Growth or reproduction: emergence of an evolutionary optimal strategy

J Grilli, S Suweis and A Maritan

Dipartimento di Fisica e Astronomia ‘G Galilei’, Università di Padova, CNISM and INFN, via Marzolo 8, I-35131 Padova, Italy
E-mail: jgrilli@pd.infn.it, suweis@pd.infn.it and amos.maritan@pd.infn.it

Received 4 September 2013
Accepted 24 September 2013
Published 24 October 2013

Online at stacks.iop.org/JSTAT/2013/P10020
doi:10.1088/1742-5468/2013/10/P10020

Abstract. Modern ecology has re-emphasized the need for a quantitative understanding of the original ‘survival of the fittest theme’ based on analysis of the intricate trade-offs between competing evolutionary strategies that characterize the evolution of life. This is key to the understanding of species coexistence and ecosystem diversity under the omnipresent constraint of limited resources. In this work we propose an agent-based model replicating a community of interacting individuals, e.g. plants in a forest, where all are competing for the same finite amount of resources and each competitor is characterized by a specific growth–reproduction strategy. We show that such an evolution dynamics drives the system towards a stationary state characterized by an emergent optimal strategy, which in turn depends on the amount of available resources the ecosystem can rely on. We find that the share of resources used by individuals is power-law distributed with an exponent directly related to the optimal strategy. The model can be further generalized to devise optimal strategies in social and economical interacting systems dynamics.

Keywords: models for evolution (theory), interacting agent models, stochastic processes

ArXiv ePrint: 1306.5877
1. Introduction

Living systems evolve and adapt to survive in an evolutionary tussle. One of the main driving forces of natural selection [1, 2] is the competition for resources that regulates survival, growth and reproduction rates. The game of life is orchestrated through an optimization program that releases energy through offspring production while simultaneously trying to conserve it through an evolutionary feedback mechanism. Growth is the key ingredient to succeed in competition with other individuals, while reproduction promotes colonization through offspring, thereby avoiding extinction.

Both empirical and theoretical evidence suggest that a trade-off across species between competition and colonization ability [3]–[6] promotes coexistence: the good competitors are typically bad colonizers, whereas the good colonizers are bad competitors. The essential idea here is borrowed from a well known ecological theory, the r/K selection theory [7, 8]. This theory states that in ecosystems with access to large (infinite) resources, the long-time dynamics approaches a stable equilibrium with higher growth and lower reproduction rates for the interacting agents (K-strategy). In contrast, in unstable environments with scarce resources, the individuals procreate more, but have smaller biomasses (r-strategy). The impact of trade-offs in competition strategies on biodiversity maintenance has also been investigated in more recent theoretical models, known as trade-off models [9, 10]. Both stochastic individual-based models [9, 11] and resource competition models in the Lotka–Volterra form [12, 6] have shown that the inclusion of the trade-off traits positively affects the maintenance of species diversity within single and multi-trophic ecological communities. Even in the deterministic limit, excluding all dynamic stochasticity, optimal and evolutionary stable trade-offs have been quantified for a structured rotifer population preying on a dynamically varying food supply [13].

The present paper will focus on an optimal trade-off between growth (through competition) and reproduction (through colonization) while simultaneously incorporating all inherent stochastic fluctuations due to natural birth, death and growth.
2. Definition of the model

The model is defined as a birth–death–growth stochastic process in the continuous time limit. It consists of a community of agents competing for a finite amount of resources \( R \). Each agent uses a fraction of resources \( R \) at any given time, e.g., at time \( t \) the \( i \)th individual uses an amount of resources \( \epsilon_i(t) \) such that \( \sum \epsilon_i(t) = R \). In our analysis, we assume \( R \) to be a constant parameter, while the number of individuals in the community \( N(t) \) varies during the process and, at stationarity, fluctuates around its time-averaged value.

The population of the community remains unchanged until one of the \( N(t) \) individuals dies. Death events occur with a rate \( dN(t) \), given that each individual has a constant death rate \( d \), independent of its history, resource usage or age. The \( k \)th individual, which is uniformly drawn from the pool of the \( N(t) \) individuals, dies and \( \epsilon^* := \epsilon_k(t) \) resources are instantly shared by the rest of individuals in the community. Individuals use those resources to grow or to have progeny. Each individual is characterized by a balance between these two processes, which is quantified in terms of a parameter \( p_i \). With probability \( p_i \) (or \( 1 - p_i \)) the \( i \)th individual uses the available energy to produce offspring, i.e., new individuals in the system, or to grow. This complementarity reflects the facts that both growth and reproduction require energy allocation, and the individuals have to find a balance between the two tasks.

We implement the above growth/birth process in the following way. When an individual dies it frees a quantity of resources \( \epsilon^* \). The rest of the community is divided into two disjoint subsets, \( B \) and \( G \): the \( i \)th individual has a probability \( p_i \) (or \( 1 - p_i \)) to belong to the set \( B \) (or \( G \)), that is, it chooses the move birth (growth). The quantity of freed resources that the \( i \)th individual manages to use is proportional to its own energy \( \epsilon_i \). This choice is solely decided by the following fact: the bigger an individual is, the more resources it will consume in order to survive. Furthermore, this hypothesis is consistent with the von Bertalanffy equation of ontogenetic growth [14]–[16]. If we define \( E_b = \sum_{i \in B} \epsilon_i \) (\( E_g = \sum_{i \in G} \epsilon_i \)) as the sum of the energies of the individuals that have chosen the move birth (growth) then the total energy allocated for the births is \( \epsilon^* E_b / (E_g + E_b) \), where the relation \( E_g + E_b = R - \epsilon^* \) holds.

Each new generated individual uses a fixed amount of resources \( \epsilon^{(0)} > 0 \). This parameter defines the minimal biomass of an individual. Given this ‘minimal energy’ \( \epsilon^{(0)} \), the number \( n_b \) of new individuals added to the system is given by the largest integer less than \( (\epsilon^*/\epsilon^{(0)})E_b/(E_g + E_b) \), i.e. \( n_b = \lfloor (\epsilon^*/\epsilon^{(0)})E_b/(E_g + E_b) \rfloor \), where \( \lfloor \cdot \rfloor \) indicates the floor function. The \( p_i \) values of these new individuals are inherited from their parents: for each of the \( n_b \) progenies, the \( i \)th individual belonging to the subset \( B \) has probability \( \epsilon_i / E_b \) to transmit its \( p_i \). Individuals belonging to the subset \( G \) grow by exploiting the remaining energy \( \epsilon_g := \epsilon^* - n_b \epsilon^{(0)} \) (i.e., energy not used for procreation). Therefore, the energy of the \( i \)th individual belonging to \( G \) changes as \( \epsilon_i \rightarrow \epsilon_i (1 + \epsilon_g / \epsilon_g) \).

The dynamics defined above conserves the total resource \( R \) of the ecosystem, but does not conserve the total number of individuals in the community. If the fluctuations of the total population \( N \) drive the system to the state \( N = 0 \), then the dynamics stops. If the system reaches the \( N = 0 \) state, we initialize the system to a new configuration with \( R/\epsilon^{(0)} \) individuals (of energy \( \epsilon^{(0)} \)). This choice may be interpreted as immigration of outside species in the community. The proposed community dynamics also has 'non-
Growth or reproduction: emergence of an evolutionary optimal strategy

Figure 1. Relation between average number of individuals \( \langle N \rangle \), total available resources \( R \) and growth/reproduction strategy \( p \) under the proposed ecosystem dynamics modeling. Numerical simulations (points of different colors/shapes) show a linear relation of the form \( \langle N \rangle = bpR/\epsilon(0) \), with \( b = 0.64 \pm 0.02 \). The simulations were performed with \( \epsilon(0) = 1 \) and averages were performed over 100 realizations. Lines represent the analytical mean-field prediction \( \langle N \rangle = (2/3)pR/\epsilon(0) \) obtained in section 3.2, where the proportionality constant is predicted to be \( b = 2/3 \).

trivial’ absorbing states. These are related to the strategy \( p \): if all the individuals share the same strategy \( p \) there is no way to introduce a new individual with a different \( p \) in the ecosystem. Therefore the stationary state of the ecosystem dynamics will be characterized by one final strategy \( p \) and not by a mixture of heterogeneous \( p_i \). From a theoretical point of view the number of these possible absorbing states is infinite (one for each value of \( p \)).

3. Fixed \( p \)

3.1. Numerical simulations

The simulations of the community dynamics are performed using Gillespie’s algorithm. The system is initialized at time \( t = 0 \) with \( N(0) = R \) individuals having the same energy usage \( (\epsilon(0) = 1) \) and the same value of \( p \). The structure of the community depends on \( R \) and \( p \). The main goal of the simulations is to study this dependence.

Suppose that at time \( t \) there are \( N(t) \) individuals in the ecosystems and that a death event occurs at time \( \tau > t \). Each individual has a constant death rate \( d \), and therefore \( \tau \) is a random variable with exponential distribution and average \( 1/dN(t) \). At time \( \tau \), we randomly remove an agent that frees its resource \( \epsilon^* \). The remaining individuals identically compete to gain their shares of the released resources.

The number of individuals, \( N(t) \), is a random variable, whose average at stationarity depends on both \( R \) and \( p \). Numerical simulations, shown in figure 1, indicate that \( \langle N \rangle = bpR \) with \( b = 0.64 \pm 0.02 \), which is compatible with our analytical estimate \( b = 2/3 \) given in section 3.2.

The community is characterized in terms of the distribution of resource usage among individuals as measured by \( n(\epsilon | p, R) \, d\epsilon \), the average number of individuals in the energy interval \( (\epsilon, \epsilon + d\epsilon) \) when all the individuals share the same value of \( p \). Figure 2(A)
Figure 2. Power-law behavior of $n(\epsilon|p,R)$. Panel (A) shows the cumulative distribution of resource usage, i.e. the average fraction of individuals using at least an amount $\epsilon$ of resources, $P(\epsilon > \epsilon) = \int_0^\infty n(x|p,R) \, dx / \int_0^\infty n(x|p,R) \, dx$, for $R = 10^5$ and different values of $p$. It turns out to be a truncated power-law, with an exponent $-\alpha(p) + 1$. Panel (B) shows the collapse of distributions obtained for different values of $R$ at fixed $p = 0.2$. We plot $\epsilon^{\alpha(p)-1} P(x > \epsilon)$ versus $\epsilon/R$, where $\alpha(p) = 2.16$ and for different values of $R$. The collapse is consistent with our finite-size scaling hypothesis, i.e. $n(\epsilon|p,R) = \epsilon^{-\alpha(p)} f(\epsilon/R)$. The inset shows $P(x > \epsilon)$ for different values of $R$. Notice the scale in the vertical axes and in the inset. In both panels $\epsilon(0) = 1$. Averages were performed over 100 realizations.

shows that resources are distributed with a truncated power-law with an exponent $-\alpha(p)$ depending on $p$. As expected, the smaller the value of $p$ is (competition strategy biased favorably), the smaller is the absolute value of the exponent of the distribution.

The cut-off of the distribution of order $R$ suggests that finite-size scaling [17] is a good candidate to describe the behavior of the resource usage in the community. This corresponds to the assumption that $n(\epsilon|p,R) = \epsilon^{\alpha(p)} f(\epsilon/R)$, where $f(x)$ tends to a constant value for small arguments whereas it rapidly approaches zero when the argument increases. If finite-size scaling holds the plot of $\epsilon^{\alpha(p)-1} P(x > \epsilon)$ versus $\epsilon/R$ should give a single data collapsed curve instead of multiple curves for different values of $R$. The quality of the collapse we get (see figure 2(B)) is consistent with the finite-size scaling ansatz.

3.2. Mean-field approximation

In this section, we perform a mean-field approximation in order to derive both the power-law decay and an estimate of the decay exponent as a function of $p$. The time evolution of the energy usage distribution in the mean-field approximation is given by (from now on we shall omit the $p$ and $R$ dependence in $n(\epsilon|p,R)$ in order to simplify the notation)

$$\frac{\partial n(\epsilon,t)}{\partial t} = -dn(\epsilon,t) + d\langle N(t) \rangle \langle n_b \rangle \delta(\epsilon - \epsilon(0))$$

$$+ d\langle N(t) \rangle (1-p) \left[ \frac{1}{D} n \left( \frac{\epsilon}{D}, t \right) - n(\epsilon,t) \right],$$

where

$$\int_0^\infty n(x|p,R) \, dx = 1.$$
where the first term represents the decay of \( n(\epsilon, t) \) due to random death events, the second term takes into account the birth events, which are \( \langle n_b \rangle \) on average, while the third term represents growth. \( \langle N(t) \rangle \) is the total number of individuals (i.e. \( \langle N(t) \rangle = \int d\epsilon \, \epsilon \, n(\epsilon, t) \)) and \( D\epsilon \) is the updated energy usage of all individuals belonging to the growing set which originally had a resource usage equal to \( \epsilon \) with

\[
D = 1 + \frac{\langle \epsilon^* - \langle n_b \rangle \epsilon(0) \rangle}{(1 - p)(R - \langle \epsilon^* \rangle)}.
\]

From equations (1) and (2) one has

\[
D(\epsilon^*) = 1 + \epsilon_g/E_g = 1 + \langle (\epsilon^* - \langle n_b \rangle \epsilon(0))/E_g \rangle \approx 1 + (\langle \epsilon^* \rangle - \langle n_b \rangle \epsilon(0))/E_g, \tag{3}
\]

where \( E_g = (1 - p)(R - \langle \epsilon^* \rangle) \). The amount of freed resources at time \( t \) depends on the probability that an individual with a resource usage \( \epsilon^* \) dies. Since the individual chosen to die is randomly selected, we have \( \langle \epsilon^* \rangle = \int d\epsilon \, \epsilon \, n(\epsilon, t) \epsilon/N \approx R/\langle N \rangle \).

At stationarity \( n(\epsilon, t) = n(\epsilon) \) and, therefore,

\[
\frac{\partial n(\epsilon)}{\partial \epsilon} = \frac{2 - b}{1 - b} n(\epsilon) + \frac{b}{1 - b \epsilon(0)} R \delta(\epsilon - \epsilon(0)),
\]

where

\[
b = \langle n_b \rangle \epsilon(0)/R,
\]

where we assumed that \( \langle \epsilon^* \rangle/R \sim 0 \), i.e. \( |D - 1| \sim 0 \), which allows us to expand \( n(\epsilon/D, t) \) in equation (1) in order to get (3). The solution of this equation for \( \epsilon > \epsilon(0) \) is the power-law

\[
n(\epsilon) = \frac{1}{\epsilon(0)} \frac{b}{1 - b \epsilon(0)} \frac{R}{\epsilon(0)} (\epsilon/\epsilon(0))^{-\alpha} \Theta(\epsilon - \epsilon(0)), \quad \alpha = \frac{2 - b}{1 - b}.
\]

This solution is consistent since \( \int d\epsilon \, \epsilon \, n(\epsilon) \epsilon = R \) without having to explicitly impose it, whereas \( \langle N \rangle = \int d\epsilon \, \epsilon \, n(\epsilon) = Rb/\epsilon(0) \), implying that \( b = \epsilon(0)/\langle N \rangle/R \) and so \( \langle n_b \rangle = 1 \). Since \( \langle n_b \rangle \) is the average number of births per dead individual, at stationarity \( \langle n_b \rangle = 1 \) assures a community of constant average size. On the other hand the average value of \( n_b \) can be explicitly written as

\[
\langle n_b \rangle = \int d\epsilon^* \langle n(\epsilon^*) \rangle \frac{p \epsilon^*}{\epsilon(0)} \frac{R}{\epsilon - \epsilon^*} \approx \int d\epsilon^* \, \epsilon \, n(\epsilon^*) \frac{p \epsilon^*}{\epsilon(0)} \frac{R}{\epsilon - \epsilon^*} \]

\[
= \frac{1}{\langle N \rangle} \epsilon(0) \frac{p}{\epsilon(0)} \sum_{i=1}^{\infty} \frac{i}{p} \int_{i/p}^{(i+1)/p} d\epsilon \, n(\epsilon^*). \tag{6}
\]

If we simply remove the floor function from the above expression we would obtain \( b(p) = p \). In order to get a better approximation we estimate the series in equation (6) by evaluating the total resource, \( R \), as follows

\[
R = \int d\epsilon \, \epsilon \, n(\epsilon) \epsilon \approx \sum_{i=1}^{\infty} \left( i + \frac{1}{2} \right) \epsilon(0) \frac{p}{i/p} \int_{i/p}^{(i+1)/p} d\epsilon \, n(\epsilon) \]

\[
= \sum_{i=1}^{\infty} \left( i + \frac{1}{2} \right) \epsilon(0) \frac{p}{i/p} \int_{i/p}^{(i+1)/p} d\epsilon \, n(\epsilon) \]

where we have used the ‘mid-point prescription’ to approximate the first term in the integrand, \( \epsilon \), in the interval \( (i\epsilon(0)/p, (i + 1)\epsilon(0)/p) \). Using the previous two equations and the definition of \( \langle N \rangle \), we get \( R = \langle N \rangle \epsilon(0)(\langle n_b \rangle + 1/2)/p = 3\langle N \rangle \epsilon(0)/(2p) \) which leads to \( b = 2p/3 \). Therefore we predict the exponent of the power-law distribution to be equal to \( (6 - 2p)/(3 - 2p) \). Figure 3 shows the analytical prediction of the exponent versus

doi:10.1088/1742-5468/2013/10/P10020

6
Figure 3. Comparison between the exponent $\alpha(p)$ obtained by fitting simulation data with a power-law (black dots) and our analytical prediction $\alpha = (6 - 2p)/(3 - 2p)$ (purple curve) based on the mean-field approximation.

the results of numerical simulation. Apart from a mismatch for very small values of $p$ the agreement is quite satisfactory. This mismatch is due to the fact that the smaller the value of $p$ is, the bigger is $\langle \epsilon^* \rangle \approx R/\langle N \rangle = 3\epsilon^{(0)}/2p$, which we assumed to be very small with respect to $R$. Moreover, when $p$ is small, the integration interval in equation (6) is wide, and the ‘mid-point prescription’ becomes less accurate. The mid-point prescription used in equation (6) fails if $p > 1 - 1/N$ and a better approximation is obtained by removing the floor function.

4. Evolutionary strategy: optimal $p$ as a function of the resources

The next step is to investigate the fate of an inhomogeneous system with randomly drawn $p$s for the individuals in the community. As already observed, the system reaches a state with a unique value of $p$. However, given that the dynamics is stochastic the selected final $p$ is not unique even in the case of the system starting from the same initial state. Figure 4(A) shows the distribution of the final values of $p$, $P^{(1)}(p)$ when we initialize the system with $N_0$ individuals each with an energy usage $\epsilon^{(0)}$ ($R = N_0\epsilon^{(0)}$), and a uniform distribution of $p$s, $P^{(0)}(p)$, between 0 and 1. Quite interestingly $P^{(1)}(p)$ is not uniform as the initial distribution, $P^{(0)}(p)$, but rather it is peaked around a certain value, $p^*(R)$ that depends on $R$. Indeed, the center of the distribution gives the optimal $p^*(R)$ value. In fact, by drawing the initial values of $p$ from $P^{(1)}(p)$, we obtain a narrower distribution, $P^{(2)}(p)$ (see figure 4(B)), and for each iteration the distribution becomes narrower and centered around $p^*(R)$. In the limit of $S \to \infty$ steps, $P^{(S)}(p)$ converges to a delta function. This result is independent of the initial distribution we choose as far as it is different from zero at $p^*(R)$. Therefore the optimal strategy $p^*(R)$ is evolutionarily selected by the community dynamics, depending on the ecosystem total resources $R$. If $R$ is small the population sizes are also small, and demographic fluctuations can lead to rapid extinction. In this condition large values of $p$ are selected, favoring procreation with respect to individual growth, and thus promoting the persistence of the ecosystem population. On the other hand, if the available resources are large, demographic fluctuations are less
dangerous and species develop a strategy in order to gain the highest share of the available resources, i.e. they prefer to grow and small \( p \) strategies are favored.

A natural follow-up of the previous analysis is an attempt to understand whether \( p^*(R) \) is an evolutionary stable strategy (ESS). If a population adopts the ESS, it cannot be invaded by a population with another strategy. In the context of stochastic dynamics every strategy can in principle be invaded, even if it is the optimal one, just because of demographic fluctuations. The ESS is thus defined as the strategy whose probability to invade another strategy is always higher than the probability to be invaded. In other words, given two strategies, say \( p^* \) and \( p \), \( p^* \) is the ESS if

\[
P_{\text{fix}}(p^* \rightarrow p | n^{(0)}, m^{(0)}) > P_{\text{fix}}(p \rightarrow p^* | n^{(0)}, m^{(0)}) \quad \forall p \neq p^*,
\]

where, given any two strategies \( p_1 \) and \( p_2 \), \( P_{\text{fix}}(p_1 \rightarrow p_2 | n, m) = \lim_{t \to \infty} P(n > 0, m = 0, t | n = n^{(0)}, m = m^{(0)}, t = 0) \) and \( P(n > 0, m = 0, t | n = n^{(0)}, m = m^{(0)}, t = 0) \) is the probability that starting at \( t = 0 \) with \( n^{(0)} \) individuals with \( p_1 \) and \( m^{(0)} \) individuals with \( p_2 \), at time \( t \) all individuals adopt the \( p_1 \) strategy. The existence of an ESS and its value is independent of the particular choice for \( n^{(0)} \) and \( m^{(0)} \). We set \( n^{(0)} = m^{(0)} \). Figure 5 highlights that \( p^*(R) \) is indeed an evolutionary stable strategy.

5. Discussion and conclusions

Our stochastic birth–death–growth model rationalizes the emergence of an optimal trade-off between growth (competition) and reproduction (colonization) strategies in evolving living systems relying on a finite pool of resources. The dynamical evolution of the system
Figure 5. Probability of extinction and fixation of two competitive strategies. In the initial state there are only two species equally populated, one with a strategy $p_i$ and the other one with a strategy $p_j$. The element in the $i$th row and $j$th column of the plotted matrices represents the probability $P_{\text{fix}}(p_j \rightarrow p_i)$ that the species with $p_i$ becomes extinct whereas the one with $p_j$ spreads through all the system ($i, j = 1, \ldots, 20$). The optimal strategy (ESS) corresponds to the choice of $p$ which has a probability greater than $1/2$ to be fixed against any other possible value of $p$. The value of $p^*(R)$ depends on the quantity of available resources $R$ and is plotted in the inset of figure 4(A).

Our model also predicts a power-law distribution of resources among individuals, and allows us to relate it with the optimal trade-off strategy for the system. Indeed, the exponent of the power-law characterizing the resource distribution depends on the trade-off between growth and reproduction and therefore is directly related to the availability of resources. A power-law emerges because of the ‘rich get richer’ feature of the individuals’ growth, and therefore it is not unexpected since preferential attachment mechanisms are known to produce power-laws. Indeed, scale-free distributions of resources among individuals are found in several different contexts: in social systems the wealth among individuals is usually described by a Pareto distribution [20]. In the context of economy the sizes and incomes of companies follow the Zipf’s power-law [21, 22]; in forest science a power-law distribution of plant height—which correlates with resource usage—has also been recently reported [23]. Interestingly, though, usually these resource distributions show non-universal power-law exponents [24]. For instance distributions of firm sizes have exponents that depend on the firms’ sector types [22] or the distribution of family names has a power-law decay with an exponent varying from 1.83 in the US to about 1 in Korea [24]. Therefore our theoretical framework can be properly generalized to model systems also in these different fields of science and to elucidate the connection between
the exponent of the power-law distributions of resources and the optimal trade-off strategy, which in turn depends on the quantity of available resources.

The proposed model is just the starting point for more complicated dynamics where more complex ingredients may be incorporated. In ecology, space plays an important role, as all individuals compete within a certain area. Therefore the proposed model can be seen as a mean-field version of a spatially explicit model, where the quantity of resources $R$ plays the role of an effective parameter that quantifies the amount of resources and space one individual typically competes for. Similarly, space plays a key role also in sociological and economical systems, where the network determining agents’ specific interactions may display complex topological properties.

Acknowledgments

We thank T Anfodillo, J R Banavar, C Borile, F Simini and L Tamburino for insightful discussions and the Cariparo Foundation for financial support. We are particularly grateful to S M Bhattacharjee and A K Chattopadhyay for a very helpful critical reading of the paper.

References

[1] Darwin C, 1859 On the Origin of Species (New York: The Harvard Classics)
[2] Wilbur H M, Tinkle D W and Collins J P, Environmental certainty, trophic level, and resource availability in life history evolution, 1974 Amer. Nat. 108 885
[3] Kraaijeveld A R, Limentani E C and Godfray H C, Basis of the trade-off between parasitoid resistance and larval competitive ability in Orosphila melanagaster, 2001 Proc. R. Soc. London B 268 259
[4] Novak M, Pfeiffer T, Lenski R E, Sauer U and Bonhoeffer S, Experimental tests for an evolutionary trade-off between growth rate and yield in E. coli, 2006 Amer. Nat. 168 242
[5] Calcagno V, Mouquet N, Jarne P and David P, Coexistence in a metacommunity: the competition–colonization trade-off is not dead, 2006 Ecol. Lett. 9 897
[6] Chesson P and Kuang J J, The interaction between predation and competition, 2008 Nature 456 235
[7] MacArthur R H and Wilson E O, 1967 The Theory of Island Biogeography (Princeton, NJ: Princeton University Press)
[8] Pianka E R, On r- and k-selection, 1970 Amer. Nat. 104 592
[9] Chave J, Muller-Landau H C and Levin S A, Comparing classical community models: theoretical consequences for patterns of diversity, 2002 Amer. Nat. 159 1
[10] Kneitel J M and Chase J M, Trade-offs in community ecology: linking spatial scales and species coexistence, 2004 Ecol. Lett. 7 69
[11] Bertuzzo E, Suweis S, Mari L, Maritan A, Rodriguez-Iturbe I and Rinaldo A, Spatial effects on species persistence and implications for biodiversity, 2011 Proc. Nat. Acad. Sci. USA 108 4346
[12] Wangersky P J, Lotka–Volterra population models, 1978 Annu. Rev. Ecol. Syst. 9 189
[13] Shertzer K W and Ellner S P, Energy storage and the evolution of population dynamics, 2002 J. Theor. Biol. 215 183
[14] von Bertalanffy L, Quantitative laws in metabolism and growth, 1957 Q. Rev. Biol. 32 217
[15] West G B, Brown J H and Enquist B J, A general model for ontogenetic growth, 2001 Nature 413 628
[16] Banavar J R, Damuth J, Maritan A and Rinaldo A, Ontogenetic growth (communication arising): modelling universality and scaling, 2002 Nature 420 626
[17] Fisher M E and Barber M N, Scaling theory for finite-size effects in the critical region, 1972 Phys. Rev. Lett. 28 1516
[18] Mueller L D, Guo P and Ayala F J, Density-dependent natural selection and trade-offs in life history traits, 1991 Science 253 433
[19] Freitas Coelho F, Deboni L and Santos Lopes F, Density-dependent reproductive and vegetative allocation in the aquatic plant Pistia stratiotes (Araceae), 2005 Rev. Biol. Trop. 53 369

doi:10.1088/1742-5468/2013/10/P10020
Growth or reproduction: emergence of an evolutionary optimal strategy

[20] Kleiber C and Kotz S, 2003 Statistical Size Distributions in Economics and Actuarial Sciences (New York: Wiley)

[21] Okuyama K, Takayasu M and Takayasu H, Zipf’s law in income distribution of companies, 1999 Physica A 260 125

[22] Axtell R L, Zipf distribution of US firm sizes, 2001 Science 293 1818

[23] Simini F, Anfodillo T, Carrer M, Banavar J R and Maritan A, Self-similarity and scaling in forest communities, 2010 Proc. Nat. Acad. Sci. USA 107 7658

[24] Baek S K, Bernhardsson S and Minnhagen P, Zipf’s law unzipped, 2011 New J. Phys. 13 043004