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Weighted fitness theory: an approach to symbiotic communities

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We see in our crystal ball that, in the near future, microbiology could have a new formulation for the theoretical conditions that explain the evolution of group selection in the symbiotic community. This formulation is a combination of the two main theories on evolutionary altruism: (i) Hamilton's (1963) theory of kin selection and (ii) the multilevel selection theory of Wilson and Wilson (2007). The first explained that the fitness (*F*) of any individual has an e_i ($0 < e_i < 1$) component that favours self-reproduction, and another ($1 - e_i$) that altruistically favours the reproduction of the other members of the group. The second demonstrated the existence of different selective pressures that can operate at different levels in the biological hierarchy. Acting simultaneously, these pressures generate what is known as the genomic conflict (i.e. different genes affecting a given character can receive opposing selective pressures as the result of acting at different levels of that hierarchy). If multilevel selective pressures exist, then different levels of environmental resistance in an ecological niche also exist, both at group and individual levels. Thus, we can estimate the proportion of selective pressure due to competition at individual p_i ($0 < p_i < 1$) and group ($1 - p_i$) levels.

If we accept the previous models, an individual's inclusive fitness (*F*) will centre on the hierarchical level at which the selective pressure is highest. This is where the battle for life is most intense and the individual is most likely to die. Thus, if selective pressure is greater at group level, the life of the individual will be more dependent on the survival of the group. This increases the chances of more efficient groups being positively selected and these groups are precisely made up of the most altruistic subjects. Conversely, if selective pressure is greater at individual level, then selfish subjects have a greater chance of being the lucky winners.

In financial investment projects, mathematical expectation (expected value, *EV*) is used to assess where the best investment is. Accordingly, future cash collections are weighted by multiplying them by their probability of return, and the project is chosen according to the highest expected value. Likewise, if we apply *EV* to inclusive fitness (*F*) multiplied by selective pressure at different levels, the weighted inclusive fitness formula (F') is the result of:

$$F' = e_i \times p_i + [(1 - e_i) \times (1 - p_i)].$$

F' represents the relative contribution that each individual makes in terms of biological fitness to himself (e_i), and his group ($1 - e_i$), but also takes into account the relative selection pressure at each of these levels, p_i and ($1 - p_i$), respectively. Given that F' weights the degree of group cohesion with multilevel pressure at each hierarchical level, it is, in our opinion, the parameter that best represents what natural selection actually does or does not do to favour each individual. Thus, an individual with a greater F' will be the one that contributes more to the hierarchical level than his ecological niche demands. It is especially worth mentioning that since F' only takes into account the percentage of individual fitness, it can be applied to any kind of biological relationship regardless of the degree of kinship, including the interactions of symbiotic mutualism between species. Mathematically, the function F' is a hyperbolic paraboloid (Fig. 1).

How does F' work?

When group pressure ($p_i < 0.5$) rather than individual pressure predominates in the niche, only the individuals with $e_i < 0.5$, that is, those with a higher F' or the most altruistic ones, will be positively selected. On the other hand, when individual pressure predominates ($p_i > 0.5$), only those with $e_i > 0.5$ (the selfish ones) will be selected.

Nonetheless, in the same way as an altruistic individual increases the fitness of the other partners in his group, these, in turn, will increase the fitness of the altruist in question. This constitutes the effect of

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reciprocity in mutual collaboration. This aid from the group (Δe_i) implies an increase of e_i, and if this effect increases the individual's F', it can be termed as *biological leverage*. F' including the effect of Δe_i is the result of:

$$F^{\Delta} = (e_i + \Delta e_i) \times p_i + [1 - (e_i + \Delta e_i) \times (1 - p_i)],$$

where extracting and simplifying:

$$F^{\Delta} = F' + (2 \times p_i - 1) \times \Delta e_i.$$

As $0 < p_i < 1$, so that $F^{\Delta} > F'$ and biological leverage can exist, selective pressure at individual level must be more intense than pressure at group level ($p_i > 0.5$). If the prevailing selective pressure is the one of the group ($p_i < 0.5$), this extra help (Δe_i) will decrease the F' of the individual. This apparent paradox makes sense only when selective pressure favors selfishness, then cooperation with other partners can be beneficial for the individual. And the greater the individual pressure with respect to group pressure (i.e. the closer p_i is to 1), the greater the biological leverage, and also the greater the benefit the selfish individual obtains from being helped by the others. Conversely, if what prevails in the environment is competition between groups, then any deviation from group fitness towards individual fitness will penalize the group and all its members. The altruists ($e_i < 0.5$) who work for the group will have to equip themselves with an increasing number of altruistic traits, because the egoistic features become deleterious for the group and would cause individuals to have a lower F'.

There is also biological leverage at group level. As the help given to the individual by the rest of the partners (Δe_i) increases his individual fitness (e_i), conversely, to increase group fitness ($1 - e_i$), individual fitness must drop. This implies that helping the individual will be the opposite of helping the group. We call the latter ($-\Delta e_i$) and it is the result of:

$$F^{-\Delta} = F' + (1 - 2 \times p_i) \times \Delta e_i$$

As expected, to achieve $F^{-\Delta} > F'$ so that group biological leverage can exist, selective group pressure must prevail ($p_i < 0.5$). This is exactly the case in eusocial animals and symbionts, in which altruistic traits only thrive for the benefit of the group ($1 - e_i$) if they are combined with help for the group ($-\Delta e_i$), as these altruistic traits are the only ones that provide a larger F' for the individual.

What about long-term evolution?

When $p_i < 0.5$, the most altruistic individuals are selected and groups increase their fitness, so that individuals can survive in previously non-attainable environments. The appearance of these new groups produces divergent and rapid evolution (adaptive radiation) that increases the concurrence of groups, and thus competition and intrinsic environmental resistance at group level ($1 - p_i$). These conditions provoke a positive feedback process given that the greater the group pressure, the greater the likelihood that more altruistic individuals – those with higher group fitness ($1 - e_i$) – will be positively selected. When adding the effect of the group's biological leverage, *ceteris paribus*, we reach the point where $p_i = 0$. At this stage, group individualization would be perfect and it would no longer be possible to consider individuals at the lower level of the biological hierarchy, as the creation of an entity with a higher hierarchical level would be complete. In sum, when $p_i < 0.5$, due to the effect of the positive feedback mentioned above, p_i tends to 0 in the long term, thus:

$$\lim_{p_i \to 0} F' = e_i \times p_i + (1 - e_i) \times (1 - p_i) = 1 - e_i.$$

This limit is actually the point of maximum altruism (point *A*, Fig. 1). The sum of positive feedback (between group pressure and evolutionary altruism) and group biological leverage is essential to explain how symbiogenesis and the formation of new and more complex entities can evolve at a higher biological hierarchy level. By way of

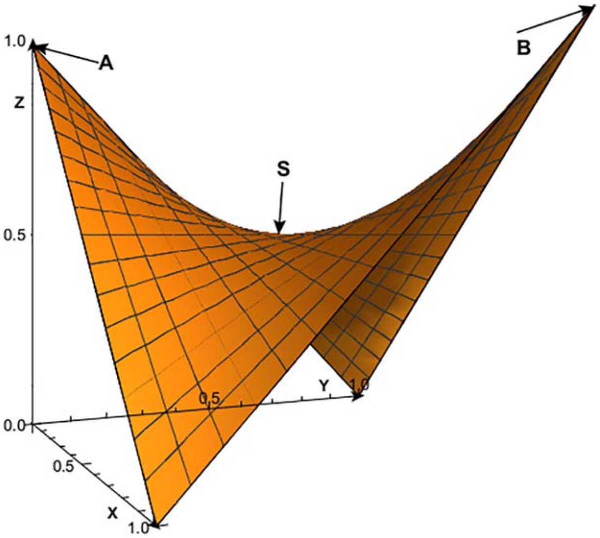

Fig. 1. The hyperbolic paraboloid, the curve of weighted fitness function (F'). The curve is a three-dimensional saddle-shaped doubly ruled surface, i.e. through every one of its points two distinct lines lie on the surface. The point where the minimum value of the maxima coincides (*S*) is the saddle point. The *X* axis represents the individual selective pressure proportion (p_i). The *Y* axis represents the individual fitness proportion (e_i). *Z* axis is F'. The coordinates of the saddle point or minimax *S* are 0.5, 0.5, 0.5. The parabola from point *A*(0, 0, 1) to point *B*(1, 1, 1), whose vertex is *S*, represents the maximum values that e_i takes for each given value of p_i. That is, the *BSA* parabola represents the fitness ratio that will be positively selected for each level of selective pressure.

example, this is actually how the symbiotic communities of insects and their endosymbionts have coevolved (López-Sanchez *et al.*, 2009) towards a common hologenome (Moran and Sloan, 2015). Conversely, when $p_i > 0.5$ and individual selection predominates, the most altruistic individuals are relegated by natural selection and *F'* tends to maximum selfishness (point *B*, Fig. 1):

$$\lim_{p_i \to 1} F' = e_i \times p_i + (1 - e_i) \times (1 - p_i) = e_i.$$

We found unequivocal cases of the two situations explained above in microorganisms. For example, bacteria of the *Myxococcus* (Travisano and Velicer, 2004) and *Pseudomonas* genera (Rainey and Rainey, 2003) usually live a solitary life until nutrients deplete. When this happens, groups of them die forming multicellular structures so others can survive and reproduce. These bacteria, like primitive eusocial animals, have an adaptive trigger that detects environmental changes and allows them to move from a free individual life, to a social one, or vice versa. However, if environmental conditions persist in one way or another, these peculiar species may reach the point of no return (Wilson, 1971) where rigid adaptations lacking phenotypic flexibility end up being selected. At this point, and under the predominant conditions, even when these adaptations impede going back, *F'* increases. Genomic reduction in the primary endosymbionts of insects (Latorre and Manzano-Marín, 2016), with the creation of more complex entities (hologenomes), is a good example of rigid adaptation towards social/eusocial/group life. As we see, neither evolutionary altruism nor hierarchical speciation requires kinship or vigilance of selfish individuals. The only factor needed is the concurrence of future partners in an ecological niche in which group pressure predominates.

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