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Reply to Johnson: Holistic evaluation of ecological models in paleobiology

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Johnson (1) argues that our paper does not falsify Red Queen (RQ) and that fitting Hubbell's neutral theory (NT) to fossil data does not "validate" NT. Our paper (2) makes similar points. We do not claim to falsify RQ; rather, we discuss deep similarities between RQ and NT and show how elevated extinction among young species emerges from RQ-like dynamics. Likewise, we argue that NT increases our understanding of extinction, not that NT model fit proves species are neutral. We welcome further paleobiological application of ecological models, including those incorporating environmental change. Yet Johnson's attempt is described and implemented incorrectly, cannot be fit to data, and is argued on flawed premises.

Johnson implements density dependence with a reflecting boundary at carrying capacity. Contrary to his assertion, this is at least as complex as the logistic model, containing five parameters including two that he never acknowledges or parameterizes: starting abundance, and the abundance below which species are considered extinct. We recreated his model using a standard definition of reflecting boundary (3) and recovered a strikingly different survivorship pattern from his, wherein species that reach carrying capacity get "stuck" there and become immortal. Two other plausible definitions of reflecting boundary did not match his figures. Thus, his model does not match his verbal description and is not replicable. Another problem is that he calculates survivorship by solving the Fokker–Planck equation (4). Fokker–Planck is inappropriate here because it calculates survivorship as the probability that a species has abundance over some threshold regardless of its history, thus allowing for "resurrected species." Johnson's figure 1B indicates something has gone wrong with his model: Environmental stochasticity σ is the only source of extinction in his model, so decreasing σ should not increase extinction rate among old species.

Johnson's model cannot produce likelihoods, meaning it cannot be tested against alternative survivorship models or test for differences between datasets. While there are no statistical panaceas, we rigorously compare NT to other models in an information criterion framework; in contrast, Johnson's supposed fit to data comes from simple "eyeballing," despite his insistence on strong tests of theory.

Johnson argues we did not consider the validity of NT's assumptions. In fact, we examine the neutrality assumption at length and discuss how models can succeed despite (or perhaps due to) making unrealistic assumptions. Johnson's model is supposed to be more biologically realistic than NT, but it assumes without justification that no species competes with any other for resources and that each species has the same carrying capacity. His model includes no differences among species, so it makes a neutral assumption as well. Johnson urges that "a holistic evaluation of NT should consider other predictions," but this is exactly what our paper is doing: testing previously unexplored aspects of NT. NT is a unified theory, able to link and explain disparate ecological phenomena across scales and data types. In contrast, Johnson's model is tailor-made to explain survivorship in one dataset, and it seems unlikely it can do even that.

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