Dynamics, Symmetry, and the Levels of Selection

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Abstract

Most attempts to answer the question of whether populations of groups can undergo natural selection focus on properties of the groups themselves rather than the dynamics of the population of groups. Those approaches to group selection that do emphasize dynamics lack an account of the relevant notion of equivalent dynamics. I present a new framework for assessing dynamical equivalence that is based upon the notion of a dynamical symmetry, a transformation of a system that commutes with its evolution through time. In this framework, structured sets of dynamical symmetries are used to pick out equivalence classes of systems. Every member of such an equivalence class is dynamically independent of all other members, and in this sense constitutes a natural unit, belonging to a natural 'dynamical kind'. By characterizing dynamical kinds via symmetry structures, the question of levels of selection becomes a precise question about which populations respect the dynamical symmetries of Darwinian evolution. Standard population genetic models suggest that populations undergoing evolution by natural selection are partially characterized by a group of fitness-scaling symmetries. I demonstrate conditions under which these symmetries may be satisfied by populations of individuals, populations of groups of individuals, or both simultaneously.

1 Framing the problem

This essay concerns the relationship between two biological facts. First, biological systems are hierarchically structured: macromolecules are parts of cells, which are parts of organisms, which are parts of demes, and so on. Second, at least some biological systems undergo evolution by natural selection. To ask how the occurrence of natural selection relates to the

structural hierarchy is to ask about the so-called 'levels of selection'. Much has been written on this subject, and over decades of discussion, a tangled bank of problems has grown up around this theme.[1] These include questions such as: On which biological entities in the structural hierarchy does natural selection act (Vrba and Gould, 1986)? Which entities possess a fitness (Brandon, 1982)? At what level of the hierarchy do we find individuals (Wilson and Sober, 1989)? Which entities replicate (Dawkins, 1976)? What entities benefit from selection (Sober and Wilson, 1994)? At what level does adaptation occur (Sober, 1993)? Can selection take place at multiple levels simultaneously (Damuth and Heisler, 1988)?

Despite the apparent diversity, all of these questions are to some extent derivative of a more basic concern: at what levels in the biological hierarchy is the process of natural selection to be found? The reference to "process" here is not coincidental.[2] Rather, the notion of process is conceptually central. Whatever else it may be, evolution by natural selection is a process. In fact, it is an instance of a special sort of process which, for lack of a better term, I'll call a *dynamical process*. Processes in general involve change through time of the state of a system. In a dynamical process, the state of the system corresponds to the values of a collection of causally connected variables. In such a system, not all states are possible, and which are accessible is determined by causal relations amongst the variables. To illustrate the contrast with processes in general, consider the change through time of the system consisting of all the coins in my left pocket along with those in the let pocket of someone in Beijing. Any number of coins in my pocket is compatible with any number of coins in my Chinese counterpart's pocket. The 'system' in question does evolve through time and so partakes in a process. But it is not a dynamical process. In contrast, the changing state of a chemical reaction described in term of the concentrations of reagents and products is a dynamical process—changing the value of one variable changes the values that are accessible to the remainder.

Evolution by natural selection is a dynamical process in this sense, one that involves the change through time of type frequencies in a population. The central question of the levels of selection is a question about the conditions under which a population of biological entities can be said to instantiate a dynamical process of the Darwinian kind. This in turn demands a theory of kinds of dynamical process, or *dynamical kinds*—an account of how particular processes sort into natural and distinct kinds. Only with such a theory can it be determined whether a process at one or another level of the structural hierarchy is an instance of evolution by natural selection or of a different sort of process altogether.

Standard approaches to the levels of selection tend not to focus on identifying characteristics of the process of natural selection but rather on identifying the conditions necessary and sufficient for it to occur. Arguably, this is what Darwin was up to in the first four chapters of the *Origin of Species* (1993), and it is certainly what Lewontin (1970) had in mind when he proposed his tripartite schema.[3] According to the latter, a population of entities (biological or otherwise) will undergo evolution by natural selection if: (i) there is phenotypic variation amongst members of the population; (ii) there is differential fitness among the phenotypes; and (iii) there is correlation in fitness between parents and offspring (i.e., fitness is heritable). To determine whether or not these conditions are or can be met by populations of entities at various levels of the structural hierarchy, one must first clarify the notions of heritability and reproduction. Unsurpisingly, those who take Lewontin's approach have developed these notions in great detail. This is, for example, the bulk of the work taken up by Godfrey-Smith (2009) in his exemplary monograph on 'Darwinian populations'.

The problem is that Lewontin's properties-first approach is question-begging. Evolution by natural selection is a dynamical process of populations. The process itself—irrespective of whatever mechanisms underly it—can be described solely in terms of variables that refer to population properties. Put differently, it is possible to characterize the process without assuming anything about the nature and characteristics of the participating populations other than that they possess properties of type frequency and type fitness. It is not necessary to know what properties of biological entities are in fact used to instantiate such a process. Assuming at the outset facts about those properties—for instance, that members of an evolving population must reproduce in a particular fashion thus begs the question about which populations can instantiate a process of the Darwinian kind. To put a sharper point on the criticism, we cannot know whether the conditions Lewontin offers are in fact necessary and sufficient unless we already have a way to decide which processes are positive instances of natural selection. For these reasons, I suggest that we should abandon the properties-first approach of Lewontin and his intellectual descendants and instead focus on directly characterizing the dynamical process of evolution. For this, we need a theory of dynamical kinds.

2 An incomplete framework

What must a theory of dynamical kinds look like if it is to serve it's intended purpose with respect to the levels of selection question? To answer this, it will be instructive to examine a prominent framework for discussing multilevel selection that explicitly emphasizes dynamics. I have in mind the formalism developed by Kerr and Godfrey-Smith (2002) to talk about evolutionary processes at both the 'individual' and 'group' level. Despite the merits of their framework, it does not provide the resources to answer the question of levels of selection as construed above. Understanding why this is the case will suggest conditions on the sort of theory of dynamical kinds that is needed, as well as motivate the specific solution I propose below.

2.1 The KGS model

Kerr and Godfrey-Smith (hereafter KGS) ask us to consider an infinite population of biological entities that are of two types, A and B. These entities, whatever they may be, I'll call 'particles' as KGS do in order to avoid confusing and prejudicial use of terms like 'individual' or 'organism'. These particles are supposed to aggregate into groups, all of which contain n particles. Each group is classified according to the number, i, of type A particles that belong to it. The frequency of groups of type i is given by f_i. The particles and groups reproduce in discrete generations—groups dissolve, particles replicate in a single, panmictic mass, and then reform groups.

According to KGS, we have two choices when modeling the behavior of this system over time. On the one hand, we can assign context-dependent fitnesses to each particle on the basis of its type and the type of group in which it occurs. Specifically, let α_i be the fitness of an A particle in a group with i A's and β_i stand for the fitness of a B particle in a group with i A's. In this approach then, groups are treated as local environments across which particle fitnesses vary.

Let p stand for the frequency of A particles in the entire meta-population and q for the overall frequency of B particles. Then, KGS tell us, the dynamics of the p and q are captured by the following recurrence relations:

$$p(t+1) = \frac{1}{\bar{w}} \sum_{i=1}^{n} f_i(t) \frac{i}{n} \alpha_i \tag{1}$$

$$q(t+1) = \frac{1}{\bar{w}} \sum_{i=0}^{n-1} f_i(t) \frac{n-i}{n} \beta_i \tag{2}$$

The variable $\bar{w}$ in the above equations is shorthand for the average particle fitness which is given by:

$$\bar{w} = \sum_{i=1}^{n} f_i(t) \frac{i}{n} \alpha_i + \sum_{i=0}^{n-1} f_i(t) \frac{n-i}{n} \beta_i$$

Equations (1) and (2) are not dynamically sufficient—they do not determine the time-course of the frequencies p and q—unless we specify the functions $f_i(t)$. In the cases considered by KGS, the $f_i(t)$ are assumed to be functions solely of $p(t)$.

In constructing (1) and (2), we took the perspective of the particles and treated groups as environments over which particle fitness varies. Of course, if we're going to be able to entertain the question of levels of selection, we're going to have to have a way to adopt the group perspective as well. KGS claim that we can do so in the following manner. To each group we assign two parameters:

π_i = total number of particle copies from a group with i A types

ϕ_i = (number of A copies in a group with i A types) / (total number of copies in a group with i A types)

The parameter π_i, represents a "group productivity" which is purportedly analogous to particle fitness. The latter parameter ϕ_i is the fraction of particles of type A produced by a group with i A-types. It has no analog from the particle perspective. Unsurprisingly, these parameters can each be written in terms of α_i and β_i, though the exact expressions are immaterial here. Using the new parameters as defined (and again assuming the functions f_i are known), we can write down a new set of dynamical equations for groups:

$$\bar{\pi}p(t+1) = \sum_{i=1}^{n} f_i(t)\phi_i\pi_i \tag{3}$$

$$\bar{\pi}q(t+1) = \sum_{i=0}^{n-1} f_i(t)(1-\phi_i)\pi_i \tag{4}$$

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In both of these equations,

$$\bar{\pi} = \sum_{i=0}^{n} f_i(t)\pi_i$$

2.2   Group dynamics in KGS

As I suggested above, this setup does not allow us to answer the question of levels of selection as it was framed in Section 1. While it is true that Equations (3) and (4) represent some facts about groups, a glance at the definitions of π_i and ϕ_i reminds us that we are still firmly rooted in the particle perspective. Groups are acknowledged as "fitness structure" in the population, but this structure is ultimately still described with reference to particles. In fact, Equations (3) and (4) only explicitly track particle frequencies. What matters for the question of levels of selection as I've posed it is whether or not the dynamics of the population of groups is a process of Darwinian evolution when those dynamics are described exclusively in terms of a population of groups. To answer this question, these equations need a little rearranging.

To begin with, it is essential to note that the f_i are the frequencies of group types. If we want to know how the population of groups changes over time, we need to keep track of the f_i, not p and q. So let's suppose that the population of particles evolves in time according to Equations (1) and (2). Recall that in order for those equations to be dynamically sufficient, we have to know what the frequencies of groups are in terms of the frequencies of particles. Let's assume that groups are formed at random in the new generation following dissolution of the groups of the preceding generation. On this assumption, we have:

$$f_i(t) = \binom{n}{i}(p(t))^i(1 - p(t))^{n-i} \tag{5}$$

For simplicity, I will assume that $n = 2$. That is, each group is composed of just two particles. From Equations (1) – (5) we can then find explicit expressions for the dynamics of the group frequencies:

$$f_0(t+1) = \frac{(\beta_0 f_0(t) + \frac{1}{2}\beta_1 f_1(t))^2}{\left(\alpha_2 f_2(t) + \beta_0 f_0(t) + \frac{1}{2}(\alpha_1 + \beta_1)f_1(t)\right)^2} \tag{6}$$

$$f_1(t+1) = \frac{2(\frac{1}{2}\alpha_1 f_1(t) + \alpha_2 f_2(t))(\beta_0 f_0(t) + \frac{1}{2}\beta_1 f_1(t))}{\left(\alpha_2 f_2(t) + \beta_0 f_0(t) + \frac{1}{2}(\alpha_1 + \beta_1)f_1(t)\right)^2} \tag{7}$$

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$$f_2(t+1) = \frac{(\frac{1}{2}\alpha_1 f_1(t) + \alpha_2 f_2(t))^2}{\left(\alpha_2 f_2(t) + \beta_0 f_0(t) + \frac{1}{2}(\alpha_1 + \beta_1)f_1(t)\right)^2} \tag{8}$$

To reiterate, what Equations (6) – (8) represent are the dynamics of a population of groups as it changes in time, assuming that the particles composing the groups are governed by Equations (1) and (2). These expressions, not Equations (3) and (4), are the group analogues of the equations governing particle dynamics. Note that the population of groups is presumed to occupy a single selective environment—there is only one group context. We should thus expect there to be a single group fitness for each type of group. In fact, we'll have reason later (in Section 4.2 and Appendix A below) to identify group fitnesses with the coefficients of the frequencies appearing in the denominators of each expression on the right-hand side, namely α_2, β_0, and $\frac{\alpha_1 + \beta_1}{2}$. These are proportional to the parameters π_i introduced as 'group fitnesses' by KGS. But this cannot be determined by simple inspection of the equations. Only the group frequencies are unambiguously recognizable. What's more, the form of, say Equation (6) is quite different from that of Equation (1) or (2). In particular, the frequency of a particle type at time $t+1$ depends on only one particle frequency at t whereas each group frequency at time $t+1$ is a function of two frequencies. The dynamics governing change in the population of groups looks quite different from the dynamics of particles.

2.3   What's missing

To take stock so far, the KGS formalism supports the construction of models of particle evolution for which groups manifest as fitness structure. With the additional assumption of a particular connection between particles and groups, we were also able to produce a model of the dynamics of the population of groups in terms of group properties alone—properties that could be assessed without any knowledge that the groups consist of particles. The result was a set of dynamical relations that look superficially quite different from those governing the particles. In this context the levels of selection question amounts to this: which, if either, dynamics is an instance of natural selection? Is the dynamics expressed by either model of the right sort to count as evolution by natural selection? There is no answer inherent in the KGS framework. Even if we assume that the particles are undergoing evolution by natural selection, we have no principled means of deciding whether the dynamics expressed in Equations (6)–(8) is "the same as" the dynamics

expressed in Equations (1) annd (2) in some relevant sense. What is it to be the same kind of dynamical process? Note that I am not asking whether either population possesses the right sort of properties apart from its dynamics—it is not directly relevant to our question whether, for instance, there is a mechanism for generating heritable variation. Of course, if a given population turns out to be undergoing evolution by natural selection, then we have good reason to suspect that there is such a mechanism. But knowing there is such a mechanism is insufficient to guarantee any particular dynamics, and it is obeying a dynamics of the right sort that makes a process one of natural selection.

Though relatively few have done so, I am hardly the first to place this kind of emphasis on dynamics. For instance, Wagner and Laubichler (2000, 32) reformulate the question, "What is an evolutionary trait?" as a question about dynamics: "given the equations that describe the dynamics of natural selection among individuals. . . how can we lump the organism 'types' (be it genotypes or phenotypes) into equivalence classes (i.e. character states), such that the dynamics of these abstract types is still predicted by the same equations without any loss of generality." But, like KGS, Wagner and Laubichler offer no account of "sameness of dynamics", though they appeal to the concept. What does it mean for the states of two different populations to be predicted by the same equations without loss of generality? Presumably, natural selection encompasses more than evolution in a haploid population with two alleles and n fitness environments as described by Equations (1) and (2) above. But even the addition of a third allele or just one more fitness environment would be described by a different set of equations. Obviously, the 'sameness' of dynamical equations should not be taken too literally. But how can we decide whether or not the dynamics of two changing populations is the 'same' in some more liberal, salient sense?

An answer to this question can only be provided by a theory of dynamical kinds. Specifically, what we need is a theory of dynamical kinds that is permissive enough to treat systems with different numbers of dynamical variables as belonging to the same kind (e.g., evolving populations with two versus three types), that can equate dynamics of differing algebraic form (e.g., Newtonian systems with differing force laws), and yet nonetheless ensures that 'equivalent' dynamical systems constitute a natural kind. In the next section, I present an account with all of these features. It is a theory of dynamical kinds built upon the notion of a 'dynamical symmetry'.

3 A theory of dynamical kinds

3.1 A motivational example

To provide some intuitive motivation for my proposed theory of dynamical kinds, consider the following toy example. Imagine I have an agar plate with lots of unidentified bacterial colonies on it, and that I wish to know how many kinds of bacterial colonies there are. To make some headway, I might perform the following experiment for each colony I can see on the plate. First, I take a sample of the colony and use it to inoculate two fresh plates, call them A and B. For plate A, I immediately add penicillin and then incubate the plate for 24 hours. For plate B, I incubate the plate for 24 hours and then add penicillin. After applying one or the other treatment, I could then examine both plates to see how much the colony on each one grew. A typical way to do this is by measuring the area each colony occupies. What sorts of results are possible? Sometimes, plate A might show no growth at all while plate B shows significant change. In such cases, the obvious explanation is that the antibiotic simply kills the bacteria, and adding it right away to plate A precluded growth. But it's also possible that the colony on A would show a little growth, but less than that on B at the end of the experiment. Or there might be no difference at all. If for one sample from the original plate, there was no difference between experimental plates A and B while for another sample, plate B showed growth and A did not, I could conclude that I had at least two kinds of bacteria on the original plate—one which is penicillin-resistant and one that isn't.[4]

Similar experimental manipulations are possible with other antibiotics, but less destructive techniques are available as well. I could, for instance, vary the concentration of nutrients in the growth medium and sort colonies on the basis of whether or not their growth rate is affected by this variation. With a little more effort, I could also vary nutrient concentrations while keeping either the differences or relative proportions fixed. In each case, I could classify colonies on the basis of whether or not the rate of growth was affected by the change in medium as evidenced by the difference in outcomes on plates A and B. A variety of more or less complex patterns are possible. While a colony's growth rate may be changed by intervention on lactose concentration alone, it might be unaffected if lactose and glucose are varied together. Regardless of the particular manipulation, I can sort bacteria into kinds depending on whether or not the outcome is the same on both plate A, for which we intervene and then incubate, and plate B, for which we incubate and then intervene.

The kinds determined in this way are dynamical kinds. What experiments of this sort discern are kinds of metabolic processes. This is clear if we focus attention on the colonies whose metabolic processes remained constant under intervention—those for which plates A and B turned out the same at the end of the experiment. What I've discovered is that for those colonies, their metabolism—however complex it may be—possesses a dynamical symmetry. Roughly speaking, the term 'dynamical symmetry' denotes any transformation of a dynamical system that leaves unchanged the way in which the states of that system unfold through time. In this case, it is the way in which metabolic process unfold through time that remains unchanged under a transformation of antibiotic or nutrient concentration.

3.2 Symmetries

Suppose we are interested in Newtonian gravity instead of Darwinian evolution. The analog to our question about levels of selection is the following: Which collections of objects comprise a gravitating system? To see the analogy more closely, we might ask whether collections of gravitating systems can also constitute a gravitating system in their own right. One way we might approach the problem is similar to the way in which we used Equations (6) – (8) above. That is, we can begin with a gravitating system of, say, n massive particles with dynamics described by Newton's laws of motion in conjunction with the inverse square law of gravitation. As with our biological 'particles', we can then redescribe the system in terms of m groups of particles (it doesn't matter whether we assume the same number of particles in each group or not). From the original dynamical equations, we can then deduce new equations describing the evolution of the meta-system entirely in terms of the groups. I won't present an explicit calculation here, but the upshot is that we will be confronted by the same sort of problem we faced above: in what specific ways and to what degree must the two dynamical descriptions be similar for us to declare them both gravitating systems.

To answer this puzzle we should focus not on the details of the dynamics, but rather on the *dynamical symmetries*. Simply put, a dynamical symmetry of a system is any physical transformation, σ, of the system that is invisible to the dynamics that govern that system in the sense that it makes no difference whether we apply σ to the system and then advance the state according to the dynamical laws, or if we instead apply the laws to advance the state and then transform the result with σ. Either way we end up with the system in the same state.[5] This idea can be put more precisely as follows:

Definition. Let S be the set of states of a system and let $\Lambda_{t_0,t_1} : S \to S$

be the time-evolution operator which takes the system from state S_0 at t_0 to S_1 at t_1. A *dynamical symmetry* is any operator $\sigma : S \to S$ with the following property: $\forall_{s \in S} \forall_{t_0} \forall_{t_1 > t_0} [\Lambda_{t_0,t_1}(\sigma(s)) = \sigma(\Lambda_{t_0,t_1}(s))]$. This property is represented in the following commutation diagram:

$$
\begin{array}{ccc}
s_0 & \xrightarrow{\ \sigma\ } & \hat{s}_0 \\
\downarrow{\scriptstyle \Lambda} & & \downarrow{\scriptstyle \Lambda} \\
s_1 & \xrightarrow{\ \sigma\ } & \hat{s}_1
\end{array}
$$

In classical mechanics, for instance, displacement by a constant distance in space is a dynamical symmetry. Imagine a system that exhibits a simple ballistic trajectory, such as a thrown baseball. We can describe the state of the system immediately after the ball leaves the pitcher's hand with the coordinates of a single point and an initial velocity. Advancing the system using the dynamical laws—Newton's Laws—yields a series of states that trace out a parabola in space. This is depicted in the left side of Figure 1. The little silhouette represents the pitcher. The baseball images indicate successive locations of the ball as it travels toward the viewer. In other words, they show successive states of the ball as we advance forward in time using the 'time-evolution operator', Λ_{t_0,t_1}, appropriate for Newtonian Mechanics. Now suppose that we transform the original system by shifting the pitcher (and thus the ball) to the right by a few meters. This transformation, σ, of the initial state is indicated in the figure by the small arrow pointing to the right-hand silhouette. The latter of course, represents the pitcher and ball in their transformed initial state. If we then advance the state through time, we would see that the ball follows a parabolic trajectory as shown on the right. Unsurprisingly, the ball ends up in a spot a few meters to the right of the where the original pitch ended up—just where it would be if we had displaced the final state of the original pitch by the same few meters to the right. As we all know from experience, it doesn't matter whether we throw a ball and then displace it to the right a few meters, or displace it and then throw. Either way, the ball ends up in the same place. In this sense, the dynamics of motion are insensitive to spatial translations.

Consider instead the bacterial example with which I began. Each colony is a dynamical system. While lots of properties of the colony change with time, let's focus strictly on biomass. As time progresses, suppose that a given colony on a particular growth medium adds biomass at a constant rate. If we change the growth medium—by adding antibiotic, for example—this constitutes a transformation of sorts. If the growth rate of the colony is insensitive to the concentration of the antibiotic, then it will not matter
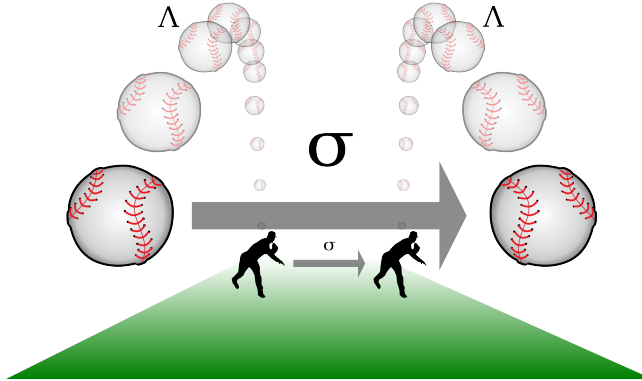
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Figure 1: Example of a Newtonian Symmetry

whether I change the antibiotic concentration of the medium and then grow the colony, or grow the colony and afterward add the antibiotic. I get the same state either way, and so this transformation is a symmetry of the colony dynamics.

Dynamical symmetries weave together into what I call symmetry structures. Suppose that σ_1 and σ_2 are symmetries of the dynamics of interest. Then so is $\sigma_2 \circ \sigma_1$, where this notation denotes the operation obtained by first applying σ_1 and then σ_2. In fact, it is easy to see that this generalizes to any composite of symmetry transformations—the symmetries of a set of dynamical equations form a group in the mathematical sense.[6] A particular group structure along with a list of the specific, concrete transformations that manifest that structure constitute the *symmetry structure* of a dynamics:

Definition. A *symmetry structure* is a collection of physical symmetry transformations, represented by $\Sigma = \{\sigma_i | i = 1, 2, \dots\}$, along with a composition function $\circ : \Sigma \times \Sigma \to \Sigma$ that indicates how those symmetries behave under composition. (For a discrete set of symmetries, the composition function can be given in the form of a multiplication table.)

It is important to emphasize that symmetry structures are *not* abstract algebraic objects. Rather, a symmetry structure is a collection of concrete, physical transformations whose behavior under composition is described by

a particular abstract algebraic object, i.e., a group. To make this point as explicit as possible, consider the close analogy between electric circuits and hydrostatics. So close is the analogy in behavior that circuits have been used to model complex hydrostatic systems with great accuracy (see Bourouina and Grandchamp, 1996). This is because the dynamics of certain sorts of electric circuits and the dynamics of certain hydrostatic systems are described by the same equations; the variables are simply interpreted differently. Though they are described by identical equations, however, these two systems have different symmetry structures in the sense I am using the term. This is because the transformations for hydrostatic systems involve operations like changes in pressure while the transformations for circuits involve completely distinct operations like changing voltage. Their symmetry structure share a common abstract group structure, but they are not identical because the concrete, physical transformations for each are different.

3.3 Dynamical kinds

Symmetry structures offer a way of classifying individual processes on the basis of their dynamical properties. For a particular system to instantiate a particular dynamics, it is a necessary condition that the system manifests the symmetry structure associated with that sort of dynamics. So, for instance, if a system is to be a Newtonian gravitating system, then it must have the dynamical symmetry structure of Newton's laws of motion and gravitation. In particular, the dynamics must be unaffected by rigid translations and rotations of the system (and a handful of other such transformations) as well as composites of these transformations. *Prima facie* this might sound like a circumspect way of saying that two systems have the same dynamics if they "obey the same equations." That would be deeply unsatisfying since we already know that some of the systems we want to lump together as Darwinian evolvers do not obey exactly the same dynamical equations. But the appeal to symmetry does not merely group systems by their specific dynamical equations. In fact, one cannot do so on the basis of symmetry conditions alone since the fact that a system respects a particular symmetry structure is not generally a sufficient condition for that system to be governed by a particular dynamics—two systems that respect the same symmetry structure might differ in dynamical details. This flexibility is appealing. For one thing, there are no difficulties under the symmetry approach with accommodating different numbers of variables corresponding to, e.g., different numbers of alleles. This is because one and the same symmetry structure may be instantiated by multiple systems with algebraically distinct dynami-

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cal relations, provided that the symmetry transformations are appropriately specified. In the gravitating system example, it doesn't matter how many gravitating bodies we consider—the notion of a rigid translation can be precisely specified with a schema such as: "add a constant vector to every position." However, the fact that symmetry structures impose a non-trivial equivalence relation on dynamical systems means that to insist on identifying dynamical kinds on the basis of symmetry is to make a substantive claim that requires defense. Why classify dynamical processes this way and not some other?

The answer is that dynamical kinds are excellent candidates for being so-called 'natural kinds'. Broadly speaking, there are two complimentary questions concerning natural kinds: one metaphysical and the other epistemic.[7] The metaphysical question has to do with 'joints' in the stuff of the world: what are the objective categories to which the individual objects composing the world belong? Though I haven't space here to pursue the point in detail, it should be noted that putting the question this way presumes that we can characterize the individuals making up the world without appeal to the natural categories to which they belong. This is a dubious claim, and so it would be better to treat the metaphysical problem of natural kinds as the problem of identifying both the objective units into which the world is divided and the objective categories into which they sort.

Dynamical kinds identify plausible candidates for both natural units and categories. To begin with, each such kind picks out a class of units that are independent of one another with regard to their dynamical properties. It is the case that if a system respects the symmetry structure of a given dynamics then its states cannot depend upon the states of other such systems that simultaneously respect that symmetry structure.[8] So for example, the state of any Newtonian gravitating system as it evolves through time must be independent of the state of any other gravitating system. Conversely, if the state of one collection of massive bodies influences the state of another, neither collection is a Newtonian gravitating system. To return to my agar plate example, any partition of colonies into S-metabolizers separates colonies into units that grow at rates independent of one another. If the growth rates of two colonies are tied together, then neither alone is an S-metabolizer. This way of dividing individual systems thus reflects a genuine division in the world. In an intuitive sense then, each system that is an instance of a dynamical kind is an individual in the sense that it bears properties independent of other such systems.

The epistemic version of the question of natural kinds concerns the identification of inductively fruitful categories. Which kinds are 'projectible' to

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use Goodman's bon mot (Goodman, 1955). Of course, here too we are really facing a pair of problems: which predicates are projectible, and how do we individuate instances of these predicates? After all, it matters whether we're looking at one or many instances of 'greenness'. Here again, dynamical kinds offer consistent solutions to both problems. Individuals are just instances of dynamical kinds. More accurately, they are collections of properties causally bound together in such a way that they respect the symmetry structure of a given kind. What of the projectibility of the kinds? For many reasons, it would be a boon if in fact dynamical kinds are the projectible kinds. It is lot easier to determine whether or not a system respects a symmetry structure than it is to determine the dynamical details of the system in terms of its internal variables. For instance, it is quite easy to identify an S-metabolizer via a few experiments with agar plates. It is very hard to determine precisely how the overall metabolic rate of the population of bacteria is caused by the distribution and concentration of nutrients. It is easier to learn these kinds than it is to learn full dynamics. Of course, this is not an argument for the claim that dynamical kinds are projectible kinds. A priori arguments are of dubious utility in this regard. I suggest that the best argument for taking dynamical kinds seriously as natural kinds is inductive success. That is, if in fact dynamical kinds generally turn out to support successful inductive generalization, then there is reason to think dynamical kinds are the right answer to the epistemic question of natural kinds.

It would lead us far astray to assess the empirical case for taking dynamical kinds seriously as natural kinds. For our present purposes, it suffices that dynamical kinds offer an attractive solution to the question of 'sameness of dynamics' with which we began. Systems with different numbers of dynamical variables (e.g., different numbers of allele frequencies) may belong to the same dynamical kind, as can systems described by dynamical equations of differing form (e.g., haploid vs. diploid models). Finally, dynamical kinds are categorically distinct and objective features of the world. Whether or not they constitute the sole answer to the question of natural kinds, they are natural enough to play the role demanded of them here.

4   Dynamical kinds and the levels of selection

4.1   Darwinian dynamical kinds

So what is a Darwinian process? I have argued that the question of the levels of selection can be settled on symmetry grounds: either the dynamics of a population described at some level of the biological hierarchy respects the

symmetries of evolution by natural selection—in which case selection does occur at that level—or it violates one or more of these symmetries, in which case selection cannot be said to operate at that level. To ascertain whether or not a particular population is a Darwinian evolver—a population evolving through a process of natural selection—we need only ascertain whether the dynamics of the population obeys the symmetries of evolution by natural selection. Of course, this means addressing the daunting question of what the 'fundamental' dynamics of evolution by natural selection are.

Restricting our attention to the deterministic models of population dynamics (which generally assume infinite populations), the list of fundamental equations is topped by the so-called 'Replicator-Mutator Equation' or RME. This equation comes in different forms for haploid and diploid populations:[9]

The RME for discrete generations (haploid):

$$x_i(t+1) = \frac{1}{\bar{w}} \sum_j q_{ji} w_j x_j(t) \tag{9}$$

The RME for discrete generations (diploid):

$$x_i(t+1) = \frac{1}{\bar{w}} \sum_{jk} x_j(t) x_k(t) R_{jk} Q_{jki} \tag{10}$$

The variable x_i refers to the frequency of a type (such as a genotype) and w_i refers to the fitness of that type. The term q_{ji} is the probability that an individual of type j produces an individual of type i in haploid reproduction, while Q_{jki} is the probability that a mating of type j with type k individuals produces an offspring of type i. In Equation (10), $R_{jk} = R_{kj}$ is the expected number of offspring produced by pairs of individuals of types j and k, and so $w_i = \sum_j x_j R_{ji}$. In both cases, $\bar{w} = \sum_i w_i x_i$.

Most if not all of the standard models in population genetics can be cast as special cases of either Equations (9) or (10). In fact, the haploid RME can be treated as a special case of the diploid RME for which $\sum_k x_k R_{jk} Q_{jki} = w_j q_{ji}$. The Price Equation, which describes the change in mean character value across a single generation, has been touted for its generality (see Okasha, 2006a). But this equation too can be derived from Equation (9) (Page and Nowak, 2002). All of these models therefore inherit the symmetry structure of the RME, and so there is good reason to take this symmetry structure as characterizing the process of evolution by natural selection. Taking the RME to be fundamental leads to the following definition:

Definition. A population is an instance of the *Darwinian Dynamical Kind (DDK)* if the dynamics that govern its evolution respect the symmetries of the RME.

A process of population change is an instance of evolution by natural selection just if the population is an instance of the DDK.

4.2 Levels of selection

If undergoing evolution by natural selection means belonging to the DDK, then it is possible to provide sharp answers to questions about levels of selection. To begin with, this criterion sanctions some intuitively plausible examples. Consider the particle and group models of KGS (introduced in Section 2) when $\alpha_1 = \beta_1$. This would be the case if, for instance, the particle types A and B are two alleles occurring at a common locus and the group types tracked by f_0, f_1, and f_2 are the frequencies of the three possible diploid genotypes. The fact that $\alpha_1 = \beta_1$ in this interpretation reflects the fact that the alleles in a genome (a group) share a common fate.[10] With these assumptions, it is straightforward to show that Equations (1)–(2), which indicate the change through time of allele (particle) frequencies in the meta-population, are instances of the diploid RME.[11] It is also the case that Equations (6)–(8) are instances of the diploid RME for three distinct types.[12] It follows that Equations (1)–(2) jointly respect the symmetries of the RME, as do Equations (6)–(8). So if we take the symmetry approach seriously, both the population of particles and the population of groups in this model is in fact a Darwinian evolver. That is, both the population of alleles and the population of genotypes in a diploid population evolve by natural selection given the KGS recurrence relations and the fact that alleles in the heterozygote have equal fitnesses.

It is worth noting that the DDK captures cases of both haploid and diploid evolution without any special pleading. This is in contrast with Godfrey-Smith's appeal to 'paradigm populations' (Godfrey-Smith, 2009). Employing a spatial analogy, Godfrey-Smith positions each population in a space defined by three parameters: fidelity of heredity, "dependence of realized fitness differences on intrinsic properties," and smoothness of the fitness landscape. Paradigm populations are located in the vicinity of the point maximizing all of these parameters. However, only haploid populations can maximize all three parameters (since diploids do not reproduce with perfect fidelity). Thus, we must either treat sexually reproducing populations as evolving in somewhat less than Darwinian fashion or we have to

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stretch the region of 'paradigm populations' to include both (Godfrey-Smith opts for the latter). But under the symmetry approach, both types of population can be exact realizations of the fundamental symmetry structure that characterizes Darwinian evolution.

Of course, if we are to believe the DDK actually picks out all and only the instances of evolution by natural selection, it must rule out some putative cases. Here again we don't have to look far for an example. To demonstrate that a population governed by a particular dynamics fails to satisfy the requirements for membership in the DDK, it is sufficient to show that it violates at least one part of the symmetry structure of the RME. Thus, rather than attempt a full explication of the symmetry structure of the RME, it will suffice for our purposes to consider only the most obvious subset of the symmetries of Equation (10): fitness scaling. More explicitly, Equation (10) is invariant under transformations that change all fitnesses at a given time by a common multiplicative constant. Thus, a necessary condition for a population to be a Darwinian population is that its dynamics must be invariant under all such fitness-scaling transformations.

Consider again the dynamics of group evolution expressed by Equations (6) – (8). In general, the α's and β's may be causally independent of one another. Suppose that the ratio $\frac{\alpha_1}{\beta_1}$ is not causally constrained to be constant. Specifically, suppose the ratio varies under interventions that scale group fitnesses. There is certainly no reason from the particle perspective why this couldn't be the case. However, if it is the case, then it is straightforward to show that fitness scaling is no longer a symmetry of Equation (7) (see Appendix A). Put differently, unless the alleles in a group retain proportional fitnesses under intervention, the population of groups does not evolve in a process of natural selection.

5   Objections and extensions

I have argued that answering questions about the levels of selection means answering questions about the equivalence of dynamics—is the process of change in a population of groups the same kind as the process in the population of individual organisms, and are either instances of the process of natural selection? I offered a general theory of dynamical kinds that carves dynamical processes into objective categories on the basis of symmetry structures, and so provides general answers to questions about dynamical equivalence. To apply this theory to questions about selection, however, I had to assume that we already know the fundamental dynamics of evolution-

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ary change, and that this is captured by the RME. There are a number of obvious objections to this move that bear comment.

5.1 Wrong theory of evolutionary dynamics

To begin with, one might simply object that the RME is not the correct choice for a fundamental evolutionary dynamics. For example, Glymour (2011) has argued that the population-level approach of classical population genetics is fundamentally misguided, and that individual-based modeling offers superior predictive and explanatory power. I am sympathetic to this line of criticism, and I am happy to concede that, in fact the RME is not the right theory of evolutionary dynamics.[13] But this is only an objection to the details of the analysis of the levels of selection offered above. The point is that whatever the correct theory of evolutionary dynamics may be, we can apply the theory of dynamical kinds to it in order to decide at what levels of the biological hierarchy evolution by natural selection occurs. A different theory means a different definition of the DDK, but the procedure is the same. And it is the procedure for which I am arguing.

5.2 There is no fundamental theory of evolutionary dynamics

One might instead worry that there just isn't a 'fundamental' evolutionary dynamics. It is distinctly possible that there is no unique dynamics governing the change through time of biological systems described in terms of population-level variables. Clearly there are some population-level regularities in the biological world, so the worry must be that there is such a variety of dynamics governing change through time of populations that there is no single dynamical kind that encompasses them all. Again, this may in fact be the case. However, in that event, the category 'population undergoing evolution by natural selection' is just not a natural kind. The question of levels of selection would then be ill-posed. We would instead have to ask about where in the structural hierarchy this or that evolutionary process may occur. It would be a mistake to speak of levels of selection as though that were a single sort of thing. But for each sort of evolutionary process there is, the dynamical kinds approach gives clear, well-motivated answers to questions about where in the structural hierarchy such change can occur.

5.3 We don't know what the right theory of evolutionary dynamics is

Finally, one might think that there exists one or more kinds of evolutionary process, each with a stable dynamics, but that we just don't know what they are. Here, the theory of dynamical kinds offers significant practical assistance. Dynamical kinds are discoverable without prior knowledge of any particular dynamics. In fact, it is possible to search for dynamical kinds without even postulating any particular dynamics. This can be done by looking directly for dynamical symmetries. These are often easier to discover than specific dynamical relations—one need only assess whether particular transformations commute with the time-development of the system in question. Thus, not only is this worry not a problem for the dynamical kinds approach to the levels of selection, it is an invitation to test the inductive power of these putative natural kinds.

6 Conclusion

I began this essay with a question about the levels of selection: if a population of biological entities evolves by natural selection, is it possible for a population of groups of those entities to do so as well? I suggested that the notion of evolution by natural selection is a dynamic one, and thus we should view the question as one about the sameness of dynamics. This in turn was given a precise meaning in terms of symmetry structures and their realizations. In short, two populations whose states form a realization of the same symmetry structure under the relevant set of transformations are said to instantiate equivalent dynamics. Since it is in fact possible for populations of groups to realize the same symmetry structure as the population of entities comprising the groups, we found the answer to our original question to be affirmative. To be a Darwinian evolver is to possess a certain sort of dynamical symmetry, and it is possible for populations of groups to possess that sort of symmetry. Of course, we need to know something about what we take to be the correct evolutionary dynamics before questions about the levels of selection can be answered. For purposes of illustration, I chose the RME as the fundamental theory, and used this to offer a precise characterization of the Darwinian Dynamical Kind (DDK)—a category of dynamical system that may be said to undergo evolution by natural selection. I then demonstrated that it possible for populations of entities at multiple levels of the structural hierarchy to simultaneously belong to the DDK.

There is one important caveat to be offered. For the symmetry approach

to say anything useful about real populations and not idealized infinite ones, it will be necessary to restate the definition of a symmetry structure as well as the DDK in terms of *approximate symmetries* (see Rosen, 1995). Doing so requires some finesse. But that is a topic for another time.

A Appendix: Violating the fitness-scaling symmetry

It is straightforward to show that fitness scaling is not a symmetry of Equations (6) – (8) unless the fitnesses α_1 and β_1 are directly proportional under all possible transformations of the system that scale group fitnesses. Each of the dynamical equations in this case is a difference equation, expressing a type frequency at time $t+1$ in terms of type frequencies and fitnesses at time t. For ease of notation, let $\vec{s}(t) = \langle f_0(t), f_1(t), f_2(t), \omega_0(t), \omega_1(t), \omega_2(t) \rangle$ stand for state of the system at a time t. The variables ω_i are meant to represent the group type fitnesses. Group fitness ω_i in the discrete-time case represents the expected total number of offspring produced by a group of type i. Group fitnesses do not appear explicitly in Equations (6) – (8), but there is a simple connection between them and the particle fitnesses $\alpha_1, \alpha_2, \beta_0, \beta_1$. Since groups are assumed to be of fixed size, it must be the case that each ω_i is proportional to π_i as defined by Kerr and Godfrey-Smith (2002). Really, each group fitness is the average of the particle fitnesses weighted by the proportion of each particle type appearing in the group. In the two-particle case, this means that $\omega_0 = \beta_0$, $\omega_2 = \alpha_2$, and $\omega_1 = \frac{1}{2}(\alpha_1 + \beta_1)$. It is this last fitness relation that is problematic.

To see why, we have to consider the relevant transformations. We are interested in fitness-scaling as a set of transformations of *group-level* variables. There is one fitness scaling transformation, $\vec{\sigma}_k$ for every positive real-valued k. These transformations have the effect of multiplying all group fitnesses by a common factor:

$$\vec{\sigma}_k(\vec{s}(t)) = \langle f_0(t), f_1(t), f_2(t), k\omega_0(t), k\omega_1(t), k\omega_2(t) \rangle$$

According to the definition of dynamical symmetry, $\vec{\sigma}_k$ is a symmetry of the group dynamics just if the system state is the same whether we apply $\vec{\sigma}_k$ and then use Equations (6) – (8) to evolve the system, or first evolve the system and then apply $\vec{\sigma}_k$. Let Λ_i be the function mapping the state of the system at time t to the value of f_i at time $t + 1$. If $\vec{\sigma}_k$ is a symmetry, then it must be that for $i = 0, 1, 2$:

$$f_i(t + 1) = \Lambda_i(f_0(t), f_1(t), f_2(t), k\omega_0(t), k\omega_1(t), k\omega_2(t)) \qquad (11)$$

Consider just $f_0(t+1)$. Dividing the numerator and denominator of the right-hand side of Equation (6) by $\frac{1}{2}\beta_1$ gives:

$$f_0(t + 1) = \frac{(2\frac{\beta_0}{\beta_1} f_0(t) + f_1(t))^2}{\left(2\frac{\alpha_2}{\beta_1} f_2(t) + 2\frac{\beta_0}{\beta_1} f_0(t) + \frac{(\alpha_1 + \beta_1)}{\beta_1} f_1(t)\right)^2} \qquad (12)$$

A transformation mapping ω_0 to $k\omega_0$ is identical with one which maps β_0 to $k\beta_0$ at the particle level. The same scaling transformation must also take α_2 to $k\alpha_2$. However, the mapping from ω_1 to $k\omega_1$ does not correspond to a unique transformation of particle-fitnesses. In the most general case, we have two functions, g and h such that $g(\alpha_1) + h(\beta_1) = k(\alpha_1 + \beta_1)$. Any choice of functions satisfying this condition is equivalent to the single group fitness transformation—the transformation is infinitely degenerate from the particle perspective. However, if the transformation is to satisfy (11), then it must be the case that the coefficient of $f_1(t)$ in the denominator is constant under the scaling transformation. In other words, it must be the case that:

$$\frac{g(\alpha_1) + h(\beta_1)}{h(\beta_1)} = \frac{\alpha_1 + \beta_1}{\beta_1} \qquad (13)$$

Since $g(\alpha_1) + h(\beta_1) = k(\alpha_1 + \beta_1)$, we have that $\frac{k(\alpha_1 + \beta_1)}{h(\beta_1)} = \frac{\alpha_1 + \beta_1}{\beta_1}$, and thus $h(\beta_1) = k\beta_1$. Likewise, since, $\frac{g(\alpha_1) + k\beta_1}{k\beta_1} = \frac{\alpha_1 + \beta_1}{\beta_1}$ it must be that $g(\alpha_1) = k\alpha_1$. Thus, in order for the group fitness scaling transformation to be a symmetry, it must be the case that:

$$\frac{g(\alpha_1)}{h(\beta_1)} = \frac{\alpha_1}{\beta_1} \qquad (14)$$

In plain language, the ratio of the particle fitnesses must remain fixed under all transformations of the group fitnesses. As a consequence, if the ratio of α_1 to β_1 is not fixed under all group fitness scaling transformations, then fitness scaling is not a symmetry of the group-level dynamics, and the population of groups is *not* a Darwinian evolver.

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Notes

[1]See Okasha (2006b) for a concise overview of the historical arc of the debate, and Lloyd (2012) for a survey of some of the conceptual issues raised.

[2]Nor is it unorthodox. In his consideration of the evidence for or against selection at various levels of the structural hierarchy, Hull (1980, pg. 312-3) proposes "...to investigate the general characteristics of the evolutionary *process* at some length and then to discuss only briefly the particular entities that mayor may not possess the characteristics necessary to function in this *process*" (emphasis added). More recently, Godfrey-Smith (2009, p. 109) dedicates a chapter to '...the idea that Darwinian *processes* occur at different "levels" (emphasis added).

[3]See also (Godfrey-Smith, 2007).

[4]I'm ignoring many biological details. For instance, kinds of the sort I'm discussing are likely mutable since plasmids carrying antibiotic resistance can be shared between strains, mutation rates in bacteria are high, and so on.

[5]This is the notion of a symmetry of the laws of nature presented in (Rosen, 1995).

[6]There is no reason a priori to rule out dynamical symmetries that have no inverse, and so it would be more accurate to say that symmetries form monoids.

[7]For a recent discussion that draws the distinction between epistemic and metaphysical questions about natural kinds, see (Slater, 2013).

[8]Suppose A and B are both instances of dynamical kind K. If the properties of A depended on those of B, then the behavior of states of A under the set of symmetry transformations in K would vary depending on the state of B. Under any but the most trivial dependence on B, such variation would mean that, contrary to supposition, the symmetry transformations on the states of A fail to realize the symmetry structure of K.

[9]The haploid version of the RME is taken from (Page and Nowak, 2002, 97). The diploid version was constructed by the author using the discrete analogues of terms appearing in the continuous time RME for sexual repro-

duction as presented in Appendix A of the same paper.

[10]It is sufficient for being an instance of the RME that the two allele types have identical fitnesses. It is not necessary for each allele in a group to share a common fate for this to be the case (I thank Peter Gildenhuys for pointing this out). In this sense, the condition of "common fate" on which Sober and Wilson (1994) have insisted is too strong.

[11]Specifically, they are instances of the diploid RME for two distinct types for which $Q_{000} = 1, Q_{010} = Q_{100} = \frac{1}{4}, Q_{110} = 0, Q_{001} = 0, Q_{011} = Q_{101} = \frac{1}{4}, Q_{111} = 1$, and $R_{00} = \alpha_2, R_{01} = R_{10} = \alpha_1 + \beta_1 = 2\alpha_1, R_{11} = \beta_0$.

[12]Specifically, they are instances of the diploid RME for which $Q_{000} = 1, Q_{010} = \frac{1}{2}, Q_{011} = \frac{1}{2}, Q_{021} = 1, Q_{110} = \frac{1}{4}, Q_{111} = \frac{1}{2}, Q_{112} = \frac{1}{4}, Q_{121} = \frac{1}{2}, Q_{122} = \frac{1}{4}, Q_{222} = 1$ (with the remaining unspecified values of $Q_{ijk} = 0$), and $R_{00} = \beta_0^2, R_{01} = \beta_0\beta_1, R_{02} = \alpha_2\beta_0, R_{11} = \beta_1^2, R_{12} = \alpha_2\beta_1, R_{22} = \alpha_2^2$. Note that the values of the Q_{ijk} are just the probabilities one would expect for Mendelian segregation.

[13]The RME is really only a partial theory. Just like Newton's Laws of Motion are empty without a specification of one or more force laws, the RME is empty without a further specification of the ways in which fitnesses can depend on time and population states.