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Evolutionary information contained in frequency spectra

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Abstract

Information concerning important details of an ecosystem's evolution are shown to be contained in an appropriately constructed power spectrum. In particular, it provides an answer to the question of just *why* power-law behavior vanishes in the absence of Darwinian competition. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

The last years have witnessed great activity in the study of physical models that mimic biological evolution processes. As a consequence, much light has been shed on diverse features of the rich Darwinian landscape. A great deal of effort has been invested in devising ingenious and at the same time *simple* theoretical models that may provide one with meaningful insights concerning punctuated equilibrium, self-organized criticality, and other features of biological evolution [1–8]. Recently, a somewhat more realistic model than those previously in existence was introduced [9,10]. It deals with several *interacting species* and its intrinsic dynamics clearly exhibit the punctuated equilibrium phenomenon. More importantly, the model *predicts* that the laws governing the extinction distribution curves should be power laws [9] and is also able to reproduce not only Sepkosky's evolutionary activity curves [11] but also lifetime species distribution ones [11,12], both kinds of curve constructed on the basis of fossil records. As reported in [9,10], the model's workings are complex enough so as to be able to

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mimic some facets of actual biological evolution. On the basis of this model one may understand that several (simple) dynamical mechanisms exist that account for these (observed) facets without recourse to catastrophic events. It should be pointed out that the aforementioned predictions are of a mathematically robust nature [9,10] (recent models, see, for instance, Refs. [5–8] seem able to allow for this kind of predictions too).

For the convenience of the reader, we briefly summarize the findings of [9,10]:

- In [9] addition to introducing the model, it was shown that it exhibits the features of punctuated equilibrium and power-law behavior. Moreover, it is seen that power-law behavior (PLB) is a direct result of Darwinian competition (as simulated by the model workings). Elimination of such competition results in the disappearance of PLB.
- In [10], it was shown that, appearances notwithstanding, the model does not exhibit self-organized criticality (SOC) [13]. A different type of dynamical evolutive process is at work, that is mathematically grounded on phenotype–genotype correlations.

If one takes inventory of the results reported in Refs. [9,10], some questions remain that deserve further clarification: The dynamical system of [9,10] can be characterized with reference to the power-law character of the extinction data obtained from an appropriately constructed time series (that reflects on the evolutive dynamics). We are interested here in extracting still more information from the paleontological data on the basis of the ideas expounded in [9,10]. In order to achieve such a purpose we compare the predictions of the model of Refs. [9,10] with relatively recent results obtained from the study of the power spectrum of the time series of extinction sizes [14–17]. These results impose severe constraints on models attempting to describe the extinction/evolution process.

2. The model

The model [9,10] deals with M distinct, interacting biological species, each of which is represented by a vector in \mathcal{R}^N . The components V_α^i of V^i represent different phenotypic features (α, β, \dots) that are to be affected and modified by the evolutionary process. The degree to which the i th species is “adapted” to the environment is represented by a quantity F_i , to be called its “fitness”, which is given by the expression

$$F_i = \sum_j^M \sum_{\alpha\beta}^N g_{\alpha\beta}^{ij} V_\alpha^i V_\beta^j + \sum_\gamma^N V_\gamma^i A_\gamma^i, \quad i = 1, \dots, M, \quad (1)$$

where the hyper-matrix $g_{\alpha\beta}^{ij}$ provides the details of the inter-species interaction and the second term on the r.h.s. is an “environmental” one (see below). In [9] one assumed $g_{\alpha\beta}^{ij} = -g_{\beta\alpha}^{ji}$.

There is a correlation between the components of V^i which is represented by recourse to mappings between a set of $k + 1$ real parameters and each of these components, i.e.

$$V_\beta^i = f_\beta(a_0^i, \dots, a_k^i), \quad (2)$$

with f_β an appropriate function. The set a_0^i, \dots, a_k^i defines in fact the i species. As a result of biological mutations, these parameters are allowed to vary with time.

The conceptual difference between the a 's (that span an “ A -space”) and the V 's (a “ V -space”) should be here emphasized. The components of V denote different phenotypic features of the species that this vector represents. These features are correlated, via the a 's, in the manner just described. Genetic changes, here mimicked by modifications in the a -values, drive the evolutionary process. The correlations just mentioned constitute an essential aspect of the model. Without them, a given species might (eventually) attain, after a series of appropriate mutations, *any* phenotypic feature whatsoever. This does not happen in nature. Summing-up, changes in our a 's are to be understood as reflecting uncorrelated genetic modifications (changes in one or more bases in one or more genes) while changes in the V 's represent the concomitant phenotypic modifications that, to a greater or lesser extent, will be mutually correlated. The a 's does not represent the genetic code in itself, but only the correlations introduced by its existence.

Our model-system evolves in the following fashion: we start with an arbitrary initial configuration (the a_i are randomly chosen within $[-1, 1]$) and, in each of a series of time steps, mutation effects are mimicked by slightly modifying the a_i for the l th species. Both the selection of l and the nature of the changes are random. The condition $|V^i| = 1$ is enforced so as to avoid unrestricted growth (with time) of $|V^i|$.

A particular mutation (change in a given a) is “accepted” if it increases the corresponding fitness (as a consequence of such a mutation F_i grows). The a -change is in this case retained. Otherwise it is discarded and the a_i end up with their previous, old values.

As the features of each species are in a state of continuous change, there is a considerable amount of “evolutive activity”, that we shall quantify with reference to the motion of a “center of mass”

$$X_{CM} = \sum_{i=1}^M V^i \tag{3}$$

whose value is to be ascertained at a series of regularly spaced times. Then, we define the evolutive activity (EA) as

$$EA = |\delta_t X_{CM}|^2$$

where δ_t represents variation in an arbitrary number t of time steps (in this and previous works we use $t = 1000$).

As a matter of fact, a better measure of evolutive activity would read

$$EA_1 = \sum_i (\delta V_i)^2$$

as one might a priori expect that the larger the system, the smaller the center of mass variation (self-averaging behavior (SAB)). However, numerical results indicate that the amount of SAB is negligible, and so is also the difference

$$|EA - EA_1|.$$

This result may be due to the fact that, on account of the high dimensionality of the relevant configuration space, the V_i tend to move in mutually orthogonal directions rather than in opposite directions. Thus, their motion is to be summed rather than averaged. As a consequence, one observes that, the larger the system, the larger EA , which indeed grows in roughly linear fashion with M .

For simplicity's sake we took in [9,10] (i) our hyper-matrix in the form

$$g_{\alpha\beta}^{ij} = k_{ij}\delta_{\alpha\beta}, \quad (4)$$

and (ii) $A_\gamma^i = 0$. Thus (1), reduces itself to

$$F_i = \sum_{j=1}^M k_{ij} V^i \cdot V^j, \quad i = 1, \dots, M, \quad (5)$$

where $k_{ij} = -k_{ji}$. These simplifications will be removed (see Section 4).

The k_{ij} are randomly chosen within $[-1, 1]$ (for $i < j$) and are kept constant throughout. The functional form of (2) was chosen in the (quite general) fashion

$$f_\beta = \sum_{n=0}^k a_n x^n, \quad x = \beta/N \quad (6)$$

so that

$$V_\beta^i = \frac{\sum_{n=0}^k a_n^i (\beta/N)^n}{\sqrt{\sum_\beta \sum_{n,m=0}^k a_m^i a_n^i (\beta/N)^{n+m}}}. \quad (7)$$

3. The evolutive time series

Both in Refs. [9,10], and in those of the pioneering authors in whose work references [9,10] were inspired, emphasis was put upon the fact that both lifetime and number of extinct species follow a power law, which is usually seen as evidence of criticality. In fact, several of the models self-organize into a critical state in which many quantities are known to scale as a power law. In general, however, inverse power laws are the signature of fractal processes [18]. There are many mechanisms other than self-organized criticality that can lead to inverse power-law scaling without requiring the system to be in a critical state. A few of them are coherent noise [19,20], random multiplicative processes [21,22], random extremal processes [23], random thermal barrier crossing [24], allometric scaling [25] and our model [10]. Thus there is a real need to characterize the information contained in the fossil record as exhaustively as possible, in order to find constraints capable of differentiating between the different mathematical models that attempt to mimic aspects of evolutive processes.

The leit motiv of the present considerations revolves around the following idea: *there is more information in the temporal series representing evolutive activity than in the power laws* of the preceding paragraph. For example, if we randomly exchange the positions of the temporal intervals in Fig. 1 of [9], the concomitant distribution will

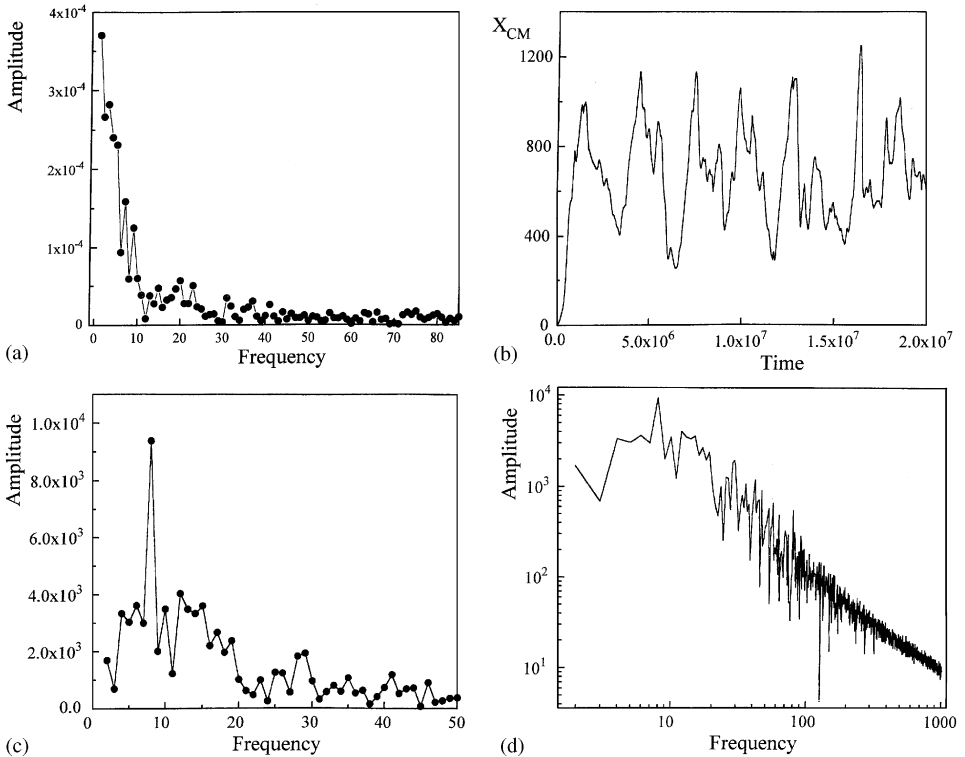


Fig. 1. Frequency spectra (arbitrary units) corresponding to a time series with $M = 25$, $N = 7$, $k = 5$. Low-frequency components contribute more than high frequency ones (the $f = 0$ component is not shown for the sake of a better visualization). (b) Time-evolution of $|X_{c.m.}|$ (arbitrary units) corresponding to a time series with $M = 25$, $N = 17$, $k = 5$. (c) frequency spectra (arbitrary units) corresponding to a time series of $|X_{c.m.}|$, with $M = 25$, $N = 17$, $k = 5$ (the $f = 0$ component is not shown for the sake of a better visualization). (d) Log-log graph of the data portrayed in Fig. 1c.

still follow a power law, which entails that power laws, by themselves, are not able to provide a complete enough characterization of the associated time series.

In other words: knowing that the extinction sizes event-distribution follows an inverse power law yields only information about the possible sizes of the events, but nothing about their temporal distribution. However, the various time scales (frequencies) contributing to a dynamic process exhibit a characteristic spectrum. An example of such a process is a simple harmonic oscillator, which has a spectrum consisting of a single frequency. In comparison, a fractal process or a fractal time series is very different. There is no characteristic scale for a fractal process, and its frequencies yield an inverse power-law spectrum [18].

Thus, the power-law spectrum and the power-law distribution have different informational contents. They are independent of each other: we can have a power-law distribution of extinction sizes but not a power-law spectrum, and vice versa. As a consequence, it should be of some importance (i) to study which type of frequency

spectrum characterizes our time series, and then (ii) to compare it with that obtained from the fossil record.

3.1. Time series and frequency spectrum

As stated, there is a strong motivation for investigating the following alternative way of extracting information contained in the pertinent time series: *the study of its frequency spectrum* [14–17,5–8]. Some results of works performed upon the fossil data [14–16] are of somewhat contradictory sort. We shall see that our model allows for a coherent view of such fossil data.

3.1.1. Spectral characteristics

First of all, it seems that actual data from fossil records display evidence of a power enhancement at low frequencies, and of a peak at intermediate frequencies, corresponding to periods of 26–32 million years [14].

Fig. 1a displays the Fourier transform of the time series of the evolutive activity, as obtained from our model. Even if not too much can be said by just glancing at the spectrum, it is clear that the behavior at low frequencies *differs* from that at high ones. A suggestive peak appears at 20 (arbitrary) units.

One must take notice, however, that our evolutive-activity time series (e.a.t.s.) is a rather noisy one. We will presently show that random fluctuations are responsible for this noise. It is then of interest to look at the frequency spectrum for $|X_{c.m.}|$ (versus t). The ensuing curve arises in direct fashion from the solution a deterministic system of differential equations (see below), and, as such, is not affected by stochastic noise. In Fig. 1b a typical such curve is displayed, the concomitant spectrum being depicted in Fig. 1c. It is clear that oscillations around a characteristic frequency are indeed present.

A more detailed analysis shows that, for fixed values of the parameters M, N, k , and k_{ij} , variation of the initial conditions (the $V_i^j(0)$) results in up to three fixed principal frequencies, of which one generally appears to be the main oscillation frequency. The concomitant widths are of variable size. If we fix the sizes of M, N , and k , and allow the k_{ij} to vary, the peak positions change, but only to a small extent. The main oscillation frequencies are not sensitive to the N value and their values diminish with M , the pertinent periods being roughly proportional to the M values.

3.1.2. Power law and periodicity

It has often been suggested that the power spectrum of the time series of extinction sizes decays as a power law [15–17]. Our model also predicts this feature. Fig. 1d depicts a log–log graph of the results portrayed in Fig. 1c. Clearly, for the most part the power-law decay is evident, with the exception of the initial portion, that gives rise to the above-mentioned oscillations. Notice then that our model “unifies” two apparently incompatible types of result that arise from the fossil data analysis: periodicity and power-law behavior. It is also worth mentioning that many working paleontologists do not accept that such power laws exist [16].

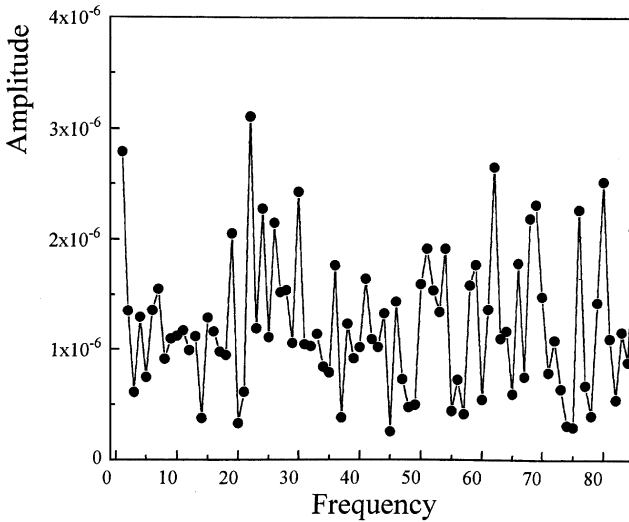


Fig. 2. Frequency spectra corresponding to a time series for random motion without Darwinian competition ($M = 25, N = 7, k = 5$). In average, all frequencies contribute in equal fashion. Additional details are as in Fig. 1.

3.1.3. Darwinian competition

Let us see now what changes can be observed in the model’s dynamics if the crucial ingredient of Darwinian competition is removed. The series of Fig. 5 of Ref. [9] corresponds to a situation in which *all* mutations are accepted (retained), whether they are “beneficial” (i.e. they produce an increase in fitness) or not. The associated spectrum is given in Fig. 2 of the present communication. The associated frequency spectrum looks quite different from that of Fig. 1: it resembles *white noise*. It is also interesting to point out that here the associated distributions of lifetime and evulsive activity *do not follow a power law* (see [9]), *and appear to be a direct consequence of Darwinian competition*, where only successful mutations survive. We discuss the concomitant implications below.

It was shown in [10] that the source of power-law behavior is to be located:

- in the details of the $A \rightarrow V$ -mapping, and
- with reference to the fact that vector \mathbf{a} traverses large regions of the A -space in recurrent fashion. As demonstrated in [10], without correlations power-law behavior (PLB) disappears, as the mapping features do not change as \mathbf{a} moves around.

3.2. Simulation invariant properties

Still to be investigated, however, is the following question: exactly why does PLB vanish in the absence of Darwinian competition, even if correlations remain present? The answer requires a more detailed analysis of the equations of motion. We will see that, in looking for it, we shall be also in a position to explain the frequency peaks

above referred to (and their absence when no Darwinian competition is allowed for).

We begin our task by looking at the temporal evolution of $|\mathbf{a}|$. An analysis of such a type was given in [10] (see its Fig. 6), but more detailed considerations are still needed, which we proceed to undertake here.

The concomitant curve could at first sight be attributed to a random character, an impression that the non-deterministic character of our model may reinforce. Appearances, however, are deceptive: if we let the system evolve many times over, starting always from an identical initial state, we always obtain the same results for the time-evolution of \mathbf{a} (a simulation invariant property), even if we vary the size of our “mutations” (and also the corresponding random generator). Of course, we always deal with fluctuations small enough that the curve $|\mathbf{a}|$ versus t remains a “smooth” one. Thus, a certain amount of “determinism” might legitimately be associated to this evolution process.

The situation is then as follows: the time series (TS) associated to the evolutive activity does change if the variations referred to in the preceding paragraph are effected: the TS strongly depends upon the nature of the fluctuations.

Although the \mathbf{a} -curve looks smooth enough, it is still subject to a small amount of “staggering”. Evolutive activity is ruled by changes in V and only *through them* by variations in \mathbf{a} (“micro-staggering”). The V -changes amplify the \mathbf{a} -micro-fluctuations, that end up giving the evolutive activity versus time curve a non-deterministic character.

However, the temporal evolution of $|\mathbf{a}|$ (in mean) *remains invariant under such circumstances*. Indeed, the evolution of \mathbf{a} can be associated to the solution of a system of non-linear, coupled differential equations (as shown in the appendix).

3.3. Darwinian competition engenders a non-linear system

Our time series are of a recurrent character, which allows for the existence of some characteristic oscillation frequencies, at least for the time scales here considered. We can confidently assert, as a consequence, that the system is able to “explore” in enough detail and in recurrent manner the A -space, which allows for the appearance of a typical peak in Fig. 1. Now, in the absence of Darwinian competition *it is impossible to conceive the curve we are concerned with here as arising from the solution of a coupled system of differential equations*. The ensuing dynamics is that of a random walk and the curve $|\mathbf{a}|$ versus t becomes a different one for each simulation run that starts from an identical initial state. The system does not “explore” and remains always in the vicinity of the initial region of A -space. The system loses both “periodicity” and power-law behavior.

In the frequency spectrum pertaining to our evolutive activity curve, a peak is detected at intermediate frequencies. This particular frequency is to be regarded as a system’s *natural* one, that depends only upon its internal characteristics, in the same fashion that a spring’s natural frequency is a function only of the mass and of the restoring force [1].

It is important to remember, in this respect, that, according to a number of analysis, extinction events are regularly spaced in geologic time [14], with periods ranging from 26 to 32 million years.

After the first evidences of such an “extinction periodicity”, several astrophysical explanations were proposed. Most suggested that perturbation of comets in the Oort Cloud raise the probability of comet impact on Earth, which establishes a link between the claimed periodicity of extinction events and the impact theory of Alvarez et al. [26]. However, as Raup suggests [14] periodicity and impact should be viewed as separate (although possibly linked) phenomena.

Alternative proposals in this vein relate the putative periodicity to “external” causes. On the basis of the present results an alternative explanation suggests itself: this periodicity could just be the manifestation of a *natural oscillation frequency* of the terrestrial ecosystem as a whole (à la Gaia [27,28]), regarded as a dynamical system. The oscillation frequency is to be associated, as explained above, to Darwinian competition, that allows one to picture the dynamical evolution of the ecosystem in terms of a set of deterministic non-linear coupled differential equations (DNLNDE). Of course, our results are based on a particular realization of a set of DNLNDE’s, the one representing our model. Even if power-law behavior and periodicity are not generic in the solution of DNLNDE’s, both characteristics jointly apply in the case of the present set of equations. A large number of numerical simulations, that start from randomly chosen initial conditions confirm such an assertion. Chaos appeared in all the instances studied here.¹ Contrarywise, in the absence of Darwinian competition we have no DNLNDE associated to the system, but rather a random walk-like evolution.

4. Conclusions

- Summing up, in this paper we have complemented the work reported in [9,10] by
- providing a mathematical explanation of the reasons that underlie the fact that, in the absence of Darwinian competition, power-law behavior is lost.
 - finding oscillation modes that introduce a certain amount of periodicity that, again disappears in the absence of Darwinian competition.
 - unifying within a same scenario apparently contradictory results from the analysis of the power spectrum of the time series of extinction sizes.

¹ In this regard some open questions may still remain. The time series of Fig. 1b is in general of a chaotic character. The oscillation frequencies do not correspond to pure modes (they exhibit variable widths). The system might be either (i) moving in the vicinity of a (periodic) stability island, or (ii) dissipating, ending up in a strange attractor. One would here be just observing what happens at initial stages, previous to the long-term relaxation one. However, the analysis of the concomitant chaotic series for very large time intervals lies beyond the scope of the present study.

Acknowledgements

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Appendix A. A system of differential equations for the present model

We investigate here the time evolution of the mean value of \mathbf{a}^i . To this end we rewrite F_i in terms of the a_k^i

$$\begin{aligned}
 F_i &= \sum_j \sum_{\alpha\beta} g_{\alpha\beta}^{ij} V_\alpha^i V_\beta^j \\
 &= \sum_j \frac{\sum_{\alpha\beta} \sum_n \sum_m g_{\alpha\beta}^{ij} a_n^i a_m^j \alpha^n \beta^m / N^{n+m}}{\sqrt{\sum_{\beta\alpha} \sum_{n,m=0}^k \sum_{p,q=0}^k a_m^i a_n^i a_p^j a_q^j \alpha^{n+m} \beta^{p+q} / N^{n+m+p+q}}}, \tag{A.1}
 \end{aligned}$$

i.e.,

$$F_i = \sum_j \frac{\sum_{nm} G_{nm}^{ij} a_n^i a_m^j}{\sqrt{\sum_{n,m,p,q=0}^k h_{pq}^{nm} a_m^i a_n^i a_p^j a_q^j}}, \tag{A.2}$$

where we introduce the constant coefficients

$$G_{nm}^{ij} = \sum_{\alpha\beta} g_{\alpha\beta}^{ij} \frac{\alpha^n \beta^m}{N^{n+m}}. \tag{A.3}$$

and

$$h_{pq}^{nm} = \sum_{\alpha\beta} \frac{\alpha^{n+m} \beta^{p+q}}{N^{n+m+p+q}}.$$

A slight variation $\delta\mathbf{a}^i$ is “accepted” if it leads to an increase in the value of F_i , being otherwise rejected. We can think of an hyper plane F_i in the K variables a_n^i . As we deal with random variations, on average some 50% of them will be acceptable ones (as evidenced by the results of our simulation runs). In a small enough time interval δt (but still able to accommodate several generations), i.e., typically of the order $\delta t = 1000$ time steps, the vector $\delta\mathbf{a}^i$ will point along the same direction as the gradient (with respect to the a_n^i) of F_i , that is

$$\frac{\delta\mathbf{a}^i}{\delta t} = \frac{|a|}{|\nabla F_i|} \nabla F_i, \tag{A.4}$$

where $|a|$ is a constant representing an average motion modulus (depending only upon the statistical distribution that governs the $\delta\mathbf{a}^i$ variations).

For such a reason we prefer working with \mathbf{a}_i and not with \mathbf{V}_i , even if F_i is a quadratic quantity in both quantities.

We proceed then to evaluate the F_i -gradient

$$\frac{\partial F_i}{\partial a_k^i} = \sum_{j \neq i} \frac{\sum_{nm spq} H_{km pq}^{ijns} a_n^i a_s^i a_p^j a_q^j a_m^j}{(\sum_{n,m,p,q=0}^k h_{pq}^{nm} a_m^i a_n^i a_p^j a_q^j)^{3/2}}, \tag{A.5}$$

where we have made use of the relation

$$\frac{\partial a_m^j}{\partial a_k^i} = \delta_{ij} \delta_{mk}. \tag{A.6}$$

due to the fact that they are independent variables.

Also,

$$H_{km pq}^{ijns} = G_{km}^{ij} h_{pq}^{ns} - G_{nm}^{ij} h_{pq}^{ks}, \tag{A.7}$$

so that replacement in (A.4) leads to

$$\frac{\delta a_k^i}{\delta t} = \frac{|a| \sum_{j \neq i} \sum_{nm spq} H_{km pq}^{ijns} a_n^i a_s^i a_p^j a_q^j a_m^j / (\sum_{n,m,p,q} h_{pq}^{nm} a_m^i a_n^i a_p^j a_q^j)^{3/2}}{\sqrt{\sum_k (\sum_{j \neq i} \sum_{nm spq} H_{km pq}^{ijns} a_n^i a_s^i a_p^j a_q^j a_m^j / (\sum_{n,m,p,q} h_{pq}^{nm} a_m^i a_n^i a_p^j a_q^j)^{3/2})^2}}, \tag{A.8}$$

$i = 1, M, \quad k = 1, K,$

that indeed leads to a set of non-linear, coupled differential equations.

In the absence of Darwinian competition Eq. (A.4) ceases to be valid, as $\delta a^i / \delta t$ becomes an entirely random *small* quantity, whose average tends to vanish on account of the fact that no preferred direction of motion exists. $|a^i|$ becomes a random walk.

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