

## SPECIATION: A CASE STUDY IN SYMMETRIC BIFURCATION THEORY

BY IAN STEWART

**Abstract.** Symmetric bifurcation theory is the study of how the trajectories of symmetric vector fields behave as parameters are varied. We introduce some of the basic ideas of this theory in the context of dynamical system models of speciation in evolution. Abstractly, these models are dynamical systems that are equivariant under the natural permutation action of the symmetric group  $\mathbf{S}_N$  on  $\mathbf{R}^{kN}$  for some integers  $N, k \geq 1$ . The general theory, which is group-theoretic in nature, makes it possible to analyse such systems in a systematic manner. The results explain several phenomena that can be observed in simulations of specific equations. In particular, in steady-state bifurcation, primary branches involve bifurcation to two-species states; such bifurcations are generically jumps; and the weighted mean phenotype of the organisms changes smoothly, whereas the standard deviation jumps. In particular, classical mean-field genetics, which focusses on allele proportions in the population, cannot detect this kind of speciation event.

### 1. INTRODUCTION

About 5 million years ago, a small number of finches belonging to the same species arrived on the Galápagos Islands, probably blown there by a storm, Lack [32]. In the absence of their usual predators, this ‘founder population’ of finches diversified into 13 species, plus a 14th on the Cocos Islands. Figure 1 shows the currently accepted phylogeny of these species. Grant [22] provides an accessible introduction to Darwin’s finches and their evolutionary history, along with pictures of the different species.

Some species now specialize in feeding on seeds, some on insects, some on cactus. This kind of process, known as *speciation*, is fundamental to evolutionary biology, and was the central point of Darwin’s *On the Origin of Species*

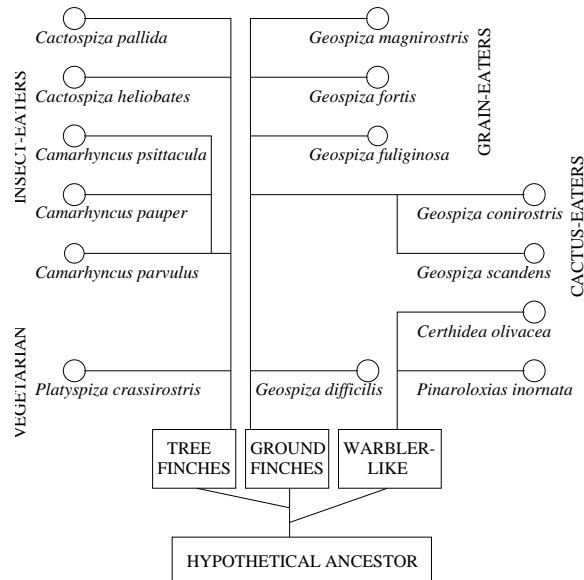


FIGURE 1. Phylogeny of Darwin's finches, after Lack [32].

of 1859. The finches of the Galápagos were a key example in his thinking, and they are known as 'Darwin's finches'. Their continuing evolution has now been observed for several decades, Grant *et al.* [24, 23], and it turns out that one of the most important features is climate. Changes to the climate affect the availability of food, and the finches evolve rapidly. The climatic changes are chaotic, and effectively unpredictable, but the evolutionary response of the birds to these changes is to some extent deterministic and predictable, Grant *et al.* [23]. It is therefore reasonable to study models of species change in which changing 'environmental' parameters drive a deterministic dynamical system.

Some recent models suggest that symmetry (which arises because different organisms in the same species are nominally identical) plays a significant role in the dynamics, and affects the generic behaviour. We focus on the underlying mathematical techniques of symmetric (or equivariant) bifurcation theory. We show how group-theoretic methods organize calculations in symmetric dynamical systems, and examine what results these methods yield in the speciation models.

**Genotype and Phenotype.** For a systematic exposition of modern evolutionary biology, see Ridley [40]. Deterministic models do not conflict with the widespread view in biology that mutations or other genetic factors in speciation are random, because natural selection within a given context is not

random — the central point made by Grant *et al.* [23]. However, the models described here are based on the possibly controversial assumption that the main role of the genes is to make it *possible* for phenotypes to change, while placing constraints (currently poorly understood) on what range of phenotypes may occur. In a physical analogy, the random movement of water molecules makes it possible for water to flow; but it is the surrounding landscape that determines *where* it flows. Thus the dynamics of rivers and lakes is predictable if we know enough about the landscape, but the motion of any given molecule of water is dominated by random fluctuations. In this analogy, the water molecule corresponds to a gene in an organism, and the role of selection corresponds to the landscape. See Cohen and Stewart [4] for further discussion. Here, our main aim is to describe the mathematics of the models, and their analysis, as a case study in symmetric bifurcation theory.

In most traditional models of speciation, the dynamical variables are proportions of *alleles* (alternative genes) in a mean-field gene-pool, see for example Maynard Smith [34]. More modern studies, under the name ‘adaptive dynamics’, introduce nonlinear effects and incorporate selection as an explicit dynamic mechanism (see for example Kisdi and Geritz [30]) but still make allele frequencies the key variables. Hofbauer and Sigmund [26] discuss many gene-based dynamic models of evolution. An alternative approach (Cohen and Stewart [4], Elmhirst [9, 10], Vincent and Vincent [47], Stewart *et al.* [44], Dias and Stewart [6]), which we focus on here, works with the phenotype, not the genotype. (The phenotype of an organism is its bodily form, markings, and behaviour. Its genotype is the DNA code in its genome.) The phenotype of a given organism is represented as a vector  $x = (x_1, \dots, x_m)$  in a *phenotypic space*  $\mathbf{R}^m$ , and the dynamic describes how  $x$  changes on an evolutionary timescale. More generally, we can replace  $\mathbf{R}^m$  by a manifold: the assumption here is that we are considering *continuous* characters, well modelled by variables taking values in  $\mathbf{R}$ . Discrete characters are another matter, and we do not consider them here.

In principle, there could be many different ways for speciation to occur. For example recent work on wallabies, Fox [16], suggests that sometimes disease organisms shuffle the genome. There is no reason to suppose that all instances of speciation fit into the same pattern; the current evolution of Darwin’s finches may not be what was involved in the appearance of *Tyrannosaurus rex*, or the divergence of chimpanzees and humans from a common ancestral species. So we should seek to understand possible mechanisms of speciation, and not expect to find a single mechanism. However, there is some prospect of finding generalities if we focus on abstract features of the process (such as ‘instability’) instead of fine details (the precise cause of the instability). For example, disease

organisms shuffling the genome is, for present purposes, just another way to render the genome ‘fluid’.

In general terms, biologists distinguish two main types of speciation process: ‘allopatric’ and ‘sympatric’, Mayr [35, 36]. For a finer classification, see Rice and Hostert [39]. In *allopatric* speciation some subpopulation of a single species becomes isolated geographically from the main population, and evolves separately under different environmental conditions. If the separation continues for long enough, eventually the two populations become unable to interbreed (Mayr’s test for ‘different species’). If, much later, the two groups end up in the same habitat, they will constitute two distinct species in the same location.

*Sympatric* speciation is less intuitive. Now the original population remains a single geographical group, but for some reason this group (which previously had cohered as one species) separates into two distinct phenotypic classes, even though all organisms are potentially able to interbreed. Eventually, reinforced by other factors such as ‘assortative mating’ — preference for a mate from the same subpopulation — the two types again become separate species. See for example Dieckmann and Doebeli [7], Higashi *et al.* [25], Kawecki [29], Kondrashov and Kondrashov [31], Rundle *et al.* [41], Tregenza and Butlin [45]. The challenge to intuition here is: if it makes evolutionary sense for one organism to evolve towards a particular new phenotype, why doesn’t it make the same sense for all the others to evolve towards the *same* phenotype? Especially when interbreeding stirs the gene-pool, just as it did when there was only one species.

Our general answer to this challenge is that it ignores issues of collective behaviour and context. It also ignores the question of stability. It therefore ignores the phenomenon of symmetry-breaking, in which symmetric causes produce less symmetric (including possibly asymmetric) effects, [21, 20].

The main aim of this paper is to summarize recent research on dynamical systems models of sympatric speciation, which represents this process as a symmetry-breaking bifurcation. The conclusion is that speciation (in some sense, possibly a rather limited one) is triggered when a diverse population is able to exploit its environment more effectively (as ‘observed’ by each individual, not just the collective) than a uniform population. In this case, selection on individual organisms drives the entire population towards a split into several (usually two) subpopulations, each representing a separate cluster in phenotypic space. Once this initial separation is established, other factors (such as assortative mating) can then reinforce this split, until eventually it becomes irreversible and the species become separate.

Of course, the biological details of this reinforcement are important. But it is the initial separation that gives evolution a ‘foot in the door’ to prise one

species apart into several, and it is this separation that is conceptually the most puzzling feature. The intuition that symmetry should be preserved is strong — and wrong.

## 2. AN IDEALIZED MODEL

In order to motivate the model, we start by representing the population of organisms by a probability density function  $P$  on phenotypic space  $\mathbf{R}^m$ . We assume that the population is large enough for a continuum model to be appropriate, in which case the probability that a randomly chosen organism has phenotype  $y$  belonging to some (measurable) subset  $Y$  of  $\mathbf{R}^m$  is

$$p(y \in Y) = \int_{y \in Y} P(y) dy,$$

where the integral is the Lebesgue integral. In order to perform simulations and analysis, we discretize this model. Choose a positive integer  $N$  and a ‘coarseness’  $\epsilon > 0$ . For any  $x \in \mathbf{R}^m$  let  $s_x(y)$  be a step function, constant on the ball of radius  $\epsilon$  centred at  $x$  and zero outside that ball, with total measure  $1/N$ . Approximate  $P$  by a finite sum

$$P(y) \sim \sum_{j=1}^N s_{x^j}(y).$$

Intuitively, each component  $s_{x^j}(y)$  of this sum represents a randomly chosen sample of the population, within tolerance  $\epsilon$  of the phenotype  $y$ . By taking  $N$  such samples (named ‘PODs’ in [4] — Placeholders for Organism Dynamics — and ‘tokens’ by Elmhirst [10]) we obtain a coarse-grained representation of the probability density function  $P$ .

As  $P$  evolves with time, the approximation evolves with it. So we can hope to replace the time-evolution of  $P$  by the time-evolution of representatives  $x^1, \dots, x^N$ . We assume that the  $x^j$  change according to a dynamical system:

$$\begin{aligned} \frac{dx^1}{dt} &= f_1(x^1, \dots, x^N, \lambda), \\ \frac{dx^2}{dt} &= f_2(x^1, \dots, x^N, \lambda), \\ &\dots \\ \frac{dx^N}{dt} &= f_N(x^1, \dots, x^N, \lambda), \end{aligned}$$

where for the moment we leave the vector field  $f = (f_1, \dots, f_N)$  unspecified. The parameter  $\lambda$  represents the effect of ‘environment’, and for simplicity we assume  $\lambda$  is 1-dimensional. For example,  $\lambda$  might be annual rainfall.

We also assume that the system can be modelled on two distinct timescales. The  $x^j$  change rapidly; the parameter  $\lambda$  changes ‘quasi-statically’, that is, so slowly that the  $x$ -dynamic treats  $\lambda$  as being constant while  $x$  responds to the current value of  $\lambda$ .

What constraints should we put on  $f$ ? The most important one stems from mathematical considerations rather than specific biological needs. It is a symmetry constraint. In sympatric speciation, the initial population is nominally identical, so all the  $x^j$  are equal. Thus the dynamics should be symmetric under all permutations of the indices  $1, \dots, N$ . Another and perhaps more compelling way to say this is that the time-evolution of  $P$  should not depend on the labels  $j$  that we assign to the representatives  $x^j$ .

We therefore arrive at the idea that the *interaction network*, a graph whose nodes represent PODs and whose edges represent interactions between them, should be *all-to-all coupled*, as in Figure 2.

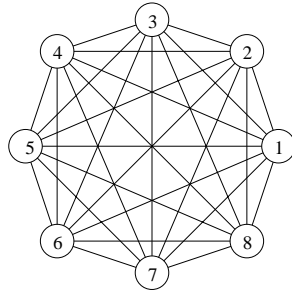


FIGURE 2. All-to-all coupled network with 8 PODs.

The symmetry of the network corresponds to a symmetry property of the Lebesgue integral. Suppose that  $P$  is an integrable function defined on a subset  $Y$ . Decompose  $Y$  into a finite set of almost disjoint measurable subsets  $Y_1, \dots, Y_s$ . (By ‘almost’ disjoint we mean that intersections have measure zero.) Let  $Z_j = Y_j + z_j$  be a translate of  $Y_j$ , for each  $j$ , and suppose that the  $Z_j$  are also almost disjoint. Finally, define a function  $Q$  by

$$Q(z) = P(z - z_j) \quad \text{if } z \in Z_j$$

with  $Q(z) = 0$  otherwise. That is,  $Q$  is a ‘shuffle’ of  $P$ . Then trivially

$$\int_{Z_j} Q(z) dz = \int_{Y_j} P(y) dy.$$

In particular, this formula holds if the  $Y_j$  are congruent boxes, and the map  $Y_j \mapsto Z_j$  permutes them. Thus the Lebesgue integral has an equivariance property under permutations of almost disjoint subsets of its domain. Permuting tokens should respect this equivariance.

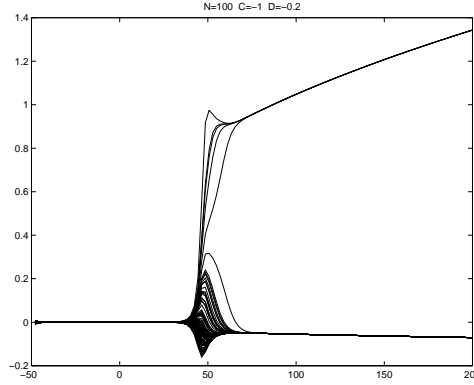


FIGURE 3. Simulation of speciation for  $N = 100$  clumps of organisms. Note division of population into two species of 16 and 84 clumps each. Time series of all cells are superposed, with  $\lambda$  horizontal and  $x_j$  vertical for each  $j$ .

Either way, we deduce that  $f$  must be *equivariant* under the action of the symmetric group  $\mathbf{S}_N$ ; that is,

$$f_{\sigma i}(x^1, \dots, x^N, \lambda) = f_i(x^{\sigma^{-1}1}, \dots, x^{\sigma^{-1}N}, \lambda)$$

for all  $\sigma \in \mathbf{S}_N$ . Again, see [4]. Equivalently,

1.  $f_i(x)$  is invariant under all permutations that fix  $i$ .
2.  $f_j(x)$  is obtained from  $f_i(x)$  by interchanging  $i$  and  $j$ .

For example, one possible choice of  $f$  takes the form

$$(2.1) \quad \begin{aligned} \frac{dx^1}{dt} &= x_1 - x_1^3 + \lambda(x^1 + \dots + x^N), \\ \frac{dx^2}{dt} &= x_2 - x_2^3 + \lambda(x^1 + \dots + x^N), \\ &\dots \\ \frac{dx^N}{dt} &= x_N - x_N^3 + \lambda(x^1 + \dots + x^N). \end{aligned}$$

This is a typical example of an  $\mathbf{S}_N$ -equivariant vector field. Below, we consider more examples. But already this example illustrates some key ideas.

Figure 3 shows a typical numerical simulation of (2.1) when  $N = 100$ . When  $\lambda < 0$  there is a unique equilibrium in which all  $x^j = 0$ . When  $\lambda > 0$  the  $x^j$  make a rapid jump away from 0: either to a positive value or a negative value. Once the transients associated with the jump have settled down, only two possible values of the phenotypic variables occur. In this particular case, 16 PODs take the positive value and 84 take the negative one.

The bifurcation appears to happen at  $\lambda \sim 40$ , which is the result of ‘slow passage effects’. Because of the way the simulation is performed, the  $x^j$  become extremely small, at an exponential rate, as  $\lambda$  increases towards 0. Once  $\lambda$  becomes greater than zero, it takes many iterations before the instability in the  $x^j$  becomes visible to the eye. See Neihstadt [37, 38].

The general theory of equivariant dynamical systems shows that typically, when there is a symmetry-breaking bifurcation of this kind, the system bifurcates to a state in which all entries  $x^i$  of  $x$  take one or other of two particular values  $u, v$ , where  $u > 0$  and  $v < 0$ . This result does not depend on the specific form of the ODE: just on its symmetries. We now explain how this behaviour comes about.

### 3. EQUIVARIANT BIFURCATION THEORY

In this section, we describe the underlying mathematical generalities: equivariant bifurcation theory. We then specialize the results to the model (2.1), and thereby explain its behaviour.

**3.1. Group-Theoretic Formalism.** The general context for a symmetry-based analysis of pattern formation in equivariant dynamical systems is symmetric (or equivariant) bifurcation theory. This is surveyed in Golubitsky *et al.* [21, 20]. We briefly summarize the main ideas, which are group-theoretic in nature.

Let  $\Gamma$  be a (compact) Lie group of linear (without loss of generality, orthogonal) transformations of  $\mathbf{R}^n$ . If  $\gamma \in \Gamma, x \in X$  we denote the action of  $\gamma$  on  $x$  by  $\gamma x$ . We say that a smooth vector field  $f : \mathbf{R}^n \times \mathbf{R} \rightarrow \mathbf{R}^n$  is  $\Gamma$ -equivariant if

$$(3.1) \quad f(\gamma x, \lambda) = \gamma f(x, \lambda)$$

for all  $\gamma \in \Gamma$ . Such an  $f$  determines a  $\Gamma$ -equivariant ODE

$$(3.2) \quad \frac{dx}{dt} + f(x, \lambda) = 0,$$

where  $x \in \mathbf{R}^n, \lambda \in \mathbf{R}$ . Steady states are zeros of  $f$ . The symmetry of  $f$  implies that for fixed  $\lambda$ , the zeros of  $f$  come in symmetrically related sets. Specifically, if  $x \in \mathbf{R}^n$  then the *orbit* of  $x$  under  $\Gamma$  is

$$\Gamma x = \{\gamma x : \gamma \in \Gamma\}$$

and if  $x(t)$  is a solution, then so is  $\gamma x(t)$ .

The *isotropy subgroup* of  $x \in V$  is

$$\Sigma_x = \{\sigma \in \Gamma : \sigma x = x\}.$$



If  $H \subset \Gamma$  is any subgroup, then its *fixed-point subspace* is

$$\text{Fix}(H) = \{x \in V : \gamma x = x \quad \forall \gamma \in H\}.$$

The isotropy subgroup of  $x$  captures the symmetry of the state  $x$ . The fixed-point subspace is a ‘dual’ notion, and describes all  $x$  with a given symmetry group  $H$ .

If  $x, y$  lie in the same  $\Gamma$ -orbit, then their isotropy subgroups are conjugate:

$$\Sigma_{\gamma x} = \gamma \Sigma_x \gamma^{-1}.$$

Conversely, conjugate  $H$  have fixed-point subspaces in the same  $\Gamma$ -orbit:

$$\text{Fix}(\gamma H \gamma^{-1}) = \gamma \text{Fix}(H).$$

For many purposes we do not need to distinguish between the conjugates of a given subgroup.

The (conjugacy classes) of isotropy subgroups of  $\Gamma$  form a partially ordered set, conventionally called the *isotropy lattice* of  $\Gamma$ , even though it is often not a lattice in the usual technical sense. The isotropy lattice provides a useful guide to the probable sequence of symmetry-breaking events: roughly speaking, each successive loss of stability results in an isotropy subgroup that is lower down in the lattice — often, but not always, one step lower down. See Field [12] and Field and Richardson [13, 14, 15]. In any case, the isotropy lattice can be used to organize computations in terms of restrictions to successively larger fixed-point subspaces. This can be done because fixed-point subspaces have a simple but crucial property: if  $f$  is  $\Gamma$ -equivariant and  $H$  is any subgroup of  $\Gamma$ , then

$$f(\text{Fix}(H)) \subseteq \text{Fix}(H).$$

Therefore we can consider the restriction

$$f|_{\text{Fix}(H)} : \text{Fix}(H) \rightarrow \text{Fix}(H)$$

which defines a dynamical system in its own right. Moreover,  $\text{Fix}(H)$  contains any trajectory  $x(t)$  that has symmetry  $H$ . The restriction  $f|_{\text{Fix}(H)}$  satisfies an equivariance condition: it is equivariant under the action of  $N(H)/H$  where  $N(H)$  is the normalizer of  $H$  in  $\Gamma$ . Sometimes it satisfies further constraints, called ‘hidden symmetries’, see [20].

**3.2. Local Bifurcation.** Next, we summarize the local bifurcation theory of symmetric vector fields. That is, we examine qualitative changes in the topology of the phase portrait (system of trajectories) as the parameter  $\lambda$  varies.

For simplicity, assume that  $f(0, \lambda) \equiv 0$ , so there exists a ‘trivial branch’ of solutions  $x = 0$ . The *linearization* of  $f$  is the derivative

$$L_\lambda = D_x f|_{0, \lambda}$$

Local bifurcation at  $\lambda = 0$  occurs when the trivial branch undergoes a change of linear stability, so that  $L_0$  has eigenvalues on the imaginary axis (often called *critical eigenvalues*). There are two cases:

1. *Steady-state bifurcation*:  $L_0$  has a zero eigenvalue.
2. *Hopf bifurcation*:  $L_0$  has a complex conjugate pair of purely imaginary eigenvalues.

Hopf bifurcation leads to time-periodic solutions and will not be considered in this paper. A bifurcating branch *breaks symmetry* if the corresponding isotropy subgroup is not the whole of  $\Gamma$ . The *critical eigenspace* is the real generalized eigenspace  $E$  for the critical eigenvalues. By equivariance,  $E$  is a  $\Gamma$ -invariant subspace of  $\mathbf{R}^n$ . For steady-state bifurcation, generically  $E$  is absolutely irreducible: the only equivariant linear maps are scalar multiples of the identity. Centre manifold reduction, Carr [2], reduces the problem to one posed on  $E$ .

The simplest and most widely used existence theorem for steady-state branches is the Equivariant Branching Lemma. To state it we require the concept of an *axial* subgroup: this is an isotropy subgroup  $\Sigma$  for which  $\dim \text{Fix}(\Sigma) = 1$ .

**THEOREM 3.1. (EQUIVARIANT BRANCHING LEMMA).** *Let  $f(x, \lambda) = 0$  be a  $\Gamma$ -equivariant bifurcation problem where  $\text{Fix}(\Gamma) = 0$ . Let  $\Sigma$  be an axial subgroup. Then generically there exists a branch of solutions to  $f(x, \lambda) = 0$  emanating from the origin with symmetry group  $\Sigma$ .*

This theorem is originally due to Vanderbauwhede [46] and Cicogna [3]. For a proof see Golubitsky *et al.* [21] Chapter XIII Theorem 3.3 p.82.

#### 4. THE SYMMETRIC GROUP

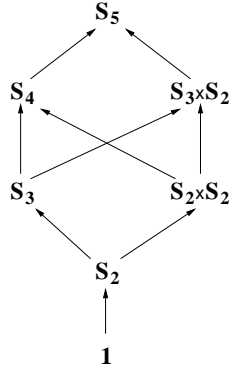
Now we specialize the above algebraic constructions to the symmetry group of the speciation models, which is the symmetric group  $\mathbf{S}_N$  acting on  $\mathbf{R}^N$  by permutation matrices.

We can compute the isotropy subgroups of  $\mathbf{S}_N$  acting on  $\mathbf{R}^N$ . If  $\sigma \in \mathbf{S}_N$  and  $\sigma x = x$ , then the only entries  $x_i, x_j$  of  $x$  that can be permuted by  $\sigma$  are those with equal values,  $x_i = x_j$ . We therefore partition  $\{1, \dots, N\}$  into disjoint blocks  $B_1, \dots, B_k$  so that  $x_i = x_j$  if and only if  $i, j$  belong to the same block. Now

$$\Sigma_x = \mathbf{S}_{b_1} \times \dots \times \mathbf{S}_{b_k}$$

where  $b_\ell = |B_\ell|$  and  $\mathbf{S}_{b_\ell}$  is the symmetric group on block  $B_\ell$ .

Conjugacy classes of isotropy subgroups of  $\mathbf{S}_N$  are in one-to-one correspondence with partitions of  $N$  into nonzero natural numbers arranged in ascending order. The isotropy lattice is isomorphic, as a partially ordered set, to the set

FIGURE 4. Isotropy lattice of  $\mathbf{S}_5$ .

of all such partitions, with the ordering being defined by refinement, [20]. For example the isotropy lattice of  $\mathbf{S}_5$  is shown in Figure 4.

Suppose that  $\Sigma$  is an isotropy subgroup corresponding to the simplest nontrivial partition  $P = \{p, q\}$  where  $p + q = N$ , and to avoid ambiguity  $p \leq N/2$ . Then  $\text{Fix}(\Sigma)$  consists of all vectors

$$\underbrace{(u, \dots, u)}_p, \underbrace{(v, \dots, v)}_q$$

for real numbers  $u, v$ . Therefore  $\dim \text{Fix}(\Sigma) = 2$ . Similarly, if  $\Sigma$  corresponds to a partition of  $N$  into  $k$  blocks, then  $\dim \text{Fix}(\Sigma) = k$ . Finally, we restrict the action of  $\mathbf{S}_N$  onto the standard irreducible  $\mathbf{R}^{N-1}$ , by imposing the relation  $x_1 + \dots + x_N = 0$ . The isotropy subgroups remain the same, but the dimension of every fixed-point subspace is reduced by 1. In particular the isotropy subgroups  $\mathbf{S}_p \times \mathbf{S}_q$ , where  $p + q = N$ , are axial. By the Equivariant Branching Lemma, generically there exist branches of equilibria with isotropy subgroups  $\mathbf{S}_p \times \mathbf{S}_q$ . We call these the *primary* branches. Such solution branches correspond to a split of the population of  $N$  identical PODs into two distinct species consisting of  $p$  and  $q$  PODs respectively, having respective phenotypes  $u$  and  $v$ . So in *all*  $\mathbf{S}_N$ -equivariant ODEs, speciation (in this sense) is a consequence of symmetry-breaking.

Already we can make an interesting *quantitative* prediction: on the above branches the mean value of the phenotypic variables changes smoothly during the bifurcation. The fixed-point space of  $\mathbf{S}_p \times \mathbf{S}_q$  is spanned by all vectors of the form

$$(u, \dots, u; v, \dots, v)$$

where there are  $p$   $u$ 's and  $q$   $v$ 's. In the irreducible  $(N - 1)$ -dimensional representation of  $\mathbf{S}_N$ , the entries sum to zero:

$$(4.1) \quad pu + qv = 0.$$

Therefore the mean value of the phenotypic variable after bifurcation is  $(pu + qv)/N = 0$ . Before bifurcation it is also 0, because we are looking for bifurcations from the trivial equilibrium and have normalised the phenotypic variables to be zero for the original single species. Now, we are working with the centre manifold reduction, which involves a nonlinear change of variables (via a diffeomorphism). Therefore the mean varies *smoothly* in the original phenotypic variables.

**4.1. Example: Darwin's Finches.** The process of speciation cannot be observed directly on very long timescales, but is sometimes observable on a shorter timescale: one example is Darwin's finches. As a substitute for evolution, we can observe two related species or subspecies that sometimes coexist in the same environment, and sometimes do not. When they do not coexist, their phenotypes should correspond to an allopatric context, without speciation; has occurred. When they coexist, their phenotypes should correspond to a sympatric context, after speciation.

With this interpretation, the 'constant mean' prediction is consistent with several field studies, normally interpreted as evidence for character displacement, Salthe [42]. See [4, 44, 43]. We mention just one example here: Darwin's finches. In this case, the relevant phenotypic variable is beak size. The species *G. fortis* and *G. fuliginosa* occur in both sympatric and allopatric populations. *G. fortis* is allopatric on Daphne, and *G. fuliginosa* is allopatric on Crossman. Moreover, the two species are sympatric on a number of islands, which occur in three groups: Abingdon, Bindloe, James, Jervis; Albemarle, Indefatigable; and Charles, Chatham. Figure 5, adapted from Lack [32], shows the differences in beak size between these species on these groups of islands. The mean beak sizes of *G. fortis* and *G. fuliginosa* are approximately 10mm in the allopatric case. In all three sympatric populations, the mean for *G. fortis* is about 12mm, while that for *G. fuliginosa* is about 8mm. Thus they diverge in opposite directions with a constant mean of about 10mm.

**4.2. The General Cubic Truncation.** The model (2.1) is extremely special, and we seek a more general family of models that displays typical behaviour. We approach this problem through the Taylor series of the vector field near the bifurcation point.

A standard way to analyse bifurcations is to expand the Taylor series of the vector field and then truncate at some (low) degree, see for example Iooss and

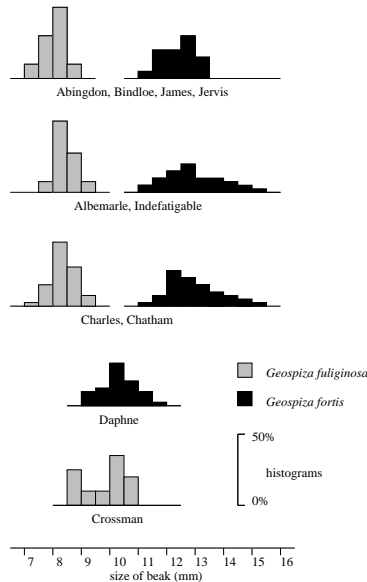


FIGURE 5. Beak sizes in allopatric and sympatric populations of *Geospiza* in the Galápagos Islands. After Lack [32].

Joseph [27]. Using methods from singularity theory or topology, it is sometimes possible to justify this truncation rigorously, but for present purposes we consider the truncation process as a way to write down a simple but interesting model. For speciation models, truncation at cubic order is highly informative. (The quadratic truncation has too low a degree to be representative.)

Cohen and Stewart [4] study the Taylor series of an  $\mathbf{S}_N$ -equivariant vector field  $f$ , and show that the general symmetry-breaking bifurcation can be transformed (by centre manifold reduction) to the form

$$(4.2) \quad \frac{dx_i}{dt} = \lambda x_i + B(Nx_i^2 - \pi_2) + C(Nx_i^3 - \pi_3) + Dx_i\pi_2$$

plus higher order terms, for  $i = 1, \dots, N$ . Here  $\lambda, B, C, D \in \mathbf{R}$  are parameters, and

$$\begin{aligned} \pi_2 &= x_1^2 + \dots + x_N^2, \\ \pi_3 &= x_1^3 + \dots + x_N^3. \end{aligned}$$

In a sense that can be made precise, (4.2) is the simplest *interesting* equation of the type we wish to consider. It has the virtue that it can be analyzed more or less explicitly, and we summarize the results.

Primary branches and their stabilities have been analysed by Elmhirst [9]. By the Equivariant Branching Lemma, primary branches of equilibria occur

on the spaces  $W_p = \text{Fix}(\mathbf{S}_p \times \mathbf{S}_q)$  where  $p + q = N$  and  $1 \leq p \leq N/2$ . We coordinatize  $W_p$  by  $\alpha \in \mathbf{R}$ , corresponding to the point

$$\alpha(\underbrace{q, \dots, q}_p; \underbrace{-p, \dots, -p}_q).$$

Define

$$\begin{aligned} n &= N(N - 2p), \\ c &= C(N^2 - 3Np + 3p^2), \\ d &= D(N^2 - N(N + 3)p + (N + 3)p^2). \end{aligned}$$

Then the branching equation on  $W_p$  is

$$\lambda = -\alpha n - \alpha^2 N(c - d),$$

which is a parabola passing through the origin. Together with the trivial solution, the bifurcation diagram on  $W_p$  looks like Figure 6.

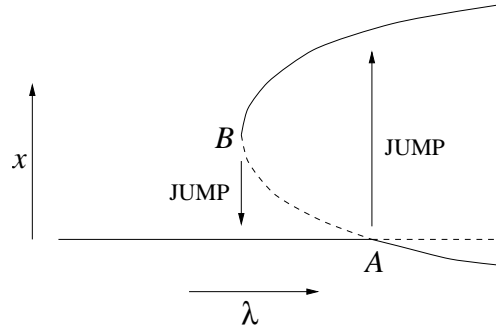


FIGURE 6. Bifurcation diagram illustrating jumps and hysteresis.

Let  $\alpha_0$  be the  $\alpha$ -coordinate of the other point at which the parabola crosses the  $\alpha$ -axis, and let  $(\lambda_c, \alpha_c)$  be the coordinates of the vertex of the parabola. Then

$$\begin{aligned} \alpha_0 &= \frac{n}{N(d - c)}, \\ \alpha_c &= \frac{n}{2N(d - c)}, \\ \lambda_0 &= \frac{n^2}{4N(c - d)}. \end{aligned}$$

Stability of a branch of equilibria depends on the eigenvalues of the linearization  $Df$  along the branch. For the primary branches, these eigenvalues

are:

$$(4.3) \quad \begin{aligned} \mu_0 &= \alpha n + 2\alpha^2 N(c - d) \\ \mu_1 &= \alpha N^2 + \alpha^2 N^2(2N - 3p)(C - D) \\ \mu_2 &= -\alpha N^2 + \alpha^2 N^2(3p - N)(C - D) \end{aligned}$$

with multiplicities  $1, p - 1, q - 1$  respectively. Note that when  $N = 3$  we have  $p = 1$  so  $\mu_1$  does not occur.

Near the origin, the eigenvalues  $\mu_1$  and  $\mu_2$  have opposite signs. Therefore the bifurcating branches are always unstable near the origin. This is why we must work with (at least) the cubic truncation, which permits primary branches to re-stabilize, for example by ‘turning round’ at a saddle-node bifurcation. There is a general reason for the instability near the origin: see subsection 4.3 below.

Simulations of 4.2 for many values of the parameters can be found in Stewart *et al.* [44] and Stewart [43].

**4.3. Local Instability of Secondary Branches.** Some features of the secondary branches in this problem can be ‘predicted’ on general grounds of symmetry. Computations (Dias and Stewart [6]) provide considerable extra detail, but these generalities put the results in context.

It is known that generically, all primary branches of equilibria in an  $\mathbf{S}_N$ -equivariant system of ODEs that can be found by applying the Equivariant Branching Lemma (that is, the branches with ‘axial’ isotropy subgroups) are locally unstable, that is, unstable close enough to the bifurcation point. Call these *axial branches*. This result applies when  $\mathbf{S}_N$  acts in its standard  $(N - 1)$ -dimensional irreducible representation, and can be traced to the existence of a non-trivial quadratic equivariant mapping. See Golubitsky *et al.* [21] Theorem XIII 4.4 and Golubitsky and Stewart [20].

We have seen that primary branches in  $\mathbf{S}_N$ -equivariant systems (in the stated representation) are axial, with isotropy subgroups of the form  $\mathbf{S}_p \times \mathbf{S}_q$  with  $p + q = N$ . Moreover, the representation of this subgroup decomposes into three irreducible subspaces, of dimensions  $1, p - 1, q - 1$  respectively: call these  $W_0, W_1, W_2$ . Both  $\mathbf{S}_p$  and  $\mathbf{S}_q$  act trivially on  $W_0$ . On  $W_1$ , the subgroup  $\mathbf{S}_q$  acts trivially and  $\mathbf{S}_p$  acts by its standard irreducible representation; and the same goes with  $p, q$  interchanged for  $W_2$ .

Follow a primary branch until an eigenvalue of the Jacobian changes sign. Generically, the kernel (eigenspace) is one of  $W_0, W_1, W_2$ . If it is  $W_0$  then the symmetry remains unbroken, and we expect a fold point in the branch. If it is  $W_1$  then the  $\mathbf{S}_q$  symmetry remains unbroken, but the  $\mathbf{S}_p$  symmetry breaks; correspondingly for  $W_2$ . Consider the case  $W_1$ . Centre manifold reduction near this bifurcation point, Carr [2], reduces the problem to a bifurcation problem on  $W_1$ . The primary branch for the original problem becomes the

‘trivial’ branch for this reduced problem, and the secondary branch becomes a primary branch in the reduced problem.

The reduced problem is equivariant under the normalizer quotient  $N(\Sigma)/\Sigma$  where  $\Sigma = \mathbf{S}_q$ , and this quotient is easily seen to be isomorphic to  $\mathbf{S}_p$ . Therefore we expect to find a generic  $\mathbf{S}_p$ -equivariant bifurcation in the reduction. But now the theory of  $\mathbf{S}_N$ -equivariant bifurcations applies (with  $N$  replaced by  $p$ ). We predict the occurrence of branches for all axial subgroups of  $\mathbf{S}_p$ ; that is, all subgroups  $\mathbf{S}_a \times \mathbf{S}_b$  with  $a + b = p$ . Moreover, generically all such branches should be locally unstable.

Lifting back to the original space, we obtain the generic existence of secondary branches, with isotropy subgroups  $\mathbf{S}_a \times \mathbf{S}_b \times \mathbf{S}_q$  with  $a + b = p$ , so  $a + b + q = N$ . Again, generically all such branches are locally unstable. Figure 7 illustrates the geometry in a schematic manner.

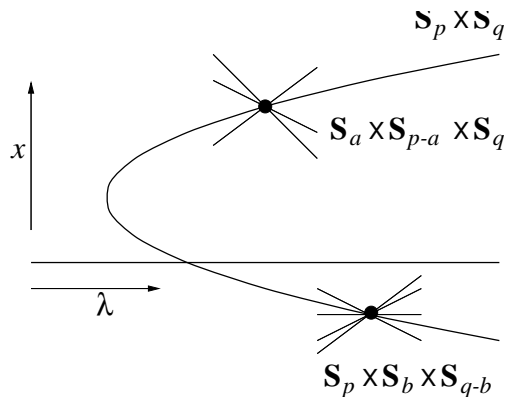


FIGURE 7. Schematic bifurcation diagram showing expected local geometry of secondary branches.

In order to make this argument rigorous we must show that there are no hidden symmetries in the sense of Dias and Stewart [5], and check that the relevant genericity conditions hold. There seems to be no obstacle to carrying out such an analysis, but the results would still be local near the secondary bifurcation points. We therefore prefer to analyse the cubic truncation from a global point of view. This also provides explicit expressions for the eigenvalues along the secondary branches and reveals phenomena that cannot be found by a purely local analysis.

Figure 8 illustrates the results that can be obtained analytically using equivariant bifurcation theory. It shows three primary branches, with isotropy subgroups  $\Sigma_1 = \mathbf{S}_6 \times \mathbf{S}_{19}$ ,  $\Sigma_2 = \mathbf{S}_2 \times \mathbf{S}_{23}$ , and  $\Sigma_3 = \mathbf{S}_8 \times \mathbf{S}_{17}$ . A secondary branch, shown shaded, links all three primary branches, and corresponds to the



isotropy subgroup  $\Sigma = \mathbf{S}_6 \times \mathbf{S}_2 \times \mathbf{S}_{17}$ . All branches are parabolic in projection, because of the cubic truncation. The equations for these branches, and their stabilities, are computed analytically in Dias and Stewart [6].

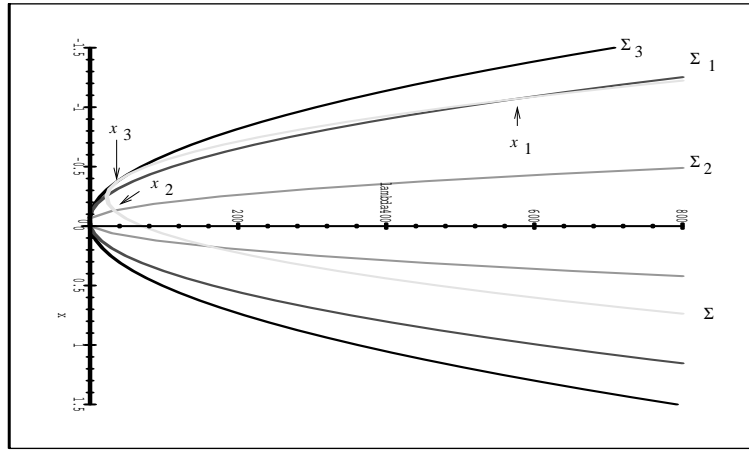


FIGURE 8. Branches of steady-state solutions of (4.2) projected on the  $(x, \lambda)$ -plane.  $N = 25$ ,  $a = 6$ ,  $b = 2$ ,  $c = 17$  and the parameter values are  $B = 1$ ,  $C = -0.8$ ,  $D = -5$ . Here  $\Sigma = \mathbf{S}_6 \times \mathbf{S}_2 \times \mathbf{S}_{17}$ ,  $\Sigma_1 = \mathbf{S}_6 \times \mathbf{S}_{19}$ ,  $\Sigma_2 = \mathbf{S}_2 \times \mathbf{S}_{23}$  and  $\Sigma_3 = \mathbf{S}_8 \times \mathbf{S}_{17}$ .

**4.4. Trimorphism in Biology.** Our results do not completely rule out the stable occurrence of 3-species states (‘secondary’ equilibria) in  $\mathbf{S}_N$ -equivariant ODEs. Our arguments merely show that such states do not occur for ODEs that are small perturbations of the cubic truncation (4.2). Large perturbations, or models unrelated to the cubic truncation, may in principle possess stable secondary branches.

In the context of polymorphism, we note that stable trimorphic states are sometimes observed experimentally. For example, Kashiwagi *et al.* [28] observe ‘balanced polymorphisms’ with three coexisting morphs at the genetic locus *glnA* of *E. coli* bacteria. This locus encodes the enzyme glutamine synthetase, which transforms glutamate into glutamine. A diverse population of randomly mutated bacteria was repeatedly selected for the ability to survive in a glutamate-limited environment—three rounds of mutagenesis and about 100 generations of adaptation per round. The anticipated outcome was the evolution of a population with *one* novel glutamine-synthesizing enzyme and no

other alleles at that locus. Instead, in several distinct experiments, trimorphic balanced polymorphisms occurred. See Lenski (2002) for a brief summary.

## 5. VARIATIONS ON A THEME

The symmetry assumption that underlies our analysis (namely,  $\mathbf{S}_N$ -equivariance) is too neat and tidy to be totally realistic. Real organisms in the same species are not identical. In a sense, this is an irrelevant objection: all models are idealizations. But we can ask whether exact symmetry is a *reasonable* idealization.

Its theoretical justification is straightforward. A good way to understand the dynamics of almost-symmetric systems is to view them as perturbations of exactly symmetric ones. Any robust phenomena that occur in the exactly symmetric system tend to occur in any small perturbation — usually at the expense of fine details regarding symmetries, but not much else. However, it is informative to consider some explicit variations on the idealized model, in which the exact symmetry is broken in specific ways.

Such variations are discussed in [43] and we merely mention them here. They include:

1. Converting deterministic ODEs onto stochastic ones by adding random noise.
2. Forcing the symmetry of the model to break by perturbing the deterministic dynamics.
3. Making the interaction network asymmetric by choosing its connections at random.
4. Randomly choosing the interaction network at each iteration of the dynamics.
5. Combining some of the above.

In each case, simulations show that the main conclusions of the idealized model are replicated in the more realistic one. In particular ‘speciation’ is robust; the typical end result is a two-species state; phenotypic means vary smoothly but the bifurcation is a jump.

Recently, a new technique has been developed to study pattern formation in networks of dynamical systems (‘coupled cell systems’) without assuming the presence of a symmetry group. Instead, attention focuses on the symmetry *groupoid*, which is a systematic way to describe relationships between subnetworks. This approach, initiated in [17], is likely to have widespread repercussions.

## 6. IS THIS SPECIATION?

From the biological point of view, there is one glaring omission from the model: the vital role of the gene.

We have chosen to present the model as a dynamic in phenotypic space, arguing that on this level of modelling the role of the gene is to allow the phenotype to change in response to selection. However, the same modelling methods can be adapted to include the effects of genetics (by, in effect, treating each allele as a ‘phenotypic’ variable in its own right). The BirdSym model of Elmhirst [10] is an example. Again, the main conclusions listed above remain valid. Indeed, Elmhirst relates his model analytically to  $\mathbf{S}_N$ -equivariant ODEs, and uses the results to explain certain features that appear in the simulations.

In particular, for genes that contribute to continuous characters we find that the mean value fails to detect the bifurcation. That is, mean field genetics is insensitive to this kind of speciation event. The standard deviation, in contrast, increases dramatically at bifurcation — an interesting instance of the principle that dispersion about the mean (‘error bar’) can be more significant than the mean itself. What changes is not the proportions of alleles in the population’s gene-pool, but how those alleles are associated in adults that survive to reproduce: see Cohen and Stewart [4], Stewart *et al.* [44]. In the jargon of equivariant bifurcation theory, the mean is not a *detective* for the primary bifurcation, but the standard deviation is, Barany *et al.* [1].

Because our models are abstract, they have many interpretations. They may be considered as models of ‘character displacement’, Salthe [42]; as models of phenotypic polymorphism (subspecies rather than species); or as models of full-blown evolutionary speciation. In all cases, they model the dynamics of the process on some coarse-grained scale, but not the fine detail.

We have chosen to ‘define’ species in terms of clustering in phenotypic space. The traditional biological meaning of ‘species’ is stronger, and its definition is not entirely satisfactory even now. The essential idea is that two species are distinct if their members cannot interbreed *to produce fertile offspring*, Mayr [35, 36]. However, this feature is not observed in many real species. For example, distinct species of Darwin’s finches often interbreed, with entirely fertile and viable offspring. Such interbreeding contributes to the finches’ ongoing evolution. Moreover, many recent papers exhibit mechanisms that can reinforce an initial phenotypic splitting, and, in effect, prevent or reduce mating between the two subpopulations. So what matters is not whether the organisms can potentially interbreed, but whether in practice they do.

A topical example here is the African forest elephant. Until recently, the conventional wisdom was that there are two species of elephant, African and Indian. For about a century, some zoologists believed that the African elephant

consisted of two species: one inhabiting the savannah, the other inhabiting the forest. There are significant differences in phenotype: the savannah elephants are big ('robust') whereas the forest elephants are smaller ('gracile'). Nonetheless, most zoologists expected them to be part of just one species, because the forests are adjacent to the savannahs, and interbreeding should create gene-flow and keep the species united. Genetic studies show that this expectation is false: the two are as distinct, genetically, as either is from the Indian elephant. Gene-flow is disrupted because either the opportunities for interbreeding are rare, or because the animals in the two species prefer not to interbreed anyway. Some zoologists now think that there may be at least five species of elephant.

At any rate, it is probably asking too much to have a definition of species that not only is valid at the start and end of the speciation process, but also holds during the sensitive and unusual period in which the nascent species are separating. Too strong a definition implies, for purely verbal reasons, that species can never split. Analogously, a single stick can never break: either it is still in one piece, in which case it hasn't broken yet, or it's in two pieces, in which case it's not a single stick. Any sensible definition of 'species' has to avoid this linguistic trap.

We therefore contend that it is reasonable to consider the above bifurcation as some primitive step towards genuine speciation. And it demonstrates one important idea: that speciation results from the *collective* response of a group of organisms: to their environment, but also *to each other*. This statement, by the way, does not conflict with the belief — almost dogma — that selection acts on organisms, not on species. In our models, the selection process does act on organisms, or at least on their representative PODs. That is to say, there is an ODE for each POD variable  $x^j$ , and that equation determines how  $x^j$  changes. However, the way it changes depends on the current state of the other PODs. So the model merely affirms that the selection process on organisms depends not only on the environment, but on the behavioural strategies adopted by competing organisms [43]. There is nothing controversial about this statement. Indeed, unless there are interactions with other organisms, there can be no competition.

## References

1. Barany E., Dellnitz M., Golubitsky M., *Detecting the symmetry of attractors*, Physica D., **67** (1993), 66–87.
2. Carr J., *Applications of Centre Manifold Theory*, Springer, New York, 1981.
3. Cicogna C., *Symmetry breakdown from bifurcation*, Lett. Nuovo Cimento, **31** (1981), 600–602.
4. Cohen J., Stewart I., *Polymorphism viewed as phenotypic symmetry-breaking*, in *Non-linear Phenomena in Physical and Biological Sciences* (ed. Malik S.K.), Indian National Science Academy, New Delhi, 2000, 1–67.

5. Dias A.P.S., Stewart I., *Hilbert series for equivariant mappings restricted to invariant hyperplanes*, J. Pure Appl. Algebra, **151** (2000), 89–106.
6. Dias A.P.S., Stewart I., *Secondary bifurcations in systems with all-to-all coupling*, preprint, Math Dept., Porto, 2002. To appear in Proc. Roy. Soc. London A.
7. Dieckmann U., Doebeli M., *On the origin of species by sympatric speciation*, Nature, **400** (1999), 354–457.
8. Eldredge N., Gould S.J., *Punctuated equilibrium: an alternative to phyletic gradualism*, in *Models in Palaeobiology* (ed. Schopf T.J.M.), Cooper, San Francisco, 1972.
9. Elmhirst T., *Symmetry-breaking Bifurcations of  $S_N$ -equivariant Vector Fields and Polymorphism*, MSc Thesis, Mathematics Institute, University of Warwick, 1998.
10. ———, *Symmetry and Emergence in Polymorphism and Sympatric Speciation*, PhD Thesis, Mathematics Institute, University of Warwick, 2001.
11. ———,  *$S_N$ -equivariant symmetry-breaking bifurcations*, Internat. J. Bif. Chaos, to appear.
12. Field M.J., *Lectures on Bifurcations, Dynamics and Symmetry*, Research Notes in Mathematics, **356**, Longman, London, 1996.
13. Field M.J., Richardson R.W., *Symmetry breaking and the maximal isotropy subgroup conjecture for reflection groups*, Arch. Rational Mech. Anal., **105** (1989), 61–94.
14. ———, *Symmetry breaking and branching patterns in equivariant bifurcation theory I*, Arch. Rational Mech. Anal., **118** (1992), 297–348.
15. ———, *Symmetry breaking and branching patterns in equivariant bifurcation theory II*, Arch. Rational Mech. Anal., **120** (1992), 147–190.
16. Fox D., *Wallaby nations*, New Scientist, (3 August 2002), 32–35.
17. Golubitsky M., Pivato M., Stewart I., *Symmetry groupoids and patterns of synchrony in coupled cell networks*, to appear.
18. Golubitsky M., Schaeffer D.G., *Singularities and Groups in Bifurcation Theory I*, Applied Mathematical Sciences, **51**, Springer, New York, 1985.
19. Golubitsky M., Stewart I., *Symmetry and pattern formation in coupled cell networks*, in *Pattern Formation in Continuous and Coupled Systems* (eds. Golubitsky M., Luss D., Strogatz S.H.), IMA volumes in Math. and Appns., **115**, Springer, New York, 1999, 65–82.
20. ———, *The Symmetry Perspective: From Equilibrium to Chaos in Phase Space and Physical Space*, Progress in Mathematics, **200**, Birkhäuser, Basel, 2002.
21. Golubitsky M., Stewart I., Schaeffer D., *Singularities and Groups in Bifurcation Theory: Vol. II*, Appl. Math. Sci., **69**, Springer, New York, 1988.
22. Grant P.R., *Natural selection and Darwin's finches*, Scientific American, (October 1991), 60–65.
23. Grant P.R., Grant B.R., *Unpredictable evolution in a 30-year study of Darwin's finches*, Science, **296** (2002), 707–711.
24. Grant P.R., Grant B.R., Smith J.N.M., Abbott I.J., Abbott L.K., *Darwin's finches: Population variation and natural selection*, Proc. Nat. Acad. Sci. USA, **73** (1976), 257–261.
25. Higashi M., Takimoto G., Yamamura N., *Sympatric speciation by sexual selection*, Nature, **402** (1999), 523–526.
26. Hofbauer J., Sigmund K., *The Theory of Evolution and Dynamical Systems*, London Math. Soc. Student Texts, **7**, Cambridge University Press, Cambridge, 1988.
27. Iooss G., Joseph D.D., *Elementary Stability and Bifurcation Theory* (2nd ed.), Springer, New York, 1990.

28. Kashiwagi A., Noumachi W., Katsuno M., Alam M.T., Urabe I., Yomo T., *Plasticity of fitness and diversification process during an experimental molecular evolution*. J. Molecular. Evol., **52** (2001), 502–509.
29. Kawecki T.J., *Sympatric speciation via habitat specialization driven by deleterious mutations*, Evolution, **51** (1997), 1751–1763.
30. Kisdi E., Geritz S.A.H., *Adaptive dynamics in allele space: evolution of genetic polymorphism by small mutations in a heterogeneous environment*, Evolution, **53** (1999), 993–1008.
31. Kondrashov A.S., Kondrashov F.A., *Interactions among quantitative traits in the course of sympatric speciation*, Nature, **400** (1999), 351–354.
32. Lack D., *Darwin's Finches. An Essay on the General Biological Theory of Evolution*, Peter Smith, Gloucester MA, 1968.
33. Lenski R.E., *First Zuckerman Prize Awarded*. J. Molecular Evol., **54** (2002), 141–142.
34. Maynard Smith J., *Models in Ecology*, Cambridge University Press, Cambridge, 1974.
35. Mayr E., *Animal Species and Evolution*, Belknap Press, Cambridge MA, 1963.
36. ———, *Populations, Species, and Evolution*, Harvard University Press, Cambridge MA, 1970.
37. Niehstadt A.I., *Persistence of stability loss for dynamical bifurcations I*, Diff. Eq., **23** (1987), 1385–1391.
38. ———, *Persistence of stability loss for dynamical bifurcations II*, Diff. Eq., **24** (1988), 171–196.
39. Rice R., Hostert E.E., *Laboratory experiments on speciation: what have we learned in 40 years?* Evolution, **47** (1993), 1637–1653.
40. Ridley M., *Evolution*, Blackwell, Oxford, 1996.
41. Rundle H.D., Nagel L., Boughman J.W., Schluter D., *Natural selection and parallel speciation in sympatric sticklebacks*, Science, **287** (2000), 306–308.
42. Salthe S.N., *Evolutionary Biology*, Holt, Rinehart and Winston, New York, 1972.
43. Stewart I., *Self-organization in evolution: a mathematical perspective*. Proceedings of Nobel Symposium on Self-Organization, Stockholm, 2002, to appear.
44. Stewart I., Elmhirst T., Cohen J., *Symmetry-breaking as an origin of species*, in *Bifurcations, Symmetry, and Patterns* (eds. Buescu J., Castro S.B.S.D., Dias A.P.S., Labouriau I.S.), Birkhäuser, Basel, to appear.
45. Tregenza T. Butlin R.K., *Speciation without isolation*, Nature, **400** (1999), 311–312.
46. Vanderbauwhede A., *Local Bifurcation and Symmetry*, Habilitation Thesis, Rijksuniversiteit Gent, 1980; Res. Notes Math., **75**, Pitman, Boston, 1982.
47. Vincent T.L., Vincent T.L.S., *Evolution and control system design*, IEEE Control Systems Magazine, (October 2000), 20–35.

Received December 10, 2002

University of Warwick  
 Institute of Mathematics  
 Coventry CV4 7AL, U.K.  
 e-mail: ins@maths.warwick.ac.uk