Individuality and Macroevolutionary Theory[1]

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The issue of whether species are individuals is now an old one; the literature abounds with arguments, counter-arguments and counter-counter-arguments for their individuality. The question I want to take up in this paper is not whether species are indeed individuals, but what ramifications their alleged individuality has for macroevolutionary theory.

According to those biologists who argue for a new theory of macroevolution, the individuality of species is one of the fundamental premises of that theory. For example, Joel Cracraft writes of himself and others that

> The issue of individuality... is at the heart of arguments of those evolutionary biologists who see a need to view the patterns and processes of evolution as being hierarchically arranged into microevolutionary and macroevolutionary levels (1987, p. 332).

Niles Eldredge, one of the originators of the Punctuated Equilibrium Theory of evolution, writes,

> The ontological status of species... is perhaps the most crucial issue so far broached that bears on the success of the synthesis as an all embracing theory of evolution. Viewing species as individuals opens the door to a more fully explicit and completely hierarchically view of nature's organization–and to a concomitantly hierarchically based theory of life's evolution (1985, p. 51).

In light of such claims, the question I want to pose is this: How much does the thesis that species are individuals contribute to a better theory of macroevolution? More specifically, does the thesis lend support to the Punctuated Equilibrium Theory of evolution? And furthermore, does the individuality of a species or a group indicate that selection works on entities more inclusive than genes or organisms?

In this paper, I will argue that the alleged individuality of species is neither necessary nor sufficient for the Theory of Punctuated Equilibrium. In addition, I will contend that the individuality of a group or species is neither necessary nor sufficient for its being a unit of selection. Before I launch into these arguments, there are two preliminary matters I would like to address.

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The first is a caveat to those who argue that species are individuals. Though the primary objective of this paper is to point out that certain implications attributed to the individuality thesis are not forthcoming, there is one aspect of the thesis which I believe does have important ramifications for evolutionary theory, namely the claim that species are not natural kinds. Some philosophers (e.g., J.J.C. Smart 1963) have questioned the status of evolutionary theory as a scientific theory because there are no laws which refer to particular species. However, if species are not kinds but particulars, this criticism of evolutionary theory is defused. According to the individuality thesis, species are no more kinds than particular chunks of gold are. Just as we do not expect there to be laws which refer only to particular chunks of gold, we should not expect there to be laws which refer only to particular species. Thus the thesis that species are individuals, in showing that species are not natural kinds, helps put the ontology of evolutionary theory in order.

That, however, is where I think the important ramifications of the individuality thesis end. Alexander Rosenberg (1987) has nicely argued that the individuality thesis does not help decide which species definition should be adopted or how the process of speciation works. Furthermore, the individuality of species does not show that species and not higher taxa are units of evolution (Ereshefsky 1988a). I will not take up these matters here; the purview of this paper is to review the alleged implications the individuality thesis has for macroevolutionary theory.

One other item needs to be taken up before that can be done. What is it for an entity to be an individual, beyond the claim that it is not a natural kind? There are, I believe, two views: The weak view of individuality holds that if the constituents of an entity must be spatiotemporally connected, then that entity is an individual. This view is maintained by Ghiselin (1987), Rosenberg (1985), and others. The strong view, on the other hand, holds that not only must the constituents of an individual be spatiotemporally connected, but they must be appropriately causally connected as well. I have argued for this latter view elsewhere (Ereshefsky 1988a, 1988b), and Ernst Mayr (1987) seems to hold a version of it. In what follows, I will argue that regardless of which view one adopts, the individuality of species is neither necessary nor sufficient for the new theory of macroevolution.

Let's turn to the connection between the individuality of species and the Theory of Punctuated Equilibrium.

According to Eldredge and Cracraft,

> if species are viewed as individuals (i.e., discrete entities with origins, subsequent histories and definite terminations), their evolution must be explained. Only a view that species are transitory, arbitrarily defined segments of an evolutionary continuum permits the notion that within-populations phenomena can be extrapolated directly to higher levels. Recognition of the existence of species as discrete entities in effect contradicts the vision of change in gene content and frequency... as a continuous process from the population on up through the phylum (1980, pp. 269-270; also see Eldredge 1985, p. 127).

In other words, the individuality thesis is supposed to support the two major tenets of the Theory of Punctuated Equilibrium. First, there is the pattern tenet that most species change very little during most of their lives, and the change they do undergo occurs during the first five percent (or so) of their existence (Sober 1984, p. 356). Thus according to the theory, species are discrete entities, with definite beginnings and endings. Second, there is the process tenet, namely that the pattern of evolution posited by the theory cannot be the result of the cumulative effects of microevolutionary processes, but must be the result of macroevolutionary processes.

Suppose species are individuals. Does their individuality support the two major tenets of the Theory of Punctuated Equilibrium? I am doubtful. First, individuals need not have discrete temporal boundaries. In fact, biological entities can be individuals on either view of individuality and still lack well defined beginnings and endings. For example, ecosystems consist of a number of spatiotemporally connected and biologically interacting organisms. Yet the temporal boundaries of some ecosystems are far from well defined. So the mere claim that species are individuals is insufficient for establishing that the pattern of evolution is the one posited by the theory. Furthermore, even if species were individuals with discrete boundaries, that would not be enough to show that the pattern of evolution is one of punctuated equilibria. Following Hennig (1966), species could have discrete boundaries, and sandwiched between those boundaries species could have patterns of gradualism. Thus the claim that species are individuals, even coupled with the assertion that they have discrete boundaries, is insufficient for establishing the first tenet of the Theory of Punctuated Equilibrium.

Second, suppose that species are individuals and that the pattern of evolution is one of punctuated equilibria. For example, suppose the members of each species are spatiotemporally and causally connected by gene flow, and most evolution within a species occurs early in its existence. Are these factors enough to establish that the pattern posited by the theory cannot be due to the cumulative effects of microevolutionary processes? Critics of the theory have argued that such a pattern can be accounted for by the traditional models of evolution: for instance, such a pattern of evolution can be accounted for by dramatic spurts of directional organismic selection, followed by long bouts of stabilizing organismic selection (see e.g., Ayala 1983). So even if species were individuals and the pattern of evolution were one of punctuated equilibria, that pattern could be due to micro and not macroevolutionary processes. Hence, the individuality of species is insufficient for establishing the second tenet of the Theory of Punctuated Equilibrium.

In brief, asserting that species are individuals is insufficient for establishing either the pattern or process tenets of the Theory of Punctuated Equilibrium. But perhaps the individuality of species is a necessary requirement of that theory. Again I will argue that this is not the case. Consider the elements of the Periodic Table. The members of each element need not be spatiotemporally or causally connected; they need only share a common element-specific atomic number. Now it is certainly possible for all the members of an element to quickly transmute into another element, remain members of that element for a long period of time, and then quickly transmute into a third element. In other words, the members of an element can exhibit a pattern of punctuated equilibria without forming an individual. Given that possibility, the individuality of an entity is not a necessary condition for its exhibiting a pattern of punctuated equilibrium. Thus the mere individuality of a species is not a necessary condition for its displaying a pattern of that type.

In summary, the individuality of species is neither necessary nor sufficient for the truth of the Theory of Punctuated Equilibrium. This result, of course, does not imply that the theory is false; it just shows that the mere metaphysical assertion that species are individuals is not so tightly connected to the theory's truth as some have claimed.

Let's turn to a specific type of process posited by that theory, namely group and species selection.

According to Eldredge,

> it is obvious that if an entity is to be selected among others of like kind, it must in some way be said to exist. It cannot be a class of things, a set with

> members, rather it must be a whole with parts. It must be a historical entity (1985, p. 104).

Similarly, Hull writes,

> Selection can act only on spatiotemporally localized entities, but if it is to act on entities more inclusive than organisms in the sense that it acts on organisms, then these entities must be cohesive wholes and not classes or groups (1980, p. 314).

So according to Eldredge and Hull, the individuality of a group, whether it be a species or some other type of group, is a necessary condition for its being a unit of selection.

Are these authors right? One way to answer this question is to see if the individuality of a group is indeed a requirement of current models of group selection. Using such a procedure, I will argue that a group need not be an individual to be a unit of selection according to either Elliott Sober's (1984) or David Hull's (1980, 1981) conceptions of group selection.

In his book (Sober 1984, p. 280), Sober presents the following model of selection: There is group selection of groups that have some property P if and only if,

1. Groups vary with respect to whether they have P, and

2. There is a common causal influence on those groups that makes it the case that

3. Being in a group that has P is a positive causal factor for the survival and reproductive success of the organisms in that group.

Given these criteria for group selection, I will argue that the following example is a case of group selection, even though the groups in question are not individuals on either the weak or the strong view of individuality.

Suppose a flying predator which feeds on groups of insects has three groups of insects within its range. Each group consists of organisms from different species, and the members of those species occupy different niches. Furthermore, each group occupies a number of acres and the distance between some of the members of each group is quite large for organisms of that size. Now the way this predator works is he surveys the average lengths of the insects in each group, and then he feeds exclusively on the members of the group with the greatest average length. Is this an example of group selection according to Sober's model? I think it is.

The three groups vary with respect to their average length, so the groups do vary with respect to some property; thus clause one of Sober's model is met. Furthermore, there is a common causal influence which affects the fitnesses of the organisms in those groups, namely the flying predator; hence the second clause of Sober's model is satisfied. Finally, the fitnesses of the organisms in the surviving groups are increased specifically because they belong to the groups with the property of having the smaller average length; thus clause three of Sober's model is fulfilled. Since this example meets all three of Sober's criteria, it is a case of group selection according to his model of selection.

The other thing to notice about this example is that the organisms in each group are neither causally connected in any biological fashion, nor are they spatiotemporally connected. Each group consists of organisms from different species, hence there is no reproductive interaction among all the members of a group. Furthermore, the insects of

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those species occupy different niches, so there is no competition for resources among all the members of a group. Since the organisms in each group are neither biologically causally connected nor spatiotemporally connected, the groups in this example are not individuals on either the strong or weak view of individuality. As I just argued, this example is a case of group selection according to Sober's model of selection. Thus according to that model, a group can be a unit of selection without being an individual.

Let me quickly respond to two objections which might be posed against this example being a genuine case of group selection. First, it is argued by many, including Sober, that group selection occurs only when an organism's chance of surviving and being reproductively successful is affected by a 'group-level' property and not merely by its own properties. One might wonder what the group-level properties are in this example. The answer is simple: The group-level properties here are the average lengths of the members of each group; these are properties which an organism cannot have on its own, but can only have by being a member of a certain group.

Second, someone might object that for group selection to occur, it is not the fitnesses of the organisms in a group that should be affected, but the fitness of the group itself. For example, a fitter group is able to produce more groups. In response to this reply, let me point out that the groups selected in the above example are fitter according to this criterion: the groups of insects with the smaller average lengths are the groups which survive; thus they are better able to produce more groups of insects than the group with the greatest average length.

In brief, Sober's model of group selection shows that a group need not be an individual to be a unit of selection. To show that this result does not depend on Sober's model of selection alone, I will quickly argue that the same result can be obtained using Hull's ideas on selection.

According to Hull (1980, 1981), group selection occurs only if groups are entities which he calls "replicators" and "interactors." A group is an interactor if and only if it has a group-level property which affects the adaptedness of that group (1980, p. 325). And a group is a replicator if and only if it exhibits some structure which can be passed on to descendant groups of that group (1980, p. 324). Are the groups in the above example interactors and replicators? I will argue that they can be.

The groups in question do have group-level properties, namely the average lengths of the members of each group. Furthermore, these properties do affect the adaptedness of the members in each group; the insects in the groups with the smaller average lengths survive while the insects in the group with greatest average length are killed off. Thus the groups in the above example satisfy Hull's description of interactors.

Are the groups in question replicators as well? Suppose the insects in the groups with the smaller average lengths have a genetic tendency for having a smaller length. In addition, suppose that such genetic tendencies can cause those groups to create new groups of insects with smaller average lengths. If that is the case, then the groups of insects have the structure, namely smaller average lengths, and the means for replicating that structure required for being replicators.

Since the groups in question can be interactors and replicators, they can be units of selection on Hull's model of group selection. As we have already seen, such groups are not individuals on either view of individuality. Thus, contrary to Hull's assertion, groups need not be individuals in order to be units of selection according to his model of selection.

In summary, both Sober's and Hull's models of selection allow that a group may be a unit of selection without being an individual. This result indicates that the claim that an entity must be an individual in order to be a unit of selection places an unnecessary metaphysical constraint on the biologist's search for the units of selection.

Before I conclude this paper, I want to point out that being an individual is not a sufficient condition for being a unit of selection either. Take any population which consists of members which are spatiotemporally and causally connected by gene flow. In other words, take any population that is an individual on both the weak and strong view of individuality. It is certainly possible, and it is probably true in many cases (see G. C. Williams 1966), that such populations lack population-level properties which affect the adaptedness of their members. Given that there are such populations, then according to both Hull's and Sober's models of selection, such populations are not units of selection, despite their being individuals. Thus according to those models, being an individual is not a sufficient condition for being a unit of selection.

In this paper, I have argued that the individuality of a group is neither necessary nor sufficient for its being a unit of selection. I have also argued that the individuality of a species is neither necessary nor sufficient for the truth of the Theory of Punctuated Equilibrium. Given these results, it seems mistaken to claim that the individuality of species "is perhaps the most crucial issue" for a new theory of macroevolution. Metaphysical work in theoretical biology and the philosophy of biology has provided a number of benefits. However, in the areas discussed in this paper, I think it has mainly side-tracked the issue.

Notes

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