0$, and $\frac{\xi}{\eta} \leq \frac{\gamma}{\beta}$ are necessary conditions for the existence of trajectories along which $v(t) \rightarrow +\infty$.

Now, we prove that the above conditions, when $\frac{\xi}{\eta} < \frac{\gamma}{\beta}$, are also sufficient. In fact, consider a trajectory starting from (u_0, v_0, n_0) , where v_0 is sufficiently high (we write $v_0 \gg 1$), $\eta u_0 \gg \xi v_0$ and $n_0 \ll v_0$. Then, $\dot{v}(0) > 0$. Being $\beta, \gamma, \eta, \xi > 0$, $\beta\xi < \gamma\eta$, consider

$$\begin{aligned} \eta \frac{\dot{u}}{u} + \beta \frac{\dot{v}}{v} &= \frac{d}{dt} \ln u^\eta v^\beta = -\alpha\eta + \beta\epsilon + (\gamma\eta - \beta\xi)v \\ &\quad + \frac{q\delta\eta}{1+v}n + \frac{(1-q)\delta\beta}{1+u}n. \end{aligned}$$

Then, also $\frac{d}{dt} \ln u^\eta v^\beta > 0$ at $t=0$. If along such a trajectory, $v(t)$ does not tend to $+\infty$, v at some \bar{t} must decrease and so must u . But, until $v > \frac{\alpha\eta - \beta\epsilon}{\gamma\eta - \beta\xi}$, $u^\eta v^\beta$ keeps increasing; then, if v decreases, u increases. Conversely, however, having u increased, when v is close to $\frac{\alpha\eta - \beta\epsilon}{\gamma\eta - \beta\xi}$ and started from a much higher value, $\dot{v} > 0$ and v cannot decrease further. It follows that both $v(t)$ and $u(t)$ tend to $+\infty$.

Our next step is to prove that along a trajectory where $v(t)$ and $u(t)$ tend to $+\infty$ and $\beta\xi < \gamma\eta$, $u/v \rightarrow a > 0$, where $a = (\gamma + \xi) / (\beta + \eta)$. In fact, assume $v(t) \rightarrow +\infty$ and write

$$\begin{aligned} \frac{du}{dv} &= \frac{uv \left(-\frac{\alpha}{v} - \beta \frac{u}{v} + \gamma + \frac{q\delta n}{(1+v)v} \right)}{uv \left(-\frac{\epsilon}{u} - \xi \frac{v}{u} + \eta + \frac{(1-q)\delta n}{(1+u)u} \right)} \\ &= \frac{u}{v} \left(\frac{-\frac{\alpha}{v} - \beta \frac{u}{v} + \gamma + \frac{q\delta n}{(1+v)v}}{-\frac{\epsilon}{u} - \xi \frac{v}{u} + \eta + \frac{(1-q)\delta n}{(1+u)u}} \right). \end{aligned}$$

Hence, posing $u = e^y$ and $v = e^x$, it follows

$$\frac{dy}{dx} = \frac{-\alpha e^{-x} - \beta e^{y-x} + \gamma + \frac{q\delta n}{(1+e^x)e^x}}{\epsilon e^{-x} + \eta e^{y-x} - \xi + \frac{(1-q)\delta n}{(1+e^y)e^y}}.$$

Moreover, as it is easily checked, when $v \rightarrow +\infty$, then $n/v < c$ for a suitable $c > 0$. Assume now, by contradiction, that $y(x)$ has infinitely many maxima and minima when $x \rightarrow +\infty$. Then, take one such extreme value \bar{x} sufficiently high. Then, for $y(\bar{x}) = \bar{y}$, in order to satisfy $y'(\bar{x}) = 0$, $e^{\bar{y}-\bar{x}}$ must be quite close to γ/β , and hence, $e^{\bar{y}-\bar{x}} > q > \frac{\xi}{\eta}$ (since $\frac{\xi}{\eta} < \frac{\gamma}{\beta}$) for a suitable q . As a consequence, through straightforward steps, we get in a neighborhood of \bar{x}

$$\frac{dy}{dx} = \frac{-\beta e^{y-x} + \gamma}{-\xi + \eta e^{y-x}} + e^{-x} \varphi(x),$$

where $\varphi(x)$ and $\varphi'(x)$ are bounded when x is sufficiently high.

Hence, assume $\frac{dy}{dx}(\bar{x}) = y'(\bar{x}) = 0$ and compute $y''(\bar{x})$. Posing $y - x = z$, it follows

$$y''(\bar{x}) = \frac{(\beta\xi - \gamma\eta)e^{\bar{z}}}{(-\xi + \eta e^{\bar{z}})^2} (y(\bar{x}) - 1) + o(e^{-x}).$$

So, being $y'(\bar{x}) = 0$ and $\beta\xi - \gamma\eta < 0$, we have $y''(\bar{x}) > 0$, and maxima and minima cannot alternate. Therefore, $y(x)$ and consequently $u(v)$ do not oscillate when x and thus v is high enough, so that $\frac{u}{v} \rightarrow a > 0$ when $v \rightarrow +\infty$, $\frac{\xi}{\eta} < a < \frac{\gamma}{\eta}$. It follows, when v is high enough, $a = \lim_{v \rightarrow +\infty} \frac{du}{dv}$, i.e.,

$$a = \frac{-\beta a + \gamma}{-\frac{\xi}{\eta} + \eta},$$

and therefore

$$a = \frac{\gamma + \xi}{\beta + \eta}.$$

As far as n is concerned, it easily follows that $n \rightarrow 0$ (when $v \rightarrow +\infty$) if $a < 1$ while, if $a > 1$, $\frac{n}{v} \rightarrow c = \theta(a - 1) + \xi - \eta a$ if the right term is strictly positive; otherwise, if $\theta(a - 1) < \eta a - \xi$, $n \rightarrow +\infty$ as v^λ , where $\lambda = \frac{\theta(a-1)}{\eta a - \xi} < 1$.

Therefore, posing $\lim_{v \rightarrow +\infty} \frac{n}{v} = c' \geq 0$, it follows that, when v is high enough, along any trajectory where $v, u \rightarrow +\infty$, $u = av + b + o\left(\frac{1}{v}\right)$, being

$$b = \frac{-\alpha - \epsilon + q\delta c' - \frac{(1-q)\delta c'}{a}}{\beta + \eta},$$

[e.g., compute $\frac{u}{v} - \frac{b}{v} = \frac{d}{dt} \ln\left(\frac{u}{v}\right)$, setting $u = av + b + o\left(\frac{1}{v}\right)$].

In fact, along any of the above trajectories, when v is high enough, for any $m > 1$

$$u = av + b + \sum_{k=1}^{m'} d_k v^{-k} + o(v^{-m-1})$$

or

$$u = av + b + v^\lambda \left[\sum_{k=1}^{m'} d'_k v^{-k} + o(v^{-m-1}) \right],$$

but clearly, the formal power series in v^{-1} may not converge (i.e., its radius of convergence may be zero). Similar arguments can be applied to $n(v)$. ■

The only other case in which diverging trajectories exist is the following.

Theorem 3. Assume $\eta \leq 0$ and $q\delta\theta/(1 + v^*) \geq \beta$, where $v^* \geq 0$ is defined by the system parameters. These are necessary conditions for the existence of trajectories along which $u(t)$ and $n(t) \rightarrow +\infty$, as $v(t) \rightarrow v^*$. Moreover, if $\eta < 0$ and $q\delta\theta > \beta$, such conditions are also sufficient, implying $v^* = 0$. In any case, along any diverging trajectory, asymptotically (i.e., when u is high enough)

$$n = \theta u + k + o\left(\frac{1}{u}\right)$$

holds, where k is defined by the system parameters.

Proof. Assume $\eta \leq 0$. So, recalling the expression of \dot{n} , if $u(t) \rightarrow +\infty$, $v(t)$ tends to some $v^* \geq 0$. Then, assume $u(t) \rightarrow +\infty$ and $v(t) \rightarrow v^*$ on some trajectory. Then, for any t_0 , there exists some interval $I \subset (t_0, \bar{t})$, $\bar{t} \leq +\infty$, where $\beta u \leq q\delta n/(1 + v^*)$, implying $n(t) \rightarrow +\infty$ as well. On the other hand

$$\frac{dn}{du} = \frac{\frac{r}{1+v} [1 + \theta(u-v) - n]}{-\frac{\alpha}{n} - \beta \frac{u}{n} + \frac{q\delta}{1+v}},$$

so that n/u must tend to θ as $u(t) \rightarrow +\infty$. Let $n = \theta u + k + o\left(\frac{1}{u}\right)$ when u is high enough. Thus, if $q\delta\theta/(1 + v^*) > \beta$, letting $u(t) \rightarrow +\infty$, we get

$$\theta = \frac{\frac{r}{1+v^*} (1 - \theta v^* - k)}{-\frac{\beta}{\theta} + \frac{q\delta}{1+v^*}},$$

and we can find the value of k . Otherwise, if $q\delta\theta/(1 + v^*) = \beta$, $k = 1 - \theta v^*$.

As to the sufficiency of the conditions $\eta < 0$ and $q\delta\theta > \beta$, let us first divide the system equations (1)–(3) by $u > 0$. In the consequent equivalent system, let $w = \ln(e^{\ln ru} n^{q\delta})$ and consider

$$\begin{aligned} r\dot{u} + q\delta \frac{\dot{n}}{n} &= \frac{d}{dt} \ln(e^{\ln ru} n^{q\delta}) = \dot{w} \\ &= -r\alpha + \frac{q\delta}{1+v} + r \left(\frac{q\delta\theta}{1+v} - \beta \right) u + r \left(\gamma - \frac{q\delta\theta}{1+v} \right) v. \end{aligned}$$

Let us start from a point (u_0, v_0, n_0) such that $u_0 \gg 1$ (i.e., very large), $q\delta n_0 \gg \beta u_0$, $-\eta u_0 \gg q\delta n_0$, $0 < v_0 < \sigma$, where σ is small enough. Then, $\dot{u}(0) > 0$, $\dot{v}(0) < 0$, $\dot{w}(0) > 0$. Suppose, at some $\tilde{t} > 0$, $\dot{u}(\tilde{t}) = 0$ holds and pose $(u(\tilde{t}), v(\tilde{t}), n(\tilde{t})) = (\tilde{u}, \tilde{v}, \tilde{n})$. Thus, $\tilde{u} > u_0$ and $\beta \tilde{u} = -\alpha + \gamma \tilde{v} + \frac{q\delta \tilde{n}}{1+\tilde{v}} \tilde{v} v^*$. Since \tilde{n} is also high, $\frac{\partial}{\partial v} \left(\gamma v + \frac{q\delta \tilde{n}}{1+v} \right) = \gamma - \frac{q\delta \tilde{n}}{(1+v)^2} < 0$ holds. Moreover, $\dot{v}(\tilde{t}) < 0$ and $\dot{w}(\tilde{t}) > 0$. Assuming, by contradiction, that u decreases in a small right

neighborhood of \tilde{t} , it follows that in such a neighborhood, as w increases, so does n , while v decreases. So, it follows that $\dot{u}(t) > 0$, leading to a contradiction. ■

Remark 1. The nongeneric cases (where the above necessary but in those cases not sufficient conditions hold) can exhibit quite different patterns. For example, assume $\gamma, \eta > 0$ and $\gamma\eta = \beta\zeta$. Then

$$\eta \frac{\dot{u}}{n} + \beta \frac{\dot{v}}{v} = \frac{d}{dt} \ln u^n v^\beta = -\alpha\eta + \beta\epsilon + \frac{q\delta\eta n}{1+v} + \frac{(1-q)\delta\beta n}{1+u}.$$

It follows that, if $-\alpha\eta + \beta\epsilon > 0$, all the trajectories in the prism Π diverge, i.e., along them $u, v \rightarrow +\infty$. Viceversa, if $-\alpha\eta + \beta\epsilon < 0$ and, for example, $\gamma/\beta < 1$, it is easily checked that no diverging trajectory exists. Similar examples can be provided for the “critical” cases of Theorem 3.

Theorem 2 tells us that a necessary and sufficient condition for the divergence of v , i.e., for the level of maladaptive traits to grow without bound (even in finite time in some cases), is that γ and η are positive and that moreover $\beta\zeta < \gamma\eta$. The positivity of γ and η implies that no corruption effects exist, and both adaptive and maladaptive traits are successfully filtered. Moreover, the product of the filtering factors $\gamma\eta$ must be larger in size of the product of the (quadratic) decay factors $\beta\zeta$. In other words, if for both types of traits decay effects are comparatively weak with respect to filtering effects and if corruption effects do not occur, there is no obstacle to the diffusion of maladaptive culture, and the same occurs for adaptive culture: the levels of both types of traits keep on growing at similar speed. The net effect on population growth is ambiguous, however, and depends on parameter values, so that we can have either unconstrained population growth with various possible speeds or an eventual extinction.

Theorem 3, instead, helps us to understand what may happen when maladaptive traits are subject to corruption (i.e., when η is weakly negative). In this case, if the combined strength (the product) of the rate of generation of new adaptive traits (q), of the factor measuring the impact of new adaptive traits on overall trait levels (δ), and of the factor measuring the impact of population growth on the net level of adaptive vs. maladaptive traits (θ) is strong enough to counterbalance the (quadratic) decay of adaptive traits, there is the possibility that both adaptive traits and population levels grow without bound, whereas the level of maladaptive traits remains bounded. If corruption of maladaptive traits strictly occurs (i.e., $\eta < 0$) and if the combined effect of the three factors described above strictly dominates the decay factor for adaptive traits, not only unbounded growth of both population and adaptive traits is ensured but also maladaptive traits eventually become extinct. Moreover, when both adaptive traits and population grow without bound, they do it at similar speed. For very specific combinations of parameters (such as $\gamma\eta = \beta\zeta$), however, as shown in Remark 1, very different dynamic behaviors may result with respect to the ones described in Theorems 2 and 3, including generalized divergence of both types of traits and absence of unbounded growth for all variables.

C. Trajectories tending to the sides of $\bar{\Pi}$

Apart from the case described in Theorem 3, a simple tool for investigating the existence of trajectories tending to some side of $\bar{\Pi}$ (i.e., to $u = 0$ or $v = 0$ or $n = 0$) is to analyze the local stability of stationary points lying on those sides. For example, consider $v = 0$. Then, a stationary point lying on the side $v = 0$, with $u, n > 0$, is a positive solution (\bar{u}, \bar{n}) of the system

$$\begin{cases} -\alpha - \beta u + q\delta n = 0 \\ 1 + \theta u - n = 0, \end{cases}$$

Assume such a solution exists (which implies $\bar{n} > 1$). Then, there exist trajectories in Π tending to $(\bar{u}, 0, \bar{n})$ if

$$\epsilon + \eta\bar{u} + (1 - q)\delta\bar{n} < 0.$$

This amounts to require that, at the stationary state where maladaptive traits become extinct, the total strength of the resilience factor of maladaptive traits decay (ϵ), of the corruption/filtering factor of maladaptive traits times the stationary level of adaptive traits, and of the combined effect of the share of generation of new maladaptive traits ($1 - q$) with the impact factor of new traits on overall trait levels (δ) times the stationary population level must be negative. In other words, there must be some force at work that negatively affects the growth of maladaptive traits strongly enough, be it decay, corruption, or weak generation of new maladaptive traits, or a combination thereof. Moreover, these adverse forces oppose the growth of maladaptive traits more and more, the higher the stationary levels of adaptive traits and of the population.

IV. SIMULATIONS

The objective of this section is to highlight, via numerical simulations, some effects on dynamics that may be observed by varying two parameters of the model, namely, η and γ : the factors controlling the corruption/filtering of maladaptive and adaptive traits, respectively. We choose to focus on these two parameters in view of the importance that their corresponding parameters played in the analysis of the dynamic properties of the constant population case studied by Antoci et al. (2018). In all our simulations, we will only consider interior equilibria where all three state variables are strictly positive ($\bar{u} > 0, \bar{v} > 0, \bar{n} > 0$).

In Fig. 1, we show how the equilibrium levels of the state variable u (for the other state variables, the simulations are similar) change with γ for three different levels of η . With H , we denote bifurcation points, and with LP , limit points. [In our simulation, the normal form coefficients for the Hopf and the limit point bifurcations were calculated. Both first Lyapunov coefficients are negative (implying that the Hopf bifurcations give rise to attractive cycles), while the LP-coefficients are both nonzero.] Each point in the blue (respectively, black and red) curves represents a saddle point with a 2-dimensional stable manifold (respectively, a saddle point with a 1-dimensional stable manifold and a sink). For instance, for $\eta = -0.2$, there are three equilibria (but no

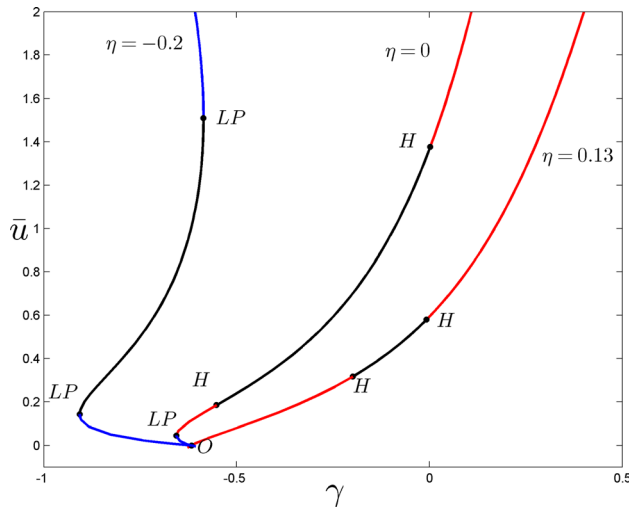


FIG. 1. Equilibrium curves varying the parameter γ . Parameter values are $r = 1.5$, $q = 0.444$, $\beta = 1$, $\zeta = 1$, $\delta = 1$, $\epsilon = 0.01$, $\theta = 7$, and $\alpha = 0.2461$.

attractor as we are in Region VI of Fig. 2). As expected, for positive values of both γ and η , the equilibrium levels of all the state variables tend to increase, and for given values of γ , the equilibrium population level increases more slowly the higher the value of η .

To investigate the bifurcation curves denoting changes in the number and stability of stationary points, we performed codimension-two bifurcation analysis with respect to the two parameters γ and η . [The bifurcation diagrams in Fig. 2 were computed for continuation from the H and LP points in Fig. 1.] The main bifurcation diagram is shown in Fig. 2, where the parameter plane (γ, η) is subdivided into eight colored regions labelled I–VIII. Each of them differs from the others with respect to the numerosity and stability of equilibrium points. Region I represents parameter

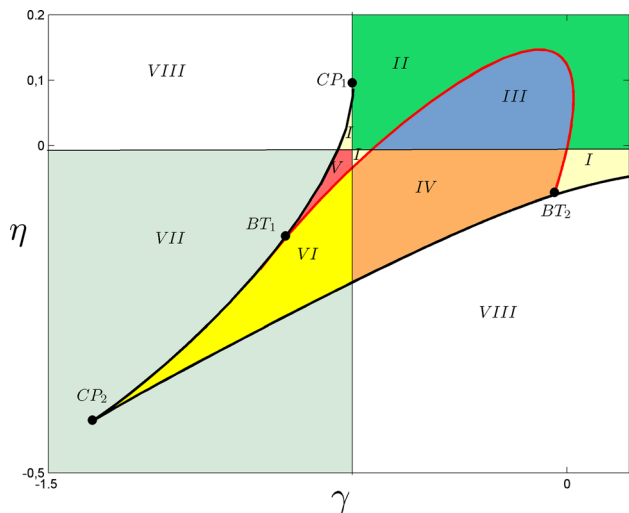


FIG. 2. Two parameter bifurcation diagram. The red curve refers to (codimension-one) supercritical Hopf bifurcation and the black curve to LP bifurcation. The symbols CP and BT indicate the points where a (codimension-two) cusp bifurcation and a Bogdanov-Takens bifurcation occur, respectively. Parameter values are $r = 1.5$, $q = 0.444$, $\beta = 1$, $\zeta = 1$, $\delta = 1$, $\epsilon = 0.01$, $\theta = 7$, and $\alpha = 0.2461$.

configurations giving rise to a saddle point with a 2-dimensional stable manifold and to a sink (with a 3-dimensional stable manifold). We use the symbol $I \rightarrow (2, 3)$ to indicate such a context. Analogously, in Region IV, two saddle points exist, one with a 2-dimensional stable manifold and the other with a 1-dimensional one [IV $\rightarrow (2, 1)$]. Regions I and IV are separated by a supercritical Hopf bifurcation curve; when such a curve is crossed, then a stable limit cycle arises. The following list associates with each of the regions I–VIII the corresponding configuration of equilibrium points, using the same symbology introduced above:

- Region I $\rightarrow (2, 3)$;
- Region II $\rightarrow (3)$;
- Region III $\rightarrow (1)$;
- Region IV $\rightarrow (2, 1)$;
- Region V $\rightarrow (2, 3, 2)$;
- Region VI $\rightarrow (2, 1, 2)$;
- Region VII $\rightarrow (2)$;
- Region VIII \rightarrow no equilibria;

Notice that a sink exists in Regions I, II, and V, while a stable limit cycle exists in Regions III, IV, and VI.

In addition to the above regions, there are four codimension-two bifurcation points denoted by black dots in Fig. 2: two cusp points (CP_1 and CP_2) and two Bogdanov-Takens bifurcation points (BT_1 and BT_2). [At each BT point, the system has an equilibrium with a double zero eigenvalue, while at the CP point, there is an equilibrium with a simple zero eigenvalue but zero coefficient of the fold normal form.] The cusp CP_1 locates at $(\gamma, \eta) = (-0.617, 0.087)$, where the value of variable u is equal to zero. The cusp CP_2 locates at $(\gamma, \eta) = (-1.385, -0.424)$, where the black LP bifurcation curve on the left and the black LP bifurcation curve on the right meet tangentially. At the BT_1 point $(-0.853, -0.166)$ and BT_2 point $(-0.037, -0.075)$, the branches of the LP curve and Hopf bifurcation curve meet tangentially.

In Fig. 3, we show two examples of an attractor and a limit cycle in the phase space, for a given level of η and two alternative values of γ . Notice how, for a mildly positive η (i.e., for a modest level of filtering of maladaptive traits), the dynamic shifts from a stable equilibrium for a comparable level of γ (i.e., a very close level of filtering of the adaptive trait) to a cyclic behavior for a negative level of γ (i.e., corruption of adaptive traits).

In Fig. 4, we have an illustration of some of the results of Theorem 2. Figure 4(a) shows an attractor $\bar{Q} = (\bar{u}, \bar{v}, \bar{n})$ for $\zeta\beta > \eta\gamma$, i.e., for a combination of parameters that violates the assumptions of the theorem. Figures 4(b) and 4(c) refer to the context in which Theorem 2’s assumptions on parameter values are satisfied. Figure 4(b) shows a trajectory along which unbounded growth of u , v , and n is observed, while Fig. 4(c) presents the dynamics of the ratio $\frac{n(t)}{v(t)}$ which, as predicted by the theorem, converges to a constant value.

Finally, Fig. 5 shows, for the same combination of parameters of Fig. 2, three different trajectories for a given couple of values of γ and η . As it can be seen, one trajectory (black curve) converges to a sink; the second one (red curve)

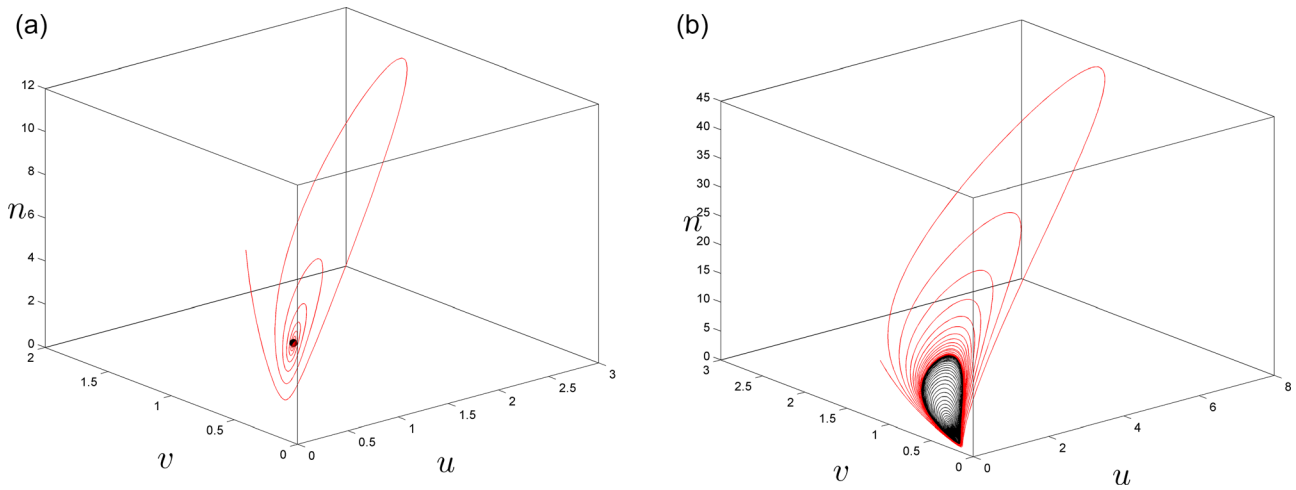


FIG. 3. Trajectories converging to sink (a) and to a limit cycle (b) arisen via a Hopf bifurcation. Parameter values are the same as in Fig. 2. (a) $\gamma = -0.22$, $\eta = 0.13$ and (b) $\gamma = -0.13$, $\eta = 0.13$.

converges to the equilibrium point where the population becomes extinct ($n = 0$) and both types of traits disappear ($u = v = 0$); the third one (blue curve) leads to unbounded growth of both types of traits and to the asymptotic extinction of the population.

V. DISCUSSION

In this paper, we have studied a nonlinear model of the interaction between trait selection and population dynamics that extends previous research by Ghirlanda *et al.* (2010) and

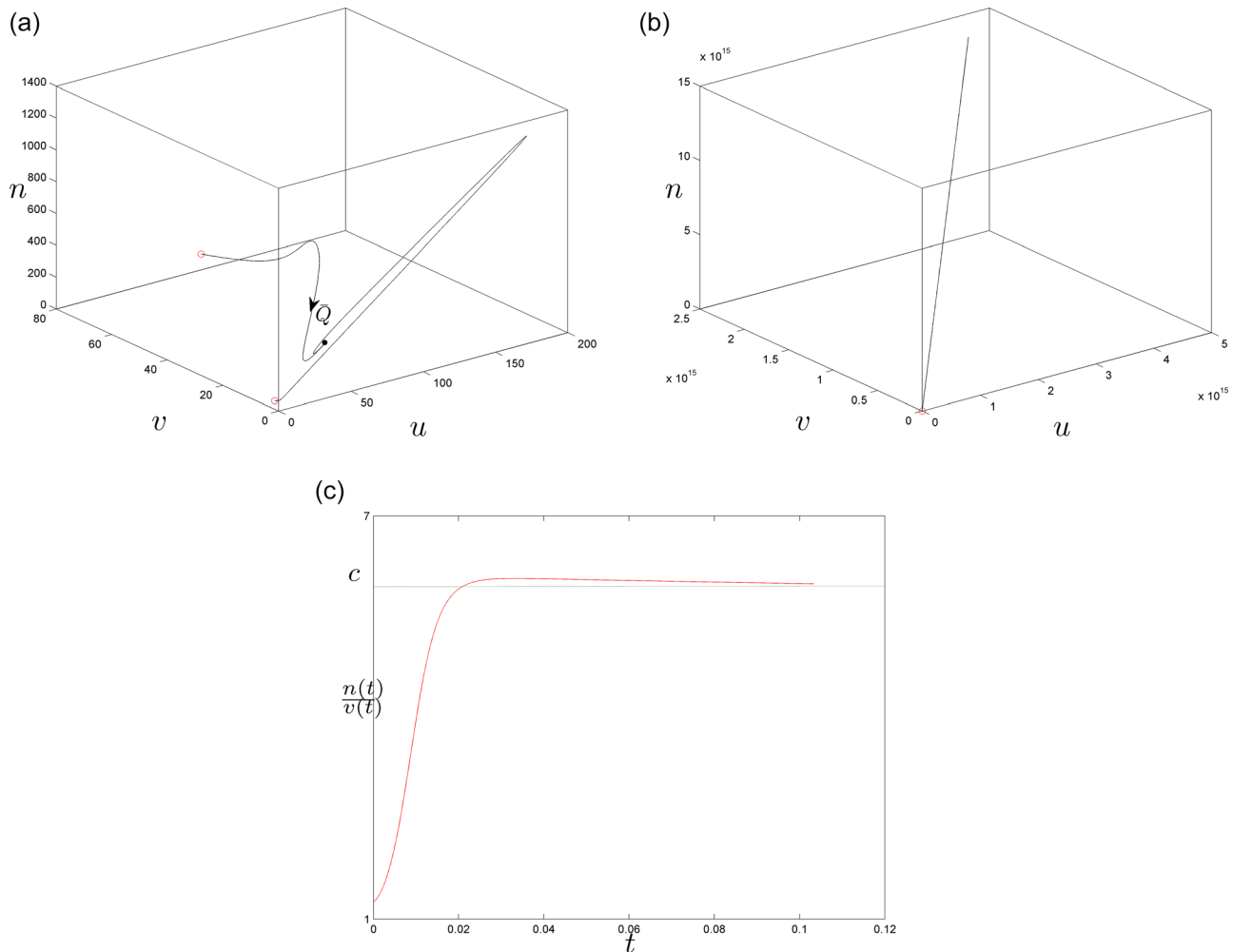


FIG. 4. Theorem 2. (a) Attractive equilibrium point in the phase space for $\xi\beta > \eta\gamma$ (theorem's assumptions not met); (b) Divergent trajectory in the phase space when theorem assumptions are met; (c) Time dynamics of the ratio $\frac{n(t)}{v(t)}$ when assumptions are met. Parameter values are $\alpha = 1, r = 0.5, q = 0.8, \beta = 1, \xi = 1, \delta = 1, \theta = 7, \epsilon = 1, \gamma = 2$. (a) $\eta = 0.1, \xi\beta > \eta\gamma$, (b) $\eta = 0.6, \xi\beta < \eta\gamma$, and (c) $\eta = 0.6, \xi\beta < \eta\gamma$.

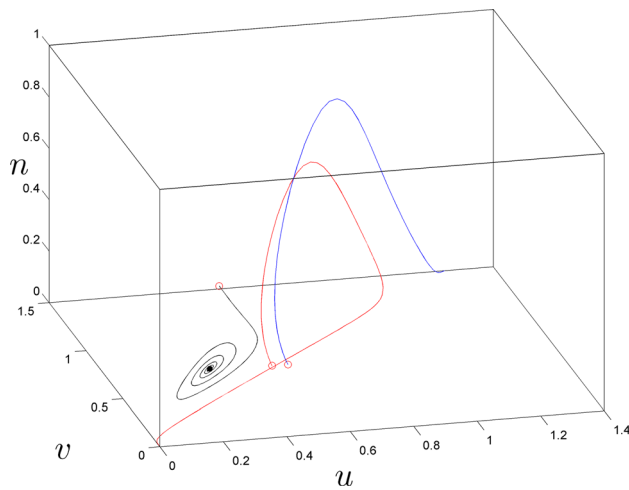


FIG. 5. Theorem 2. Black curve converging to the attractive equilibrium point; red curve converging to the origin $(0, 0, 0)$; blue curve such that $u(t) \rightarrow +\infty$, $v(t) \rightarrow +\infty$, $n(t) \rightarrow 0$. $\eta = 1.2$, $\gamma = 1$, the other parameter values are the same as in Fig. 2.

Antoci *et al.* (2018). As in the latter paper, we find that the factors that control corruption/filtering of adaptive vs. maladaptive traits play an especially important role. In particular, through some simulation analysis, we find that for relatively small variations of the values of the parameters η and γ , major changes in the dynamic properties of the model can occur. Moreover, even when locally stable equilibrium points are shown to exist, the dynamics nonetheless exhibit a variety of possible behaviors for different initial conditions. This shows that the simple dynamic patterns that are found in many economically motivated models of cultural transmission are possibly obtained under very specific conditions and possibly over-simplified theoretical frameworks. In order to refine our understanding of these complex dynamics, a closer look at the microforces that shape the corruption vs. filtering of adaptive and maladaptive traits in specific contexts and situations is needed, so as to arrive at a precise calibration of model parameters and to the formulation of reliable predictions of the model's asymptotic dynamics.

Our model shows that when both adaptive and maladaptive traits find favorable conditions to develop, they can both thrive and spread over the population, and it is their relative, precarious balance that determines whether this entails unbounded population growth or, to the contrary, eventual extinction. The basic message of the model is therefore that unless structural forces are at work to determine parameter constellations that limit the risk of population extinction, this possibility cannot be ruled out in principle and is actually very possible for certain parameter regions. As remarked in the introduction, the fact that contemporary societies have typically created ideal conditions for the proliferation of maladaptive traits as a consequence of the pursuit of short-term corporate profits is a cause of concern, in that, in terms of our model, this can be reflected into the prevalence of parameter constellations where we find a strong filtering of maladaptive traits, and possibly an increasing relative share of such traits among newly created ones. As we have seen, such shifts make it less likely to reach a situation where

maladaptive traits go extinct or are limited in their growth. These results confirm that there is a need to take account of this kind of effect in economic growth models, so as to evaluate the cultural implications of growth strategies that are directly or indirectly conducive to favorable social environments for maladaptive traits.

This model has clearly many limitations due to its simplified structure that explores the dynamic interaction of a limited number of ecological effects. Although such a structure is not derived from a micro-founded social interaction model, it has the merit of generalizing existing models which have long served as benchmarks in the literature and can therefore be regarded as a conceptual improvement which introduces a basic level of theoretically grounded sources of nonlinear complexity of the traits-population coevolution dynamics. Future research should build more detailed models that account for even more complex nonlinear effects and provide richer and more finely grained policy implications. For instance, one could consider population-dependent filtering of adaptive vs. maladaptive traits. In large populations, lower levels of social control could make the filtering of maladaptive traits progressively more difficult, thereby incentivizing forms of social dysfunction that are typical of large scale societies (Cumming *et al.*, 2006), while at the same time, a large population pool could make space for richer forms of cultural selection of adaptive traits (Bell *et al.*, 2009), with an ambiguous net effect. Policy approaches would consequently become sensitive to population size and could be based upon dynamic adaptive strategies whose parameters could provide further sources of complex dynamic behavior at system level and interact in subtle ways with the structural parameters studied in the present model. However, the analysis of models with a realistic amount of nonlinearity easily becomes very challenging and calls for simulation experiments. This is a major difficulty that cannot be easily dealt with and requires a further improvement of our analytic capacity and a substantial effort toward modeling accuracy and parameter calibration. Nevertheless, this paper makes a first important step toward relaxing linearity assumptions that greatly limit the complexity of the dynamic behavior of trait selection-population models with little guarantee of theoretical legitimacy if not in terms of tractability. We feel that the most promising direction for future research is not in modeling over-simplification, but rather in the improvement of the capacity to understand the complexity of socio-economies, and to take it into account when formulating our policy strategies and more generally when reflecting on the unintended consequences of our social and individual attitudes in a variety of dimensions that have major consequences for the adaptive success of our species.

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