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Versão corrigida

Dissertação apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção de Título de Mestre em Ciências, na Área de Ecologia de Ecossistemas Terrestres e Aquáticos.

Orientador(a): Tiago Bosisio Quental

São Paulo

2020

Ficha Catalográfica

Graciotti, Rodolfo Pereira

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Rodolfo Pereira Graciotti; orientador Tiago Bosisio Quental -- São Paulo, 2020.

68 p. + anexo

Dissertação (Mestrado) -- Instituto de Biociências da Universidade de São Paulo. Departamento de Ecologia.

1. Macroevolução. 2. Registro Fóssil. 3. Especiação. 4. Extinção.

I. Universidade de São Paulo. Instituto de Biociências. Departamento de Ecologia.

Comissão Julgadora:

Prof(a). Dr(a).

Prof(a). Dr(a).

Prof(a). Dr.(a).
Orientador(a)

Resumo

Compreender os padrões da biodiversidade e os processos que os geram são objetivos centrais em estudos ecológicos e macroevolutivos. Os efeitos de fatores bióticos e abióticos na geração e manutenção da biodiversidade, incialmente analisados isoladamente, são hoje considerados interligados e importantes em determinar o balanço da diversidade de espécies. Os modelos de diversificação dependente de diversidade postulam que um aumento no número de espécies resultaria em reduções na taxa de especiação e aumentos na taxa de extinção. À essa dinâmica é atribuído o efeito da competição interespecífica, porém de forma indireta e interpretativa, pois os modelos tipicamente carecem de abordagens mais mecanísticas. Neste estudo, incorporamos mais explicitamente aspectos espaciais e eco-morfológicos, construindo métricas que capturam além da coexistência no tempo, coexistência no espaço e interação no morfoespaço. Desta forma, testamos como inferências indiretas se comparam com nossas inferências que utilizam uma abordagem mais mecanística para estudar a competição. Utilizamos o registro fóssil da família Canidae na América do Norte, um grupo amplamente estudado e bem caracterizado do ponto de vista eco-morfológico e paleontológico. Testamos a hipótese de que a intensidade da competição resultaria tanto na diminuição das taxas de especiação quanto no aumento das taxas de extinção. Encontramos que a competição atuou de forma mais intensa durante as fases iniciais da radiação de Canidae, resultando na supressão da taxa de especiação no momento em que o grupo apresentava expansão de diversidade. Entretanto, não detectamos uma associação entre a intensidade da competição e a dinâmica de extinção esperada pelo efeito competitivo. Os resultados sugerem que a queda de diversidade e aumento na extinção próxima do presente estariam relacionadas a fatores externos à competição de espécies de Canidae, como por exemplo mudanças climáticas e competição com outros grupos como Felidae. Nossos resultados estão de acordo com estudos anteriores que apontaram assimetrias no efeito da competição nas taxas de especiação e de extinção. A novidade apresentada aqui foi mostrar que os efeitos da competição interespecífica não se manifestaram ao longo de toda a história evolutiva de Canidae. Também mostramos que modelos mais mecanísticos de fato sugerem que, ao menos parcialmente, os efeitos dependentes de diversidade podem ser influenciados por competição de recursos. Concluímos então que a relevância de fatores bióticos e abióticos na dinâmica de diversificação de um grupo pode se alterar ao longo do tempo, e que não apenas um mecanismo atua em detrimento do outro.

Palavras-chave: Macroevolução. Registro Fóssil. Especiação. Extinção.

Abstract

Understanding biodiversity patterns and the processes that generate them are key goals in ecology and macroevolutionary studies. The deep time effects of biotic and abiotic factors on biodiversity, initially considered in isolation, have been shown to be interconnected and important on determining biodiversity dynamics. Diversity-dependent models of diversification postulate that an increase in diversity should result in a decrease in speciation rate and an increase in extinction rate. Interspecific competition is typically considered to be the underlying mechanism of such dynamics but the evidence is indirect and interpretive as such models typically lack a more mechanistic view of competition. In this study, we more explicitly incorporated spatial and eco-morphological aspects to test how the aforementioned effects manifest in deep time. We built different metrics that capture not only species temporal coexistence, but also their coexistence in space and morphospace. We hence tested how indirect inferences compare with our inferences that use a more mechanistic approach to study competition. We used the North American fossil record of the family Canidae, a group that has been extensively studied and well characterized both from the eco-morphological and paleontological points of view. We tested the hypothesis that an increase in the intensity of competition would result in both a decrease in speciation rate and an increase in extinction rate. We found that interspecific competition only affected diversification dynamics during the early stages of Canidae radiation, resulting only in the suppression of speciation rate at the time the clade was expanding in diversity. On the other hand, we found no association between the intensity of the competition and extinction dynamics as expected by a competitive effect. The results suggest that the decrease in diversity and increase in extinction rate close to the present might be better explained by external factors, such as climate change and competition with other clades such as Felidae, and not by interspecific competition within Canidae. Our results are in line with previous studies that showed asymmetric effects of competition on speciation and extinction dynamics. We have demonstrated that more mechanistic models suggest that diversity-dependence effects could indeed result from resource competition, but these effects are not present throughout the whole evolutionary history of Canidae. We therefore conclude that the relevance of biotic and abiotic factors on driving diversification dynamics changes over time and that neither is likely to be the sole responsible for changes in biodiversity in deep time.

Keywords: Macroevolution. Fossil Record. Speciation. Extinction.

Introduction

Understanding the patterns and processes that promote biodiversity is a key goal in ecological and macroevolutionary studies. As a first order approach to diversity, one can measure how the number of species vary whether across different regions, different communities, or even how the number of species vary through time. Macroevolutionary questions are often directed towards understanding how patterns of species diversity changed in deep time, a multimillion-year time scale, as well as what are the processes governing these patterns. Traditional views on the controls of diversity through time often antagonize the roles of the abiotic environment and the biotic interactions between species, however those different approaches are not self-excluding (Benton, 2009). In fact, Benton (2009) proposes that the so-called abiotic and biotic factors act on different scales, where species interactions would be relevant at local shallow time scales, and extrinsic factors would preferentially operate on a regional/global deep time scale.

Much of the ongoing debate regarding abiotic and biotic factors as drivers of species diversity revolve around the interplay between these factors and how they affect diversification dynamics (Ezard et al., 2011). Diversification rates are described as the balance between the processes of speciation and extinction, and many authors have tried to disentangle how abiotic and biotic factors may affect the underlying diversification dynamics. The role of species interactions in shaping diversification dynamics remain far from fully understood (Harmon & Harrison, 2015; Rabosky & Hurlbert, 2015). This topic has attracted great interest in the paleontological/macroevolutionary community, with special interest on how interspecific competition, and to lesser extent, predation, might regulate biodiversity dynamics (Sepkoski et al., 2000; Van Valkenburgh, 2007; Vermeij, 1987). Recent studies (Pires et al., 2017) have shown that speciation may be driven by competitive interactions between species. The idea that competitive interactions may be a driving force in speciation or extinction is central to the theory of diversity-dependence mechanisms of diversification (Rabosky, 2013). Diversity-dependence theory proposes that species diversity might be self-regulated at large continental scales in an observed feedback between species richness and macroevolutionary rates (Rabosky, 2013; Rabosky & Hurlbert, 2015; Sepkoski, 1996). Drawing from the theoretical concept of competitive exclusion (Gause, 1935) and Hutchinsonian niche concepts (Hutchinson, 1959), Hermoyian et al. (2002) hypothesized that in the absence of disturbing factors, "species that are too morphologically similar […] experience interspecific competition sufficient to drive one of the species locally extinct". Although these ideas date back to Darwin (1859), it is still difficult to understand how competition scale up to higher hierarchical levels of diversity (Marshall & Quental, 2016; Sepkoski, 1996). Although most theory in diversity-dependence has been centered on how species within a given clade regulate the dynamics of such focal clade, it has also been proposed that clades might in fact regulate and even drive other clades to extinction. This mechanisms have been termed “clade competition” (Sepkoski, 1996; Sepkoski et al., 2000).

Two main mechanisms of clade competition are said to influence species diversity trajectories. In the first, one clade prevents another competing clade to radiate and its replacement can only happen due to its extinction (the incumbent clade) driven by mechanisms other than the clades interaction. Such process is termed passive replacement or incumbent replacement (Rosenzweig & McCord, 1991). In the second, the appearance of a new competing clade might actively outcompete the former, leading to its demise (Sepkoski, 1996). Although passive replacement has been considered to be prevalent, there is a growing number of examples that seem to be congruent with active displacement (Pires et al., 2017; Silvestro et al., 2015; Van Valkenburgh, 2007). The fossil record (as opposed to molecular phylogenies) might be particularly relevant to study diversity-dependence because it allows not only a direct inference of diversity trajectories, but also to directly estimate speciation and extinction rates (Quental & Marshall, 2010). In fact, inferences about diversity-dependence, either within or between clades have moved beyond the study of diversity curves, e.g., fitting logistic models to diversity trajectories or contrasting diversity curves of potential competitor clades (Sepkoski, 1996), to directly investigate the effect of diversity on the dynamics of speciation and extinction separately (Alroy, 1996; Foote et al., 2018; Pires et al., 2017).

Diversity-dependence has been interpreted as being produced by competition between species that overlap in space and time (Sepkoski, 1978, 1996), through mechanisms such as competitive exclusion acting on extinction, or limited resources acting on suppressing speciation (Rabosky, 2009, 2013; Sepkoski, 1978, 1996). Only a handful few different clades have been investigated at the species level, so it is an open question if different lineages might be more or less prone to such diversity-dependence mechanisms driven by competition. Although seemly relevant, it is possible that our perception of the prevalence of such mechanism might be driven by our study systems. Studies on carnivorous mammals have demonstrated the importance of competition in diversification dynamics (Silvestro et al., 2015; Van Valkenburgh, 1988, 1999). Large predatory mammals are expected to present intense competitive interaction, both in modern and fossil faunas (Van Valkenburgh, 1985, 1988). In fact, competition might indeed have shaped diversification of Canidae species in North America during the Cenozoic (Pires et al., 2017; Silvestro et al., 2015; Van Valkenburgh, 1999), and it might have acted differently in speciation and extinction dynamics (Pires et al., 2017; Silvestro et al., 2015).

Canidae is a family of predatory mammals comprising both extant and extinct lineages, with its origins in the Paleogene of North America, having existed for some 40 million years until the present day (Wang & Tedford, 2008). The Canidae fossil record of North America is considerably well documented in both its taxonomic diversity and sampling (Tedford et al., 2009; Wang, 1994; Wang et al., 1999), and eco-morphological characterization (Balisi et al., 2018; Balisi & Van Valkenburgh, 2020; Janis et al., 1998; Slater, 2015; Van Valkenburgh et al., 2004). Extinct canid species display a wide array in both body size and diet, ranging from small predators of small prey and plant matter (hypocarnivory), to large-bodied bone-crushing or hypercarnivore (whose diet is almost entirely composed of meat) dogs (Van Valkenburgh, 1991; Wang & Tedford, 2008). The succession of canid sub clades in the fossil record also suggests repeated patterns of increase in species diversity, followed by stability and subsequent demise of at least two extinct subfamilies (Silvestro et al., 2015; Van Valkenburgh, 1999; Van Valkenburgh et al., 2004; Wang & Tedford, 2008). The extinction of both Hesperocyoninae and Borophaginae subfamilies seems to be driven by the expansion of the next subfamily, as well as by other Carnivora clades, in a pattern congruent with active displacement (Silvestro et al., 2015). This pattern is also repeatedly observed in other Carnivora clades, and it is argued that the large predator adaptive zone remained fairly unchanged in the Cenozoic, promoting intense competition of Carnivora (Van Valkenburgh, 1999).

Many studies concerning macroevolutionary competitive dynamics of canids (as well as on other lineages) have focused either on diversity-dependence diversification dynamics (Silvestro et al., 2015), or morphological evolution of species traits (Slater, 2015), or on the implications of such morphological evolution on species survival and extinction risk (Balisi et al., 2018; Balisi & Van Valkenburgh, 2020; Van Valkenburgh et al., 2004). The effect of competition on diversification dynamics has been tested fairly indirectly and relied on the assumption that an increase in diversity implies in stronger competition, which would lead to a drop in speciation or rise in extinction rates. Although a reasonable interpretation, to better understand the effect of competition on diversification dynamics it might be more interesting to explore how the occupancy of morphospace might be linked to speciation and extinction dynamics. Canidae exhibit a trend of increasing body size as lineages evolve over time (Van Valkenburgh et al., 2004), a pattern known as Cope's Rule (Hone & Benton, 2005). Such increase in body size seems to be correlated with increasing adaptations to hypercarnivory, an ecological specialization towards large prey consumption (Van Valkenburgh et al., 2004). Specialization to extreme morphologies (either small hypocarnivores or larger hypercarnivores) seems to lead to short living species (Balisi et al., 2018), but hypercarnivory *per se* seems to imply an extinction selective regime only at certain time periods and do not seem correlated to extinction dynamics as a whole (Balisi & Van Valkenburgh, 2020). Slater (2015) has argued that the evolution of canid morphological traits followed patterns of repeated ecological radiations in a bounded morphospace of restricted diet categories. Thus, suggesting that morphospace is rapidly saturated and paving the way to better understanding the complex interactions between the evolution of body size, diet ecology and diversification dynamics. We therefore argue that the role of resource mediated competition in diversification dynamics still remains to be explicitly investigated, as studies mentioned earlier have focused either on diversity-dependence mechanisms assuming that all species coexist with no information regarding ecological overlap; or in studies that investigated the rates of morphological evolution without a direct relationship to diversification dynamics.

Conclusions

1. We developed a new approach to study the potential effects of interspecific competition in diversification dynamics that goes beyond the usual diversity-dependent models.

2. Our new approach takes into account not only temporal coexistence, but also spatial coexistence and ecological overlap in an explicit manner by using geographical information from fossil occurrences and the morphology of fossil and extant species.

3. We recovered the usual signal of diversity-dependence when using "global" diversity trajectories, which do not explicitly account for spatial coexistence; but we show that diversity-dependence is detected even when the spatial distribution of species is explicitly taken into account.

4. We showed that changes in speciation rate were associated with changes in diversity and with changes in different metrics used to describe the intensity of competition, but only at the moment in time when Canidae was expanding its diversity. We found that an increase in extinction rate was not related to an increase in competition intensity or an increase in diversity, as expected by competition models.

5. We hence confirm previous results, which suggested that diversity-dependence imposed by the species within a clade only operate through the speciation dynamics. We expanded this view by showing that mechanistic models of competition also suggest that interactions among species within the focal clade only affect speciation dynamics.

6. We discussed our results in the light of the roles of biotic and abiotic factors on controlling biodiversity in deep time and suggest that, in long-lived clades, self-diversity-dependence and resource competition might preferentially act during the initial radiation phases, while later on their history such effects might be overwhelmed by external factors such as climatic changes or clade competition.

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