

## Re: Species Selection Redux

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**From:** Guy Hoelzer ([hoelzer\\_at\\_unr.edu](mailto:hoelzer_at_unr.edu))

**Date:** 03/12/05

Date: Fri, 11 Mar 2005 20:06:38 -0500 (EST)

in article [d0rc88\\$1dde\\$1@darwin.ediacara.org](mailto:d0rc88$1dde$1@darwin.ediacara.org), Perplexed in Peoria at [jimmenegay@sbcglobal.net](mailto:jimmenegay@sbcglobal.net) wrote on 3/10/05 10:01 PM:

> "Guy Hoelzer" <[hoelzer@unr.edu](mailto:hoelzer@unr.edu)> wrote in message  
> news:[d0qtar\\$17uv\\$1@darwin.ediacara.org](mailto:d0qtar$17uv$1@darwin.ediacara.org)...  
>> in article [d0on9t\\$gus\\$1@darwin.ediacara.org](mailto:d0on9t$gus$1@darwin.ediacara.org), Perplexed in Peoria at  
>> [jimmenegay@sbcglobal.net](mailto:jimmenegay@sbcglobal.net) wrote on 3/9/05 9:51 PM:  
>>  
>>> "Guy Hoelzer" <[hoelzer@unr.edu](mailto:hoelzer@unr.edu)> wrote in message  
>>> news:[d0nbfi\\$1ci\\$1@darwin.ediacara.org](mailto:d0nbfi$1ci$1@darwin.ediacara.org)...  
>>>> in article [d0m6mq\\$2ndm\\$1@darwin.ediacara.org](mailto:d0m6mq$2ndm$1@darwin.ediacara.org), Perplexed in Peoria at  
>>>> [jimmenegay@sbcglobal.net](mailto:jimmenegay@sbcglobal.net) wrote on 3/8/05 10:56 PM:  
>>>>  
>>>>> "Tim Tyler" <[tim@t1lock.org](mailto:tim@t1lock.org)> wrote in message  
>>>>> news:[d0kipq\\$2654\\$1@darwin.ediacara.org](mailto:d0kipq$2654$1@darwin.ediacara.org)...  
>>>>>> [bryophyta@hotmail.com](mailto:bryophyta@hotmail.com) <[bryophyta@hotmail.com](mailto:bryophyta@hotmail.com)> wrote or quoted:  
>>>>>> Also, it is widely expected that species selection will be a rather weak  
>>>>>> force – since its effects will often be swamped by individual selection –  
>>>>>> which will act to destroy some of the variation on which species  
>>>>>> selection would otherwise act.  
>>>>  
>>>> The strength of selection at any level is always determined by the same  
>>>> factor: the extent of heritable variation in fitness.  
>>>  
>>> I agree, but there is a need to be cautious here. In comparing fitnesses  
>>> at different levels, you need to be sure you are not comparing apples  
>>> and oranges. The most important thing is to be sure that you are using  
>>> the same time scale in both cases. You can't naively take fitness to be a  
>>> growth rate per generation but use organism generations in one case and  
>>> species generations in another.  
>>  
>> While I appreciate the importance of temporal (and spatial) scale  
>> compatibility in the interaction among processes, I don't think that your  
>> concern is relevant here. I don't think that the interaction between  
>> selection manifested at different levels of organization generally depends  
>> on the relative fitnesses of entities existing at the different scales. For  
>> example, it is not like a species can be more fit than an individual  
>> organism, or vice versa. Instead, the strength of selection at any level

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>> *depends on "the extent of heritable variation in fitness" at that level*  
>> *alone, and the evolutionary response to selection can (but does not*  
>> *necessarily) include a cascade of effects that spill over into systems at*  
>> *other scales of organization.*  
>>  
>> *You seem to be focused on situations where selection within systems existing*  
>> *at different scales conflict, ...*  
>  
> *Yes, I was focused on that. The topic was whether selection at the species*  
> *level is "weak", and to address that we have to ask "weak as compared to*  
> *what?".*  
> *Tim's original claim that it is weak was clearly meant to compare the strength*  
> *of species selection with that of classical Fisherian individual selection.*  
>  
> *In raising the issue of time scales, I did not intend to compare the fitness*  
> *of an individual with the fitness of a species. However, to answer the*  
> *question of relative strength, we do need to compare the "variation" of the*  
> *two, and the only way I know of to quantify variation is to compute a*  
> *variance. A variance is not a pure number – it has the "dimensions" of*  
> *fitness<sup>2</sup>, so to compare variances we need to measure the two kinds of*  
> *fitnesses in the same units.*

OK.

>>>> *The view that forms of group selection, including species selection, is*  
>>>> *usually weak implies that heritable variation in fitness among groups is*  
>>>> *usually small. That may be the case, but I think it would be useful to*  
>>>> *have someone explain why this situation might be common in today's*  
>>>> *biosphere, or in general (temporally speaking) if that is part of the*  
>>>> *argument.*  
>>>>  
>>>> *Well, in some sense (regarding group selection at least) this is simply a*  
>>>> *theorem of analysis-of-variance. The (per capita) variance within the*  
>>>> *population as a whole is partitionable into within-group and among-groups*  
>>>> *components. The part is always smaller than the whole.*  
>>>>  
>>>> *How does this lead to the conclusion that group selection is usually weak*  
>>>> *compared with selection at the individual level?*  
>>>>  
>>>> *It seems self explanatory to me. Heritable variation (variance) in fitness*  
>>>> *among groups is always less than or equal to the heritable variation in*  
>>>> *fitness among individuals.*

This assumes that the fitness of groups is an additive function of the fitnesses of its components. As JE is so fond of pointing out, under this condition groups simply do not exist as a potential target of selection. It doesn't make any sense to me to even discuss the strength of group selection and make this assumption in your argument. Your fitness is not an additive function of the fitnesses of your genes, or your cells, etc.. Fitnesses at different levels of selection are mostly independent from one another, so knowing the fitnesses of agents at one level gives you little to no

information about fitnesses at other levels. So heritable variation for fitness at the group level CAN be greater than the heritable variation for fitness at the individual level. In fact, heritable variation for fitness at the group level can be great even when there is no heritable variation for fitness at the individual level.

>>> *The entity that evolves is different.*

>>

>> *I presume you are referring to the entity that evolves in DIRECT response to the selection pressure, as opposed to entities that evolve due to indirect correlation with the entity under selection.*

>

> *Of course. While I agree that ecosystems "evolve", I think that it would be incorrect to say that they evolve under natural selection. An ecosystem doesn't have a fitness. Of course, an understanding of NS is certainly necessary for an understanding of ecosystem evolution.*

Do you recognize your claim that ecosystems don't have a fitness is an assertion without empirical support? Many professionals (perhaps most ecosystem scientists, for example) would disagree. I admit that the data contradicting your position are also wanting, but I think it is important to recognize that this is an open question actively debated among scientists.

>>> *In group selection, as in individual selection,*

>>> *it is the species that evolves.*

>>

>> *Who told you this? The network of populations evolves under group selection. This may be a metapopulation or a species or any other kind of network of populations that might exist (including networks of populations involving multiple species!).*

>>

>>> *That is, in both cases, the effect is*

>>> *to change the average character of individual organisms within the species.*

>>

>> *This is major misconception, IMHO. The average character of individual organisms will only evolve (indirectly) as a result of group selection when individual level traits are correlated with factors affecting heritable variation in fitness among groups. This need not be the case, and I know of no reason to think that it would be the norm.*

>

> *I am referring to models of "group selection" such as the Price model, or the "trait group" model in which the fitness of a group is equal to the average of the fitnesses of its members \*\*\*by definition\*\*\**

So your comments are not aimed at the notion of group selection in general, right? They are only aimed at this (what I consider to be) naïve attempt to model group selection. This seems to me like either an attack on a straw man, or a failure to appreciate the importance of functional independence (though possibly correlated through indirect effects) of fitnesses at different levels of organization to the complex process of multilevel selection.

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> *The source of our disagreement is becoming obvious. You are thinking in terms  
> of models in which the group (or species) has a fitness of its own which is  
> distinct from the average fitness of its members.*

>

>>>>> *It is true that the process of individual selection does tend to reduce  
>>>>> variation between groups.*

>>>>

>>>> *Funny. I would make exactly the opposite argument. I think that selection  
>>>> at higher levels is better able to reduce the effects of selection at lower  
>>>> levels than it is for the exertion of control to reach upward. Higher  
>>>> level phenomena emerge from the activities of their lower level components,  
>>>> so their existence and their potential as a unit of selection is  
>>>> automatically promoted by the interests of lower level agents. I see no  
>>>> advantage to individual organisms in somehow stifling group selection  
>>>> (including species selection).*

>>>>

>>> *You seem to have misinterpreted me. I agree with the points you are making  
>>> about "emergence" and about control hierarchies. I was talking about  
>>> versions of group selection (such as Price's or D.S.Wilson's) in which  
>>> there is no "emergence" and in which groups act as pure units of selection  
>>> rather than as levels of functional organization.*

>>

>> *I'm not sure that D.S. Wilson still holds that view, but I think I  
>> understand your perspective.*

>

> *After reading "Unto Others" I am quite sure that he does NOT hold that view.  
> However, his "trait group" model of group selection very definitely does  
> treat group fitness as an aggregate of the fitnesses of the members.*

I agree. This is another model that misses the mark IMHO by making a simplifying assumption that obscures an essential part of the process.

>> *I guess I would argue that the functionalist  
>> viewpoint solves most of these issues.*

>>

>> *I think it is a big mistake to define a group by the identities of the  
>> individuals that compose it, as opposed to its functional coherence.  
>> Otherwise we can be talking about ghosts, which as we all know don't really  
>> exist. Do you see a problem in simply limiting the purview of group  
>> selection theory (multilevel selection theory, really) to functional  
>> entities, without changing any of the conceptual aspect of the theory?*

>

> *No problem at all. I wish Price and D.S. Wilson had never muddied the  
> waters by calling their models "group selection" models.*

I agree in retrospect, although at the time I think they served the purpose of pushing the dialogue ahead.

> *Best of all, our argument over the relative strength of individual and  
> group selection becomes moot, because the two no longer can oppose each*

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- > *other. Individual selection acts on individual traits and higher level*
- > *selection acts on higher level traits.*

Yes, although I think that they can still conflict as their effects cascade across levels.

Regards,

Guy