

## Reply to Speijer: Does complexity necessarily arise from selective advantage?

We recently pointed out that the distantly related alveolate and euglenozoan protist lineages share several otherwise rare traits and inferred that these traits arose by convergent evolution (1). We also emphasized that such complex molecular traits may evolve through the accumulation of neutral mutations (constructive neutral evolution) rather than selection. Speijer (2) questions both inferences.

Convergence is inescapably linked to level of organization: traits may be similar at one level but fundamentally different at deeper levels. For example, vertebrate and cephalopod camera eyes arose by independent reorganization of homologous subcomponents (3). Similarly, widespread RNA editing exists in dinoflagellate and kinetoplastid mitochondria, but their different mechanisms reinforce the phylogenetic conclusion that these processes originated convergently. The same can be said for characteristics of plastids and nuclear gene expression we highlighted (1). “Epistatic constraints” are not an alternative to convergence: They may economize the role of convergence for evolutionarily related changes, but the ultimate origin of the traits is still convergent.

Whether characters originated because of selection is a thornier question. The assumption that complex systems must confer some advantage and therefore evolve by positive selection is rarely questioned, even in cases with no obvious advantage (or for which multiple mutually exclusive explanations have been proposed), such as kinetoplastid RNA editing. We suggest instead that such systems arise without positive selection through a process of constructive neutral evolution (4).

Speijer (2) raises three objections: Drift is required, editing is expensive, and reversals are impossible. However, drift must fix neutral changes in any explanation of editing (unless every mutation is selected, a ridiculous extreme). Similarly, there is no evidence that eukaryotic genomes are so sensitive to ATP economics that complexity must be meaningfully deleterious. Moreover, in a neutral origin of editing, complexity increases

incrementally and in a ratchet-like fashion in which new neutral changes render previous ones essential. This directionality favors the system's persistence but does not exclude reversal any more than if the system originated by positive selection.

It also is essential to distinguish how a system originated and what it does today. A complex system may originate without selective advantage and subsequently acquire secondary attributes. Secondary attributes may be beneficial, but they do not explain the system's origin. Speijer's model (5) does not seek to explain the origin of kinetoplastid editing but only its later expansion in some lineages. In evoking selection, this model demands uncertain conditions such as strong competition between kin and few cheaters. However, the ratchet-like expansion predicted by a neutral model (4) requires no special conditions: As long as the correction machinery is in place, expansion simply requires the emergence of new guide RNAs, mutation, and drift.

The conventional route taken by most molecular biologists is to explain complexity by positive selection. However, we should not dismiss the purely neutral origin of complex systems like editing without evidence. Indeed, the absence of a working model for the origin of editing through positive selection renders the neutral model even more appealing, because it is liberated from the need to justify such an absurd molecular system with “Just-So” stories.

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Author contributions: P.J.K., B.S.L., and J.L. wrote the paper.

The authors declare no conflict of interest.

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