How Economic Exchange Can Favour Human Genetic Diversity

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Abstract

By allowing individuals to use goods they do not produce, economic exchange is recognized as driving the wide diversity of economic activities seen in human societies. Since productivity also depends on innate abilities, we ask whether economic exchange could also have influenced human evolution and promoted adaptive genetic diversity. We model a system where individuals produce and exchange goods under a Walrasian equilibrium, with abilities determined by an evolving quantitative genetic trait. We then analyse how exchange shapes the evolutionary pressures on this trait. Our analysis demonstrates that exchange consistently promotes negative frequency-dependent selection, which favours the maintenance of genetic diversity. Exchange also generates stable long-term adaptive polymorphism when the production of goods requires different abilities. Importantly, we establish that the mode of exchange matters: markets, where individuals can switch trading partners, promote genetic diversity under broader conditions than when exchange occurs in isolated pairs. Finally, we show that genetic diversity and economic specialisation can co-evolve, each facilitating the emergence of the other under a wider range of conditions. Our findings suggest that economic exchanges play a crucial role in fostering biological diversity and offer insights into how a culturally determined mode of organization may have shaped human adaptive genetic evolution.

1 Introduction

The practice of exchanging goods and services is one of the hallmarks of human societies (Oka and Kusimba, 2008; Feinman and Garraty, 2010) and has profoundly impacted the social organisation of human groups. The development of economic exchange played a central role in state formation (Service, 1978; Bates, 1983; Fenske, 2014; Depetris-Chauvin and Ozak, 2015), influenced subsistence strategies (Stiles, 1993), and, perhaps most notably, is regarded as the primary cause of economic specialisation, leading different individuals within many societies to specialise in producing distinct goods and services (Smith, 1776; Stigler, 1951). From its earliest origins, human history has been intertwined with exchange, as evidenced by archaeological findings of long-distance exchange dating back to the emergence of Homo sapiens 200,000 to 300,000 years ago (Blegen, 2017; Potts et al., 2018). Then, could economic exchange shape characteristics of a population other than just its social and economic organisation?

If exchange has driven individuals to specialise in producing certain goods, it may have also shaped the evolution of biological heritable traits associated with producing these goods. Indeed, a wide range of heritable traits are likely involved in the key tasks required to produce goods (Polderman et al., 2015; Houmark et al., 2024). For instance, among the Tsimane people, individuals with strong visual acuity and high running speed appear to be more successful hunters (Apicella, 2014). Bajau people of Southeast Asia are able to spend considerable time fishing at great depths of up to 70 meters (Sopher, 1977), thanks to particular physiological adaptations (Ilardo et al., 2018). More generally, individuals' earnings and, presumably their work performance correlate with the main dimensions of personality traits (Denissen et al., 2018; Barth et al., 2020), which, like physical traits, are partially heritable and shaped by evolution (Loehlin et al., 1998).

These biological traits evolve by natural selection through their effects on survival and reproduction. Since economic exchange alters the benefit of producing certain goods, it can also affect the reproduction and survival of individuals producing these goods, and therefore change the selective pressures on the traits involved in production. For instance, in the same way that exchange drives diversity in economic activities, are there conditions under which exchange would lead to the emergence of adaptive diversity in genetic traits? This possibility cannot be taken for granted. Evolutionary changes in genetic traits are governed by particular dynamics, with changes generally occurring gradually over multiple generations, in contrast to economic processes, where individuals can freely and nearly instantly adopt strategies when it benefits them. As such, genetic diversity is thought to be favored only in restricted cases where parents and offspring occupy the same economic roles across generations (Smaldino, 2014), while arguments proposing that exchange and specialisation lead to phenotypic diversity typically apply to plastic behavioural traits or skills acquired through learning (Montiglio et al., 2013; Lukaszewski et al., 2017; Smaldino et al., 2019; Durkee et al., 2022). Yet debate persists (Hunt and Jaeggi, 2022), and it remains an open question whether adaptive genetic diversity—and, by extension, phenotypic diversity across a wider range of traits—can be favoured by economic exchange in diverse societies, or whether it requires stricter conditions, such as individuals exclusively dedicating their time to distinct roles.

It also remains unclear whether biological traits, such as physical aptitudes or personality differences, influence the conditions under which individuals tend to specialise in producing distinct goods in the presence of economic exchange. The importance of these interactions—on one side biological traits and on the other side a humanly devised mode of organization—is increasingly recognized, as shown by the development of the gene-culture co-evolution theory (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1988; Feldman and Laland, 1996) and the recent integration of genetic data to explain economic outcomes (Barth et al., 2020; Biroli et al., 2022; Pereira et al., 2022). Interaction between genetic diversity and economic specialisation has also been prompted by recent evidence showing that the emergence of distinct economic roles happened earlier in areas where migration events have led to greater neutral genetic diversity (Depetris-Chauvin and Ozak, 2015, 2020).

Given these open and complex questions, a theoretical analysis appears relevant and even necessary to understand whether economic exchange might influence adaptive genetic diversity and whether this changes the relationships between exchange and economic specialisation. Yet, previous studies have tended to stay within the domains of their specific disciplines and did not explore the interaction between exchange, genetic diversity, and economic specialisation. For example, models focusing on the evolution of genetic diversity under various modes of social organization have not explicitly considered the role of exchange (Henrich and Boyd, 2008; Vásárhelyi et al., 2015; Vásárhelyi and Scheuring, 2018; Nakahashi and Feldman, 2014). Conversely, the Ricardian model of economic specialisation assumes that the abilities of individuals to produce one good or another are exogenous and constant parameters (Varian, 2009).

We address these open questions here by building a comprehensive mathematical model that combines standard economic and evolutionary approaches. We examine a population of individuals who produce and exchange goods, explicitly modelling exchange within the Walrasian general equilibrium framework. In addition, the quantities of goods individuals produce depend on (i) their innate abilities modelled as a quantitative trait and (ii) their allocation of time to produce each good modelled as a behavioural strategy. We use this model to investigate (i) how much exchange can affect the adaptive dynamics of genetic traits and (ii) how genetic diversity and economic specialisation interact. We do this under two scenarios that reflect distinct modes of exchange experienced by humans at different periods in history: individuals exchanging goods in isolated pairs, and individuals engaging in exchange within a large market. We also compare both scenarios to a baseline case of autarky.

2 Model

2.1 Biological scenario

We consider a randomly mixing population of constant and large size N where individuals have economic interactions according to the following non-overlapping generation life cycle. (i) Each individual produces up to two goods, one of type x and the other of type y. (ii) Individuals can exchange goods with each other. (iii) Individuals produce a large number of offspring proportional to their payoff, which depends on the amount of goods they consume after exchange. As commonly done in evolutionary models with individual interactions, we assume for simplicity, but without loss of qualitative generality, that individuals reproduce asexually, meaning that bearing mutations genetic traits are passed intact from parent to offspring (rather than combining with those of a mating partner). (iv) Adults die and offspring compete for the breeding spots vacated by the adults and mature, i.e. Wright-Fisher population process (Ewens, 1979). We next detail each of these events.

Production. The quantity of each good that individuals produce depends on (i) an evolving genetic quantitative trait affecting their innate abilities to produce the good and (ii) the time they allocate to the production of the good. Formally, an individual with genetically encoded trait $\tau_i \in \mathbb{R}$ and time $h_i \in [0, 1]$ allocated to produce good x, produces an amount $q^{\mathrm{x}}(\tau_i, h_i)$ and $q^{\mathrm{y}}(\tau_i, h_i)$ of goods x and y, respectively. These quantities are assumed to take the following functional forms:

$$\begin{aligned} q^{\mathrm{x}}(\tau_i, h_i) &= h_i^{\eta} \cdot r^{\mathrm{x}}(\tau_i), \\ q^{\mathrm{y}}(\tau_i, h_i) &= (1 - h_i)^{\eta} \cdot r^{\mathrm{y}}(\tau_i). \end{aligned} \tag{1}$$

The first component in the products on the right-hand sides of eq. (1) describes the returns of allocating time to produce each good. The parameter $\eta \in [0, 1)$, which we refer to as the elasticity of scale, quantifies the decreasing returns to scale of allocating more time to the production of each good. A low value of η describes production with strong decreasing returns to scale such as foraging and hunting, where resources become increasingly difficult to find and extract, while η close to one represents constant returns to scale.

The second component on the right-hand sides of eq. (1), the quantity $r^k(\tau_i)$, captures the dependence of the production of good $k \in \{\mathrm{x}, \mathrm{y}\}$ by individual i on trait τ_i and is assumed to be given by

$$r^k(\tau_i) = \exp\left[-\frac{(\tau_i - o_k)^2}{\sigma^2}\right] \tag{2}$$

(see top panel of Figure 1 for an illustration). The parameter o_k represents the optimal trait value for which the production of good k is maximal. Different values of o_k for different goods capture the notion that different goods require distinct abilities and thus traits. Thus, there is a trade-off as a trait value that is optimal for one task is often not optimal for another. For instance, high muscle mass benefits tasks requiring strength, such as heavy lifting or sprinting but can reduce flexibility, impair fine motor skills and increase fatigue in endurance activities. The parameter $\sigma^2 > 0$ represents the production breadth of goods, that is, how deviations from the optimal trait value decrease production. A low σ^2 describes a knife-edge production breadth where a small deviation from the optimal trait value leads to a sharp drop in production and so only individuals with a narrow range of traits can effectively produce each good. In other words, when σ^2 is low, production requires highly tailored abilities—for instance, some prey may be inaccessible without the exact strength-endurance balance needed to dive to certain depths. A high σ^2 represents a plateau production breadth where a large deviation from the optimal trait value leads to a modest drop in production and so individuals with a wide range of traits can effectively produce each good.

Exchange. Individuals can exchange the goods they produce with others by giving up a quantity of one good in return for another. Individual i producing quantity $q^k(\tau_i, h_i)$ of good k, exchanges e_i^k units of this good and ends up consuming $c_i^k = q^k(\tau_i, h_i) + e_i^k$ units of good k. The quantity exchanged e_i^k is negative for an individual that gives up some good ("sell" the good), positive for an individual that receives it ("buys" the good) and equal to 0 when exchange does not take place. The quantity of good y given in exchange of one unit of good x is defined as the price p of good x.

We consider two possible modes of exchange on top of a baseline situation where individuals live in *autarky* and do not exchange with each other. First, *dyadic exchange* where individuals are randomly paired and each pair is isolated from all others, meaning that they each settle on a potentially different price. This scenario describes early human societies where the large distances between human groups

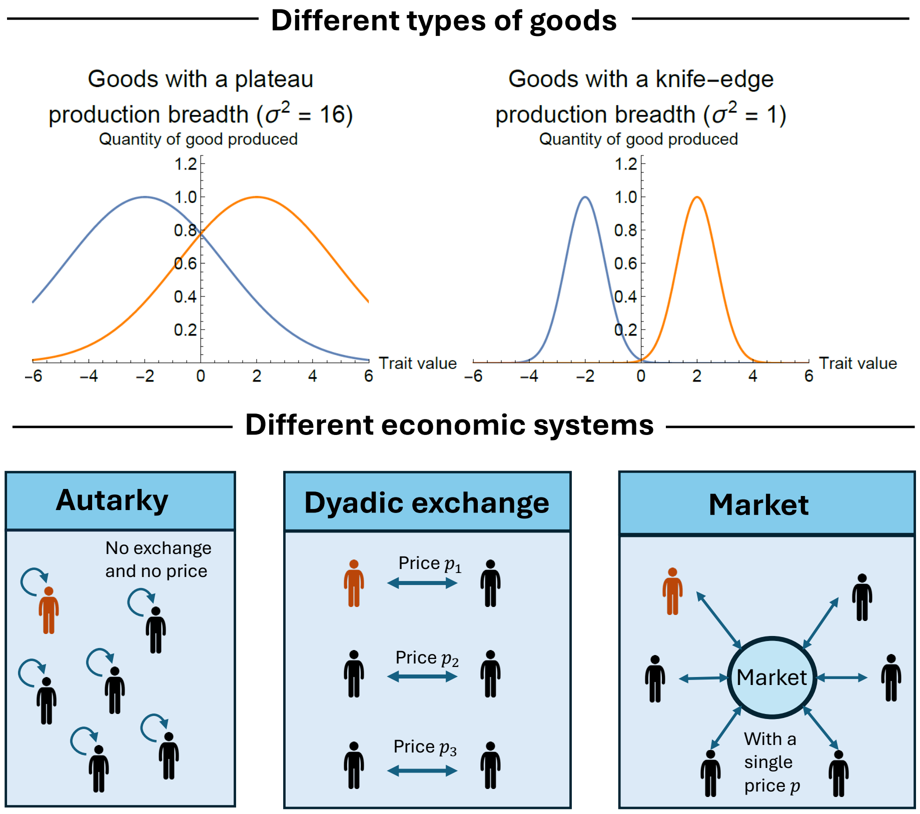

Figure 1: (Top) Quantity of good x and y produced, namely eq. (2), as a function of trait value, assuming an equal time allocated to the production of each good. The plots illustrate two types of goods, differing in production breadth σ^2, with either high or low values. The optima of production of each good are $o_{\mathrm{x}} = -2$ and $o_{\mathrm{y}} = 2$. (Bottom) Modes of exchange considered: (i) autarky where exchange is not possible, (ii) dyadic exchange, where individuals exchange in randomly formed pairs, with each pair potentially settling on different prices independently, and (iii) market, where a single price is determined by aggregate production across all individuals.

would have limited the number of partners with whom to exchange (Polanyi et al., 1957; Dupuy, 2016; Huck et al., 2023). Second, we consider *market exchange*, where individuals can freely switch trading partners. This scenario reflects later societies, where exchanges occurred in large markets, as it has been described in many different preindustrial societies (Feinman and Garraty, 2010; Garraty and Stark, 2010; Blanton and Feinman, 2024).

Payoff After exchange, the payoff π_i of individual i depends on the amounts of the two goods he consumes according to a Cobb–Douglas form: $\pi_i = (c_i^{\mathrm{x}})^{\alpha}(c_i^{\mathrm{y}})^{1-\alpha}$. Hence, the goods are essential and both need to be consumed to entail a positive payoff. The parameter $\alpha \in (0,1)$ captures the relative importance of good x compared to y for the individual payoff. Unlike classical economic models, where α typically reflects individual preferences, here α represents the effective contribution of each good to reproductive success. When $\alpha < 0.5$, good y is more valuable for fitness than good x. When $\alpha > 0.5$, the opposite holds. If $\alpha = 0.5$, goods x and y are equally valuable.

Our aim is to conduct an evolutionary analysis of this model under autarky, dyadic exchange, and market exchange. To do so, we first need to determine the outcomes of the economic interactions that determine individuals' payoffs. Because the evolutionary dynamics unfold more slowly than individuals' behaviour within a generation, we assume that prices and quantities settle at an equilibrium when determining payoffs.

2.2 Behavioural equilibrium

We assume that individuals are producer-consumers that maximise their payoffs over three decision variables: the quantities consumed of the two goods and the time allocated to produce each good. Thus, the decision problem that consumer-producer i with trait τ_i and time allocation h_i faces is

$$\max_{c_i^{\mathrm{x}} \in \mathbb{R}, c_i^{\mathrm{y}} \in \mathbb{R}, h_i \in [0,1]} \left(c_i^{\mathrm{x}}\right)^{\alpha} \left(c_i^{\mathrm{y}}\right)^{1-\alpha}, \tag{3}$$

subject to the budget constraint

$$p\, c_i^{\mathrm{x}} + c_i^{\mathrm{y}} = p\, q^{\mathrm{x}}(\tau_i, h_i) + q^{\mathrm{y}}(\tau_i, h_i). \tag{4}$$

The left-hand side of eq. (4) describes the value of the goods individual i consumes measured in units of good y (the price of good x is p and the price of good y is normalized to 1), while the right-hand side represents the value of the goods individual i produces.

Solving the optimization problem (3)-(4) provides the equilibrium quantities of each good, $\hat{c}_i^{\mathrm{x}}(p)$ and $\hat{c}_i^{\mathrm{y}}(p)$, and the time allocation $\hat{h}_i(p)$ that maximise the payoff to individual i for a given price p. Note that this procedure determines the quantity $\hat{c}_i^k(p) - q^k(\tau_i, \hat{h}_i(p))$ of good k the individual is willing to exchange at this price. To close the model, we thus need to determine the equilibrium price. We assume that the price at equilibrium $\hat{p}$ is the one at which the quantities of a good that interacting individuals want to sell (or buy) are exactly equal to the quantities that other individuals want to buy (or sell). In other words, we assume a Walrasian equilibrium—the fundamental equilibrium concept of exchange economics—whereby no surplus nor shortage of resources occurs (Walras, 1874; Arrow, 1951; Debreu, 1951; Mas-Colell et al., 1995). Beyond this assumption, we remain agnostic about the mechanism by which the equilibrium is obtained. Walrasian equilibrium has been shown to arise under different types of bargaining procedures in dyadic exchange (Yildiz, 2003; Dávila and Eeckhout, 2008), and has been observed countless times in experimental markets, even when the number of traders is small (Kagel and Roth, 1995; Lin et al., 2020).

At a Walrasian equilibrium, the equilibrium price, $\hat{p}$, has to satisfy the following condition

$$\sum_{i=1}^{N_{\mathrm{int}}} \hat{c}_i^{\mathrm{x}}(\hat{p}) = \sum_{i=1}^{N_{\mathrm{int}}} q^{\mathrm{x}}(\tau_i, \hat{h}_i(\hat{p})), \tag{5}$$

where N_{int} is the number of interacting individuals. Under dyadic exchange, $N_{\mathrm{int}} = 2$, while for market exchange, we have $N_{\mathrm{int}} = N$. The solution to the optimisation problem (3)-(4) and eq. (5) determines the equilibrium allocation $(\hat{c}_i^{\mathrm{x}}(\hat{p}), \hat{c}_i^{\mathrm{y}}(\hat{p}), \hat{h}_i(\hat{p}))$ for each individual i in the population. At the Walrasian equilibrium, we have the unique feature that all individuals end up consuming precisely the quantities that would maximise their payoff, and thus, we take this consumption to determine the payoff that determines their survival and reproduction (recall our life-cycle). We solve this equilibrium explicitly for the two modes of exchange along the special case of autarky in Appendix A to obtain the quantities consumed for each good, the time allocation and the price at equilibrium for any distribution of types of individuals. Having established the equilibrium behaviour as a function of traits of individuals, we can now proceed to the evolutionary analysis.

2.3 Evolutionary analysis

To perform our evolutionary analysis we make the standard assumptions of quantitative trait evolution that the mutation rate is low and the effect size of mutations on trait values are small (e.g. Eshel et al., 1997; Geritz et al., 1998; Rousset, 2004; Walsh et al., 2018; Avila and Mullon, 2023). With these assumptions, we can characterize long-term gradual evolution by focusing on the payoff $\pi(\tau, \theta)$ of a single individual with trait τ — henceforth called a mutant — which arises in a population of individuals that are monomorphic for trait θ — henceforth called the resident population (a full description of the method can be found in Appendix B.1). According to our model, the payoff of a mutant, derived in Appendix B.2, is given by

$$\pi(\tau, \theta) = \left[\hat{c}^{\mathrm{x}}(\tau, \theta)\right]^{\alpha} \left[\hat{c}^{\mathrm{y}}(\tau, \theta)\right]^{1-\alpha}, \tag{6}$$

with equilibrium consumption of goods x and y given by

$$\hat{c}^{\mathrm{x}}(\tau, \theta) = \alpha \left[q^{\mathrm{x}}(\tau, \hat{h}(\tau, \hat{p}(\tau, \theta))) + \frac{1}{\hat{p}(\tau, \theta)} q^{\mathrm{y}}(\tau, \hat{h}(\tau, \hat{p}(\tau, \theta))\right] \tag{7}$$

$$\hat{c}^{\mathrm{y}}(\tau, \theta) = (1-\alpha)\hat{p}(\tau, \theta) \left[q^{\mathrm{x}}(\tau, \hat{h}(\tau, \hat{p}(\tau, \theta))) + \frac{1}{\hat{p}(\tau, \theta)} q^{\mathrm{y}}(\tau, \hat{h}(\tau, \hat{p}(\tau, \theta)))\right], \tag{8}$$

and equilibrium time an individual with trait $\tau_i \in \{\tau, \theta\}$ faced with price p allocates to produce good x given by

$$\hat{h}(\tau_i, p) = \frac{1}{1 + \left[\dfrac{1}{p} \dfrac{r^{\mathrm{y}}(\tau_i)}{r^{\mathrm{x}}(\tau_i)}\right]^{\frac{1}{1-\eta}}}. \tag{9}$$

The equilibrium price $\hat{p}(\tau, \theta)$ a mutant individual faces in eqs. (7)–(8) satisfies

$$\hat{p}(\tau, \theta) = \frac{\alpha}{1-\alpha} \cdot \frac{q^{\mathrm{y}}(\tau, \hat{h}(\tau, \hat{p}(\tau, \theta))) + q^{\mathrm{y}}(\theta, \hat{h}(\theta, \hat{p}(\tau, \theta)))}{q^{\mathrm{x}}(\tau, \hat{h}(\tau, \hat{p}(\tau, \theta))) + q^{\mathrm{x}}(\theta, \hat{h}(\theta, \hat{p}(\tau, \theta)))}, \tag{10}$$

for dyadic exchange, while for market exchange the equilibrium price satisfies

$$\hat{p}(\tau, \theta) = \hat{p}(\theta) = \frac{\alpha}{1-\alpha} \cdot \frac{q^{\mathrm{y}}(\theta, \hat{h}(\theta, \hat{p}(\theta)))}{q^{\mathrm{x}}(\theta, \hat{h}(\theta, \hat{p}(\theta)))}. \tag{11}$$

At the behavioural equilibrium, the quantities consumed, $\hat{c}^{\mathrm{x}}(\tau, \theta)$ and $\hat{c}^{\mathrm{y}}(\tau, \theta)$, consist of fractions of the total budget an individual can consume, measured in units of good y (expression in square brackets in eqs. 7–8). These quantities depend on the relative importance of each good for the individual's payoff, α for good x and $1-\alpha$ for good y.

The fraction of time devoted to producing good x at equilibrium $\hat{h}$ increases with the relative value of good x compared to good y (noting that the price of good y is normalized to 1) and with the individual's relative efficiency in producing x versus y. The strength of this relationship depends on η: when η is close to 1, time allocation is highly responsive to changes in price and productivity, whereas as η approaches 0, time allocation becomes nearly independent of both price and individual traits (and economic specialisation remains limited).

Finally, the price at Walrasian equilibrium depends on (i) how much good x contributes to the payoff relatively to good y, and (ii) how rare good x is relative to good y—between the two individuals in dyadic exchange or among the resident population in exchange, where the mutant is ignored due to the large group size.

We can now infer the evolutionary dynamics from eqs. (6)–(11) as follows. In a first time, the population will evolve by directional selection with the average trait value in the population changing in the direction indicated by the payoff gradient, $\partial\pi(\tau,\theta)/\partial\tau|_{\tau=\theta=\theta^*}$, until a singular point θ^* is reached where the payoff gradient vanishes. Once the population has converged to such a trait value θ^* under directional selection, i.e. a so-called "convergence stable" trait value has been reached (a point at which $\mathrm{d}S(\theta)/\mathrm{d}\theta|_{\theta=\theta^*} = \partial^2\pi(\tau,\theta)/\partial\tau^2\big|_{\tau=\theta=\theta^*} + \partial^2\pi(\tau,\theta)/\partial\tau\partial\theta\big|_{\tau=\theta=\theta^*}$ must be negative), the nature of selection at that point can be of two types. Either (a) selection is stabilising so that the trait value is "locally uninvadable" and evolution stops; or (b) selection is disruptive, in which case the population evolves further. Disruptive selection requires that the uninvadibility coefficient is positive ($\partial^2\pi(\tau,\theta)/\partial\tau^2\big|_{\tau=\theta=\theta^*} > 0$), which entails that the population will subsequently divide into two distinct morphs with different trait values (polymorphism), i.e. evolutionary branching occurs. It follows from these considerations that polymorphism evolves by gradual evolution if directional selection is first convergent and subsequently disruptive. A necessary condition for this to occurs is the presence of negative-frequency dependent selection (which requires that $\partial^2\pi(\tau,\theta)/\partial\tau\partial\theta\big|_{\tau=\theta=\theta^*} < 0$).

As our full model is involved, we divide our evolutionary analysis into two parts in order to be able to distinguish between the role of exchange and time allocation in favouring genetic diversity. First, we analyse the effect of exchange on adaptive genetic diversity holding time allocation fixed and set $q^k(\tau,h) = q^k(\tau)$. Second, we let the time allocation depends on the trait (as per eq. 9) and analyse the full model. For each case, we also start by analysing what is the trait value that would be favoured by evolution in the absence of exchange (autarky).

3 Evolutionary analysis with fixed time allocation

3.1 Autarky

In the absence of exchange, the quantities that an individual consumes are equal to what it produces whereby the mutant payoff in eq. (6) can be simplified to

$$\pi(\tau,\theta) = [q^{\mathrm{x}}(\tau)]^{\alpha}[q^{\mathrm{y}}(\tau)]^{1-\alpha}, \tag{12}$$

which does not depend on the resident trait value. Using eqs. (1)–(2), the payoff gradient derived from this expression yields a single equilibrium point

$$\theta^* = \alpha o_{\mathrm{x}} + (1-\alpha) o_{\mathrm{y}}, \tag{13}$$

which is both convergence stable and uninvadable (see A-46). In the absence of exchange, the population is expected to evolve towards and remain at a single trait value located between the two optimal production values. Hence, evolution will favour individuals to express a generalist genetic trait, leading them to produce similar quantities of each good when α is close to 0.5, albeit with reduced efficiency compared to the maximum achievable production for each good. Further, each individual will express the same genetic trait, namely, no adaptive genetic diversity is favoured under autarky.

3.2 Dyadic exchange

Now consider that individuals can exchange in dyadic interactions. Using eqs. (6)–(10), we find that there is a unique interior equilibrium $\theta^* = \alpha o_{\mathrm{x}} + (1-\alpha) o_{\mathrm{y}}$, which is exactly the same as in the absence of exchange (eq. (13)). Furthermore, this trait value is convergent stable (Appendix B.3.2). Hence, exchange does not alter the nature of directional selection and the population first evolves towards the same equilibrium point as under autarky. Yet, exchange will affect the evolutionary stability of the convergence stable trait value. To understand this, we first note that the presence of exchange always entails negative-frequency dependent selection, since

$$\left.\frac{\partial^2 \pi(\tau,\theta)}{\partial\tau\partial\theta}\right|_{\tau=\theta=\theta^*} = -q^{\mathrm{x}}(\theta^*)^{(-2+\alpha)} q^{\mathrm{y}}(\theta^*)^{(1-\alpha)} \left(\frac{1}{4}\right)\left(\frac{\alpha}{1-\alpha}\right)\left(\left.\frac{\partial q^{\mathrm{x}}(\tau)}{\partial\tau}\right|_{\tau=\theta=\theta^*}\right)^2 < 0, \tag{14}$$

which is true for any relationship between the trait and the productivity, e.g. any functions as defined in eqs. (1) and (2). The rationale behind this result is that when an individual deviates from the singular point by producing more of one good as a result of an increase in trait value, that good becomes more common, leading to a decrease in its price and value, while the other good becomes rarer and more valuable. As a result, individuals in the population whose traits deviate in the opposite direction produce more of the now scarcer good, and achieve a higher payoff than those who continue producing the more abundant good. This generates selective pressures that favour individuals producing the rarer good, ensuring that in a population with two distinct types, neither can completely replace the other.

Eq. (14) establishes that economic exchange generically creates selection favouring coexistence of distinct morphs, but it does not ensure that exchange will result in distinct morphs from a monomorphic population. This second statement is true if selection is disruptive at θ^*, as it means that mutants deviating from the mean have a higher payoff than those at the mean. We find that disruptive selection occurs when

$$\left.\left(\alpha q^{\mathrm{y}}(\tau)\frac{\partial^2 q^{\mathrm{x}}(\tau)}{\partial\tau^2} + (1-\alpha) q^{\mathrm{x}}(\tau)\frac{\partial^2 q^{\mathrm{y}}(\tau)}{\partial\tau^2}\right)\right|_{\tau=\theta=\theta^*} > -\frac{3}{4}\left.\left(\frac{\partial q^{\mathrm{y}}(\tau)}{\partial\tau}\frac{\partial q^{\mathrm{x}}(\tau)}{\partial\tau}\right)\right|_{\tau=\theta=\theta^*}. \tag{15}$$

This requires that the second derivatives of the quantities produced with respect to the trait are large enough (note that the right-hand side is positive as the partial derivatives are of opposite signs at the generalist singular point). This condition implies that having a trait deviating from the singular point must increase the production of the goods at a rate much greater than linear. Substituting eqs. (1)–(2) into eq. (15), the condition for polymorphism to emerge translates as

$$\frac{(o_\mathrm{x} - o_\mathrm{y})^2}{\sigma^2} > \frac{2}{(1-\alpha)\alpha}. \tag{16}$$

The left-hand side of eq. (16) is the ratio of the squared difference between the trait values o_x and o_y (which maximise production of goods x and y, respectively) to the production breadth σ^2. This measures how much an individual excelling at producing one good performs poorly at producing the other and represents the degree of trade-off between producing the two goods. The population becomes polymorphic when this trade-off is strong, as it would be the case for goods that require very different traits to be produced. The right-hand side of eq. (16) depends on the relative importance for fitness of good x compared to good y. Since the denominator is largest when $\alpha = 0.5$, the condition is easier to satisfy when the two goods are equally valuable for fitness. When one of the goods is much more valuable for fitness than the other, that is, α is either close to 0 or 1, the condition is harder to satisfy.

We validate these analytical results using individual-based simulations (see Appendix B.5 for details), which allow us to illustrate the typical trajectory of trait evolution in a scenario where the population initially lives in autarky and exchange is introduced after 5000 generations (see top left panel of Figure 2). Individuals initially have a trait value close to the optimum for producing good y, and both goods are equally valuable for fitness ($\alpha = 0.5$). Prior to the introduction of exchange, the population evolves first under autarky towards the singular trait value, as predicted by the analytical results. During this time, (i) the population shifts from producing predominantly good y (indicated by a large proportion of red in the top left panel of Figure 2) to producing both goods (a combination of blue and red), and (ii) the total quantities of goods produced decreases drastically (bottom left panel of Figure 2). This is because both goods are equally valuable for fitness, and in absence of exchange, individuals must produce sufficient quantities of both goods. When exchange is introduced, the population quickly divides into two morphs, with selection pushing the traits of each morph away from each other until each of the morphs has a trait close to the optimal trait value for production of one of the two goods (top left panel of Figure 2). During this process of diversification, the quantities produced, exchanged, and consumed largely increase, demonstrating the benefits of exchange (bottom left, top right, and bottom right panels of Figure 2). At the long-term evolutionary equilibrium, one fraction of the population produces predominantly good x, while the other fraction produces almost exclusively good y, yet all individuals consume both goods (bottom right panel of Figure 2). Exchange allows for genetic diversity, raising production of both goods while maintaining an optimal allocation of goods. This is why the population composed of the two morphs who exchange with each other has an average payoff 13 times higher than a population of generalists who do not exchange (generation 12401 vs. 4801).

Supplementary Figure S1 illustrates the dynamics of the trait when one good is more important for the payoff than the other. It confirms that (i) a population in autarky converges and remain towards a singular point which is closer to the optimal of production of the most important good, and (ii) diverges once exchange is introduced. At the long-term evolutionary equilibrium, the majority of individuals have a trait close to the optimum of the good that is most valuable for fitness.

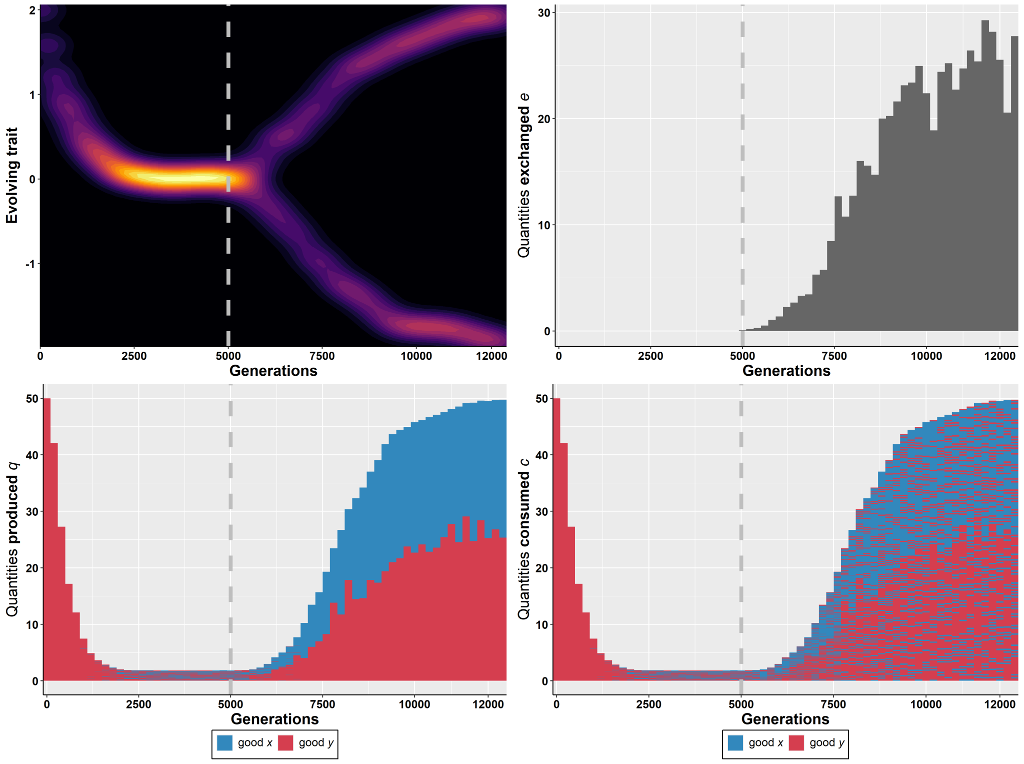

Figure 2: Distribution of trait values (top left), of the quantities produced q (bottom left), exchanged e (top right), and consumed c (bottom right) as a function of generations. The population remains in autarky for the first 5000 generations, after which exchange is introduced (indicated by the grey dotted line). We consider dyadic exchange where exchange takes place between pairs of isolated individuals. For clearer visualization, the quantities shown are of a subset of 100 randomly selected individuals. In the plots showing production and consumption, the quantities for each individual of goods x and y are stacked on top of one another, with individual 1 at the bottom and individual 100 at the top. The parameters used are production breadth $\sigma^2 = 1$, an equal importance of each good $\alpha = 0.5$, optima of production of each good $o_\mathrm{x} = -2$, $o_\mathrm{y} = 2$, population size $N = 1000$, mutation rate $\mu_\mathrm{m} = 0.01$ and variance of mutations $\sigma_\mathrm{m}^2 = 0.0004$.

3.3 Market exchange

We have shown that dyadic exchange (i) always creates negative frequency-dependent selection and (ii) even generates stable adaptive genetic diversity when the abilities necessary to produce the goods are different enough. Do these results hold when exchanges take place in a market rather than through isolated dyadic interactions? Under market exchange, the mutant payoff (eq. 6) and the quantities consumed (eq. 8) remain the same as under pairwise interactions, only the price needs to be changed (eq. (11)). Our analysis under market exchange (detailed in Appendix B.3.3) shows that $\theta^* = \alpha o_\mathrm{x} + (1-\alpha) o_\mathrm{y}$ is again convergent stable and that negative frequency-dependent selection will occur at this point. Yet for this case, the condition for disruptive selection becomes

$$\left(\alpha q^\mathrm{y}(\tau)\frac{\partial^2 q^\mathrm{x}(\tau)}{\partial \tau^2} + (1-\alpha) q^\mathrm{x}(\tau)\frac{\partial^2 q^\mathrm{y}(\tau)}{\partial \tau^2}\right)\bigg|_{\tau=\theta=\theta^*} > 0 \tag{17}$$

When this condition is satisfied, polymorphism emerges as long as the increase in production due to a deviation in the trait are superlinear. This condition ensures that the gain in production in one good for a mutant is higher than its loss in the other good. Substituting eqs (1)–(2) into eq. (17) yields

$$\frac{(o_{\mathrm{x}} - o_{\mathrm{y}})^2}{\sigma^2} > \frac{1}{2(1-\alpha)\alpha}. \tag{18}$$

Comparing the right-hand sides of eqs. (16) and eq. (18) shows that polymorphism emerges under a broader range of conditions in market compared to dyadic exchange. This suggests that the development of markets can favor genetic diversity in contexts where dyadic exchange alone is insufficient. The reason for this difference is that in dyadic exchange, genetic diversity is hindered because an individual producing more of a good lowers its price at the same time. As a result, genetic diversity only evolves when the increase in production associated is sufficiently large. However, this effect does not take place in a market, as an individual does not affect the price by himself.

4 Evolutionary analysis with time allocation decision

Thus far, we have examined the influence of exchange exclusively on the evolution of genetic diversity by keeping the time allocation h constant. We now examine how exchange shapes both genetic diversity and economic specialisation by letting individuals decide how much time they want to allocate to producing each good. We first carry out the evolutionary analysis along the same line as in the previous sections, before examining more closely the interplay between genetic diversity and economic specialisation using simulations.

4.1 Autarky

In autarky, we find that the time allocation at equilibrium in eq. (A-3) entails that all individuals allocate a fraction $\hat{h} = \alpha$ of their time to produce good x. Substituting this time allocation into the mutant payoff (eq. (12)) and then into computing the payoff gradient (eq. (A-30)) yields the same single equilibrium point $\theta^* = \alpha o_{\mathrm{x}} + (1-\alpha) o_{\mathrm{y}}$ than when time allocation was fixed. Furthermore, we find that this singular point is convergent and evolutionary stable (see Appendix B.4.1). In autarky, individuals thus evolve to have a similar genetic trait between the two optimals of production, as we found in the case of fixed time allocation.

4.2 Exchange

We now conduct the evolutionary analysis in presence of exchange using eqs. (6)–(11). While we can derive analytical results with market exchange, part of the analysis with dyadic exchange must be carried out numerically since the price can not be explicitly solved analytically. Thus, our analysis with dyadic exchange focuses on varying two parameters: the elasticity of scale η in increments of 0.05 and the production breadth σ^2 over the range $[1, 20]$ in increments of 1, while setting $o_{\mathrm{x}} = -2, o_{\mathrm{y}} = 2$ and $\alpha = 0.5$.

In the presence of exchange, whether dyadic or market based, we find that there is a unique singular point taking the usual form $\theta^* = \alpha o_{\text{x}}+(1-\alpha)o_{\text{y}}$ (see numerical analysis in the accompanying Mathematica notebook for dyadic exchange and Appendix B.4.3 for market exchange). Furthermore, this trait value is convergence stable on the range of η and σ^2 considered. As under fixed time allocation, the population thus first evolve by directional selection towards having the same generalist value of the trait.

At this generalist value, the synergy coefficient is negative on the range of η and σ^2 considered for dyadic exchange and is always negative for market exchange (eq. (A-64)). Hence, there is again negative frequency-dependent selection at the singular trait value, which opens up the possibility that a polymorphism might emerge. We next examine the conditions under which disruptive selection occurs and thus polymorphism emerges by gradual evolution. For dyadic exchange, we assess these conditions numerically across the parameter space considered and the results are displayed in the left panel of Figure 4. For market exchange, we obtain the following analytical condition (Appendix B.4.3)

$$\frac{(o_{\text{x}}-o_{\text{y}})^2}{\sigma^2} > \frac{1-\eta}{2(1-\alpha)\alpha}. \tag{19}$$

This expression is identical to the one derived under fixed time allocation in eq. (18), except that the right-hand side now includes the additional term $1-\eta$.

These results show that for both dyadic and market exchange, when η is close to 0, the time allocation is largely independent of the evolving traits and selection is disruptive under the same conditions as derived in eqs. (16) and (18), consistent with the results obtained under fixed time allocation. When η is higher, meaning when the effect of diminishing returns is less pronounced, the range of values of production breadth σ^2 within which polymorphism emerges broadens. When η close to 1, individuals tend to allocate a significant proportion of their time to producing either one good or the other (see eq. (9)). As a result, polymorphism emerges almost inevitably, even when σ^2 is high, that is, even when the production of goods does not require tailored abilities. The key result is that a context favourable to economic specialisation significantly broadens the conditions for genetic diversity to emerge. Comparing the conditions for polymorphism to emerge between dyadic and market exchange (Figure 4) reveals that polymorphism arises under a broader range of conditions in market exchange than in dyadic exchange.

4.3 Interplay between economic specialisation and genetic diversity

We now examine how the interaction between exchange and genetic diversity affects the distribution of time allocation in the population. The expression for h in eq. (9) describes how the time allocation of individuals depends on their traits and the price in a monomorphic population, but it did not clarify how h is distributed across an evolving population when individuals vary in their traits. To address this, we return to individual-based simulations under the scenario where the population first evolves in autarky, and exchange is introduced after a period of time. First, when η is high and exchange is introduced, individuals—particularly those at the extremes of the evolved trait distribution—shift their time allocation from producing both goods x and y (spending a fraction α of their time on x and $1-\alpha$ on y) to focusing almost entirely on a single good (their h is close to 1 or 0, see Figure 3). In other words, individuals become specialised in the production of goods. As generations go by, the population

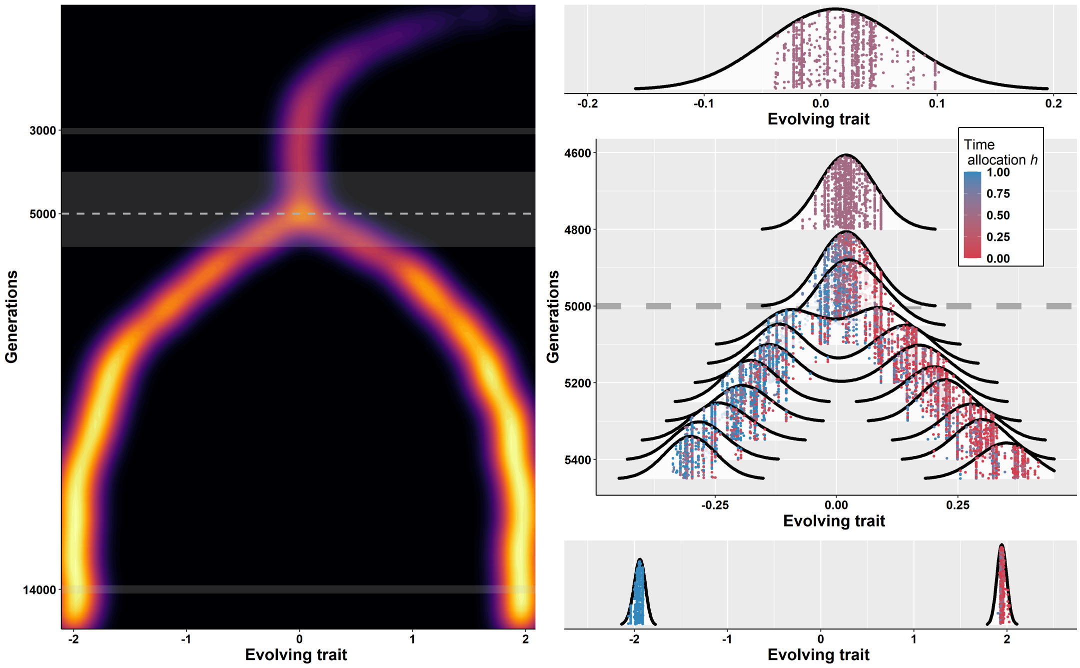

Figure 3: Evolution of genetic diversity and economic specialisation. (Left) Evolution of trait over generations. The population remains in autarky for the first 5000 generations, after which exchange is introduced (indicated by the grey dotted line). We consider dyadic exchange where exchange takes place between pairs of isolated individuals. (Right) Distribution of trait (x-axis) and time allocation (colour). Each point represents a single individual. The plot is divided in three parts, each focusing on a particular time period, (top) at 3000 generations when exchange is absent, (middle) at 5000 generations when exchange is introduced and (bottom) at 14000 generations to show the long-run outcome. The parameters used are elasticity of scale $\eta = 0.9$, production breadth $\sigma^2 = 1$, equal importance of goods $\alpha = 0.5$, optima of production $o_{\mathrm{x}} = -2, o_{\mathrm{y}} = 2$, population size $N = 1000$, mutation rate $\mu_{\mathrm{m}} = 0.01$ and variance of mutations $\sigma^2_{\mathrm{m}} = 0.0004$.

splits into two morphs where morphs closer to the optimal of production of a good allocate more time to produce that good (when interacting with the other morph). At equilibrium, the population consists of individuals with distinct genetic traits and distinct time allocation patterns.

We refer to this variation in time allocation across individuals as economic specialisation and we measure it by the difference between the highest and lowest h values observed in the population. We then examine this measure of economic specialisation in the generation immediately after exchange is introduced and across the parameter space to assess the role of economic specialisation in the emergence of genetic diversity. Our results show that the transition from autarky to exchange can lead to varying degrees of economic specialisation, with the greatest differences in time allocation occurring when returns to scale are high and production breadth is low (Figure 4, supplementary Figures S3, S4). For these parameter values at which economic specialisation is strongest, genetic diversity consistently emerges, as shown by the two panels of Figure 4. However, genetic polymorphism can also be favoured even when the population is not fully economically specialised. For instance, at moderate values of the elasticity

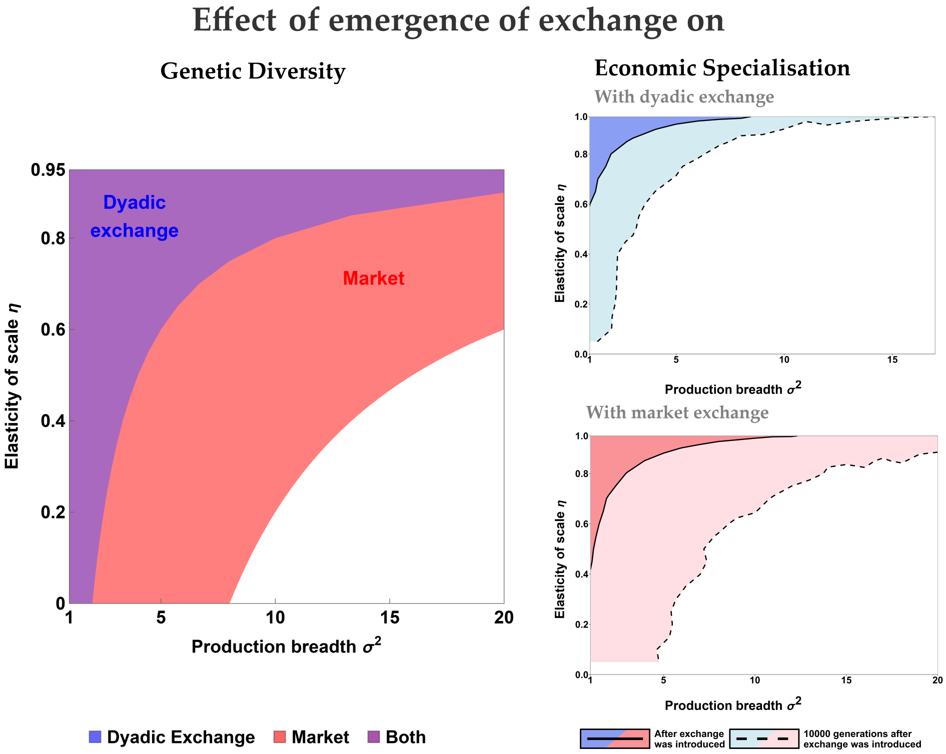

Figure 4: Effect of the emergence of exchange on genetic diversity and economic specialisation as a function of production breadth σ^2 and elasticity of scale η. The shaded areas in the left panel show the conditions under which genetic diversity is predicted to emerge, identified by locating the cases where the singular trait value is both convergence stable and invadable (i.e. selection is disruptive). The right panel shows the conditions under which economic specialisation is observed after 1 generation (dark shaded area) and after 10,000 generations (light shaded area) following the introduction of dyadic exchange (top) or market exchange (bottom). These conditions are determined by identifying when the average difference between the highest and lowest values of h exceeds 0.8 across 10 replicates of numerical simulations. The parameters used are equal importance of goods $\alpha = 0.5$, optima of production $o_x = -2, o_y = 2$. The parameters used specifically for the simulations to obtain the right panels are for population size $N = 1000$, mutation rate $\mu_m = 0.01$, variance of mutations $\sigma_m^2 = 0.0004$, and the initial population is drawn from a Normal distribution centered on the singular point with small variance 0.0025.

of scale and low production breadth, individuals continue to allocate a substantial portion of their time to producing both goods, yet genetic diversity still emerges. This suggests that economic decisions regarding time allocation promote genetic diversity not only when individuals engage in entirely distinct production activities, but also under partial specialisation.

To evaluate how genetic diversity, once established at a long-term evolutionary equilibrium, influences economic specialisation, we examine economic specialisation after 10,000 generations. At this stage, economic specialisation is observed across a much broader range of parameter combinations than when exchange was just introduced (supplementary Figures S3, S4). Notably, the conditions under which economic specialisation is present now closely align with those that initially favoured the emergence of genetic diversity (Figure 4). This demonstrates that the emergence of diverse morphs favour economic specialisation, and importantly, that in some cases, the emergence of genetic diversity has even enabled the development of economic specialisation. We illustrate this possibility under a scenario where η is low (presented in Supplementary Figure S5). Here, when exchange is introduced into the population, the time allocation of individuals remains close to 0.5. However, the variance in the trait quickly increases and as traits diverge, individuals increasingly focus on producing the good for which they are better suited (h approaches 0 or 1). In summary, over time, adaptive genetic diversity and economic specialisation reinforce each other, resulting in a population divided into two morphs, each with traits near the production optimum of one good and entirely specialising in its production (when interacting with the other morph).

5 Discussion

The impact of economic exchange on the organisation of human societies has long been recognised, yet its possible footprint on innate human abilities is less understood. In this paper, we introduced an individual producer-resource model that we combined with a standard economic model of exchange and a standard evolutionary model to investigate how the presence of economic exchange might shape the selective pressures acting on quantitative traits involved in the production of goods by individuals. In our model, the evolving trait can represent a wide range of biological characteristics, provided it has a heritable genetic component. This includes most morphological and physiological traits, as well as a substantial proportion of behavioural traits (Polderman et al., 2015). Our findings are summarized in the following key points.

First, our theoretical analysis reveals that the development of exchange can shift the nature of selection pressures, from maintaining by stabilising selection an homogeneous population, where all individuals express a similar generalist trait in autarky, to favouring adaptive genetic diversity in presence of economic exchange. Specifically, with exchange, selection (i) consistently promotes, at least temporarily, the coexistence of different morphs through negative frequency-dependent selection, and (ii) can generate stable long-term adaptive polymorphism by disruptive selection. This occurs because exchange allows individuals whose heritable traits make them efficient at producing a single good, to still access the other good, and thus to have a higher survival and reproduction. At the same time, the price dynamics—

where an increase in production of a given good lowers its relative value and, consequently, the fitness of these producers—prevent any single type from completely replacing others. Importantly, these processes, despite resulting in an increase in the overall payoff to individuals and thus the average payoff in the population, do not require conditions such as population structure, competition between groups, or groups facing different environments.

Second, we identify the conditions under which exchange promotes adaptive genetic diversity. As we have seen, a polymorphism is favoured by selection when small deviations from a generalist trait lead to disproportionately higher production of one good, meaning the gain in production of one good outweighs the loss in production of the other. This translates in our model in three conditions. First, production of the two goods must require sufficiently different innate abilities, that is, the trait values that maximize production of each good, must lie sufficiently far apart. Second, the goods must display a knife-edge production breadth where small deviations from the optimal trait values (o_{x} and o_{y}) lead to large reductions in quantities produced, that is, the production breadth (σ^2) cannot be too large. Third, one good can not be much more valuable than the other in terms of fitness, that is the relative importance of good x (α) cannot be too close to 0 or 1. Our results further show that when exchange takes place through a market involving many participants, selection generates stable polymorphism in a wider range of conditions. This suggests that the transition from localised, bilateral exchanges between individuals to broader market economies, could also have resulted in an increase in human genetic diversity.

Third, our model clarifies how genetic diversity—variation in individuals' innate productive abilities—and economic specialisation—variation in time individuals allocate producing each good—can co-evolve. The interactions between adaptive genetic diversity and economic specialisation have been hard to study as they can feed back into each other (Buchanan and Yoon, 2002), but our theoretical approach allows us to disentangle their roles. The presence of economic specialisation on top of economic exchange greatly widens the range of conditions under which natural selection generates adaptive genetic diversity. This extends the verbal argument that different economic and social roles promote phenotypic diversity through learning (Lukaszewski et al., 2017; Smaldino et al., 2019; Durkee et al., 2022) (i) to include phenotypic diversity arising from genetic variation, as proposed by (Hunt and Jaeggi, 2022) and (ii) to include traits that are more rigidly determined by genetic factors. However, our results also clarify that different economic roles are not always necessary for genetic diversity to emerge, as the presence of economic exchange can result in genetic diversity even when individuals do not differ in the time they spend producing one good or the other. In contrast, it can even be the emergence of genetic diversity which allows for the development of different economic roles.

Identifying the conditions and processes that favour genetic diversity has long been a central question in evolutionary biology, as it underpins the adaptability of populations to environmental changes and provides insights into past evolutionary processes. Importantly, it is well understood that cultural phenomena could affect genetic diversity, as for instance change in descent system led to a large decrease in the Y-chromosome diversity (Chaix et al., 2007; Zeng et al., 2018; Guyon et al., 2024). Yet, such examples remain rare. Our work adds a new example of such relationship by showing that the development of economic exchanges, and the factors that allowed it (Demps and Winterhalder, 2019), such as changes in technology, infrastructure and population density, could have resulted in significantly increased genetic diversity. So far, a correlation between exchange and genetic diversity has only been tested indirectly, as previous studies have examined correlations between neutral genetic diversity and economic specialisation rather than exchange directly (Depetris-Chauvin and Ozak, 2015). Integrating more detailed data on economic systems, as done in large comparative databases, could allow for a more direct test (Turchin et al., 2017). Alternatively, a population such as the Tsimane people presents a particularly interesting case study, as different groups vary in their market integration, and this variation has already been shown to influence the social structure of these groups (Gurven et al., 2015; von Rueden, 2023).

Our work also predicts, albeit less directly, that the development of exchange and the transition to market exchange could be associated with an increase in trait diversity. Actually, by removing the assumptions of asexual population, our model predicts less that the development of exchange would lead to the emergence of extreme distinct traits, but rather to an increase in the overall adaptive diversity of traits (Rueffler et al., 2006, see Figure 1 of Dieckmann and Doebeli 1999 for an example). As such, our results resonates with the recent observation that personality traits can be described by fewer dimensions in small-scale societies, where exchanges take place to a smaller degree and labour division is limited (Kelly, 1995), than in industrialised societies (Lukaszewski et al., 2017; Durkee et al., 2022). Again, previous explanations have mostly explored the role of the number of distinct economic roles to explain this observation (Lukaszewski et al., 2017; Smaldino et al., 2019; Durkee et al., 2022), but our results suggest that the prevalence of economic exchange and participation in large markets could also be key factors.

In economics, specialisation was first considered a direct and almost inevitable consequence of economic exchanges, as illustrated by the famous quote by Adam Smith: “the division of labour is limited by the extent of the market.” Yet, since Adam Smith, a large body of evidence has shown that this statement should be tempered, as past and current human societies exhibit wide variability in their levels of specialisation. While specialists are prevalent in early states (Claessen and Skalník, 1978), small-scale societies tend to have very limited division of labour, aside from gendered divisions (Kelly, 1995). Therefore, a crucial question is what factors could account for the emergence of specialisation in some societies, while it remains absent in others. Previous hypotheses usually focus on the role of changes in technology, group size (Ben-Oren et al., 2023), or political elites, and ignore the potential role of biological factors. Recently, Depetris-Chauvin and Ozak (2015, 2020) have proposed that genetic diversity could also have been an important factor, based on evidence that economic specialisation emerged first in groups with higher genetic diversity. Our analysis supports this verbal model and confirms that there are scenarios where economic specialisation could emerge only under conditions favouring genetic diversity first. In addition, our findings identify some of these conditions, with for instance the presence of goods whose production requires different skills, which likely depends on the heterogeneity of the environment.

Essentially no model in the literature has previously explored the conditions under which adaptive diversity can emerge in heritable traits related to the production of goods when economic exchange is modelled explicitly, as we have done here. Previous models have demonstrated that diversity in an evolving trait is expected when social interactions favour anti-coordination (Henrich and Boyd, 2008;

Vásárhelyi et al., 2015; Vásárhelyi and Scheuring, 2018); for example, tasks where two individuals performing different actions achieve a higher payoff than two individuals performing the same action (Henrich and Boyd, 2008). Yet, these models focus on how heritable differences can be maintained given a particular fixed payoff structure. In contrast, our model takes a different perspective by identifying exchange itself as the process which generates this payoff structure under which specialisation and genetic diversity emerge. In line with this distinction, our model is particularly related to that of Nakahashi and Feldman (2014), who show that the custom of sharing goods can also promote genetic diversity. However, their result depends on having sufficiently large groups, whereas our results show that genetic diversity could emerge with economic exchange regardless of group size. This raises the broader question of how transitions from food-sharing practices to market-based exchanges may have influenced the evolution of adaptive genetic diversity.

A central assumption of our model is that it focuses on exchange under a Walrasian equilibrium, a framework with strong theoretical (Mas-Colell et al., 1995; Yildiz, 2003; Dávila and Eeckhout, 2008; Mandel and Gintis, 2016) and robust empirical support (Lin et al., 2020), demonstrated across numerous experimental setups (Kagel and Roth, 1995) and diverse cultural contexts (Roth et al., 1991). However, anthropological evidence has long pointed out that exchange in small-scale societies may also depend on other factors (Hann, 2017; Polanyi et al., 1957; Sahlins, 1974). For example, while price in our model dictates that rarer goods are more expensive, in small scale societies, social norms entails that those taking advantage of owning a desired good are frowned upon or even punished (Lee, 1979; Woodburn, 1982; Kelly, 1995; Boehm, 2001). Furthermore, price might directly deviate from its value under a Walrasian equilibrium when it is imposed by a political authority, as commonly observed in past societies (Polanyi et al., 1957). Investigating how exchange could promote adaptive genetic diversity in alternative economic systems would be a valuable extension of our analysis.

Our model may seem to overlook the fact that individual's abilities to produce a given good is also determined by culturally learned traits. However, this omission does not affect our conclusions. Even if cultural factors predominantly determine certain productive abilities compared to genetic traits, as long as skill acquisition is independent of the evolving genetic traits under focus, selection would still act on these traits as described by our results. Exploring more complex interactions between genetic and cultural traits, where individuals learn skills that are either well suited or poorly suited to their genetic predispositions, could be an interesting extension for future work. Furthermore, the quantitative evolving trait in our model can also be interpreted as a cultural trait, when it is learned from parents (vertical learning) or from successful individuals (payoff-biased learning). Accordingly, our model predicts that exchange should favour cultural diversity as well as genetic diversity. In doing so, it extends the idea that exchange fosters cultural diversity not only by facilitating the spread and recombination of ideas (Ridley, 2009) but also by shaping the evolution of culturally transmitted traits linked to production of goods.

When Adam Smith famously proposed that exchange leads to specialisation, he asserted that “the difference between the most dissimilar characters, between a philosopher and a common street porter, for example, seems to arise not so much from nature, as from habit, custom, and education.” (Smith,

1776) Two centuries later, it is widely accepted that biological and cultural factors interact in shaping human traits, making the picture far more complex than Smith initially envisioned. Our study extends this insight by demonstrating that exchange itself—the very mechanism Smith described—not only influences learning and skill acquisition, but may also have shaped adaptive genetic diversity through evolutionary pressures. The historical transitions from simple exchange to complex markets may not have merely reorganized production but actively reinforced biological differentiation, making exchange a long-term evolutionary pressure.

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Appendix A Behavioural equilibrium

In this section, we derive the behavioural equilibrium solving the individual optimisation problem (3)-(4) of the main text, which determines how individuals produce and exchange goods.

Appendix A.1 Autarky

In autarky, the optimization problem (3)-(4) faced by the producer-consumer individual i reduces to simply choosing the optimal time allocation and is thus defined by

$$\max_{h_i \in [0,1]} \left[q^{\mathrm{x}}(\tau_i, h_i)\right]^{\alpha} \left[q^{\mathrm{y}}(\tau_i, h_i)\right]^{1-\alpha}. \tag{A-1}$$

The necessary first-order condition for an interior optimum is obtained by solving the following equation for $\hat{h}_i$

$$\left.\frac{\partial\left(\left[q^{\mathrm{x}}(\tau_i, h_i)\right]^{\alpha} \left[q^{\mathrm{y}}(\tau_i, h_i)\right]^{1-\alpha}\right)}{\partial h_i}\right|_{h_i=\hat{h}_i} = 0. \tag{A-2}$$

Substituting eqs. (1) therein and solving for $\hat{h}_i$, we find

$$\hat{h}_i = \alpha. \tag{A-3}$$

Since the payoff is concave in $\hat{h}_i$, this is also the optimal solution. Hence, in autarky, each individual allocates a fraction α of their time to producing good x.

Appendix A.2 With exchange

Appendix A.2.1 Consumer-producer decision problem

In the presence of exchange, recall from section 2.1 that the decision problem (3)-(4) that consumer-producer i with trait τ_i and time allocation h_i faces is

$$\max_{c_i^{\mathrm{x}} \in \mathbb{R}, c_i^{\mathrm{y}} \in \mathbb{R}, h_i \in [0,1]} \left(c_i^{\mathrm{x}}\right)^{\alpha} \left(c_i^{\mathrm{y}}\right)^{1-\alpha}, \tag{A-4}$$

subject to the constraint

$$p\ c_i^{\mathrm{x}} + c_i^{\mathrm{y}} = p\ q^{\mathrm{x}}(\tau_i, h_i) + q^{\mathrm{y}}(\tau_i, h_i), \tag{A-5}$$

where c_i^k is the quantity of good $k \in \{x, y\}$ consumed by individual i, $q^k(\tau_i, h_i)$ is his "endowment" of good $k \in \{x, y\}$, which depends on the time allocation h_i, and p is the price of good x.

To solve this problem we use standard constrained maximization method (Sydsaeter et al., 2008), and form the associated Lagrangian function

$$L(h_i, c_i^{\mathrm{x}}, c_i^{\mathrm{y}}) = \left(c_i^{\mathrm{x}}\right)^{\alpha} \left(c_i^{\mathrm{y}}\right)^{1-\alpha} - \lambda_i \Big[p c_i^{\mathrm{x}} + c_i^{\mathrm{y}} - p q^{\mathrm{x}}(\tau_i, h_i) - q^{\mathrm{y}}(\tau_i, h_i)\Big], \tag{A-6}$$

where λ_i is a Lagrange multiplier. A necessary condition to solve the decision problem is that the Lagrangian $L(h_i, c_i^{\mathrm{x}}, c_i^{\mathrm{y}})$ is maximized with respect to the choice variables $c_i^{\mathrm{x}}, c_i^{\mathrm{y}}$ and h_i. Using eqs. (1), the necessary first-order conditions characterising the solutions to the problem are

$$\left.\frac{\partial L(h_i, c_i^{\mathrm{x}}, c_i^{\mathrm{y}})}{\partial h_i}\right|_{h_i=\hat{h}_i, c_i^{\mathrm{x}}=\hat{c}_i^{\mathrm{x}}, c_i^{\mathrm{y}}=\hat{c}_i^{\mathrm{y}}} = 0 \quad \Longrightarrow \quad \lambda_i \left[p\eta(\hat{h}_i)^{\eta-1} r^{\mathrm{x}}(\tau_i) - \eta(1-\hat{h}_i)^{\eta-1} r^{\mathrm{y}}(\tau_i)\right] = 0, \tag{A-7}$$

$$\left.\frac{\partial L(h_i, c_i^{\mathrm{x}}, c_i^{\mathrm{y}})}{\partial c_i^{\mathrm{x}}}\right|_{h_i=\hat{h}_i, c_i^{\mathrm{x}}=\hat{c}_i^{\mathrm{x}}, c_i^{\mathrm{y}}=\hat{c}_i^{\mathrm{y}}} = 0 \quad \Longrightarrow \quad \alpha\,(\hat{c}_i^{\mathrm{x}})^{\alpha-1}\,(\hat{c}_i^{\mathrm{y}})^{1-\alpha} = \lambda_i p, \tag{A-8}$$

$$\left.\frac{\partial L(h_i, c_i^{\mathrm{x}}, c_i^{\mathrm{y}})}{\partial c_i^{\mathrm{y}}}\right|_{h_i=\hat{h}_i, c_i^{\mathrm{x}}=\hat{c}_i^{\mathrm{x}}, c_i^{\mathrm{y}}=\hat{c}_i^{\mathrm{y}}} = 0 \quad \Longrightarrow \quad (1-\alpha)\,(\hat{c}_i^{\mathrm{x}})^{\alpha}\,(\hat{c}_i^{\mathrm{y}})^{-\alpha} = \lambda_i. \tag{A-9}$$

Time allocation. To solve the first-conditions, we first focus on the time allocation. Solving eq. (A-7) for $\hat{h}_i$ gives

$$p\eta(\hat{h}_i)^{\eta-1} r^{\mathrm{x}}(\tau_i) - \eta(1-\hat{h}_i)^{\eta-1} r^{\mathrm{y}}(\tau_i) = 0 \tag{A-10}$$

$$\Longleftrightarrow p\,(\hat{h}_i)^{\eta-1} r^{\mathrm{x}}(\tau_i) = (1-\hat{h}_i)^{\eta-1} r^{\mathrm{y}}(\tau_i) \tag{A-11}$$

$$\Longleftrightarrow \frac{(\hat{h}_i)^{\eta-1}}{(1-\hat{h}_i)^{\eta-1}} = \frac{1}{p}\frac{r^{\mathrm{y}}(\tau_i)}{r^{\mathrm{x}}(\tau_i)} \tag{A-12}$$

$$\Longleftrightarrow \left(\frac{\hat{h}_i}{1-\hat{h}_i}\right)^{\eta-1} = \frac{1}{p}\frac{r^{\mathrm{y}}(\tau_i)}{r^{\mathrm{x}}(\tau_i)} \tag{A-13}$$

$$\Longleftrightarrow \left(\frac{1-\hat{h}_i}{\hat{h}_i}\right)^{1-\eta} = \frac{1}{p}\frac{r^{\mathrm{y}}(\tau_i)}{r^{\mathrm{x}}(\tau_i)} \tag{A-14}$$

$$\Longleftrightarrow \frac{1-\hat{h}_i}{\hat{h}_i} = \left[\frac{1}{p}\frac{r^{\mathrm{y}}(\tau_i)}{r^{\mathrm{x}}(\tau_i)}\right]^{\frac{1}{1-\eta}} \tag{A-15}$$

$$\Longleftrightarrow \frac{1}{\hat{h}_i} - 1 = \left[\frac{1}{p}\frac{r^{\mathrm{y}}(\tau_i)}{r^{\mathrm{x}}(\tau_i)}\right]^{\frac{1}{1-\eta}}, \tag{A-16}$$

which gives

$$\hat{h}_i(p) = \frac{1}{1 + \left[\frac{1}{p}\frac{r^{\mathrm{y}}(\tau_i)}{r^{\mathrm{x}}(\tau_i)}\right]^{\frac{1}{1-\eta}}}. \tag{A-17}$$

Owing to the fact that $0 \leq \eta < 1$, the Lagrangian is concave in h_i, which is sufficient for this solution to maximize the Lagrangian, holding everything else constant. Eq. (A-17) thus describes the time allocation which maximises the payoff of the individual as function of the price.

Quantities consumed. Let us now focus on consumption. Dividing eq. (A-8) by eq. (A-9), we have

$$\frac{\alpha\,(\hat{c}_i^{\mathrm{x}})^{\alpha-1}\,(\hat{c}_i^{\mathrm{y}})^{1-\alpha}}{(1-\alpha)\,(\hat{c}_i^{\mathrm{x}})^{\alpha}\,(\hat{c}_i^{\mathrm{y}})^{-\alpha}} = p.$$

Solving for $\hat{c}_i^{\mathrm{y}}$ gives

$$\hat{c}_i^{\mathrm{y}} = \frac{1-\alpha}{\alpha} p\,\hat{c}_i^{\mathrm{x}}. \tag{A-18}$$

Substituting into eq. (A-5) and solving for $\hat{c}_i^{\mathrm{x}}$, we get the consumption at equilibrium for good x as function of the price

$$\hat{c}_i^{\mathrm{x}}(p) = \alpha\left[q^{\mathrm{x}}(\tau_i, \hat{h}_i(p)) + \frac{1}{p} q^{\mathrm{y}}(\tau_i, \hat{h}_i(p))\right], \tag{A-19}$$

which is called demand function of good x in economics. Substituting back this expression into eq. (A-18), we get the demand function for good y by individual i

$$\hat{c}_i^{\mathrm{y}}(p) = (1-\alpha)p\left[q^{\mathrm{x}}(\tau_i, \hat{h}_i(p)) + \frac{1}{p} q^{\mathrm{y}}(\tau_i, \hat{h}_i(p))\right]. \tag{A-20}$$

Because the Lagrangian (A-6) is concave in the consumptions c_i^{x} and c_i^{y} and the solutions eqs. (A-19)–(A-20) are unique, these are the optimal solutions to the decision problem (Sydsaeter et al., 2008). The consumptions so obtained depend on the price, and to close the model we need an expression for the equilibrium price to which we next turn.

Appendix A.2.2 Price at equilibrium

Owing to our assumption of a Walrasian equilibrium (section 2.1), the equilibrium price $\hat{p}$ is the one at which the total quantities produced by the interacting individuals equals total consumption. This requires that the price satisfies

$$\sum_{i=1}^{N_{\mathrm{int}}} \hat{c}_i^{\mathrm{x}}(\hat{p}) = \sum_{i=1}^{N_{\mathrm{int}}} q^{\mathrm{x}}(\tau_i, \hat{h}_i(\hat{p})), \tag{A-21}$$

where recall N_{int} is the number of interacting individuals, either 2 in dyadic exchange or N in market exchange.

Substituting eq. (A-19) into eq. (A-21) and solving for $\hat{p}$, we get the equilibrium price

$$\hat{p} = \frac{\alpha}{1-\alpha} \frac{\sum_{i=1}^{N_{\mathrm{int}}} q^{\mathrm{y}}(\tau_i, \hat{h}_i(\hat{p}))}{\sum_{i=1}^{N_{\mathrm{int}}} q^{\mathrm{x}}(\tau_i, \hat{h}_i(\hat{p}))}. \tag{A-22}$$

Under market exchange we set $N_{\mathrm{int}} = N$ into this expression. Under dyadic exchange $N_{\mathrm{int}} = 2$, there are two interacting individuals, say i and j, whereby the price can be simplified to

$$\hat{p} = \frac{\alpha}{1-\alpha} \frac{q^{\mathrm{y}}(\tau_i, \hat{h}_i(\hat{p})) + q^{\mathrm{y}}(\tau_j, \hat{h}_j(\hat{p}))}{q^{\mathrm{x}}(\tau_i, \hat{h}_i(\hat{p})) + q^{\mathrm{x}}(\tau_j, \hat{h}_j(\hat{p}))}. \tag{A-23}$$

These expressions for the equilibrium price $\hat{p}$ are only implicit, since $\hat{p}$ appears on both sides. To solve for the price, we substitute eq. (A-17) along eqs. (1) for each player into eq. (A-22) (or eq. (A-23)) and solve the resulting equation numerically for $\hat{p}$. Note that when the time allocation is fixed, the price is directly given by the explicit expressions in eq. (A-22) and eq. (A-23). We later show in Appendix B.2.2 that this is also the case under market exchange in a monomorphic population. The above method allows us to determine the equilibrium price, which we next show to be unique.

Uniqueness of equilibrium price We now demonstrate that eq. (A-22) has a unique solution. To do so, we first reformulate eq. (A-22) as a root-finding problem, by defining the function $f(\hat{p})$ for $\hat{p} \in [0, \infty)$ such that solving eq. (A-22) is equivalent to solving $f(\hat{p}) = 0$, which yields

$$f(\hat{p}) = \frac{\alpha}{1-\alpha} \frac{\sum_{i=1}^{N_{\mathrm{int}}} q^{\mathrm{y}}(\tau_i, \hat{h}_i(\hat{p}))}{\sum_{i=1}^{N_{\mathrm{int}}} q^{\mathrm{x}}(\tau_i, \hat{h}_i(\hat{p}))} - \hat{p}. \tag{A-24}$$

We first assess the monotonicity of $f(\hat{p})$. Differentiating $f(\hat{p})$ with respect to $\hat{p}$ gives

$$\frac{\mathrm{d}f(\hat{p})}{\mathrm{d}\hat{p}} = -1 + \frac{\alpha}{1-\alpha} \sum_{i=1}^{N_{\mathrm{int}}} \frac{1}{q^{\mathrm{x}}(\tau_i, \hat{h}_i(\hat{p}))^2} \cdot \frac{\partial \hat{h}_i(\hat{p})}{\partial \hat{p}} \cdot \left(q^{\mathrm{x}}(\tau_i, \hat{h}_i(\hat{p})) \frac{\partial q^{\mathrm{y}}(\tau_i, \hat{h}_i(\hat{p}))}{\partial \hat{h}_i(\hat{p})} - q^{\mathrm{y}}(\tau_i, \hat{h}_i(\hat{p})) \frac{\partial q^{\mathrm{x}}(\tau_i, \hat{h}_i(\hat{p}))}{\partial \hat{h}_i(\hat{p})} \right). \tag{A-25}$$

Using eqs. (1), the partial derivatives in the brackets satisfy $\frac{\partial q^{\mathrm{y}}(\tau_i, \hat{h}_i(\hat{p}))}{\partial \hat{h}_i(\hat{p})} < 0$, i.e. increasing time allocated to produce good x decreases production of good y, and $\frac{\partial q^{\mathrm{x}}(\tau_i, \hat{h}_i(\hat{p}))}{\partial \hat{h}_i(\hat{p})} > 0$, i.e. increasing time allocated to produce good x increases production of good x. Since these signs imply that the bracketed term is negative over the domain of $\hat{p}$, the entire derivative $\frac{\mathrm{d}f(\hat{p})}{\mathrm{d}\hat{p}}$ is always negative if and only if $\frac{\partial \hat{h}_i(\hat{p})}{\partial \hat{p}} > 0$ for all $\hat{p} \in [0, \infty)$. Using eq. (A-17) shows that this is always true as

$$\frac{\mathrm{d}\hat{h}_i(\hat{p})}{\mathrm{d}\hat{p}} = \frac{\left(\frac{1}{\hat{p}}\frac{r^{\mathrm{y}}(\tau_i)}{r^{\mathrm{x}}(\tau_i)}\right)^{\frac{1}{1-\eta}}}{\hat{p}(1-\eta)\left(1+\left(\frac{1}{\hat{p}}\frac{r^{\mathrm{y}}(\tau_i)}{r^{\mathrm{x}}(\tau_i)}\right)^{\frac{1}{1-\eta}}\right)^2} > 0. \tag{A-26}$$

Thus, $\frac{\mathrm{d}f(\hat{p})}{\mathrm{d}\hat{p}}$ is always negative and the function $f(\hat{p})$ is strictly decreasing.

We then evaluate the sign of the function at the boundaries of its domain. Using the functional forms of $q^{\mathrm{x}}(\tau_i, \hat{h}_i(\hat{p}))$ and $q^{\mathrm{y}}(\tau_i, \hat{h}_i(\hat{p}))$ in eqs. (1), along $\hat{h}_i(\hat{p})$ in eq. (A-17) , we note that as the equilibrium price approaches 0 ($\hat{p} \to 0$), the equilibrium time allocated to produce good x also converges to 0 ($\hat{h}_i(\hat{p}) \to 0$), and thus the production of good x vanishes while the production of good y increases to its maximum.

$$\lim_{\hat{p}\to 0} q^{\mathrm{x}}(\tau_i, \hat{h}_i(\hat{p})) = 0, \quad \lim_{\hat{p}\to 0} q^{\mathrm{y}}(\tau_i, \hat{h}_i(\hat{p})) = r^{\mathrm{y}}(\tau_i), \tag{A-27}$$

while, as the equilibrium price approaches its maximum ($\hat{p} \to \infty$), equilibrium time allocated to produce good x converges to its maximum too ($\hat{h}_i(\hat{p}) \to 1$), and thus the production of good x increases to its maximum while the production of good y vanishes.

$$\lim_{\hat{p}\to \infty} q^{\mathrm{x}}(\tau_i, \hat{h}_i(\hat{p})) = r^{\mathrm{x}}(\tau_i), \quad \lim_{\hat{p}\to \infty} q^{\mathrm{y}}(\tau_i, \hat{h}_i(\hat{p})) = 0. \tag{A-28}$$

Substituting these limits into $f(\hat{p})$ shows that

$$\lim_{\hat{p}\to 0} f(\hat{p}) = \infty, \quad \text{and} \lim_{\hat{p}\to \infty} f(\hat{p}) = -\infty. \tag{A-29}$$

Thus, $f(\hat{p})$ is positive at the lowest bound of $\hat{p}$, and negative at the highest bound of $\hat{p}$. Since $f(\hat{p})$ is strictly decreasing, it follows that there exists a unique root, and thus a unique price satisfying $f(\hat{p}) = 0$.

Appendix A.2.3 Equilibrium consumption and time allocation

With the equilibrium price determined, we now turn to the final step, determining time allocation and the quantities ultimately consumed by individuals. The time allocation at equilibrium is obtained by substituting the equilibrium price satisfying eq. (A-22) into eq. (A-17). For consumption, substituting the equilibrium price into eqs. (A-19)–(A-20) gives the demand functions at the Walrasian price. Since at this price, the market clears (eq. (A-21)), there is no surplus or shortage, and all individuals end up exchanging and consuming precisely the quantities specified by their demand functions (this being an unique property of Walrasian equilibrium). Thus, the quantities consumed at equilibrium for each individual $i \in \{1, 2, \dots, N\}$ are $\hat{c}_i^{\mathrm{x}}(\hat{p})$ and $\hat{c}_i^{\mathrm{y}}(\hat{p})$, which determine the payoff to each individual. This completes the derivation of the behaviour equilibrium and price, which we can now use in the evolutionary analysis, whether the analytics or the individual-based simulations.

Appendix B Evolutionary analysis

Appendix B.1 Adaptive dynamics

To study the evolutionary dynamics of the quantitative trait τ, we make the standard assumptions that the mutation rate is low and that the phenotypic effects of mutations are small. Accordingly, we can describe the long-term evolutionary dynamics of the trait by focusing on the invasion fitness (geometric growth ratio) $W(\tau, \theta)$ of a mutant with trait τ introduced in a population monomorphic for trait θ (e.g. Eshel, 1983; Taylor, 1989; Christiansen, 1991; Eshel et al., 1997; Geritz et al., 1998; Avila and Mullon, 2023). We further assume that invasion fitness is of the form $W(\tau, \theta) = w(\pi(\tau, \theta), R(\theta))$, where w is a monotonically increasing function of payoff $\pi(\tau, \theta)$ and $R(\theta)$ is a one dimensional regulating variable entailing that in a fully monomorphic population the consistency condition $W(\theta, \theta) = w(\pi(\theta, \theta), R(\theta)) = 1$ holds for all $\theta \in \mathbb{R}$. Then, it is sufficient to focus on the payoff $\pi(\tau, \theta)$ of a mutant τ in a resident θ population to characterise the evolutionary dynamics (e.g. McNamara and Leimar, 2020). The direction in which the trait value changes in a population at θ can then be evaluated from the payoff gradient

$$S(\theta) = \left. \frac{\partial \pi(\tau, \theta)}{\partial \tau} \right|_{\tau=\theta} . \tag{A-30}$$

A trait value θ^* satisfying $S(\theta^*) = 0$ will be called a singular trait value and is a candidate evolutionary equilibrium.

The local evolutionary dynamics around a singular points can be characterised by the sign of the three components of the following expression:

$$\left. \frac{\mathrm{d}S(\theta)}{\mathrm{d}\theta} \right|_{\theta=\theta^*} = \left. \frac{\partial^2 \pi(\tau, \theta)}{\partial \tau^2} \right|_{\tau=\theta=\theta^*} + \left. \frac{\partial^2 \pi(\tau, \theta)}{\partial \tau \partial \theta} \right|_{\tau=\theta=\theta^*} , \tag{A-31}$$

which are, respectively, the convergence stability, uninvadability, and synergy coefficients at θ (e.g. Eshel, 1983; Eshel et al., 1997; Geritz et al., 1998). The convergence stability coefficient $\left. \frac{\mathrm{d}S(\theta)}{\mathrm{d}\theta} \right|_{\theta=\theta^*}$ indicates the direction of selection on the trait value when the resident population is in the neighbourhood of the singular point θ^*. A negative coefficient means that a population with a trait higher than the singular point θ^* will evolve towards a smaller value and thus the singular point is an evolutionary attractor (and vice versa for a lower trait value). The uninvadability coefficient $\left. \frac{\partial^2 \pi(\tau, \theta)}{\partial \tau^2} \right|_{\tau=\theta=\theta^*}$ in turn describes what happens when the singular points are reached in the evolutionary process. If the uninvadability coefficient is negative then selection is stabilising and the population remains at the singular point. If the uninvadability coefficient is positive then selection is disruptive. If a singular trait θ^* is both convergence stable and invadable, then it is an evolutionary branching point; namely, an attractor of the evolutionary dynamics that subsequently splits the population into distinct morphs leading to the coexistence of different types in a protected polymorphism (e.g. Eshel et al., 1997; Geritz et al., 1998). Branching points are of particular focus in this paper and it is useful to note from eq. (A-31) that a necessary condition for $\left. \frac{\partial^2 \pi(\tau, \theta)}{\partial \tau^2} \right|_{\tau=\theta=\theta^*} > 0$ and $\left. \frac{\mathrm{d}S(\tau)}{\mathrm{d}\tau} \right|_{\tau=\theta=\theta^*} < 0$ to hold is that the synergy coefficient is negative:

$$\left. \frac{\partial^2 \pi(\tau, \theta)}{\partial \tau \partial \theta} \right|_{\tau=\theta=\theta^*} < 0. \tag{A-32}$$

A negative expression implies that individuals achieve higher payoffs when interacting with partners possessing different traits rather than similar ones, thereby favouring the coexistence of different morphs.

Note that the focus on mutant payoff in a resident population to characterise selection in the above analysis does not imply that the evolutionary process needs to unfold in a purely monomorphic population. All the above concepts apply to populations with distributions of traits following standard quantitative genetics modelling assumption, whereby the resident trait θ can be always be though of to be the average trait in the population where variation is segregating through the constant influx of mutations (see Mullon and Lehmann, 2019 for more details on these connections between invasion analysis and quantitative genetics).

Appendix B.2 Mutant payoff

We now turn to defining the mutant payoff $\pi(\tau,\theta)$ required for the invasion analysis. Following our definition in section 2.1, the payoff of a mutant with trait τ in a population composed of residents with trait θ is

$$\pi(\tau,\theta) = \left[\hat{c}^{\mathrm{x}}(\tau,\theta)\right]^{\alpha}\left[\hat{c}^{\mathrm{y}}(\tau,\theta)\right]^{1-\alpha}, \tag{A-33}$$

where $\hat{c}^{\mathrm{x}}(\tau,\theta)$ and $\hat{c}^{\mathrm{y}}(\tau,\theta)$ denote the mutant consumption of respectively goods x and y at equilibrium. To get these expressions, we adapt the previously derived expressions in Appendix A as follows, where we denote the equilibrium price that the mutant faces $\hat{p}(\tau,\theta)$, the time allocation of the mutant $\hat{h}(\tau,\hat{p}(\tau,\theta))$ and the time allocation of a resident $\hat{h}(\theta,\hat{p}(\tau,\theta))$.

The equilibrium consumptions of the mutant are obtained by assigning mutant type τ to individual i in eqs. (A-19) and (A-20) while replacing the price p by the equilibrium price faced by the mutant $\hat{p}(\tau,\theta)$ and the time allocation at equilibrium $\hat{h}_i(p)$ by the time allocation at equilibrium of the mutant $\hat{h}(\tau,\hat{p}(\tau,\theta))$. These substitutions yield the expressions in eqs. (7)–(8).

The equilibrium time allocation for mutant and resident for a given price are obtained by respectively assigning type τ and type θ to individual i in eq. (A-17), leading to the expression given in eq. (9).

The equilibrium price under dyadic exchange, $\hat{p}(\tau,\theta)$ is obtained by assigning type τ to individual i and type θ to individual j in eq. (A-23), leading the time allocation $\hat{h}_i(\hat{p})$ and $\hat{h}_j(\hat{p})$ to be rewritten as the time allocation of mutant and resident $\hat{h}(\tau,\hat{p}(\tau,\theta))$ and $\hat{h}(\theta,\hat{p}(\tau,\theta))$. These substitutions yield eq. (10). With market exchange, the mutant τ is assumed to have no effect on equilibrium price (since population is large). The price at equilibrium is then obtained by assigning type θ to all individuals in (A-22) with $N_{\mathrm{int}} = N$, which simplifies to eq. (11) of the main text.

Appendix B.2.1 Validity of the monomorphic approximation for the equilibrium price with market exchange

In the case of market exchange, the equilibrium price obtained depends only on the monomorphic population, which may seem counterintuitive since no exchange should take place if all individuals produce the same amount. However, recall that our evolutionary model can be interpreted in a quantitative genetics way such that there is always some variance in trait values in the population owing to the constant influx of mutations (recall the last paragraph of Appendix B.1). The price obtained in the monomorphic population is then an approximation of the price in a population where individuals exhibit variation in trait values. To demonstrate the validity of this approximation, we show that taking it in account does not affect the equilibrium price, which still converges to the same value as long as the population is large enough and the variance in the unimodal trait distribution remains sufficiently small, both of which hold in our model.

Let us now assume, for this section only, that the population trait follows some unimodal distribution with mean trait value θ and small variance σ_z^2. First, by the law of large numbers, and because the population is very large ($N \to \infty$), the price in eq. (A-22) can be rewritten as

$$\hat{p} = \frac{\alpha}{(1-\alpha)} \cdot \left(\frac{N \cdot \mathbb{E}[q^{\mathrm{y}}(\tau_i, \hat{h}(\tau_i, \hat{p}))]}{N \cdot \mathbb{E}[q^{\mathrm{x}}(\tau_i, \hat{h}(\tau_i, \hat{p}))]} \right), \tag{A-34}$$

where the numerator and denominator represent expectations over the quantities produced and where we have used $\hat{h}_i(\hat{p}) = \hat{h}(\tau_i, \hat{p})$ to make the trait dependence of individual i explicit. Second, if a random variable X has a small variance, then we can approximate the expectation of a function by the function of the expectation $\mathbb{E}[q^k(\tau_i, \hat{h}(\tau_i, \hat{p}))] \approx q^k(\mathbb{E}[\tau_i], \hat{h}(\mathbb{E}[\tau_i], \hat{p}))$. Furthermore, by definition, we have $\mathbb{E}[\tau_i] = \theta$. Applying this approximation, eq. (A-34) can be rewritten as

$$\hat{p} = \hat{p}(\theta) \approx \frac{\alpha}{1-\alpha} \cdot \frac{q^{\mathrm{y}}(\theta, \hat{h}(\theta, \hat{p}(\theta))}{q^{\mathrm{x}}(\theta, \hat{h}(\theta, \hat{p}(\theta))}, \tag{A-35}$$

where $\hat{h}(\theta, \hat{p}(\theta))$ is the equilibrium time allocation of a resident individual. The last equation is equal to the equilibrium price in the mutant resident approximation when exchange takes place through a market in eq. (11). This shows that even if individuals exhibit small variations in their traits, the monomorphic approximation remains valid, as the price still converges to the same equilibrium value.

Appendix B.2.2 Explicit expression of equilibrium price in a monomorphic resident population with market exchange.

The equilibrium price in a mutant-resident population is explicitly defined by eqs. (10)–(11) when time allocation is fixed. However, when time allocation is a decision, these expressions become implicit because the price appears on both sides of the equation, requiring a numerical solution. While the equilibrium price under dyadic exchange can only be determined numerically, we show that for market exchange, a fully analytical expression for the price, and thus the equilibrium time allocations can be derived. This allows for evolutionary analysis to be conducted without the need for numerical computations.

In a mutant-resident population, the price at equilibrium is given from eq. (11)

$$\hat{p}(\theta) = \frac{\alpha}{1-\alpha} \frac{q^{\mathrm{y}}(\theta, \hat{h}(\theta, \hat{p}(\theta)))}{q^{\mathrm{x}}(\theta, \hat{h}(\theta, \hat{p}(\theta)))}, \tag{A-36}$$

where $\hat{h}(\theta, \hat{p}(\theta))$ is the time allocation at equilibrium of a resident individual with trait θ facing an equilibrium price $\hat{p}(\theta)$. Substituting the functional forms of the quantities produced from eqs. (1) into the last equation yields

$$\hat{p}(\theta) = \frac{\alpha}{1-\alpha} \frac{[1-\hat{h}(\theta, \hat{p}(\theta))]^{\eta}}{\hat{h}(\theta, \hat{p}(\theta))^{\eta}} \frac{r^{\mathrm{y}}(\theta)}{r^{\mathrm{x}}(\theta)}, \tag{A-37}$$

Substituting this last equation into the equation defining the equilibrium time allocation—where we adopt the formulation from eq. (A-13) for ease of derivation— and simplifying notation by writing $\hat{h}(\theta, \hat{p}(\theta)) = \hat{h}(\theta)$, gives

$$\left(\frac{\hat{h}(\theta)}{1-\hat{h}(\theta)}\right)^{\eta-1} = \frac{1-\alpha}{\alpha} \frac{\hat{h}(\theta)^{\eta}}{[1-\hat{h}(\theta)]^{\eta}} \frac{r^{\mathrm{x}}(\theta)}{r^{\mathrm{y}}(\theta)} \frac{r^{\mathrm{y}}(\theta)}{r^{\mathrm{x}}(\theta)} \tag{A-38}$$

$$\iff \left(\frac{\hat{h}(\theta)}{1-\hat{h}(\theta)}\right)^{\eta-1} = \frac{1-\alpha}{\alpha} \frac{\hat{h}(\theta)^{\eta}}{[1-\hat{h}(\theta)]^{\eta}} \tag{A-39}$$

$$\iff \left(\frac{\hat{h}(\theta)}{1-\hat{h}(\theta)}\right)^{\eta-1} = \frac{1-\alpha}{\alpha} \left(\frac{\hat{h}(\theta)}{1-\hat{h}(\theta)}\right)^{\eta} \tag{A-40}$$

$$\iff \left(\frac{\hat{h}(\theta)}{1-\hat{h}(\theta)}\right)^{-1} = \frac{1-\alpha}{\alpha} \tag{A-41}$$

$$\iff \frac{1-\hat{h}(\theta)}{\hat{h}(\theta)} = \frac{1-\alpha}{\alpha}, \tag{A-42}$$

which gives

$$\hat{h}(\theta, \hat{p}(\theta)) = \alpha. \tag{A-43}$$

Hence, resident individuals allocate a proportion α of their time to produce good x. Substituting back the time allocation into eq. (A-37), the price simplifies to

$$\hat{p}(\theta) = \left(\frac{\alpha}{1-\alpha}\right)^{1-\eta} \frac{r^{\mathrm{y}}(\theta)}{r^{\mathrm{x}}(\theta)}. \tag{A-44}$$

Substituting this price into eq. (9), the equilibrium time allocated to produce good x of a mutant is

$$\hat{h}(\tau, \hat{p}(\tau, \theta)) = \frac{1}{1 + \frac{1-\alpha}{\alpha}\left[\frac{r^{\mathrm{x}}(\theta)}{r^{\mathrm{y}}(\theta)} \frac{r^{\mathrm{y}}(\tau)}{r^{\mathrm{x}}(\tau)}\right]^{\frac{1}{1-\eta}}} \tag{A-45}$$

If we finally substitute the equilibrium price from eq. (A-44) and the time allocation from eq. (A-45) into the mutant payoff in eq. (6), it yields an explicit expression, which is used to conduct the invasion analysis

Appendix B.3 Evolutionary analysis with fixed time allocation

Appendix B.3.1 Autarky

We first carry out the evolutionary analysis under autarky (main text Section 3.1). Substituting the mutant payoff in eq. (12) into eq. (A-30), the payoff gradient for this case is

$$S(\theta) = \left.\frac{\partial \pi(\tau, \theta)}{\partial \tau}\right|_{\tau=\theta} = q^{\mathrm{x}}(\theta)^{(\alpha-1)} q^{\mathrm{y}}(\theta)^{-\alpha} \left[\alpha q^{\mathrm{y}}(\theta) \left.\frac{\partial q^{\mathrm{x}}(\tau)}{\partial \tau}\right|_{\tau=\theta} + (1-\alpha) q^{\mathrm{x}}(\theta) \left.\frac{\partial q^{\mathrm{y}}(\tau)}{\partial \tau}\right|_{\tau=\theta}\right]. \tag{A-46}$$

The terms in square brackets describe the sum of the gain or loss in the production of each good due to a change in the value of the trait, weighted by how much each good contributes to the payoff. When the population trait lies between the two optimal values of production, the derivatives have opposite signs since a different value of the trait increases the production of one good but reduces the production of the other good. The sign of the payoff gradient will be equal to the sign of one of the derivatives, meaning that selection will push the population to increase the production of one good at the expense of the other. Which good would be favoured depends on how much a change in the trait translates to a change in the production of goods, how important the good is for the payoff and in particular, the quantity of the other good that the individual consumes. As consuming a larger quantity of one good increases the benefit of producing the other good, this ultimately favours generalists who can produce both goods.

Setting $S(\theta) = 0$ and rearranging shows that a singular point θ^* must satisfy

$$\left.\frac{\frac{\partial q^{\mathrm{y}}(\tau)}{\partial \tau}/q^{\mathrm{y}}(\tau)}{\frac{\partial q^{\mathrm{x}}(\tau)}{\partial \tau}/q^{\mathrm{x}}(\tau)}\right|_{\tau=\theta=\theta^*} = -\frac{\alpha}{1-\alpha}. \tag{A-47}$$

Hence, at a singular point, the relative gain of production in one good is proportional (equal for $\alpha = 0.5$) to the relative loss in production of the other good. Substituting eqs. (1)–(2) into eq. (A-47) and solving for θ^* yields eq. (13).

Using the payoff gradient payoff along eqs. (1)–(2), we obtain

$$\left.\frac{\mathrm{d}S(\theta)}{\mathrm{d}\theta}\right|_{\theta=\theta^*} = -\frac{2\left(\exp\left(-\frac{(o_{\mathrm{x}}-o_{\mathrm{y}})^2(1-\alpha)^2}{\sigma^2}\right)\right)^{\alpha}\left(\exp\left(-\frac{(o_{\mathrm{x}}-o_{\mathrm{y}})^2\alpha^2}{\sigma^2}\right)\right)^{(1-\alpha)}}{\sigma^2} < 0. \tag{A-48}$$

This expression is always negative, and thus the singular point is convergent stable. Using the mutant payoff in eq. (12) along eqs. (1)–(2), we obtain the uninvadability coefficient

$$\left.\frac{\partial^2 \pi(\tau,\theta)}{\partial \tau^2}\right|_{\tau=\theta=\theta^*} = -\frac{2\left(\exp\left(-\frac{(o_{\mathrm{x}}-o_{\mathrm{y}})^2(1-\alpha)^2}{\sigma^2}\right)\right)^{\alpha}\left(\exp\left(-\frac{(o_{\mathrm{x}}-o_{\mathrm{y}})^2\alpha^2}{\sigma^2}\right)\right)^{(1-\alpha)}}{\sigma^2} < 0. \tag{A-49}$$

This expression is equal to the convergence coefficient and is always negative. The singular point is thus evolutionary stable.

Appendix B.3.2 Dyadic exchange

We now turn to the evolutionary analysis for the case of dyadic exchange (results of section 3.2). The mutant payoff in this section is the one defined in eq. (6) with price in eq. (10). Substituting it into eq. (A-30) but keeping the price in its symbolic form, the payoff gradient is

$$\begin{aligned} S(\theta) = \left.\frac{\partial \pi(\tau,\theta)}{\partial \tau}\right|_{\tau=\theta} =& \Big((1-\alpha)(\hat{p}(\theta,\theta)q^{\mathrm{x}}(\theta) + q^{\mathrm{y}}(\theta))\Big)^{-\alpha}\left(\alpha\left(q^{\mathrm{x}}(\theta) + q^{\mathrm{y}}(\theta)\frac{1}{\hat{p}(\theta,\theta)}\right)\right)^{\alpha} \\ & (1-\alpha)\left(\left.\frac{\partial q^{\mathrm{x}}(\tau)}{\partial \tau}\right|_{\tau=\theta}\hat{p}(\theta,\theta) + \left.\frac{\partial q^{\mathrm{y}}(\tau)}{\partial \tau}\right|_{\tau=\theta}\right. \\ & \left. - \left.\frac{\partial \hat{p}(\tau,\theta)}{\partial \tau}\right|_{\tau=\theta}\left(\alpha q^{\mathrm{y}}(\theta)\frac{1}{\hat{p}(\theta,\theta)} - (1-\alpha)q^{\mathrm{x}}(\theta)\right)\right). \end{aligned} \tag{A-50}$$

The last part of the expression can be rewritten using the definition of the quantity consumed of good x in eq. (A-19)

$$\begin{aligned} S(\theta) = \left.\frac{\partial \pi(\tau,\theta)}{\partial \tau}\right|_{\tau=\theta} =& \Big((1-\alpha)(\hat{p}(\theta,\theta)q^{\mathrm{x}}(\theta) + q^{\mathrm{y}}(\theta))\Big)^{-\alpha}\left(\alpha\left(q^{\mathrm{x}}(\theta) + q^{\mathrm{y}}(\theta)\frac{1}{\hat{p}(\theta,\theta)}\right)\right)^{\alpha} \\ & (1-\alpha)\left(\left.\frac{\partial q^{\mathrm{x}}(\tau)}{\partial \tau}\right|_{\tau=\theta}\hat{p}(\theta,\theta) + \left.\frac{\partial q^{\mathrm{y}}(\tau)}{\partial \tau}\right|_{\tau=\theta}\right. \\ & \left. - \left.\frac{\partial \hat{p}(\tau,\theta)}{\partial \tau}\right|_{\tau=\theta}(\hat{c}^{\mathrm{x}}(\theta) - q^{\mathrm{x}}(\theta))\right). \end{aligned} \tag{A-51}$$

The part of the expression in the first line does not influence the sign of the payoff gradient. The rest of the expression can be decomposed in two parts. A change in the trait has again a direct cost and benefit by changing the quantities of goods produced. Here, the importance of a loss or gain in production of a good is captured by its price. Second, a change in the trait also has an indirect cost or benefit, described on the third line, as changing the quantities produced also modifies the price of goods. An increase in the price of good x is costly if the mutant is a net buyer of the good x, i.e. $(\hat{c}^{\mathrm{x}}(\theta) - q^{\mathrm{x}}(\theta)) > 0$ but beneficial if it is a net seller $(\hat{c}^{\mathrm{x}}(\theta) - q^{\mathrm{x}}(\theta)) < 0$.

Substituting the equilibrium price from eq. (10), evaluated in a resident population into eq. (A-51), the term in the third line vanishes

$$
\begin{aligned}
-\left.\frac{\partial \hat{p}(\tau,\theta)}{\partial \tau}\right|_{\tau=\theta}\left(\alpha q^{\mathrm{y}}(\theta)\frac{1}{\hat{p}(\theta,\theta)} - (1-\alpha)q^{\mathrm{x}}(\theta)\right) &= -\left.\frac{\partial \hat{p}(\tau,\theta)}{\partial \tau}\right|_{\tau=\theta}\left(\alpha q^{\mathrm{y}}(\theta)\left[\frac{(1-\alpha)}{\alpha}\frac{2q^{\mathrm{x}}(\theta)}{2q^{\mathrm{y}}(\theta)}\right] - (1-\alpha)q^{\mathrm{x}}(\theta)\right) && \text{(A-52)}\\
&= -\left.\frac{\partial \hat{p}(\tau,\theta)}{\partial \tau}\right|_{\tau=\theta}\Big((1-\alpha)q^{\mathrm{x}}(\theta) - (1-\alpha)q^{\mathrm{x}}(\theta)\Big) && \text{(A-53)}\\
&= 0, && \text{(A-54)}
\end{aligned}
$$

and the remaining expression is

$$
\begin{aligned}
S(\theta) = \left.\frac{\partial \pi(\tau,\theta)}{\partial \tau}\right|_{\tau=\theta} &= \left((1-\alpha)\left(\left[\frac{\alpha}{1-\alpha}\frac{2q^{\mathrm{y}}(\theta)}{2q^{\mathrm{x}}(\theta)}\right]q^{\mathrm{x}}(\theta) + q^{\mathrm{y}}(\theta)\right)\right)^{-\alpha}\left(\alpha\left(q^{\mathrm{x}}(\theta) + q^{\mathrm{y}}(\theta)\left[\frac{1-\alpha}{\alpha}\frac{2q^{\mathrm{x}}(\theta)}{2q^{\mathrm{y}}(\theta)}\right]\right)\right)^{\alpha} && \text{(A-55)}\\
&\quad (1-\alpha)\left(\left.\frac{\partial q^{\mathrm{x}}(\tau)}{\partial \tau}\right|_{\tau=\theta}\left[\frac{\alpha}{1-\alpha}\frac{2q^{\mathrm{y}}(\theta)}{2q^{\mathrm{x}}(\theta)}\right] + \left.\frac{\partial q^{\mathrm{y}}(\tau)}{\partial \tau}\right|_{\tau=\theta}\right).
\end{aligned}
$$

This simplifies as

$$
\begin{aligned}
S(\theta) = \left.\frac{\partial \pi(\tau,\theta)}{\partial \tau}\right|_{\tau=\theta} &= \Big(\alpha q^{\mathrm{y}}(\theta) + (1-\alpha)q^{\mathrm{y}}(\theta)\Big)^{-\alpha}\Big(\alpha q^{\mathrm{x}}(\theta) + (1-\alpha)q^{\mathrm{x}}(\theta)\Big)^{\alpha} && \text{(A-56)}\\
&\quad \left(\alpha\frac{q^{\mathrm{y}}(\theta)}{q^{\mathrm{x}}(\theta)}\left.\frac{\partial q^{\mathrm{x}}(\tau)}{\partial \tau}\right|_{\tau=\theta} + (1-\alpha)\left.\frac{\partial q^{\mathrm{y}}(\tau)}{\partial \tau}\right|_{\tau=\theta}\right)\\
&= q^{\mathrm{y}}(\theta)^{-\alpha}q^{\mathrm{x}}(\theta)^{\alpha}\left(\alpha\frac{q^{\mathrm{y}}(\theta)}{q^{\mathrm{x}}(\theta)}\left.\frac{\partial q^{\mathrm{x}}(\tau)}{\partial \tau}\right|_{\tau=\theta} + (1-\alpha)\left.\frac{\partial q^{\mathrm{y}}(\tau)}{\partial \tau}\right|_{\tau=\theta}\right). && \text{(A-57)}
\end{aligned}
$$

Factoring $1/q^{\mathrm{x}}(\theta)$ from inside the parentheses out gives

$$
\begin{aligned}
S(\theta) = \left.\frac{\partial \pi(\tau,\theta)}{\partial \tau}\right|_{\tau=\theta} &= q^{\mathrm{y}}(\theta)^{-\alpha}q^{\mathrm{x}}(\theta)^{\alpha}\left(\alpha\frac{q^{\mathrm{y}}(\theta)}{q^{\mathrm{x}}(\theta)}\left.\frac{\partial q^{\mathrm{x}}(\tau)}{\partial \tau}\right|_{\tau=\theta} + (1-\alpha)\frac{q^{\mathrm{x}}(\theta)}{q^{\mathrm{x}}(\theta)}\left.\frac{\partial q^{\mathrm{y}}(\tau)}{\partial \tau}\right|_{\tau=\theta}\right) && \text{(A-58)}\\
&= q^{\mathrm{y}}(\theta)^{-\alpha}\frac{q^{\mathrm{x}}(\theta)^{\alpha}}{q^{\mathrm{x}}(\theta)}\left(\alpha q^{\mathrm{y}}(\theta)\left.\frac{\partial q^{\mathrm{x}}(\tau)}{\partial \tau}\right|_{\tau=\theta} + (1-\alpha)q^{\mathrm{x}}(\theta)\left.\frac{\partial q^{\mathrm{y}}(\tau)}{\partial \tau}\right|_{\tau=\theta}\right) && \text{(A-59)}\\
&= q^{\mathrm{x}}(\theta)^{(\alpha-1)}q^{\mathrm{y}}(\theta)^{-\alpha}\left(\alpha q^{\mathrm{y}}(\theta)\left.\frac{\partial q^{\mathrm{x}}(\tau)}{\partial \tau}\right|_{\tau=\theta} + (1-\alpha)q^{\mathrm{x}}(\theta)\left.\frac{\partial q^{\mathrm{y}}(\tau)}{\partial \tau}\right|_{\tau=\theta}\right), && \text{(A-60)}
\end{aligned}
$$

where the last line is equivalent to eq. (A-46), the payoff gradient without exchange.

This simplification can be intuitively understood by observing that in the approximation of a monomorphic population, individuals produce the same quantities and thus do not exchange with each other. Note that considering that all individuals have the same trait is an approximation of a model where residents do exhibit minimal, yet present, variation among themselves. What our analysis shows is that even in a population where individuals have different production abilities, and within which exchange occurs, exchange has no effect on selective pressures if the variance in the traits is small.

Because the payoff gradient with dyadic exchange is equal to the one in autarky, it follows that the singular point, which is the root of the payoff gradient, and the convergence coefficient $\left.\frac{\mathrm{d}S(\theta)}{\mathrm{d}\theta}\right|_{\theta=\theta^*}$ remain the same than in autarky, described respectively in eq. (13) and eq. (A-48).

The synergy coefficient is given in the main text in eq. (14). Using the mutant payoff, we obtain the uninvadability coefficient

$$\left.\frac{\partial^2\pi(\tau,\theta)}{\partial\tau^2}\right|_{\tau=\theta=\theta^*} = q^{\mathrm{x}}(\theta^*)^{(-1+\alpha)}q^{\mathrm{y}}(\theta^*)^{-\alpha}\Bigg[\left.\left(\alpha q^{\mathrm{y}}(\tau)\frac{\partial^2 q^{\mathrm{x}}(\tau)}{\partial\tau^2}+(1-\alpha)q^{\mathrm{x}}(\tau)\frac{\partial^2 q^{\mathrm{y}}(\tau)}{\partial\tau^2}\right)\right|_{\tau=\theta=\theta^*} - \frac{3}{4}\left.\left(\frac{\alpha}{1-\alpha}\frac{q^{\mathrm{y}}(\tau)}{q^{\mathrm{x}}(\tau)}\left(\frac{\partial q^{\mathrm{x}}(\tau)}{\partial\tau}\right)^2\right)\right|_{\tau=\theta=\theta^*}\Bigg]. \tag{A-61}$$

The expression can be rewritten by substituting one of the partial derivatives in the expression $\left(\frac{\partial q^{\mathrm{x}}(\tau)}{\partial\tau}\right)^2$ with its explicit form obtained from the condition that holds at a singular point, given in eq. (A-47).

$$\left.\frac{\partial^2\pi(\tau,\theta)}{\partial\tau^2}\right|_{\tau=\theta=\theta^*} = q^{\mathrm{x}}(\theta^*)^{(-1+\alpha)}q^{\mathrm{y}}(\theta^*)^{-\alpha}\Bigg[\left.\left(\alpha q^{\mathrm{y}}(\tau)\frac{\partial^2 q^{\mathrm{x}}(\tau)}{\partial\tau^2}+(1-\alpha)q^{\mathrm{x}}(\tau)\frac{\partial^2 q^{\mathrm{y}}(\tau)}{\partial\tau^2}\right)\right|_{\tau=\theta=\theta^*} + \frac{3}{4}\left.\left(\frac{\partial q^{\mathrm{y}}(\tau)}{\partial\tau}\frac{\partial q^{\mathrm{x}}(\tau)}{\partial\tau}\right)\right|_{\tau=\theta=\theta^*}\Bigg]. \tag{A-62}$$

Identifying when this expression is positive and rearranging the terms yields the condition stated in the main text in eq. (15).

Appendix B.3.3 Market exchange

We here describe to the evolutionary analysis for the case of market exchange (results of section 3.3). In this case, the mutant payoff is the one described in eq. (6) with the price at equilibrium in eq. (11). Substituting it into eq. (A-30), the payoff gradient is

$$S(\theta) = \left.\frac{\partial\pi(\tau,\theta)}{\partial\tau}\right|_{\tau=\theta} = q^{\mathrm{x}}(\theta)^{(\alpha-1)}q^{\mathrm{y}}(\theta)^{-\alpha}\left(\alpha q^{\mathrm{y}}(\theta)\left.\frac{\partial q^{\mathrm{x}}(\tau)}{\partial\tau}\right|_{\tau=\theta}+(1-\alpha)q^{\mathrm{x}}(\theta)\left.\frac{\partial q^{\mathrm{y}}(\tau)}{\partial\tau}\right|_{\tau=\theta}\right), \tag{A-63}$$

which is again equal to the one without exchange in eq. (A-46). Because the payoff gradient with market exchange is equal to the one in autarky, it follows that the singular point, which is the root of the payoff gradient, and the convergence coefficient $\left.\frac{\mathrm{d}S(\theta)}{\mathrm{d}\theta}\right|_{\theta=\theta^*}$ remain the same as described respectively in eq. (13) and eq. (A-48). Thus, there is a single convergent stable singular point.

Using the mutant payoff, we obtain the synergy coefficient

$$\left.\frac{\partial^2\pi(\tau,\theta)}{\partial\tau\partial\theta}\right|_{\tau=\theta=\theta^*} = -q^{\mathrm{x}}(\theta^*)^{(-2+\alpha)}q^{\mathrm{y}}(\theta^*)^{(1-\alpha)}\frac{\alpha}{(1-\alpha)}\left(\left.\frac{\partial q^{\mathrm{x}}(\tau)}{\partial\tau}\right|_{\tau=\theta=\theta^*}\right)^2 < 0. \tag{A-64}$$

This expression is always negative and there is always negative frequency dependent selection at the singular point. Finally, using the mutant payoff, we obtain the uninvadability coefficient.

$$\left.\frac{\partial^2\pi(\tau,\theta)}{\partial\tau^2}\right|_{\tau=\theta=\theta^*} = q^{\mathrm{x}}(\theta^*)^{(-1+\alpha)}q^{\mathrm{y}}(\theta^*)^{-\alpha}\left.\left(\alpha q^{\mathrm{y}}(\tau)\frac{\partial^2 q^{\mathrm{x}}(\tau)}{\partial\tau^2}+(1-\alpha)q^{\mathrm{x}}(\tau)\frac{\partial^2 q^{\mathrm{y}}(\tau)}{\partial\tau^2}\right)\right|_{\tau=\theta=\theta^*}. \tag{A-65}$$

Identifying when this expression is positive and rearranging the terms yields the condition stated in the main text in eq.(17).

Appendix B.4 Evolutionary analysis with time allocation decision

Appendix B.4.1 Autarky

We now turn to the evolutionary analysis when time allocation is a decision variable (results of section 4). In autarky, the mutant payoff in eq. (6) simplifies to $\pi(\tau,\theta) = [q^{\mathrm{x}}(\tau,\hat{h}(\tau,\theta))]^{\alpha}[q^{\mathrm{y}}(\tau,\hat{h}(\tau,\theta))]^{1-\alpha}$ where we showed in Appendix A.1 that $\hat{h}(\tau,\theta)=\alpha$. The payoff gradient derived from this expression yields

$$S(\theta) = \left.\frac{\partial\pi(\tau,\theta)}{\partial\tau}\right|_{\tau=\theta} = \frac{2\exp\left(-\frac{\alpha(o_{\mathrm{x}}-\theta)^2+(1-\alpha)(o_{\mathrm{y}}-\theta)^2}{\sigma^2}\right)\cdot(1-\alpha)^{(1-\alpha)\eta}\cdot\alpha^{\alpha\eta}\cdot(\alpha o_{\mathrm{x}}+(1-\alpha)o_{\mathrm{y}}-\theta)}{\sigma^2}. \tag{A-66}$$

Setting this payoff gradient to zero, and solving it at $\theta=\theta^*$, yields the singular point

$$\theta^* = \alpha o_{\mathrm{x}} + (1-\alpha)o_{\mathrm{y}}. \tag{A-67}$$

This singular point is equal to 0 for the parameters specified in the main text $\alpha = 0.5$, $o_{\mathrm{x}} = -2$ and $o_{\mathrm{y}} = 2$.

Using the payoff gradient, we obtain

$$\left.\frac{\mathrm{d}S(\theta)}{\mathrm{d}\theta}\right|_{\theta=\theta^*} = -\frac{2\left(\exp\left(-\frac{(o_{\mathrm{x}}-o_{\mathrm{y}})^2(1-\alpha)^2}{\sigma^2}\right)\alpha^{\eta}\right)^{\alpha}\left(\exp\left(-\frac{(o_{\mathrm{x}}-o_{\mathrm{y}})^2\alpha^2}{\sigma^2}\right)(1-\alpha)^{\eta}\right)^{(1-\alpha)}}{\sigma^2} < 0. \tag{A-68}$$

This expression is always negative, and thus the singular point is convergent stable. Using the mutant payoff, we obtain the uninvadability coefficient

$$\left.\frac{\partial^2\pi(\tau,\theta)}{\partial\tau^2}\right|_{\tau=\theta=\theta^*} = -\frac{2\left(\exp\left(-\frac{(o_{\mathrm{x}}-o_{\mathrm{y}})^2(1-\alpha)^2}{\sigma^2}\right)\alpha^{\eta}\right)^{\alpha}\left(\exp\left(-\frac{(o_{\mathrm{x}}-o_{\mathrm{y}})^2\alpha^2}{\sigma^2}\right)(1-\alpha)^{\eta}\right)^{(1-\alpha)}}{\sigma^2} < 0. \tag{A-69}$$

The uninvadability coefficient is again equal to the convergence stability coefficient (as we found in the corresponding model with fixed time allocation). The population is thus expected to remain at the singular point, which is evolutionary stable.

Appendix B.4.2 Dyadic exchange

For the case of dyadic exchange, as the price needs to be found numerically, the evolutionary analysis is carried out in the accompanying Mathematica notebook.

Appendix B.4.3 Market exchange

We now turn to the evolutionary analysis for the case of market exchange (results of section 4). Substituting the mutant payoff in eq. (6) with the price at equilibrium in eq. (A-44) and the time allocation in eq. (A-45) into eq. (A-30) gives the payoff gradient.

$$S(\theta) = \left.\frac{\partial\pi(\tau,\theta)}{\partial\tau}\right|_{\tau=\theta} = \frac{2\exp-\left(\frac{\alpha(o_{\mathrm{x}}-\theta)^2+(1-\alpha)(o_{\mathrm{y}}-\theta)^2}{\sigma^2}\right)\cdot(1-\alpha)^{(1-\alpha)\eta}\cdot\alpha^{\alpha\eta}\cdot(\alpha o_{\mathrm{x}}+(1-\alpha)o_{\mathrm{y}}-\theta)}{\sigma^2}, \tag{A-70}$$

which is equal to the one without exchange in eq. (A-66). Because the payoff gradient with market exchange is equal to the one in autarky, it follows that the singular point, which is the root of the payoff gradient, and the convergence coefficient $\left.\frac{\mathrm{d}S(\theta)}{\mathrm{d}\theta}\right|_{\theta=\theta^*}$ remain the same as described respectively in eq. (A-67) and eq. (A-68). Thus, there is a single convergent stable singular point.

Using the mutant payoff, we obtain the synergy coefficient

$$\left.\frac{\partial^2\pi(\tau,\theta)}{\partial\tau\partial\theta}\right|_{\tau=\theta=\theta^*} = -\frac{4\exp\left(-\frac{(o_\mathrm{x}-o_\mathrm{y})^2(1-\alpha)^2}{\sigma^2}\right)^{\alpha}\exp\left(-\frac{(o_\mathrm{x}-o_\mathrm{y})^2\alpha^2}{\sigma^2}(1-\alpha)^{\eta}\right)^{1-\alpha}(o_\mathrm{x}-o_\mathrm{y})^2(1-\alpha)\alpha^{1+\alpha\eta}}{(1-\eta)\sigma^4}. \tag{A-71}$$

This expression is always negative and there is always negative frequency dependent selection at the singular point.

Using the mutant payoff, we obtain the uninvadability coefficient.

$$\left.\frac{\partial^2\pi(\tau,\theta)}{\partial\tau^2}\right|_{\tau=\theta=\theta^*} = \frac{2\left(\exp(-\frac{(o_\mathrm{x}-o_\mathrm{y})^2\alpha^2}{\sigma^2}(1-\alpha)^{\eta}\right)^{1-\alpha}\left(\exp(-\frac{(o_\mathrm{x}-o_\mathrm{y})^2(1-\alpha)^2}{\sigma^2}\alpha^{\eta}\right)^{\alpha}\left[2(o_\mathrm{x}-o_\mathrm{y})^2(1-\alpha)\alpha-(1-\eta)\sigma^2\right]}{(1-\eta)\sigma^4}, \tag{A-72}$$

which is positive if the expression in the square brackets is positive. Rearranging this expression yields the condition given in the main text in eq. (19)

Substituting the parameters used in the main text $\alpha = 0.5$, $o_\mathrm{x} = -2$ and $o_\mathrm{y} = 2$, into eq. (19), we obtain the condition for polymorphism to emerge used to generate the left panel of figure 4

$$\sigma^2 < \frac{8}{1-\eta}. \tag{A-73}$$

Appendix B.5 Simulations

We used individual-based stochastic simulations to confirm our analytical results and further explore long term evolution. These simulations describe the evolution of a haploid population of fixed and even size N. Each individual $i \in \{1, ..., N\}$ is characterised by its trait τ_i. The initial population is a monomorphic population where all individuals have a trait of the same value. The life cycle of individuals consists of discrete and non-overlapping generations as described in section 2.1, where the following occurs: (i) individuals are randomly paired with each other; (ii) time allocations are set (detailed below) (iii) individuals produce a quantity of each good as described in equation (1); (iii) individuals exchange quantities of goods and end up with quantities described in eqs. (A-19)–(A-18); (iv) individuals reproduce following a Wright-Fisher process (see eq. (A-74) below) during which mutations occur; and (v) adults of the previous generation perish. We repeat the procedure for a fixed number of generations.

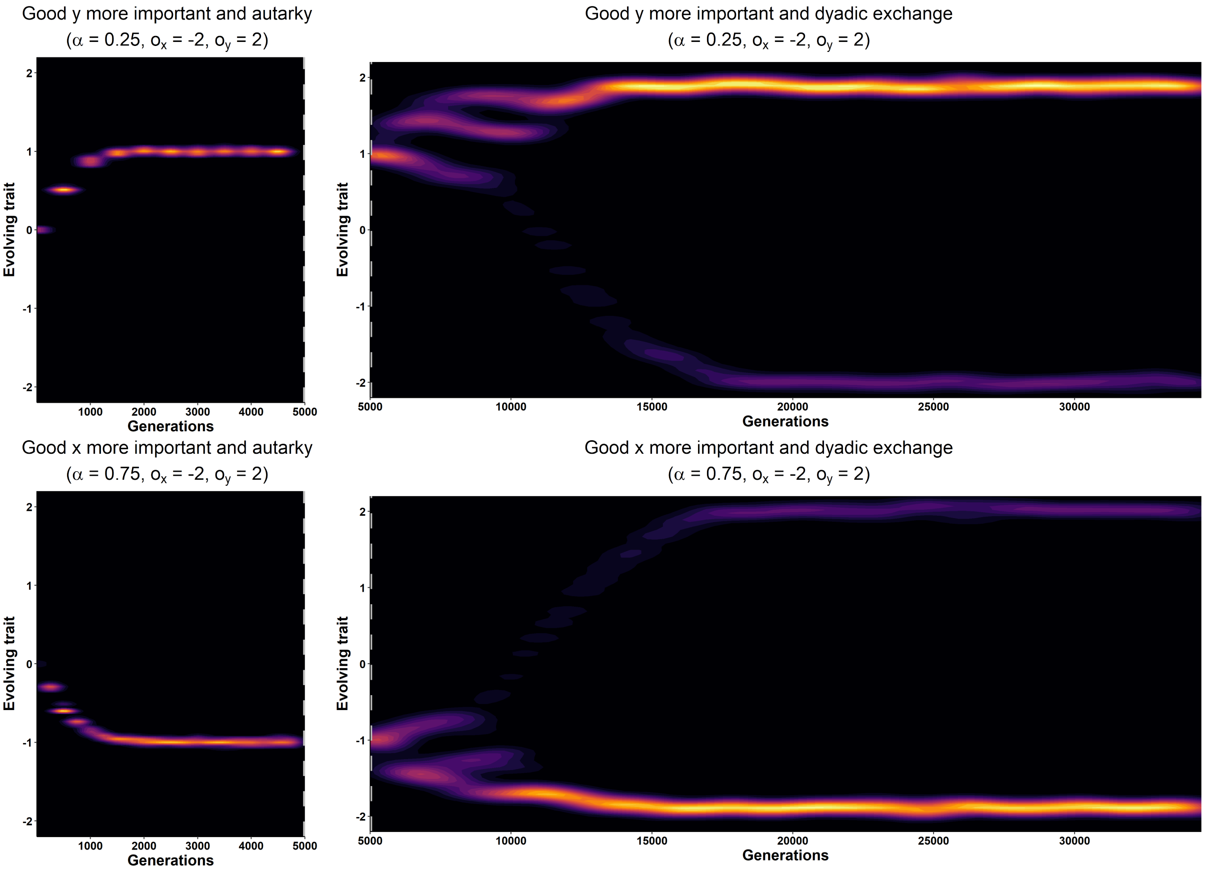
Time allocation. In the version of the model where time allocation is fixed, the time allocation is automatically set to 0.5 for all individuals during step (ii). In the second version of the model where individuals choose their time allocation, the time allocation is given by eq.(A-17), where the price is found by solving eq. (A-22) numerically.

Reproduction. During the reproduction stage, a new population of the same size N is created by sampling randomly with replacement in the parent population according to their payoff. The probability that an individual i with payoff π_i is the parent of an offspring is

$$\frac{\pi_i}{\sum_{j=1}^{N}\pi_j}. \tag{A-74}$$

Mutation For each newborn, mutation occurs with probability μ_{m}. When a mutation occurs, a random value is sampled from a Normal distribution centered on the parent's trait value, with variance σ_{m}^2.

Supplementary Figures



Good y more important and autarky (α = 0.25, o_x = -2, o_y = 2)

Good y more important and dyadic exchange (α = 0.25, o_x = -2, o_y = 2)

Good x more important and autarky (α = 0.75, o_x = -2, o_y = 2)

Good x more important and dyadic exchange (α = 0.75, o_x = -2, o_y = 2)

Figure S1. Evolution of the distribution of trait over generations when goods have different importance and for fixed time allocation. The top panel represents a scenario where good y is more important than good x ($\alpha = 0.25$), while the bottom panel represents the opposite case, where good x is more important than good y ($\alpha = 0.75$). The population remains in autarky for the first 5000 generations, after which exchange is introduced (indicated by the grey dotted line). We consider dyadic exchange where exchange takes place between pairs of isolated individuals. For better visualization of the density distributions, the plots are split into two phases: the autarky period and the period with dyadic exchange. The parameters used are production breadth $\sigma^2 = 1$, optima of production of each good $o_{\mathrm{x}} = -2$ and $o_{\mathrm{y}} = 2$, population size $N = 5000$, mutation rate $\mu_{\mathrm{m}} = 0.01$ and variance of mutations $\sigma_{\mathrm{m}}^2 = 0.0004$.

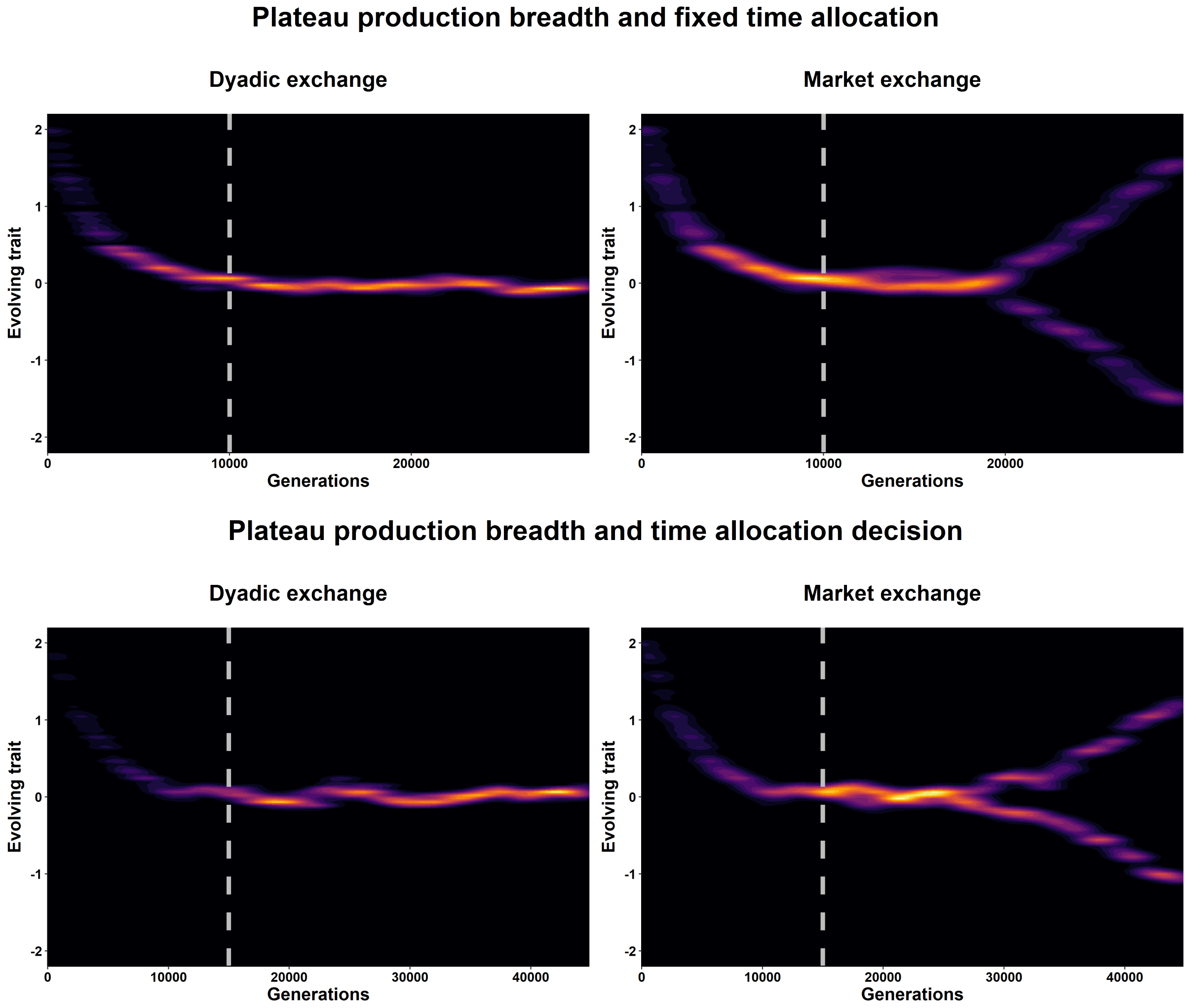


Figure S2. Evolution of the distribution of the trait over generations under two exchange regimes: dyadic exchange, where trade occurs between isolated pairs of individuals, and market exchange, where all individuals interact through a common market. The goal is to illustrate how market exchange creates conditions more conducive to the emergence of polymorphism than dyadic exchange. To highlight this effect, we select high values of production breadth for which our theoretical results predict the emergence of polymorphism under market exchange but not under dyadic exchange: specifically, $\sigma^2 = 5$ for dyadic exchange and $\sigma^2 = 10$ for market exchange. Exchange is initially absent and is introduced only after 10000 or 15000 generations (indicated by the grey dotted line). The parameters used are optima of production of each good $o_{\mathrm{x}} = -2$ and $o_{\mathrm{y}} = 2$, population size $N = 1000$, mutation rate $\mu_{\mathrm{m}} = 0.01$ and variance of mutations $\sigma_{\mathrm{m}}^2 = 0.0004$.

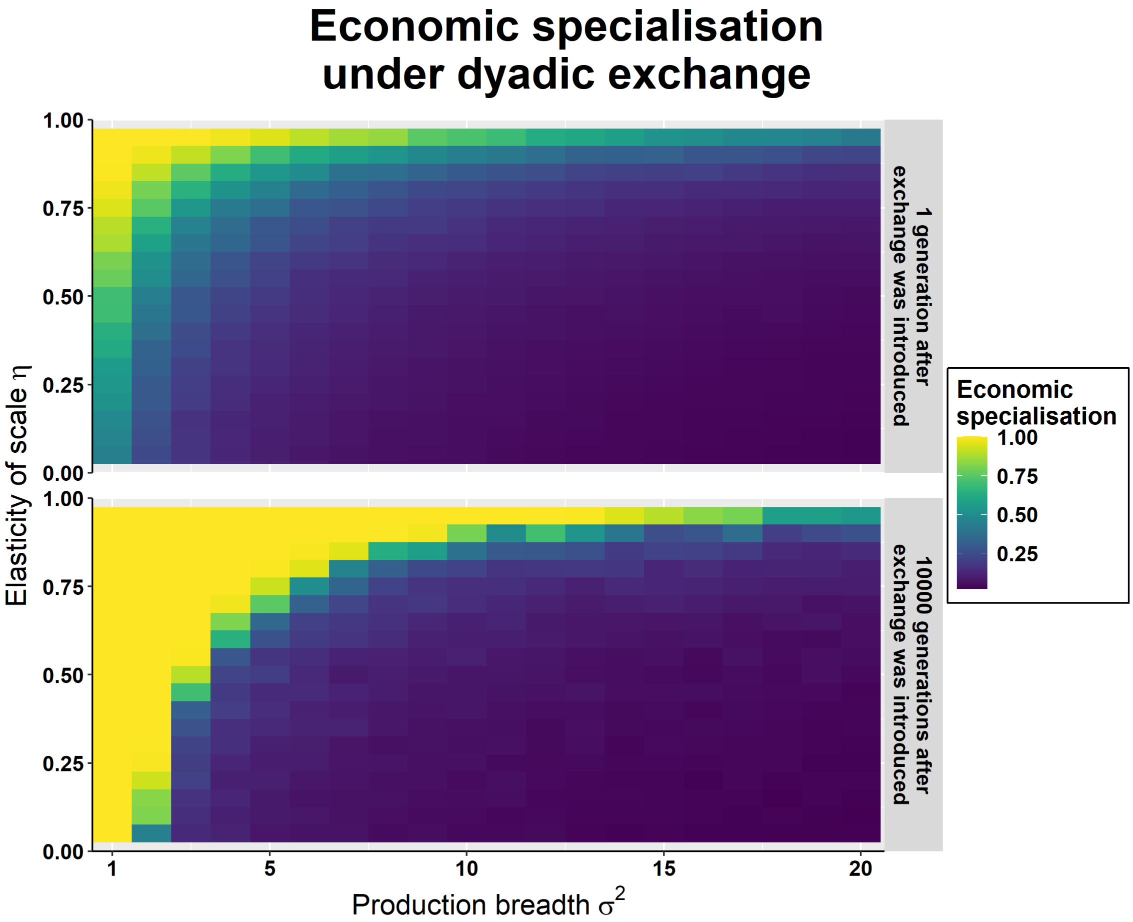


Figure S3. Effect of emergence of exchange on economic specialisation as a function of production breadth σ^2 and elasticity of scale η. The panels show average economic specialisation across 10 replicates and after 1 generation (top) and after 10,000 generations (bottom) following the introduction of exchange. Specialisation is measured as the difference between the highest and lowest values of h in the population. We consider dyadic exchange where exchange takes place between pairs of isolated individuals. The parameters used are equal importance of goods $\alpha = 0.5$, optima of production $o_{\mathrm{x}} = -2$ and $o_{\mathrm{y}} = 2$, population size $N = 1000$, mutation rate $\mu_{\mathrm{m}} = 0.01$, variance of mutations $\sigma_{\mathrm{m}}^2 = 0.0004$, and the initial population is drawn from a Normal distribution centered on the singular point with small variance 0.0025.

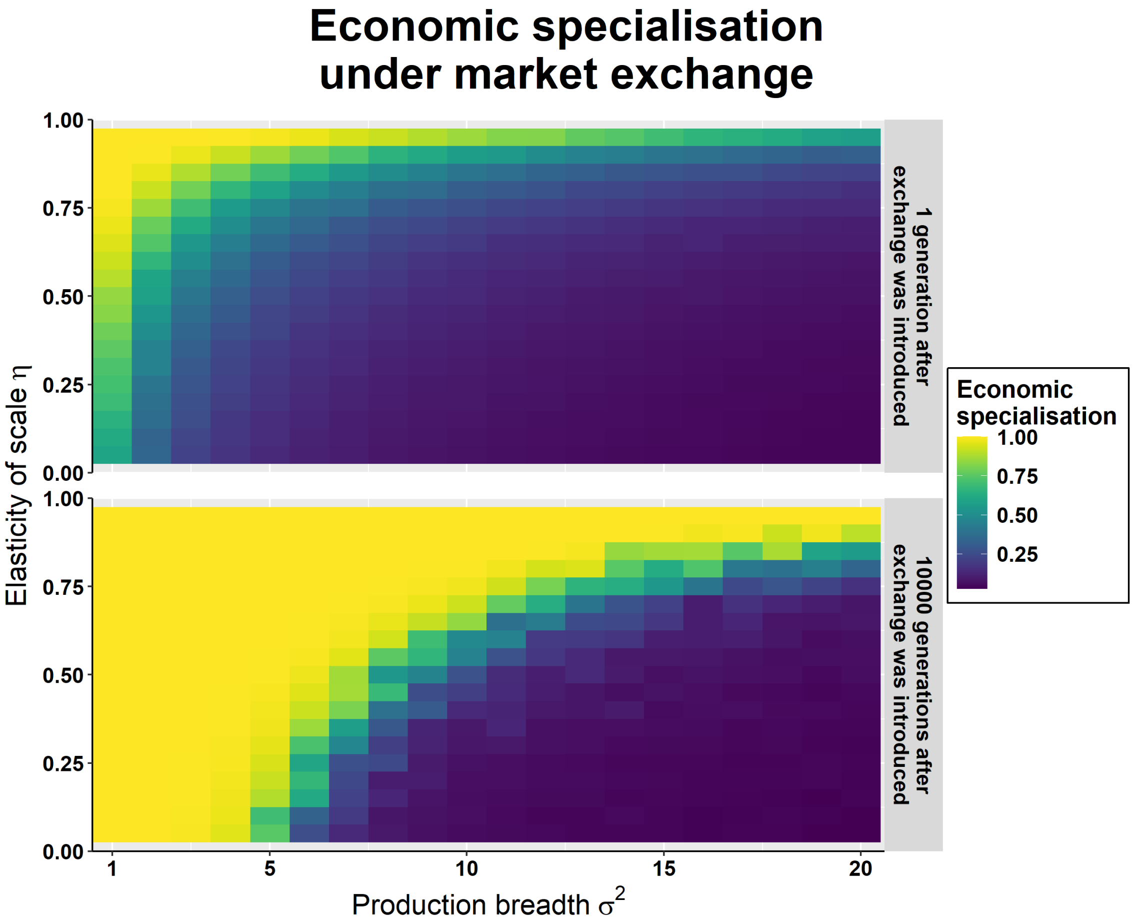


Figure S4. Effect of emergence of exchange on economic specialisation as a function of production breadth σ^2 and elasticity of scale η. The panels show average economic specialisation across 10 replicates and after 1 generation (top) and after 10,000 generations (bottom) following the introduction of exchange. Specialisation is measured as the difference between the highest and lowest values of h in the population. We consider market exchange where exchange takes place between all individuals. The parameters used are equal importance of goods $\alpha = 0.5$, optima of production $o_{\mathrm{x}} = -2$ and $o_{\mathrm{y}} = 2$, population size $N = 1000$, mutation rate $\mu_{\mathrm{m}} = 0.01$, variance of mutations $\sigma_{\mathrm{m}}^2 = 0.0004$, and the initial population is drawn from a Normal distribution centered on the singular point with small variance 0.0025.

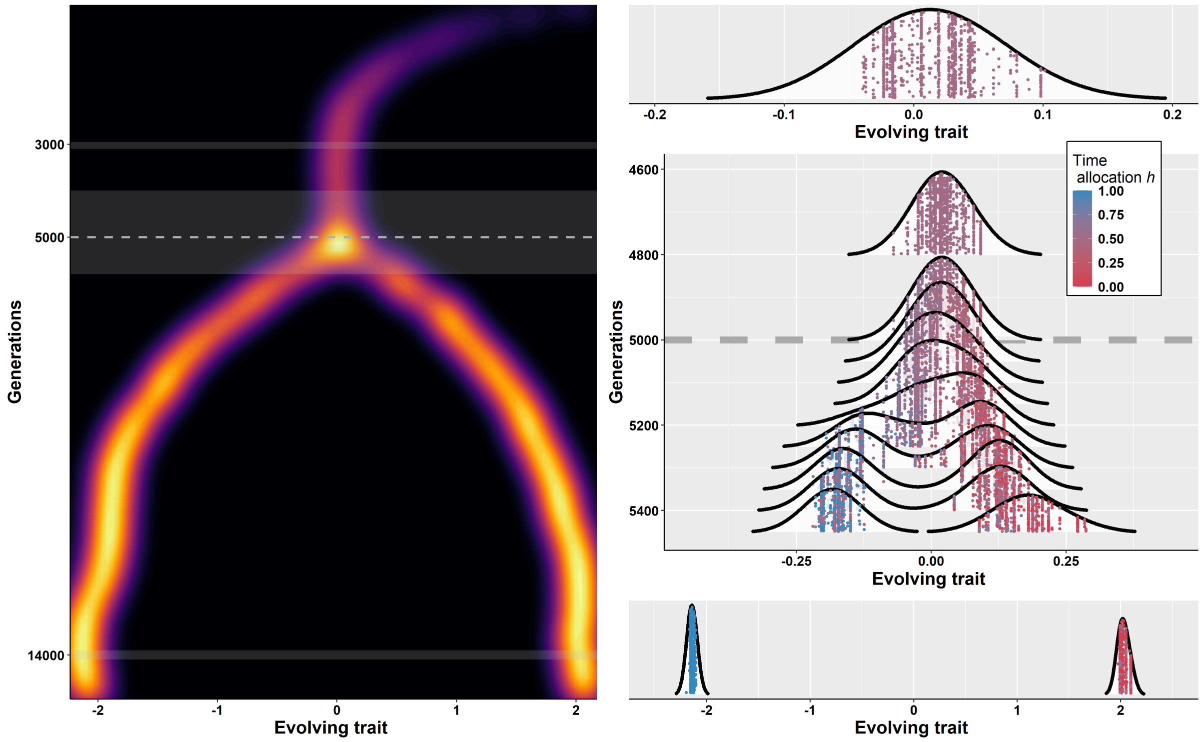


Figure S5. Evolution of genetic diversity and economic specialisation. (Left) Evolution of trait over generations. The population remains in autarky for the first 5000 generations, after which exchange is introduced (indicated by the grey dotted line). We consider dyadic exchange where exchange takes place between pairs of isolated individuals. (Right) Distribution of trait (x-axis) and time allocation (colour). Each point represents a single individual. The plot is divided in three-part, each focusing on a particular time period, (top) at 3000 generations when exchange is absent, (middle) at 5000 generations when exchange is introduced and (bottom) at 14000 generations to show the long-run outcome. The parameters used are elasticity of scale $\eta = 0.5$, production breadth $\sigma^2 = 1$, equal importance of goods $\alpha = 0.5$, optima of production $o_\mathrm{x} = -2$ and $o_\mathrm{y} = 2$, population size $N = 1000$, mutation rate $\mu_\mathrm{m} = 0.01$ and variance of mutations $\sigma_\mathrm{m}^2 = 0.0004$.