

## On the bifurcation of species

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We propose and analyze a model of evolution of species based upon a general description of phenotypes in terms of a single quantifiable characteristic. In the model, species spontaneously arise as solitary waves whose members almost never mate with those in other species, according to the rules laid down. The solitary waves in the model bifurcate and we interpret such events as speciation. Our aim in this work is to determine whether a generic mathematical mechanism may be identified with this process of speciation. Indeed, there is such a process in our model: it is the Andronov homoclinic bifurcation. It is robust and is at the heart of the formation of new solitary waves, and thus (in our model) new species. © 2008 American Institute of Physics.

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**Individual organisms are grouped into species with well-defined distinguishing characteristics, whose members generally do not mate successfully with those of other species. Here, we formulate in a simple mathematical model some of the tenets of evolution theory for mating and survival rules expressed in a continuous space of organism characteristics (phenotypes). Our mathematical description naturally produces solitary waves in characteristic space. We interpret these waves as species and their bifurcation as speciation, using numerical simulations to reveal the wealth of behavior. We then perform extensive asymptotic analyses of the model to seek an answer to a question raised by Darwin: why are there discrete species rather than individuals with a continuum of characteristics? In the context of our model, the process underlying speciation is a known mechanism called the Andronov homoclinic bifurcation. We go on to suggest that models of this kind may be used to explore other issues, such as the role of species competition and geographical effects.**

### I. INTRODUCTION

Discussions of evolution make use of the imagery of a branching tree. In the usual representation, this is done in the Cartesian plane with the vertical direction—the direction of branching—representing time  $t$ . The horizontal coordinate in the branching picture gives the value of a defining characteristic feature of typical individual organisms, such as length of neck or size of beak (e.g., [Gingerich, 1980](#), Figs. 2 and 3, on the mean and standard error of the tooth size of early Cenozoic mammals). Of course, the restriction to a single

characteristic is made only for the ease of drawing the picture; in reality there should be a large number of axes representing all the  $N$  (say) macroscopic characters of the organisms. A point in  $\mathbb{R}^N$  then prescribes what is called the phenotype of an organism and we refer to this  $N$ -dimensional space as *phenospace*. The branching tree of evolution that is commonly drawn may then be thought of as showing the trajectories (or worldlines) of species.

When the phenospace is one-dimensional, a richer imagery is conventionally used in which the number of organisms as a function of phenotype and time is included in the description. This leads to graphical representations of the evolutionary process in which species are indicated in the manner that nonlinear dynamicists represent propagating solitary waves in physical space and time. This way of seeing things makes it clear that organisms do not form an uninterrupted continuum but rather that they separate into discrete groupings or species in what Darwin referred to as the “mystery of mysteries.” The representation of species as solitary waves makes for a convenient description of speciation and it has been used in many qualitative discussions of that process, though typically without a statement of the analogy between the representations of waves and species. Indeed the way in which new species evolve does resemble the formation and splitting of solitary waves such as one sees in the solutions of the complex Ginzburg–Landau equation and other nonlinear partial differential equations (PDEs).

In *On the Origin of Species* Darwin asked “... why, if species have descended from other species by fine gradations, do we not everywhere see innumerable transitional forms? Why not a blur...of continuous variations?” And, of course, we would answer that a nonlinear mechanism is a natural choice to explain this observation: modern dynamical studies show how discrete coherent structures such as solitary waves are prevalent in nonlinear systems and that observation is the starting point of the present work. To us, a key question to consider in formulating models of evolution is

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whether there is a robust bifurcation process that may be basic to the formulation of such structures. Moreover, the question is not limited to biology. The Darwinian imagery has been invoked in other disciplines such as the social sciences and, recently, even in cosmology (Smolin, 1997). This apparent universality of the Darwinian ideas leads us to ask whether there is an underlying mathematical structure for thinking about the notions of evolution

After some effort in the search for appropriate mechanisms, we feel that there is a mechanism that can serve to describe the bifurcation of species as it is generally depicted. Here we illustrate the nature of such a speciation bifurcation with an analysis of a simple nonlinear model of evolution (Bees, 1994) that captures the qualitative feature of the speciation process that Darwin alluded to. Having first prescribed the equations of the model, we provide some numerical solutions of the model equations that show the speciation. In a sense, this gives the short answer to the question posed by Darwin: a simple model that embodies the tenets of biological evolution does lead to distinct species and it involves nonlinearity. We then go on to an analysis whose aim is to uncover the mathematical mechanism underlying this nucleation process. That analysis is essentially qualitative and makes use of standard approximations. The results suggest that the underlying mechanism is the (Andronov) homoclinic bifurcation (Kuznetsov, 2006; Izhikevich, 2007).

In proceeding in this way we recall the outlook of Turing, who, in another context, wrote that “This model will be a simplification and an idealization and consequently a falsification. It is to be hoped that features retained for discussion are those of greatest importance in the present state of knowledge.” In that spirit we do not apologize for having only one dimension in our phenospace since it is always best to begin simply. But one might reasonably object that such a discussion might better be formulated in what might be called genospace. Indeed, one should certainly aim to make models at that level. However, as in the physical sciences, it is an instructive and often effective practice to simplify matters by coarse-graining and we have chosen that route for the present study. One could go even further in that direction: Gould (2002) has proposed thinking of species themselves as organisms. In that spirit, our level of coarsening is only intermediate. We are aiming for a level of coarseness somewhat analogous to the Boltzmann description of kinetic theory, though at a lower dimensionality than is usual in that context. In any case, as we shall see, the model we study here does lead to the formation of coherent objects that bifurcate by a known robust process. We suggest that these coherent objects and their dynamics may be of use in testing suggestions about how to modify evolutionary models by including, for example, geographic effects and other such external influences.

## II. THE MODEL

### A. General features

Before presenting our model (see also Bees 1994) we describe some of its general properties. We consider an evolutionary dynamics that is adaptive (sympatric) without any

reliance on geographic (allopatric) influences. Though this reflects perhaps a minority view of things, it has been well defended in Dieckmann and Doebeli (1999), for instance, where a useful, if brief, discussion of the issues is presented. Unlike their model, however, our model does not rely on any explicitly stochastic inputs such as are frequently included in evolutionary models (see, for example, Newman *et al.*, 1985). From that point of view, our approach may be considered deterministic. However, it is statistical in the sense that Boltzmann’s kinetic theory (or wave mechanics) is. That is, we formulate a model in terms of a probability density in the state space that we call *phenospace*. (Also as in Boltzmann’s theory, the model is based on pair interactions: reproduction is assumed to be sexual.)

As mentioned above, we introduce a single phenotype descriptor and regard it as a quantification of a more general characteristic. To represent the effects of environmental pressures we could also require a second independent variable that characterizes the environmental resource. To reduce complications, we choose this to be the same variable as that used to specify phenotype. If the organisms are giraffes, for instance, the species descriptor might be neck length and the corresponding environmental parameter would be tree height, which would here both be given by the same variable. [See Roughgarden (1972) and, for discussion of such distinctions, Weiner (1994).]

We do not introduce any specific modeling of genetics (Hall *et al.*, 2002) or clines in allele space (see Veronka and Keller, 1975; Ewens, 1969; O’Brien, 1985; Spencer and Barakat, 1992). That is, we represent the phenotype by an independent variable and disregard genetic makeup. Moreover, we do not include geographical variations in the interests of simplicity. Nor do we model selective pressure by imposing an environmental gradient in phenotype space (Doebeli and Dieckmann, 2003; Tang and Waxman, 2003). We do not dictate nor limit the “fitness” of individuals with particular characteristics (Geritz *et al.*, 1997), but let this arise from the dynamics. What we do is to construct a self-consistent system modeling species and environment in phenotype-space and time and address its bifurcational structure.

With phenotype characterized by the variable  $\alpha$  we write the number of individuals in a range  $d\alpha$  at time  $t$  as  $f(\alpha, t)d\alpha$ . The use of this continuum description for a discrete number of organisms is not a problem when we are dealing with sufficiently large populations; a mechanism for killing off very small populations is a desirable feature (emergent or prescribed) of such descriptions, and we find such a regulation in our model. In our dynamical description a *species* is made up of a collection of selfish individuals as discussed by Dawkins (1989) with an  $f$  that falls off rapidly outside some narrow interval of  $\alpha$ . The width of this interval is not specified *ab initio*, but arises from the dynamics.

We introduce a density of environmental resource,  $e(\alpha, t)$ , which depends on the same variable  $\alpha$  as the phenotype density, in the sense just explained. In general the environmental resource should be characterized in some other way—call it  $\beta$ . There has to be, then, an additional equation (or equations) indicating which  $\beta$ -objects nourish which  $\alpha$ -organisms. A simple version of such an equation would be

one giving  $\beta$  as a function of  $\alpha$  (or vice versa). In such a formulation, phenospace is one-dimensional and visualization of the solutions is readily achieved. The simplest version with  $\beta$  as a function of  $\alpha$  would be to set  $\beta = \alpha$ , and that is what we have done. This choice is rather in keeping with the story of Darwin's finches, but that is not our main reason for this choice. It was to formulate the simplest model we could that would reproduce the phenomenology we are trying to understand. Once that is done, we may seek to bring in more realistic features such as competing species, predators, evolving environments, geographical differences, and so on.

## B. Model equations

Our evolution equation for the density in phenospace of organisms with characteristic  $\alpha$  is

$$\begin{aligned} \partial_t f(\alpha) = & r \iint \mathcal{K}_\alpha(\alpha_1, \alpha_2) f(\alpha_1) f(\alpha_2) d\alpha_1 d\alpha_2 - v f(\alpha) \\ & + \gamma \int \mathcal{M}(\alpha_1, \alpha) f(\alpha_1) d\alpha_1, \end{aligned} \quad (1)$$

where  $\partial_t$  is an abbreviation for partial derivative with respect to time. The three terms on the right side of this equation for the rate of change of  $f(\alpha, t)$  are, respectively, (a) increase by binary mating, (b) losses through either death or mutation, and (c) gains by mutation.

In designing the kernel  $\mathcal{K}_\alpha$  in the first term on the right, we need to be aware of the various possible complications of real mating rules. Recent data for Panama butterflies (Bull *et al.*, 2006) suggest that inter-species breeding is not as rare as was once thought and can result in hybrids that are highly fertile and viable; gene flow between species in similar habitats is present. Moreover, Hendry *et al.* (2006) report that a species of Galapagos finch with a bimodal distribution of beak size that enabled them to specialize in eating two different types of seed, have merged back into just one group with a single common beak size. Such a collapse is hypothesized to be due to the increase in bird feeders on the island. There is similar evidence for merging of almost-speciated populations of stickleback in lakes in Canada fish in Lake Victoria. Though it is possible to try to build such complications into the mating kernel, we settle here for a relatively simple form and impose only two mating rules consistent with most definitions of a species. First, the organisms of the model mate by pairs whose members are close to each other in phenotype: this is usually regarded as central to the existence of a distinct species. (Since our phenospace is  $\mathbb{R}$ , there is no problem in defining closeness.) In other words, an individual that has a "rare" phenotype relative to most other members of the population does not produce many viable offspring. Hence, we define a reproduction kernel  $\mathcal{R}(|\alpha_1 - \alpha_2|)$  for the probability that an individual with characteristic  $\alpha_1$  will have viable offspring with an individual of characteristic  $\alpha_2$ .  $\mathcal{R}$  could of course also include such features as selective breeding, but we leave this out in the interests of simplicity.

The second feature of our mating protocol has been discussed some time ago by Roughgarden (1972) and used by Levin and Segel (1982): when two organisms mate they pro-

duce an offspring that is not very far from their mean characteristic. [See Slatkin and Lande (1976) for an interesting variation on this.] Hence, we employ a birth kernel  $\mathcal{B}(|(\alpha_1 + \alpha_2)/2 - \alpha|)$  for the probability that offspring will have characteristic  $\alpha$  given parents of characteristics  $\alpha_1$  and  $\alpha_2$ . To express these two effects, we write

$$\mathcal{K}_\alpha(\alpha_1, \alpha_2) = \mathcal{R}(|\alpha_1 - \alpha_2|) \mathcal{B}\left(\left|\frac{\alpha_1 + \alpha_2}{2} - \alpha\right|\right), \quad (2)$$

where both  $\mathcal{R}$  and  $\mathcal{B}$  fall off steeply as their arguments depart from zero (and, of course, are normalized).

In the model, the overall reproduction rate is regulated by the factor  $r$ . In modern studies of the evolution of the finches in the Galapagos (see, for instance, Weiner, 1994), the reproductive success of the birds depends on the abundance of food. Such a direct influence of the environment on reproduction is translated directly into the model by letting  $r$  be a function of the environmental density. Thus, we set  $r = r(e)$ , the dependence to be specified below. We shall also need to provide an equation for  $e$  on this account.

For the mutation kernel  $\mathcal{M}$ , we assume that

$$\mathcal{M}(\alpha_1, \alpha) = \mathcal{M}(|\alpha_1 - \alpha|) \quad (3)$$

and take its overall rate  $\gamma$  to be a constant. Like  $\mathcal{R}$  and  $\mathcal{B}$ , the kernel  $\mathcal{M}$  is without dimension. Further, we treat the loss rate  $v$  as constant; a piece of this term of course comes from mutations as in the expression  $\gamma \int \mathcal{M}(|\alpha - \alpha_1|) f(\alpha_1) d\alpha_1$ , though we do not need to specify this explicitly.

To describe the environmental abundance density  $e$ , we adopt an equation in which the abundance goes to a fixed value in the absence of the organisms. Since the basic notions of the mechanism are already incorporated into Eq. (1), we have chosen to add no further complications in modeling the environmental capacity. (In more advanced discussions, one may also wish to allow for evolution of the environment.) Here, we employ the simple description

$$\partial_t e = se(E - e) - aef, \quad (4)$$

where  $s$  is a linear growth rate that could be related to  $f$ , for example, though we simply assume that  $s$ ,  $E$ , and  $a$  are constants. We find that similar descriptions give similar behavior (e.g., simple piecewise linear models rather than the above logistic growth). The depletion of resource is described by a term linear in  $f$ . Furthermore, we may distribute the impact of a species over a range of environment by replacing this term by  $ae(\alpha) \int \mathcal{C}(|\alpha - \alpha_1|) f(\alpha_1) d\alpha_1$  for some suitable peaked resource consumption kernel  $\mathcal{C}$ , but we find that this does not lead to qualitative changes in solution behavior, so we retain the simplified form. Finally, we posit  $r(e) = r_o e$ , where  $r_o$  is a constant.

To reduce the number of parameters to be varied, we introduce natural units. We measure  $e$  with the unit  $E$  and let  $\tau = (Es)^{-1}$  be the unit of time. The unit of  $\alpha$  is  $\alpha_0$  and we scale  $f$  with  $f_0 = sr_0^{-1}$ . The nondimensional equations then become

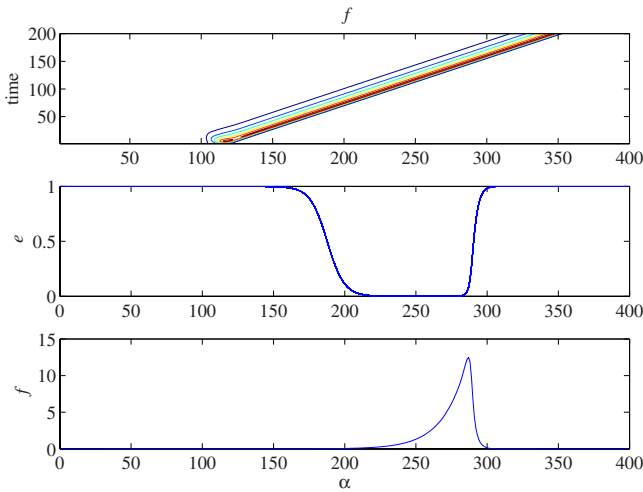


FIG. 1. (Color online) A traveling solitary wave. Top: contour plot of species  $f$  with characteristic  $\alpha$ , and time. Middle and bottom: environment  $e$ , and species  $f$ , at time=300 units.  $dx=0.50$ ,  $dt=0.20$ ,  $m=1.0$ ,  $p=0.42$ ,  $D=0.30$ ,  $\sigma_m=2.2$ ,  $\sigma_R=0.5$ ,  $\sigma_B=0.5$ .

$$\begin{aligned} \partial_t f = & e \iint \mathcal{B} \left( \left| \frac{\alpha_1 + \alpha_2}{2} - \alpha \right| \right) \mathcal{R}(|\alpha_1 - \alpha_2|) f(\alpha_1) f(\alpha_2) d\alpha_1 d\alpha_2 \\ & - \mathcal{D}f + \varrho \int \mathcal{M}(|\alpha_1 - \alpha|) f(\alpha_1) d\alpha_1 \end{aligned} \quad (5)$$

and

$$\partial_t e = e(1 - e) - \varpi e f, \quad (6)$$

where  $\varpi = a(Er_0)^{-1}$  quantifies the environmental impact of a species, while  $\varrho = \tau\gamma$  and  $\mathcal{D} = v\tau$  reflect timescale ratios of mutation and species “death” to environmental recovery, respectively. Though  $\mathcal{D}$  can vary in principle, this does not affect things much, and certainly not in the asymptotic regime that we shall discuss below. So, for the rest of this discussion, we shall treat  $\mathcal{D}$  as a constant; the key point is that it is positive. Thus, we have only three control parameters,  $\mathcal{D}$ ,  $\varrho$ , and  $\varpi$ , besides those that are needed to specify the shapes of the kernels that arise.

### III. SOME NUMERICAL SOLUTIONS

We begin the exploration of the content of the model by presenting some numerical solutions of Eqs. (5) and (6) subject to the boundary conditions  $(e, f) = (1, 0)$  at each endpoint. We used the procedure sketched in the Appendix. It gives robust results and is not sensitive to details like time step. We represent the various kernels as truncated normal distributions with compact support; they vanish when their arguments exceed a certain value, which we take to be three times their standard deviations. (This simplification disfavors hybridization.) The size of the computational domain is taken sufficiently large that it has no effect on the results.

The initial condition for the organism distribution was taken to be a truncated exponential and it leads to results such as are seen in Fig. 1, for the parameter values shown in the caption. This is a case where a pulse persists indefinitely and drifts slowly through phenospace. Thus, the properties of the organisms evolve *gradually* toward ever larger values of

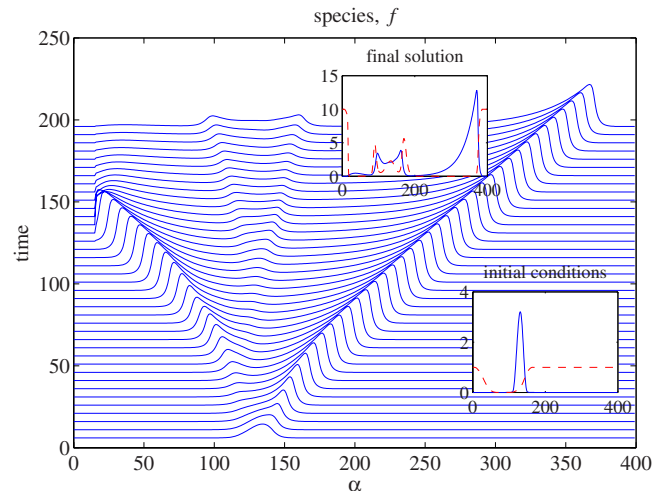


FIG. 2. (Color online) A splitting wave. Inset are the initial conditions and the solution at the final time.  $dx=0.50$ ,  $dt=0.20$ ,  $m=1.0$ ,  $p=0.43$ ,  $D=0.10$ ,  $\sigma_m=2.0$ ,  $\sigma_R=0.5$ ,  $\sigma_B=0.5$ .

$\alpha$  as the environment becomes too depleted to support the population at smaller  $\alpha$ . This illustrates one way that shortages of environmental resources of the right kind may drive evolution. We note that species tend to die out if both the environment and species are sufficiently small, but these levels are not necessarily close to zero (a piecewise linear logistic model for the environment, for example can lead to larger “depleted” levels). Other mechanisms, such as intrinsic time dependence of the environment, provide similar environmental pressures as in the classic example of Darwin’s finches (Weiner, 1994). The main result seen in Fig. 1 of course is that the feedbacks between the two components produce the expected solitary wave—the “species” of this model. For a suitable other choice of initial condition, the pulse could travel in the opposite direction, toward smaller  $\alpha$ .

On varying the parameters  $\mathcal{D}$  and  $\varpi$ , and the standard deviations of the kernels, we find other kinds of behavior. Increasing  $\mathcal{D}$  sufficiently will cause the pulse to decay away in time. Decreasing  $\mathcal{D}$  can increase the pulse height, while increasing the variance of  $\mathcal{M}$  or  $\mathcal{B}$  broadens the pulses and makes them move more quickly. However, an increase in  $\varpi$  or the variances of  $\mathcal{R}$  or  $\mathcal{B}$  or even a decrease in  $\mathcal{D}$  can lead to the bifurcation of the pulse into two pulses. This behavior, our metaphor for speciation, is seen in Fig. 2.

A more striking version of this process is shown in Fig. 3, where pulse pairs seem to appear spontaneously from suitably chosen initial conditions and parameters. In this case, some organisms out on the tail of a pulse have the right properties to take advantage of a situation in which the environment is already recovering from the pulse that has just passed. These marginal survivors will have a surge in reproductive rate and can evolve in a new direction.

There are also parameter ranges with low levels of activity in which two pulses can go off in the two directions but leave a behind some survivors; this seems to be a preferred mode at large  $\varpi$  or  $var(\mathcal{R})$  (the width of  $\mathcal{R}$ ). In Fig. 2 we have the appearance of a local equilibrium punctuated by speciation bifurcations. The new species then evolve away

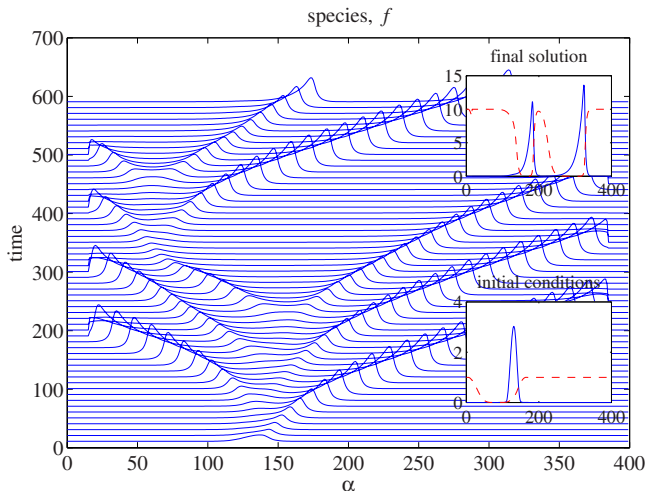


FIG. 3. (Color online) A “pulse tree.” Inset are the initial conditions and the solution at the final time.  $dx=0.50$ ,  $dt=0.20$ ,  $m=1.0$ ,  $p=0.35$ ,  $D=0.47$ ,  $\sigma_m=2.0$ ,  $\sigma_R=0.5$ ,  $\sigma_B=0.5$ .

gradually and may bifurcate again as they do so, as seen in Fig. 2.

Our terminology perhaps recalls the issues raised by Eldredge and Gould (1972) with respect to how evolution proceeds between the bifurcations of species (Futuyma, 1995). In fact, we started this work in an attempt to see more clearly into the discussion that once surrounded this topic. But, now that the controversy seems to have quieted down, we would only remark that the various possibilities can be mimicked by suitable choices of parameter values. What is of interest here is that the gap in  $\alpha$  between the newly formed pulse and the original pulse that we see represents a more abrupt process than just the driving by environmental pressure (natural selection). In terms of our specific model, the speciation is actually caused when a dying component of the population is left behind and isolated in phenospace from the main body of the original species. The newly forming species suddenly finds a recovering environment to take advantage of. Similar effects may be achieved by including geographical factors, but here they are inherent to the process and are reminiscent of what is called on/off intermittency in dynamical systems theory.

Though there are clearly many aspects of this model and its consequences that merit elaboration and variation, we prefer to bypass such variations here and inquire into the qualitative causes of the dynamics that emerge from the model. The basic mathematical mechanism of the process is what we are after and, to find it, we next simplify the mathematical description. Although this simplification is achieved by approximations, those are not essential since we can obtain accurate solutions by numerical methods. In any case, the simplified version of the model we shall obtain could perhaps have been set down as a model in its own right, though we introduce it to simplify the analysis and to permit us to advance an interpretation of the behavior we have just seen in the numerical results.

#### IV. THE REDUCED SYSTEM

We have seen how our model produces solutions that behave in the manner that is often used to represent speciation in qualitative discussions. Our aim here is to try to identify the basis of this behavior so as to provide guidance in modeling the process. To do this, we simplify the model we have presented while attempting to keep it sufficiently rich as to retain the essential features of the basic bifurcation process revealed in the full version. Our simplification consists mainly in reducing the master equation of the model to a partial differential equation on the assumption that the kernels in the integrals in Eq. (5) are sharply peaked. In that case, we can approximate the integrals by expanding  $f$  in Taylor series about the peaks of the kernels. This application of Laplace’s method to Eq. (5), in leading order, turns the integral operators into local, or diffusion, operators. The coefficients in these terms show the influence of environmental and other effects. The notation we use is illustrated by this bare bones statement:

$$\int \mathcal{F}(\alpha - \alpha')f(\alpha')d\alpha' = f(\alpha) + \mathcal{F}_1\partial_\alpha f + \dots, \tag{7}$$

where

$$\mathcal{F}_n = \int_{-\infty}^{\infty} \frac{\mathcal{F}z^n}{n!} dz. \tag{8}$$

By truncating the development, we then obtain the reduced equation

$$\partial_t f = ef^2 + \beta^+ ef\partial_\alpha^2 f + \beta^- e(\partial_\alpha f)^2 - \mu f + \chi\partial_\alpha^2 f, \tag{9}$$

where

$$\beta^\pm = 2B_2 \pm \frac{1}{2}R_2, \quad \mu = D - \varrho > 0, \quad \text{and } \chi = \varrho M_2. \tag{10}$$

Thus, together with  $\varpi$  from Eq. (6), we have a total of five parameters. The first term on the right side of Eq. (9) is a simple breeding term and the terms with second derivatives show how the organisms’ characteristics evolve under the various pressures acting. The death term retains its elemental character and Eq. (6) is unchanged. We provide a glimpse of the solution richness from this system by presenting six simulations of Eqs. (6) and (9) in Figs. 4(a)–4(f) obtained as indicated briefly in the Appendix. One may see aspects both gradualism [Fig. 4(b)] and punctuated equilibrium [Fig. 4(e)] in these images. Direct numerical solution of the original integro-differential equations produce complex explosive evolution patterns that look sufficiently like those in Figs. 4(a)–4(f) that it did not seem useful to reproduce them here.

Now we make some further notational changes for cosmetic purposes. We let

$$\varkappa(e, f) = \beta^+ ef + \chi, \quad \beta = \beta^-, \tag{11}$$

where we note that  $\varkappa > 0$ . The model equations become

$$\partial_t f = ef^2 + \varkappa\partial_\alpha^2 f + \beta e(\partial_\alpha f)^2 - \mu f, \tag{12}$$

$$\partial_t e = e(1 - e) - \varpi ef. \tag{13}$$

The first and third terms on the right-hand side of Eq. (12) represent the nonlinear effect of reproduction and its linear

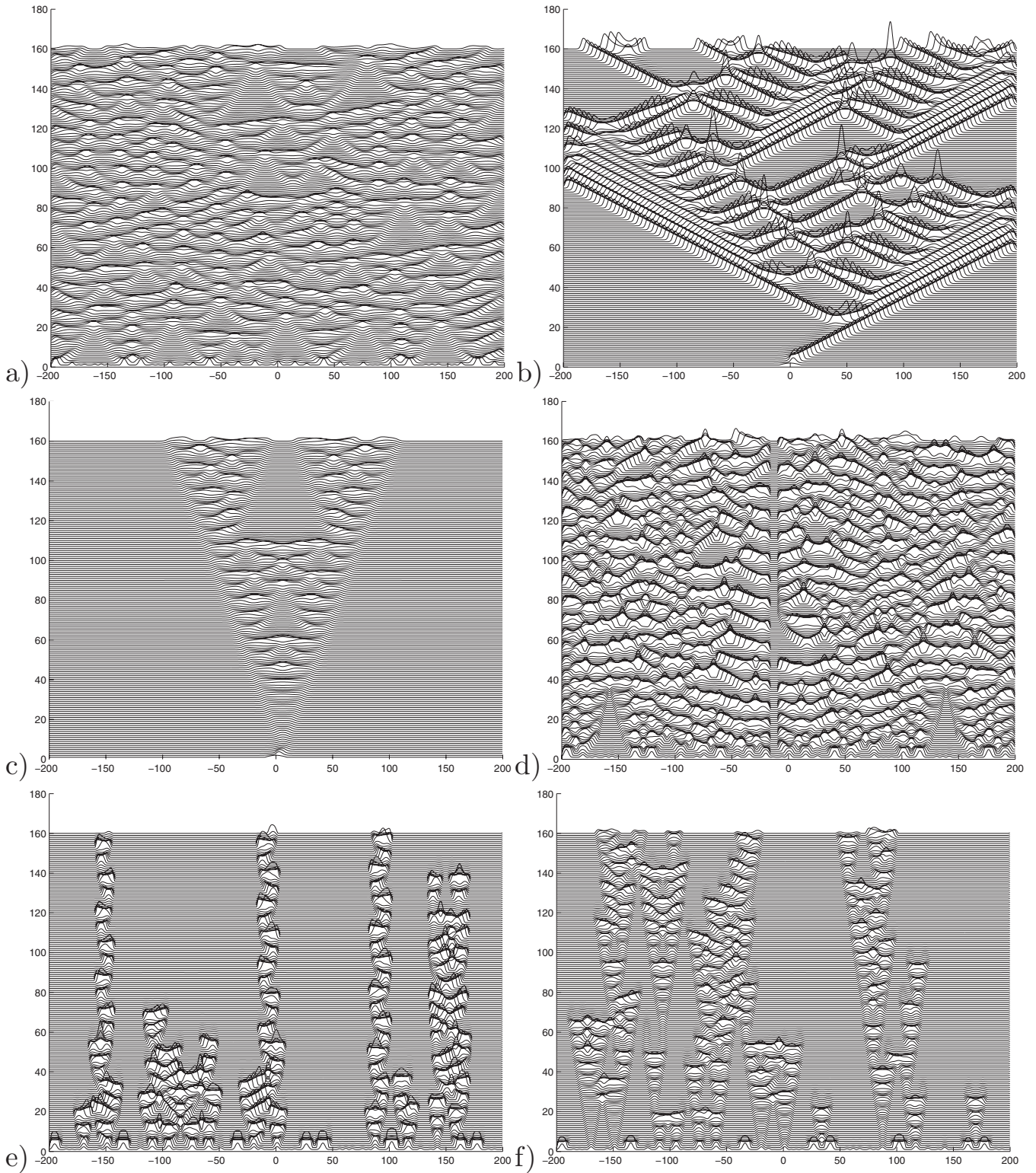


FIG. 4. Numerical simulation of PDE system (see the Appendix; note that there are many more time steps than lines plotted). (a)  $\varpi=0.5, \chi=1.2, \mu=0.4, \beta^+=1.2, \beta^-=-0.2$ . (b) Same as (a) but with  $\varpi=0.35, \beta^+=1.0, \beta^-=-0.85$ . (c) Same as (a) but with  $\beta^+=1.0, \beta^-=-0.4$ . (d)  $\varpi=0.5, \chi=0.0, \mu=0.2, \beta^+=2.2, \beta^-=0.0$ . (e)  $\varpi=0.4, \chi=0.0, \mu=0.3, \beta^+=1.5, \beta^-=-0.2$ . (f)  $\varpi=0.46, \chi=0.01, \mu=0.37, \beta^+=1.5, \beta^-=-0.1$ .

dependence on environment, whereas the second term describes the spread of species characteristics due to mutation and reproduction and the fourth term is due to mortality. A special feature of this system is the requirement that both  $e$  and  $f$  must be positive. Apart from this feature, the system has some mathematical similarities to other equations that

result in the so-called Andronov homoclinic bifurcation (such as those studied by Argentina and co-workers 1997, 1998).

To bring out the contents of this system, we study three special kinds of solution: (a) the case where  $e$  and  $f$  depend on time but not on phenotype, (b) the time-independent so-

lutions with variation in phenospace, and (c) waves traveling through phenospace. However, perhaps the most revealing aspect of the following discussions is the treatment of the case of small  $\mu$ , which leads to a simple yet instructive version of the model.

**V. PHENOSPATIALLY HOMOGENEOUS SOLUTIONS**

When  $f$  and  $e$  do not depend on  $\alpha$ , Eqs. (12) and (13) reduce to the ordinary differential equations

$$\dot{f} = f(e f - \mu), \tag{14a}$$

$$\dot{e} = e(1 - e - \varpi f). \tag{14b}$$

These equations have just two parameters,  $\mu$  and  $\varpi$ , and they control the number and locations of the fixed points that guide the phase flow.

When we set the right side of Eq. (14b) to zero, we get a choice between a solution with  $e=0$  and one with  $e=1-\varpi f$ . The combination of these two loci makes up the nullcline of Eq. (14b). Similarly, the nullcline of Eq. (14a) is made up of the curves  $f=0$  and  $ef=\mu$ . The two nullclines meet at the fixed points of the system (14). For  $e=0$  (and  $\mu \neq 0$ ), the nullcline of Eq. (14a) gives us  $f=0$ . That is, the vacuous state  $(f,e)=(0,0)$  is always an allowed state of the system. We call this fixed point  $T$  (for trivial).

More interestingly, when the second choice for  $e$ , condition  $e=1-\varpi f$ , is introduced into Eq. (14a), we obtain the cubic

$$F := f(-\mu + f - \varpi f^2) = 0. \tag{15}$$

We see that, for  $4\mu\varpi > 1$ , the cubic has only one root with  $(f,e)=(0,1)$ . In that case, there is environmental abundance but no organisms survive; we call this solution  $A$ . Finally, as we enter the parameter regime  $4\mu\varpi < 1$ , another pair of solutions emerges. These two fixed points exist when the line  $e=1-\varpi f$  intersects the hyperbola  $ef=\mu$  in the phase plane  $e-f$ . They appear as a new fixed point when the straight line becomes tangent to the hyperbola when the condition  $4\mu\varpi = 1$  is first met. The new fixed point then splits into a pair as this critical condition is passed in what is known as a saddle-node bifurcation (Strogatz, 1994). We denote the two fixed points that appear at that point in parameter space as  $B_{\pm}$ . By solving Eq. (15) we find the pair of fixed points

$$f_{\pm} = \frac{1}{2\varpi}(1 \pm \sqrt{1-4\mu\varpi}) \quad \text{and} \quad e_{\pm} = \frac{1}{2}(1 \mp \sqrt{1-4\mu\varpi}). \tag{16}$$

A more direct way to view this result is to draw the nullclines  $ef=\mu$  and  $e+\varpi f=1$ , which are, respectively, a hyperbola and a straight line with negative slope. For large  $\varpi$  these curves do not intersect but, as  $\varpi$  decreases, the curves touch at point of tangency with  $e=1/2$  when  $4\mu\varpi=1$ .

When we linearize about the various equilibria, we find that the solution  $T$ , the origin, is always unstable with the growth rates (the eigenvalues of the linear problem) 1 and  $-\mu$ . This shows that when the environment is empty and there are a few organisms, they die off. On the other hand, the equilibrium with  $e=1$  and  $f=0$  is a global attractor, so

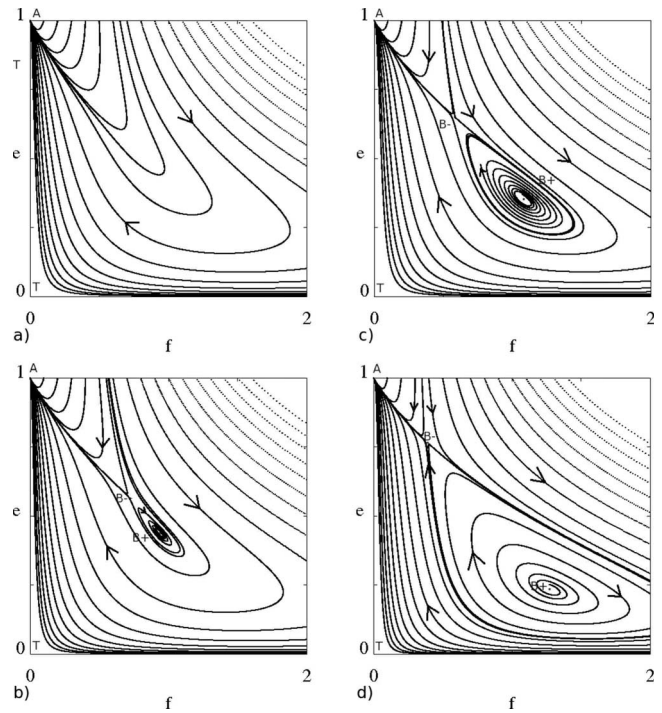


FIG. 5. Bifurcation structure of phenospatially homogeneous equations (14) with  $\varpi=0.6$ . Thus, we can compute  $\mu_c \approx 0.42$ ,  $\mu_{\text{Hopf}} \approx 0.40$ , and  $\mu_{\text{homoclinic}} = 0.34$ . (a) Extinction results when  $1/4\varpi = \mu_c < \mu$ ;  $\mu = 0.45$ . (b) Excitability occurs when  $\mu_{\text{Hopf}} < \mu < \mu_c$ ;  $\mu = 0.41$ . (c) Spatiotemporal intermittency is possible when  $\mu_{\text{homoclinic}} < \mu < \mu_{\text{Hopf}}$ ;  $\mu = 0.38$ . (d) Extinction again results when  $\mu < \mu_{\text{homoclinic}}$ ;  $\mu = 0.30$ .

that when  $e$  is only slightly positive it is drawn toward the point  $A$ . In the absence of the fixed points  $B_{\pm}$ , the environment fills up to full capacity but the organisms die out. However, things liven up when the other two fixed points ( $B_{\pm}$ ) make their appearance as  $\mu$  goes below the critical value  $\mu_c := 1/(4\varpi)$ .

Denoting either of the equilibria  $B_{\pm}$  by  $(f_0, e_0)$ , we look for solutions in the form  $f=f_0(1+\varphi)$  and  $e=e_0(1+\varepsilon)$ . Since  $e_0 f_0 = \mu$ , we then find the linearized equations for the perturbations about  $B_{\pm}$  equilibria to be

$$\dot{\varphi} = \mu\varphi + \mu\varepsilon, \quad \dot{\varepsilon} = -\varpi f_0\varphi - e_0\varepsilon, \tag{17}$$

where a dot indicates time derivative. If the solutions vary like  $\exp(\sigma t)$  we find, on using Eq. (16), that

$$\sigma^2 - (\mu - e_0)\sigma \pm \mu\sqrt{1-4\mu\varpi} = 0, \tag{18}$$

where  $1-4\mu\varpi \geq 0$  in the parameter regime of interest. Each pair of roots for each sign in this quadratic is associated to one of the fixed points  $B_{\pm}$ . When the pair  $B_{\pm}$  first appears, the system is excitable. That is, even though the fixed point  $A$  is globally stable, following a sufficiently large displacement from  $A$ , the system must follow a roundabout route (a loop around  $B_{\pm}$ ) to return to  $A$  (see Fig. 5). This sort of behavior is familiar from many biological examples (Griffith, 1971). It is also worth mentioning that an excitable medium, when subject to external noise, can produce limit cycles (Muratov et al., 2005).

If, for fixed  $\varpi$  such that  $\frac{1}{2} < \varpi < \varpi_M$  (where  $\varpi_M$  represents the point in parameter space where homoclinic and

Hopf bifurcations collide), we continue to lower the value of  $\mu$  below the critical value for the creation of  $B_{\pm}$ , we encounter a Hopf bifurcation at the value of  $\mu$  where  $B_+$  becomes an unstable spiral. Equation (18) then takes the form  $\sigma^2 + \omega^2 = 0$ , where  $\omega$  is a real number. The onset of this behavior occurs when  $\mu = e_0$ , which condition can be seen to imply that a growing oscillation about  $B_+$  occurs as we cross the line segment  $\mu = 1 - \varpi$  in parameter space. (We may also note that  $\omega = 0$  when we have  $\mu = 1/2$  and  $\varpi = 1/2$ . In the neighborhood of this point we have a Takens–Bogdanov bifurcation.) At the Hopf bifurcation we see the formation of a limit cycle around  $B_+$  and, as we continue to decrease  $\mu$ , the limit cycle becomes an increasingly larger loop until it runs into  $B_-$ . At that point, a homoclinic orbit forms through what is known as a homoclinic bifurcation. Figure 5 shows the behavior sequence corresponding to these events, including the destruction of the homoclinic orbit as  $\mu$  decreases further and  $A$  once again becomes a global attractor. Such behavior has been studied in detail (e.g., Argentina and Couillet, 1998). For  $\varpi > \varpi_M$  the order of the homoclinic and Hopf bifurcations is reversed.

The possibility of forming homoclinic orbits is the first hint of the kinds of structure we would hope to find in a model describing the behavior of species. Loosely speaking, a homoclinic trajectory is one that approaches the same fixed point as  $t \rightarrow +\infty$  and  $t \rightarrow -\infty$ . If we plot the value of  $e$  (say) versus time along the orbit, we obtain a pulse in time. However, in this special case of homogeneous phenospace, the pulses do not yet correspond to solitary waves or species. This deficiency will be remedied when we restore  $\alpha$  to the problem and look at (pheno)spatially inhomogeneous solutions when there are indeed emergent structures in the model that may be identified with species. Our intention in this section has been to give a look into the underlying structure of the simplest aspects of the model equations to learn what kind of temporal behavior the equations can produce. However, the spatially varying solutions, to which we turn next, are more suggestive of the formation of species.

## VI. STATIONARY SOLUTIONS

Our representation of a species is a solitary structure in phenospace that goes to zero away from its peak value. The simplest example of such an object occurs in the steady state. The equations in that case become

$$\chi f'' + \beta e (f')^2 = -F(f); \quad e = 1 - \varpi f, \tag{19}$$

where the prime indicates differentiation with respect to  $\alpha$  and  $F(f)$  is the cubic defined in Eq. (15). For a qualitative understanding of the content of this equation, we may think of Eq. (19) as a dynamical system, though the independent variable is not really time, so that we are dealing with a reversible system with the special feature that only solutions with positive  $f$  and  $e$  are realizable.

Homogeneous solutions  $f_0$  occur when  $F(f_0) = 0$ , and these are the same ones that are given in Eq. (16). We may perturb these to  $f = f_0 + \psi$  and linearize in  $\psi$  to study the “stability” of these “equilibria.” We obtain the linear equation

$$\chi_0 \psi'' = (\mu - 2f_0) \psi. \tag{20}$$

The eigenvalues of this problem aid in drawing the phase portraits in the  $f' - f$  plane. Alternatively, we may compute the trajectories numerically with the results shown in the accompanying figure (Fig. 6). Beyond a certain value of  $\mu$ , homoclinic solutions going to zero away from the peak value of  $\alpha$  appear. These are the species of the model. However, we naturally require that  $f = 0$  at  $\alpha = 0$  and  $\infty$  so these solutions are not realistic, though they provide some guidance, and we return to Eq. (19). The portions of the figure extending into negative  $f$  are shown to give a fuller feeling for the phase portraits.

To get a qualitative idea of where the species solutions first appear, we may omit the  $\beta$  term in Eq. (19), assume  $\chi$  constant and examine the equation

$$\chi f'' = -\frac{\partial V}{\partial f}, \tag{21}$$

where  $\partial V / \partial f = F$ . The neglected terms are actually small in the asymptotic study of the next chapter. Numerically, we find that they do not play a dominant role in this problem and we leave them out for this qualitative discussion. In this simplified case, we may integrate once to find the equation

$$\chi (f')^2 - \frac{\varpi}{4} f^4 + \frac{1}{3} f^3 - \frac{\mu}{2} f^2 = 0, \tag{22}$$

where a possible integration constant has been set equal to zero to give the reasonable condition that  $f'$  vanishes at the extreme values of  $\alpha$ . We may think of Eq. (22) as we would a dynamical system with  $\alpha$  playing the role of time. Then a homoclinic orbit approaching the origin as  $\alpha \rightarrow \infty$  and in the fictitious case  $\alpha \rightarrow -\infty$  represents a solitary structure of  $f$  as a function of  $\alpha$ .

The three extrema of  $V$  suggested by the phase portraits occur at the zeros of  $F$ , namely, the points  $A$ , at  $f = 0$ , and  $B_{\pm}$ . When the two maxima of  $V$  are at the same height, we have a heteroclinic stationary solution. This happens when  $\mu$  has the value  $\mu_S = 2/9\varpi$ , for then we may write

$$V = -\frac{1}{4} \varpi f^2 \left( f - \frac{2}{3\varpi} \right)^2. \tag{23}$$

The maxima at  $A$  and  $B_+$  are then at the same height. And, when  $\mu < \mu_S$ , the one at  $B_+$  is the higher and so homoclinic solutions emerging from  $A$  and returning to it again are possible. Those are the solutions representing species. Such steady solutions recall the model suggested by Eldridge and Gould (1972) with species that hardly evolve. However, the relevance of such solutions may be lessened by their instability. We next look at traveling wave solutions whose behavior points to the possibility of such instability. This is an aspect of the solutions that provides yet more guidance into what is happening in the numerical solutions of the model equations.

## VII. TRAVELING WAVES

Here we examine the case in which  $e$  and  $f$  depend only on  $\xi = \alpha - ct$ :



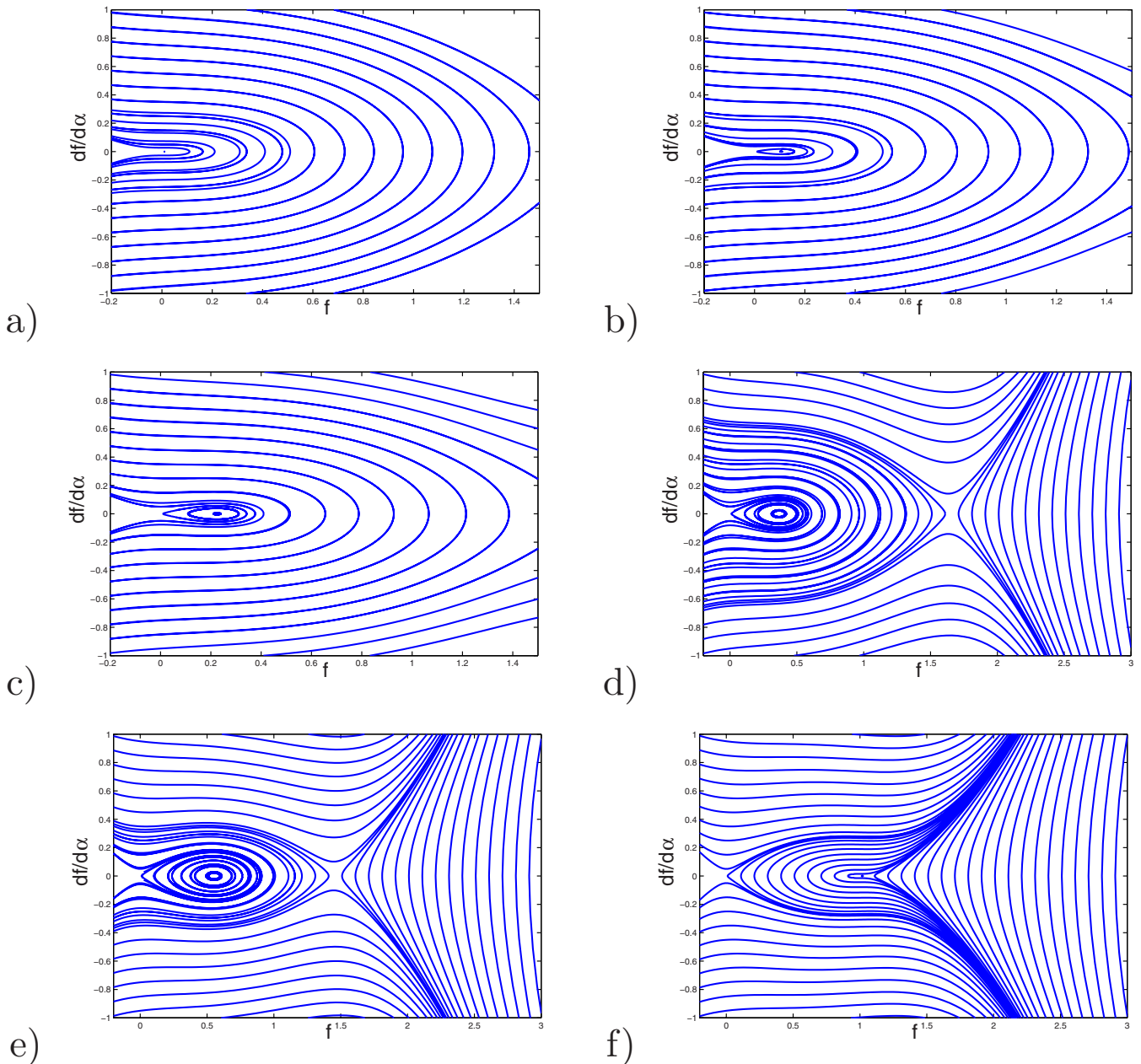


FIG. 6. (Color online) Numerical phase portraits for Eqs. (19).  $\varpi=0.5$ ,  $\kappa=1.0$ ,  $\beta=0.125$ . (a)  $\mu=0.01$ , (b)  $\mu=0.1$ , (c)  $\mu=0.2$ , (d)  $\mu=0.3$ , (e)  $\mu=0.4$ , (f)  $\mu=0.5$ .

$$f(\alpha, t) = f(\xi), \quad e(\alpha, t) = e(\xi). \tag{24}$$

This leads us to a system of three ordinary differential equations:

$$f_\xi = g, \tag{25}$$

$$\kappa g_\xi = -\mu f - cg - \beta e g^2 + e f^2, \tag{26}$$

$$c e_\xi = e(1 - e) - \varpi e f, \tag{27}$$

where the subscript stands for differentiation with respect to  $\xi$  and Eq. (25) is a definition of  $g$ .

The fixed points of this system all have  $g=0$  so that in the  $g=0$  plane, we find the fixed points associated with the stationary solutions studied earlier. For brevity, we shall not spell out the stability characteristics of the fixed points but

they may be easily read off from the phase portrait for this system shown in Fig. 7. We also show the homoclinic orbit of the reduced system that goes from  $(e, f, g)=(1, 0, 0)$  at  $t=-\infty$  and returns to the same point again at  $t=\infty$ . This homoclinic orbit corresponds to a pulse in  $\xi$ , and, thus, to a species. Significant features of the portrait are the hyperbolic fixed points lying off the axes; these correspond to the equilibria found in Eq. (16).

A trajectory that hugs the homoclinic orbit describes a clean-looking pulse. However, much as was seen in the previous section, this pulse is unstable to the formation of a small secondary pulse. This causes the trajectory in the state space of the traveling wave to be deflected so that it approaches the unstable manifold of the hyperbolic point. This encounter of the trajectory with that unstable equilibrium

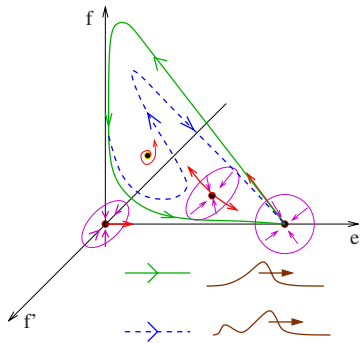


FIG. 7. (Color online) Sketch of the phase space for the traveling wave system.

results in the rapid formation of a new pulse with speed  $c$  moving in the opposite direction (in phenspace) from the parent. The computed orbit for this case is shown in Fig. 8. Though more elaborate schemes to follow the propagation and interaction of the pulses are available (e.g., Elphick *et al.*, 1990; Muratov, 2000), the present discussion may suffice to suggest the way in which the formation of a new species can become rapid when the phase space has a suitable structure. In the next section, we shall take a more quantitative look at the nature of the instability in the relatively simple case when  $\mu$  is very small.

**VIII. SMALL  $\mu$**

It is revealing to probe the core of the problem with a study of the asymptotic regime of small  $\mu$ . In examining this limit, we need to specify how  $\varpi$  behaves as  $\mu$  becomes small. Since the product  $\mu\varpi$  is central to many aspects of the problem, we might let  $\mu$  go to zero while keeping that product fixed. This gives the fullest version of the case of small  $\mu$  and it leads to an approximation of the species solutions in terms of elliptic functions. However, for our purpose of looking at the basic structure of the problem, it will suffice to consider the simpler case where  $\varpi$  remains of order unity as  $\mu$  goes to zero. To do this, we introduce new variables through these statements:

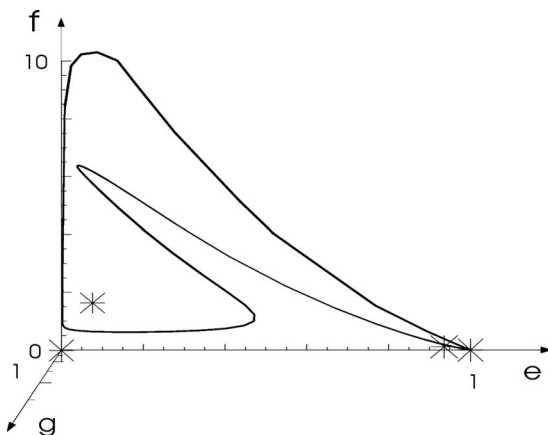


FIG. 8. Computed trajectory of a splitting pulse (thicker lines are in the foreground). Numerical simulations of the full system have been plotted in  $e$ - $f$ - $f'$ -space.

$$f(\alpha, t) = \mu\phi(x, \tau), \quad e(\alpha, t) = 1 - \mu\eta(x, \tau) \tag{28}$$

with

$$x = \sqrt{\mu}\alpha \quad \text{and} \quad \tau = \mu t. \tag{29}$$

When we introduce the indicated change of variables, we get, for  $\mu \rightarrow 0$ , the equation

$$\phi_\tau = \chi\phi_{xx} + \frac{\partial V}{\partial \phi}, \tag{30}$$

where

$$V = -\frac{1}{2}\phi^2 + \frac{1}{3}\phi^3 \tag{31}$$

and the subscripts  $x$  and  $\tau$  stand for differentiation with respect to those variables. In this limiting case, the  $\beta$ -term is negligible; it does not have an important qualitative effect on the solutions in general, as we have already suggested. Equation (30) is a nonlinear diffusion equation. It differs from the time-dependent Ginzburg–Landau equation most significantly in that its solutions are real and thus we avoid the drawback of having underlying modes that oscillate about zero, which would be inappropriate in the present context. Because the  $\beta$ -term is negligible in the asymptotics, the orbits in the  $f$ - $f'$  plane are periodic, except for those going off to infinity.

In this asymptotic case as well, we observe the formation of a solitary wave that represents a species. These solitary waves, appearing already in the steady solutions, are easily calculated. To see this we write the steady version of Eq. (30) as

$$\chi\phi'' = \phi(1 - \phi), \tag{32}$$

where the prime now denotes differentiation with respect to  $x$ . We multiply by  $\phi'$  and integrate once to obtain

$$\chi(\phi')^2 = \phi^2 - \frac{2}{3}\phi^3. \tag{33}$$

A constant of integration has been set to zero to allow  $\phi'$  to vanish when  $\phi$  does. This equation may be simplified by the substitution

$$\phi = \frac{6y^2}{(1 + y^2)^2}. \tag{34}$$

The resulting equation for  $y$  is easily integrated to yield

$$y = e^{\pm(x-x_*)/2\sqrt{\chi}}, \tag{35}$$

where  $x_*$  is a constant of integration. Together, Eqs. (34) and (35) represent a stationary species in the asymptotic limit. Both  $\phi$  and  $\phi'$  vanish when  $y$  is zero or infinity; that is, when  $x$  is very different from  $x_*$ . The two signs correspond to the two kinds of asymmetric (in  $\alpha$ ) solitary waves seen in the numerical solutions of the full equations. However, a single solitary structure, or species, such as we have just found is not the only possible solution. We may also obtain a series of structures with either periodic or chaotic spacings. These richer solutions can be found numerically or asymptotically in the limit where the species are widely spaced but we shall not present that analysis here.

To study the stability of the steady solution, we set

$$\phi(x, \tau) = \phi_0(x) + \psi(x, \tau), \quad (36)$$

where  $\phi_0$  is the steady solution and  $\psi$  is a perturbation. For perturbations with small  $|\psi|$ , we linearize Eq. (30) and obtain

$$\psi_\tau = \chi \psi_{xx} - \psi + 2\phi_0 \psi. \quad (37)$$

We then introduce a solution of the form

$$\psi(x, \tau) = e^{\nu\tau} \Psi(x) \quad (38)$$

into Eq. (37). This leads to

$$\nu\Psi = \chi\Psi_{xx} - \Psi + 2\phi_0\Psi. \quad (39)$$

For  $\nu=0$ , this equation has the solution

$$\Psi(x) = (\phi_0)_x. \quad (40)$$

In the case where the steady solution is the basic single solitary species  $\phi_0$ ,  $\Psi$  will have a single node. The qualitative significance of this is understandable by analogy with wave mechanics.

The eigenvalue equation (39) is the time-independent Schrödinger equation for the stationary states of a single particle whose energy is proportional to  $-\nu$ . The particle is moving in a potential  $1-2\phi_0$ . For the case where  $\phi_0$  describes a single species,  $1-2\phi_0$  represents a potential well in the wave mechanical analogue. For this case, the solution (40) is a zero energy state and, as it is the derivative of the single solitary structure, it has one node. By the known rules for ordering such solutions, we can expect only one mode with no nodes and it will have negative energy; that is, it will have  $\nu>0$  and be unstable in the present context. The other modes, will have more than one node and be stable. The unstable mode with no nodes is an incipient species that bifurcates from the original one. The case where  $\phi_0$  represents an array of species in phenospace is more complicated and, in the wave mechanical analog, it corresponds to a particle moving in a lattice.

## IX. DISCUSSION

Our aim in this work has been to construct a simple yet general model that embodies accepted macroscopic features of evolution theory to see whether qualitative features that emerge in discussions of the process of the evolution of species could be reproduced. We have analyzed our model to reveal how such processes may have mathematical counterparts, in the belief that there is some value in having a mathematical language for such things. A key feature of our discussion is the representation of a species by a solitary wave in the space whose coordinates represent macroscopic properties of organisms (phenospace). The phenomena that we have included in the model seem to be generic; these include mutation and inability to cross-breed easily, and we suggest that the general character of the results are not very dependent on the details of the description. The splitting and formation of solitary waves are processes that should illuminate discussions of speciation, with the possible occurrences of behaviors like gradualism and punctuated equilibrium arising quite naturally according to parameter choices.

For example, in some discussions, the notion of punctuated equilibrium seems to mean mainly a rapid speciation,

such as we saw in some of our results. On the other hand, qualitative drawings of the process seem to imply oscillations of the properties of a species consisting of periods of rapid change separated by stasis. That sort of behavior is not evident in our present results, but by enriching the model, we can produce that as well.

To the extent that this kind of model offers a way to test qualitative ideas about evolution, we believe that it would be worth extending the model beyond its present simplified form. Many of the simplifications we have introduced can be dispensed with. The most apparent of our simplifications is the use of a one-dimensional phenospace, and it is far too great a simplification. The model should be extended to allow for many more characteristics and their interaction with breeding potential. Such a generalization raises the possibility of richer behavior.

Our description of the environment and its depletion by a species is also too schematic. We need especially to allow for geographical variations in our discussions. These have a certain similarity to the introduction of more phenotypical parameters, as far as their complicating effects are concerned, but they have a different meaning with respect to the interpretation of results and the comparison with observations. These are already well-studied issues, but we need to see how these effects couple to the propagation in phenospace. Another direction that lies open is the inclusion of species competition and the introduction of predator-prey dynamics. It is clear that such moves toward increased reality will take us down the road to enhanced complexity, but that is the nature of the problem.

## ACKNOWLEDGMENTS

Over the years we have thought about the issues raised here, there have been many who have made comments and suggestions. They are too numerous to name, even if we could remember them all. Among them are our fellow participants in the 1994 GFD Summer Program at the Woods Hole Oceanographic Institution as well as audience members in many seminars on this work. Above all, we are grateful for their kind reception of our efforts.

## APPENDIX: NUMERICAL METHODS

In Sec. III we solved a set of integro-differential equations numerically. Solutions are obtained by discretizing in  $\alpha$ -space and evolving the system in time with a Runge–Kutta scheme.  $f$  is set to zero in a region close to the boundaries. In Sec. IV we solved a set of partial differential equations. Newton's method is used to do this efficiently, employing band-diagonal LU decomposition and a semi-implicit scheme. Time derivatives are replaced by their forward differences and other terms are replaced by weighted averages of the future unknown values of the variables and their present values. Initial conditions are either generated with a random superposition of sinusoidal modes (keeping  $e$  and  $f \geq 0$ ) or an offset lump for  $f$  and dip for  $e$  as for previous simulations.  $f$  is set to zero on the boundaries.

- <sup>1</sup>Argentina, M., and Couillet, P., "A generic mechanism for spatiotemporal intermittency," *Physica A* **257**, 45–60 (1998).
- <sup>2</sup>Argentina, M., Couillet, P., and Mahadevan, L., "Colliding waves in an excitable medium: preservation, annihilation and bifurcation," *Phys. Rev. Lett.* **79**, 2803 (1997).
- <sup>3</sup>Bees, M., "A mathematical model of speciation," in *Geophysical Fluid Dynamics: Bio-physical Models of Oceanic Population Dynamics*, Woods Hole Oceanog. Inst. Tech. Rept., WHOI-97-18, 1994.
- <sup>4</sup>Bull, V., Beltrn, M., Jiggins, C. D., McMillan, W. O., Bermingham, E., and Mallet, J., "Polyphyly and gene flow between non-sibling *Heliconius* species," *BMC Biology* **4** (2006).
- <sup>5</sup>Dawkins, R., *The Selfish Gene* (Oxford University Press, Oxford, 1989).
- <sup>6</sup>Dieckmann, U., and Doebeli, M., "On the origin of species by sympatric speciation," *Nature (London)* **400**, 354–357 (1999).
- <sup>7</sup>Doebeli, M., and Dieckmann, U., "Speciation along environmental gradients," *Nature (London)* **421**, 259–264 (2003).
- <sup>8</sup>Eldredge, R., and Gould, S. J., "Punctuated Equilibria: An alternative to phyletic gradualism," *Models in Paleobiology*, edited by T. J. M. Schopf (Freeman, Cooper, San Francisco, 1972), pp. 82–115.
- <sup>9</sup>Elphick, C., Meron, E., Rinzel, J., and Spiegel, E. A., "Impulse patterning and relaxational propagation in excitable media," *J. Theor. Biol.* **146**, 249–268 (1990).
- <sup>10</sup>Ewens, W. J., *Population Genetics* (Methuen, London, 1969).
- <sup>11</sup>Futuyama, D. J., *Evolutionary Biology*, 2nd ed. (Sinauer, Sunderland, MA, 1994).
- <sup>12</sup>Geritz, S. A. H., Metz, J. A. J., Kisdi, É., and Meszéna, G., "Dynamics of adaptation and evolutionary branching," *Phys. Rev. Lett.* **78**, 2024–2027 (1997).
- <sup>13</sup>Gingerich, P. D., "Evolutionary patterns in early Cenozoic mammals," *Annu. Rev. Earth Planet Sci.* **8**, 407–424 (1980).
- <sup>14</sup>Gould, S. J., *The structure of evolutionary theory* (Belknap Press/Harvard University Press, Massachusetts, 2002), p. 1433.
- <sup>15</sup>Griffith, J. S., *Mathematical Neurobiology* (Academic, New York, 1971).
- <sup>16</sup>Hall, M., Christensen, K., di Collobiano, S. A., and Jensen, H. J., "Time-dependent extinction rate and species abundance in a tangled-nature model of biological evolution," *Phys. Rev. E* **66**, 011904 (2002).
- <sup>17</sup>Hendry, A. P., Grant, P. R., Grant, B. R., Ford, H. A., Brewer, M. J., and Podoset, J., "Possible human impacts on adaptive radiation: beak size bimodality in Darwin's finches," *Proc. R. Soc. London, Ser. B* **273**, 1887–1894 (2006).
- <sup>18</sup>Izhikevich, E. M., *Dynamical Systems in Neuroscience* (MIT Press, Cambridge, MA, 2007).
- <sup>19</sup>Kuznetsov, Y. A., *Elements of Applied Bifurcation Theory* (Springer, New York, 2006).
- <sup>20</sup>Levin, S. A., and Segel, L. A., "Models of the influence of predation on aspect diversity in prey populations," *J. Math. Biol.* **14**, 253–284 (1982).
- <sup>21</sup>Muratov, C. B., "A quantitative approximation scheme for the traveling wave solutions in the Hodgkin-Huxley model," *Biophys. J.* **79**, 2893–2901 (2000).
- <sup>22</sup>Muratov, C. B., Vanden-Eijnden, E., and Weinan, E., "Self-induced stochastic resonance in excitable systems," *Physica D* **210**, 227–240 (2005).
- <sup>23</sup>Newman, C. M., Cohen, J. E., and Kipnis, C., "Neo-Darwinian evolution implies punctuated equilibria," *Nature (London)* **315**, 400 (1985).
- <sup>24</sup>O'Brien, P., "A genetic model with mutation and selection," *Math. Biosci.* **73**, 239–251 (1985).
- <sup>25</sup>Roughgarden, J., "Evolution of niche width," *Am. Nat.* **106**, 683–718 (1972).
- <sup>26</sup>Slatkin, M., and Lande, R., "Niche width in a fluctuating environment-density independent model," *Am. Nat.* **110**, 31–55 (1976).
- <sup>27</sup>Smolin, L., *The Life of the Cosmos* (Oxford University Press, Oxford, 1997).
- <sup>28</sup>Spencer, H., and Barakat, R., "Random genetic drift and selection in a triallelic locus: a continuous diffusion model," *Math. Biosci.* **108**, 127–139 (1992).
- <sup>29</sup>Strogatz, S., *Nonlinear Dynamics and Chaos: With Applications to Physics, in Biology, Chemistry and Engineering* (Perseus Books, New York, 1994).
- <sup>30</sup>Tang, Q., and Waxman, D., "An integral equation describing an asexual population in a changing environment," *Nonlinear Anal. Theory, Methods Appl.* **53**, 683–699 (2003).
- <sup>31</sup>Veronka, R., and Keller, J. B., "Asymptotic analysis of stochastic models in population genetics," *Math. Biosci.* **25**, 331–362 (1975).
- <sup>32</sup>Weiner, J., *The Beak of the Finch: Evolution in Real Time* (Knopf, New York / Jonathan Cape, London, 1994), p. 332.