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The evolutionary palaeoecology of species and the tragedy of the commons

Peter D. Roopnarine[1,*] **and Kenneth D. Angielczyk**[2]

[1]*Department of Invertebrate Zoology and Geology, California Academy of Sciences, San Francisco, CA 94118, USA*
[2]*Department of Geology, Field Museum of Natural History, Chicago, IL 60605, USA*
**Author for correspondence* (*proopnarine@calacademy.org*).

The fossil record presents palaeoecological patterns of rise and fall on multiple scales of time and biological organization. Here, we argue that the rise and fall of species can result from a tragedy of the commons, wherein the pursuit of self-interests by individual agents in a larger interactive system is detrimental to the overall performance or condition of the system. Species evolving within particular communities may conform to this situation, affecting the ecological robustness of their communities. Results from a trophic network model of Permian–Triassic terrestrial communities suggest that community performance on geological timescales may in turn constrain the evolutionary opportunities and histories of the species within them.

Keywords: tragedy of the commons; complexity; complex adaptive systems; palaeocommunity

1. INTRODUCTION

Waxing and waning of entities is a dominant feature of the palaeontological record. For example, species often increase in abundance and geographical range early in their histories, but undergo range contractions and become increasingly rare as they approach extinction [1]. Other taxonomic and non-genealogical entities, such as genera, so-called evolutionary faunas and types of ecological communities exhibit similar patterns [2–4]. Many of these macro-palaeoecological patterns result from the ecological histories of species, which themselves are the results of population dynamics that lie mostly below the resolution of the stratigraphic record. Individual species histories, however, are embedded in complex adaptive systems at a higher hierarchical level of biological organization, comprising biotic interactions among individually acting species. The feedback of species interactions and evolutionary change to both the abiotic contexts and the dynamics of the systems affect species histories.

Species evolution may therefore be constrained by the higher level systems that they create and in which they are embedded. Similarly, extinction would frequently be the result of an exhaustion of species' adaptive capacities in the face of a system's changing dynamics. From this, it is apparent that individual entities must balance selective pressures arising at various hierarchical levels, and that their waxings and wanings are the result of coupled dynamics at multiple scales of organization. Positive patterns or changes at one level need not be so at all levels, and species may evolve adaptations that do not benefit aspects of system performance, such as productivity or resistance to cascading or collateral extinctions; this is an evolutionary–ecological tragedy of the commons [5]. Here, we explore this argument by examining the manner in which the trophic breadths of species and relative guild species' richnesses determine community resistance to cascades of secondary extinction, and the top-down constraints subsequently exerted by communities on species. Specifically, certain combinations of species richness and ecological diversity may constrain the evolutionary histories of individual species because of their impact on community properties. We will first conduct a thought experiment and then provide an empirical example.

2. A THOUGHT EXPERIMENT

Imagine a marine community in the Late Pre-Cambrian comprising many ancestors of modern animal phyla, into which we introduce a proficient or novel adaptation in a single species [6]. Proficient adaptations are a hallmark of the Cambrian Explosion; the 'vacancy' of morpho-ecological niches and simpler interspecific interactions would have made them highly probable. The result of the adaptation would be a rapid increase in both the relative abundance and spatial range of the species possessing it, but the increase would be unlikely to continue unabated for two reasons. First, in ecological time, a population cannot increase infinitely because of density-dependent effects of limited resources, even in the absence of interspecific biotic interactions. Second, antagonistic interactions are likely to evolve on evolutionary timescales because the species itself now represents a valuable resource for adapting predators, parasites and pathogens. The species would also be an agent of selection on any other species using a common resource, thereby driving the evolution of competitors. The result is the onset or acceleration of biotic interactions, hypothesized to be a major driver of the Explosion [7]. Biotic interactors are agents of selection, and the feedback of communities of interacting species into their own selective environments is a source of diversification and complexification [8].

Even an explosion of evolutionary ecological activity, either the Cambrian Explosion or any community early in its history, is not without constraint. Rapid inflation will be followed by a deceleration of the proliferation of new ecological types. In the case of the Cambrian Explosion, developmental and genetic constraints [9] and ecological saturation [10] or exhaustion [7] are probable decelerating mechanisms. Ecologically, there is, however, more than saturation or exhaustion at work. Theoretically, there may always be room enough for new adaptations [10]. Species evolution, however, is an exploration of fitness landscapes that respond dynamically to abiotic variation and are coupled dynamically to the landscapes of other species in the community. We hypothesize that the long-term success of a species

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