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Biotic interactions and climate change, drivers of life

Interacciones bióticas y cambio climático: factores determinantes de la vida

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Abstract: Abiotic and biotic factors have continually shaped life on our planet. Understanding the mechanisms and processes that influence the evolutionary dynamics of biodiversity is crucial for addressing contemporary challenges. This review is aimed to achieving three objectives: first, to provide an overview of the diversity and significance of biotic interactions in nature throughout evolutionary history. Second, to emphasize the importance of integrating current ecological research with fossil data to gain deeper insights on life's evolution and the causality of extinction events. Finally, I advocate for the integration of living organisms' ecology with evolutionary biology and genetics, into the training of 21st-century palaeontologists.

Resumen: Los factores abióticos y bióticos han moldeado continuamente la vida en nuestro planeta. Comprender los mecanismos y procesos que influyen en la dinámica evolutiva de la biodiversidad es crucial para enfrentar los desafíos contemporáneos. Esta revisión tiene tres objetivos: primero, proporcionar una visión general de la diversidad y la importancia de las interacciones bióticas en la naturaleza a lo largo de la historia evolutiva. Segundo, enfatizar la importancia de integrar la investigación ecológica actual con los datos fósiles para obtener una comprensión más profunda de la evolución de la vida y la causalidad de las extinciones. Finalmente, abogo por la integración de la ecología de los organismos vivos, junto con la biología evolutiva y la genética, en la formación de los paleontólogos del siglo XXI.

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LIFE AND BIOTIC INTERACTIONS

The history of life on Earth has been shaped by both abiotic and biotic conditions. Life cannot be understood outside a given environment, with inorganic and organic matter, physical and chemical conditions, and the interaction with other individuals. That is, life must be understood within an ecosystem. Unveiling the origin of life on Earth remains the biggest unsolved mystery, although there exist different possible geochemical scenarios (Martin & Russell, 2003). The chemical environment that facilitated abiogenesis (origin of life) was rich in organic and inorganic compounds with highly heterogeneous activities. In this complex chemical environment or "primordial soup," some organic molecules were able to display very particular behaviours at certain stages, including self-assembly, self-replication, and autocatalysis, thus setting the basis for the conservation and transmission of organic information, metabolism and reproduction (*i.e.*, life and the processes that enabled life and evolution). Our Last Universal Common Ancestor, **LUCA**, an autotrophic acetogen form, evolved in an environment rich in hydrogen, carbon dioxide, and iron around 4,200 My ago (Fig. 1; Fox *et al.*, 1980; Moody *et al.*, 2024; Weiss *et al.*, 2016). There is robust evidence that, as early as 3,800 My ago, bacteria or bacteria-like organisms evolved from LUCA in an anoxic atmosphere consisting of ammonia, carbon dioxide, carbon monoxide, methane, nitrogen, and water vapour (Catling & Zahnle, 2020; Mojzsis, 1996), where they had access to food and energy directly from their environment. Moreover, it is not unlikely that bacteria might have shared the environment with viruses from their very beginning (Domingo, 2019; Moody *et al.*, 2024). In addition to the origin of life, another major evolutionary step of life was the evolution of the three main domains of life, the Bacteria and the Archaea during the Archean aeon around 3,500 My ago, and the Eukarya during the Proterozoic, as fossil evidence supports, although molecular studies indicate that eukaryotes may be much older (Fig. 1; Dacks *et al.*, 2016; Maynard Smith & Szathmáry, 1997; Porter, 2020; Woese *et al.*, 1990).

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In the very moment two organisms meet, a biotic interaction is established. Nearly, if not all species, establish at least one type of interaction at some stage during their life history, which impact on their biological fitness in different ways (biological fitness is a measure of an organism's ability to survive and reproduce in its environment; at the species level, it refers to the overall ability of the species to survive and thrive over time). There are many different types of biological interactions, classified based on their impact on the biological fitness of each interacting species: competition, amensalism, antagonism (predation, parasitism, grazing), commensalism, and mutualism. All the biotic interactions were very likely occurring between prokaryotes during the Archean and early Proterozoic aeons (Fig. 1):

1) Competition for resources (food, niche, mate…), which occurs when the fitness of both interacting individuals or species is lowered (-, -), and can be intra- or inter-species. Examples are bacteria competing for the same substrate (Hibbing *et al.*, 2010).
2) Amensalism, which is a unidirectional interaction where one individual inflicts a negative impact on another with no benefit for the individual that inflicts the impact (0, -), *e.g.*, an example is the microbial production of secondary metabolites that inhibits or kills other bacteria species, such as *Bacillus* spp. or *Streptomyces* spp. (Schatz *et al.*, 1944; Siewert & Strominger, 1967).
3) Antagonism, which is when one individual benefits at the expense of another (+, -). There are different antagonistic scenarios:
   3.1) Predation, which is when one individual kills another individual for eating, which results in a benefit for the former, the predator, and the maximum damage for the latter, the prey; *e.g.*, examples are the predatory bacteriovorous bacteria, such as *Bdellovibrio bacteriovorus* or *Micavibrio aeruginosavorus* (Davidov & Jurkevitch, 2004).
   3.2) Parasitism, in its two forms, parasites and parasitoids, which is when an individual lives in or on another individual, obtaining a benefit at the expense of the host, with mild to drastic damage. For example, *Vampirococcus* sp., bacteria that parasitise other bacteria (Guerrero *et al.*, 1986), or viruses in bacteria (Domingo, 2019).
   3.3) Grazing is when an individual feeds on another, but not necessarily killing it, which is particularly frequent within multicellular eukaryotes. However, in the microbial world, we also find many examples of grazers feeding on bacterial mats: Myxobacteria, unicellular eukaryotes such as protists, marine invertebrates, molluscs, crustaceans, fish, and amphibians feed on them as well (Cubillos *et al.*, 2024; Muñoz-Dorado *et al.*, 2016).
4) Commensalism, which is when an individual benefits from the presence of another individual without harming it (+, 0). A good example is methanotrophic bacteria, which facilitate the growth of sulfate-reducing bacteria (Boetius *et al.*, 2000).
5) Mutualism, which is when the interacting individuals or species benefit each other (+, +). Some examples in bacteria can be those of green sulfur bacteria associations with sulfide-oxidizing bacteria, or syntrophic bacteria with methanogenic archaea in anaerobic environments, where each partner provides the substrate for the other (McInerney & Bryant, 1981).

All these interactions, however, already existed in the chemical world prior to life (Tab. 1), and we must question ourselves whether biotic interactions are a by-product of life or represent inherent emerging properties of the self-organisation of matter under specific conditions. Understanding whether these interactions are uniquely biological or a continuation of prebiotic chemistry will provide profound insights into the origins of life and the universal principles governing the organization of matter. Living beings can be considered emergent systems of organised chemical species, whose functioning depends on interactions between biomolecules, making them highly organized and dynamic "complex chemical species" with emergent capabilities. Just as chemical species have a defined chemical identity (composition, structure, reactivity…), living beings possess a defined biological identity (genome, cellular organization…) that determines their ability to interact with the environment and other organisms. The inherent properties that differentiate living beings from chemical species—such as their level of organizational complexity, autonomy, and self-replication—can be regarded as emergent properties of these "complex chemical species." In this context, the so-called biotic interactions will be dynamic processes occurring at the molecular, cellular, and organismal levels, with cascading effects on other levels of organisation.

The eukaryotic cell developed during the Proterozoic as a result of a new type of interaction between prokaryote ancestors, the so-called endosymbiosis (Markov, 2005). This complex co-evolutionary process is responsible for some major evolutionary transitions, such as the emergence of the eukaryote cell and its many characteristics, such as the nucleus, the mitochondria, the plastids, and undulipodia (Margulis & Bermudes, 1985; Wernegreen, 2012). The endosymbiotic process, however, is far from being a benevolent mutualistic relationship, and represents a potential dramatic conflict of a microbial species being engulfed by another microbial species (Keeling & McCutcheon, 2017). Under this scenario, the "struggle for life" was solved in the form of a surviving chimaera of two coexisting species, possibly a predator trying to digest the prey and the prey resisting digestion, which finally resulted in an equilibrium after a long co-evolutionary process that resulted in the eukaryotic cell (Archibald, 2015; Margulis, 1970). During this

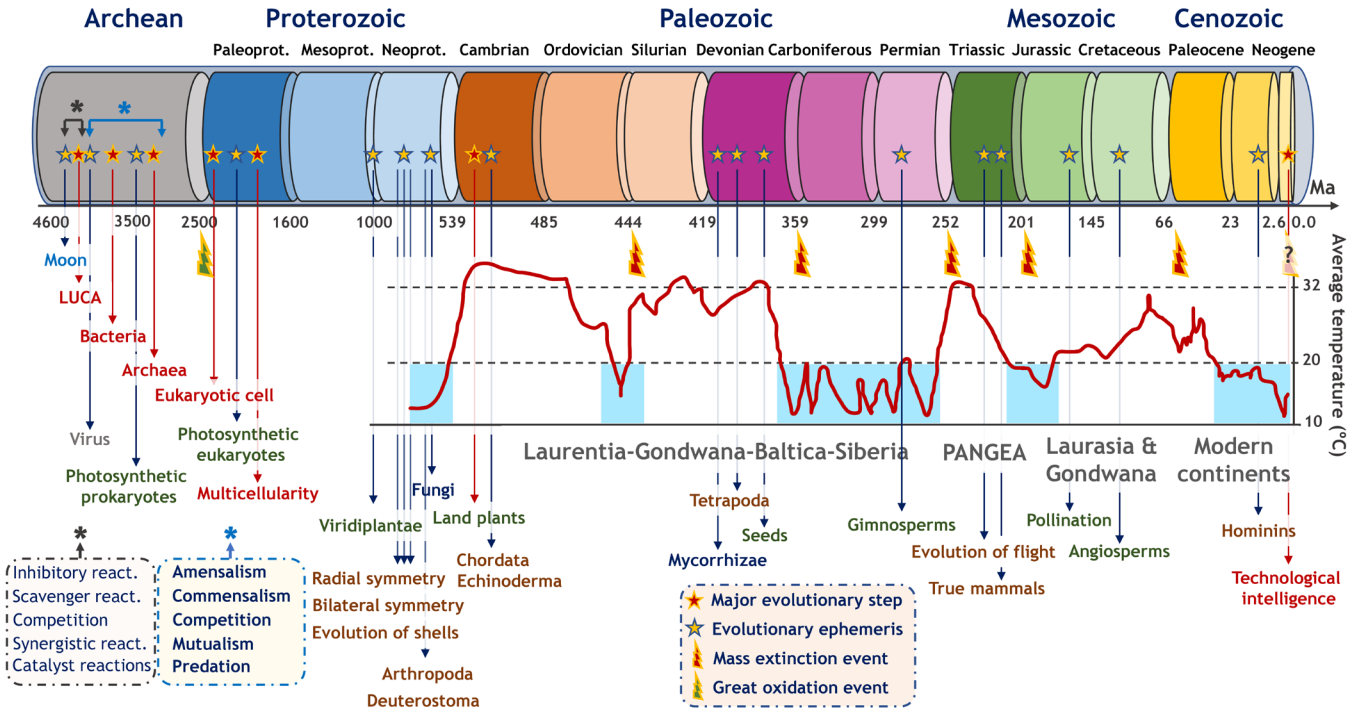

Figure 1. Planetary and evolutionary ephemeris. The major evolutionary steps are highlighted with dark red stars and arrows. Orange stars and blue arrows point to evolutionary ephemeris in the history of Earth life, such as the emergence of the main body plans or the acquisition of evolutionary novelties. Lightnings indicate the five biggest extinction events (I agree with the potential occurrence of the sixth extinction during the Anthropocene as human-mediated). Geological ages after the International Chronostratigraphic Chart 2023-24 (https://stratigraphy.org/). During the Archean aeon and the Palaeoproterozoic era, all types or ecological interactions should have been established (yellow rectangle). The average global temperature dynamics data since Precambrian were acquired from https://www.climate.gov/ (25/06/2024); light blue rectangles indicate ice ages, but, before, also happened the Huronian (2400–2100 Ma) and the Pongola (2900–2780 Ma) glaciations during the Palaeoproterozoic and Archean, respectively (Chumakov, 2005). The first main continents characterising Cambrian and Ordovician geography grouped during the Mesozoic in the Pangea continent that later separated in Gondwana and Laurasia, and in today's modern continents by continental drift (Meert, 2012).

process, a large number of genes from the genome of the prey species that would become an organelle were lost, either because they were redundant with host genes or encoded unnecessary products. Moreover, some genes were transferred to the host genome through horizontal gene transfer (Ponce-Toledo *et al.*, 2019; Van Etten & Bhattacharya, 2020). Meanwhile, both organisms "learnt" how to reproduce and survive in a close and intimate relationship, avoiding death.

Biotic interactions, since those first tentative experiments of life, drove the evolution of species, shaping the behaviour, morphology, physiology, abundance, and distribution of organisms, resulting in fine-tuned ecosystems, and organising Earth's biodiversity. Competition for resources leads to spatial and temporal niche differentiation (Gao *et al.*, 2020; Tilman, 2004). Antagonist interactions exert strong selective pressures that lead to evolutionary arms races and red queen dynamics, which result in highly specific behaviours and traits (Brodie III & Brodie Jr., 1999; Van Valen, 1973). As Charles Darwin stated, strong competitors and predators acted as selective agents in the evolution of interacting species. This is also known as the hypothesis of escalation (Vermeij, 1994). However, depending on the origin and strength of the selective pressure, an alternative and non-exclusive process is the coevolution of species, were both evolve in response to changes in each other (Thompson, 1994). Mutualistic interactions have evolved as well, through these complex coevolutionary processes, into highly specific outcomes, some of them as famous as Darwin's orchid and its predicted pollinator (Darwin predicted in 1862 the existence of a pollinator with 35 cm long proboscis, so it could pollinate the Madagascar endemic orchid, *Angraecum sesquipedale*; after being ridiculed for years, such a pollinator, the butterfly *Xanthopan morganii praedicta*, was found in 1903). The evolution and maintenance of mutualisms depend on the outcome of the balance of costs and benefits (Bronstein, 1994).

The co-evolutionary process between species can be analysed under many different approaches: observational, experimental, genetic or genomic, phylogenetic, mathematical modelling, ecological, functional, and experimental evolution studies (Brockhurst & Koskella, 2013; Bronstein, 1994; Page, 2003; Thompson, 1994; Thompson & Cunningham, 2002). Among interacting species, we observe reciprocal phenotypic changes that may or may not be directional, thus producing temporal behavioural,

Table 1. Biotic interactions and their counterparts in the pre-biotic world (Nelson & Cox, 2017).

Interaction	Chemical reaction and example
Competition (-,-)	Two chemicals or molecules compete for the same active site on an enzyme. For example, in biochemical pathways, substrate molecules and inhibitors may compete for the same active site on an enzyme, affecting the reaction rate.
Amensalism (0, -)	A chemical inhibitor binds to an enzyme (the host), decreasing its activity and harming the enzyme's normal function.
Antagonism, predation (+,-)	A catalyst (the predator) interacts with a reactant (the prey) and renders it inactive or converts it into an entirely different product. For example, proteases that break down proteins into smaller peptides or amino acids. The protease (the predator) targets and digests the protein (the prey), effectively breaking it down into its constituent parts.
Antagonism, parasitism (+,-)	A molecule (the parasite) mimics the substrate of an enzyme (the host) and binds to the active site, inhibiting the enzyme's normal function and using the enzyme's resources without contributing to the intended reaction. It is molecular mimicry in competitive inhibition. For example, the antibiotic sulfanilamide, which mimics para-aminobenzoic acid (**PABA**) and inhibits the enzyme dihydropteroate synthase in bacteria. This enzyme normally uses PABA to synthesize folic acid, but when sulfanilamide binds to it, the enzyme's activity is blocked, depriving the bacteria of folic acid and leading to its death.
Commensalism (+, 0)	One chemical species benefits from the presence of another without affecting it. For instance, in some catalytic processes, a scavenger molecule may benefit by reacting with by-products or impurities, cleaning up the reaction mixture without affecting the primary reaction.
Facilitation (0, +)	A catalyst (the facilitator) accelerates a chemical reaction without being consumed in the process, thus benefiting the reactants. An example is the role of enzymes in biochemical reactions, where they lower the activation energy and speed up the reaction.
Mutualism (+,+)	In this type of interaction, two chemicals or reactants work together to produce a greater effect than they would individually. For example, in certain types of polymerization, a combination of heat and a chemical initiator can produce a polymer more efficiently than either would alone.

ecological, morphological, or physiological polymorphisms that might revert to the original phenotypes after the interaction (Agrawal, 2001). Biotic interactions, however, are more complex than single pairs of interacting species. Thus, the existence of multipartite associations involving bacteria, fungi, plants, and animals might very likely be the rule rather than the exception (*e.g.*, Poulsen & Currie, 2009; Rohfritsch, 2008; Ruiz-González *et al.*, 2011).

BIOTIC INTERACTIONS AND THE ABIOTIC ENVIRONMENT

The 21st century has begun with a strong awareness of the role that humans are playing in accelerating climate change and a strong concern about generating resilience against its effects (IPCC, 2021). Both directly and indirectly, human beings are responsible for causing the biological annihilation of biodiversity (Ceballos *et al.*, 2017). Indeed, nature is strongly threatened by multiple pressures of anthropogenic origin, such as habitat transformation, changes in the composition of ecosystems, the introduction of invasive species, overexploitation of resources, pollution, and the effects of climate change (Ruiz-González & Vicente, 2023). Thus, many researchers support the idea of humans as responsible for initiating a biodiversity crisis that might lead to the sixth biggest extinction (Fig. 1; Cowie *et al.*, 2022).

Life in a specific place is the result of both macro- and microevolutionary processes shaped by complex interactions between organisms and their environments over millions of years. These processes involve multiple factors, including geological changes, climatic shifts, biotic interactions, and genetic changes driven by natural selection, genetic drift, gene flow, and mutation. Locally, advantageous traits within a population increase in frequency because they confer survival or reproductive advantages. Thus, the ability of an organism, or a population, to survive and reproduce in a given place and at a certain moment is the result of its evolutionary history. To a large extent, this will determine the physiological, morphological, behavioural, and genetic plasticity to face abiotic change and biotic challenges.

The change of local abiotic conditions (high or low temperatures, water availability by excess or deficiency, salinity…) has deep effects on the biota and their interactions, threatening the survival of species at the microevolutionary scale. Change in climatic conditions produces phenological shifts, altering the timing of biological events, such as flowering, migration, and breeding (Parmesan, 2007), thus affecting key biotic interactions such as those between plants and their pollinators or predators with their prey. Climate change can alter species distributions, resulting in species dispersal to areas with more suitable conditions (latitudinal or altitudinal shifts), thus leading to new biotic interactions (Parmesan, 2007; Parmesan & Yohe, 2003). Another effect of climate change is the alteration of species abundances, thus affecting the strength of existing interactions such as predation or competition, and their ecological balance (Bowler *et al.*, 2017; Harley *et al.*, 2006). In addition, climate change can drastically modify the habitat and the ecosystem by affecting resource availability and the suitability of environments for different species, *e.g.*, by increasing salinity or acidifying the environment (Hoegh-Guldberg *et al.*, 2007). Therefore, climate change facilitates the spread of invasive species and

alters symbiotic relationships (Hughes *et al.*, 2017; Walther *et al.*, 2009). At the macroevolutionary level, climatic conditions have profound consequences on the composition of life on Earth, forcing strong competition between groups of species (*e.g.*, gymnosperms *vs* angiosperms; Condamine *et al.*, 2020), driving to speciation, extinction, migration, adaptation, and ecosystem restructuring. The fossil record, along with modern observations, provides valuable insights on the complex dynamics that past climate changes produced on life, thus providing priceless information for predicting and mitigating the effects of ongoing and future climate change on biodiversity.

BIOTIC INTERACTIONS AS DRIVERS OF EXTINCTION

An extinction event immediately brings to mind a mass extinction event and, very likely, a dramatic collection of Hollywood made scenes. However, there are two types of extinction depending on the extinction intensity: mass extinctions and background extinction. A mass extinction event represents the abrupt disappearance of a large number of species across several habitats and ecosystems, that is, the loss of a considerable percentage of the planet's species within a relatively short geological period, often spanning thousands of years (*e.g.*, the end Cretaceous extinction) to a few million years (*e.g.*, the late Permian extinction event), and leading to profound and lasting impacts on the biosphere.

There are five well known mass extinctions (Fig. 1): Ordovician–Silurian (443 Ma), late Devonian (359 Ma), Permian–Triassic (252 Ma), Triassic–Jurassic (201 Ma), and Cretaceous–Paleogene (66 Ma) extinctions. However, a total of 18 intervals, heterogeneous in intensity, selectivity, or timing, has been found to qualify as mass extinctions during the Phanerozoic (Bambach, 2006). Ten of these events took place since the late Permian and follow a 26-Ma periodicity pattern (Raup & Sepkoski, 1984). Mass extinction events resulted from multiple abiotic causes, such as catastrophic events (*e.g.*, asteroid impacts), tectonics and volcanic activity, climate change, sea-level fluctuations, and changes in atmospheric and oceanic chemistry (Bond & Grasby, 2017). However, very little is known about the full causality because predation and other biotic pressures are often overlooked (Bambach, 2006). Successful species with wide geographic distributions, ecological tolerance, and adaptations to their environmental abiotic and biotic conditions were quickly driven to extinction (Raup, 1994). That is, under mass extinction regimes, many traits that previously boosted species survival became insufficient to cope with the new conditions faced during the biotic crisis. Conversely, other traits may begin to contribute to species survival (Jablonski, 1986). Thus, it is not difficult to imagine how, during this critical time for the species or the biological community, biotic interactions might have contributed to the outcomes of mass extinctions (Jablonski, 2003). The loss of keystone species during mass extinctions can trigger trophic cascades, where changes at one trophic level cause significant alterations throughout the ecosystem. This can lead to the collapse of food webs and the extinction of additional species that depended on the disrupted interactions. Moreover, changes in predation and competition dynamics can lead to the rapid decline of certain species and drastic changes in the landscape and the ecosystem (Estes *et al.*, 2011). For instance, the introduction of new predators or competitors after mass extinction events can prevent the recovery of previously dominant species and promote the rise of new ones. Disease outbreaks can exacerbate the effects of mass extinction events. By eliminating a large number of species, these events create ecological vacancies and open up niches for surviving to evolve and diversify in new species. This process can lead to adaptive radiations, where the survivors diversify rapidly under conditions of relaxed selective pressures to fill the available ecological roles that became empty after the mass extinction event.

A mass extinction event can be driven by biotic factors as well. The emergence of photosynthetic organisms, particularly cyanobacteria, drastically changed Earth's history approximately 2.4 billion years ago during the Great Oxygenation Event (Olejarz *et al.*, 2021; Yoon *et al.*, 2004; Fig. 1). This period, also known as the Oxygen Catastrophe, resulted in significant environmental changes due to the production of oxygen as a by-product of photosynthesis. As cyanobacteria evolved the ability to harness sunlight to split water molecules and release oxygen, atmospheric oxygen levels began to rise. This rapid accumulation of oxygen proved toxic to many anaerobic organisms, thus leading to what is hypothesized as one of the earliest mass extinction events, as anaerobic species experienced widespread die-offs due to oxygen poisoning (Lyons *et al.*, 2014). The extinction of these anaerobic organisms, which had previously dominated various ecological niches, paved the way for the emergence and diversification of aerobic life forms capable of utilizing oxygen for energy production, and eventually facilitated the evolution of complex multicellular organisms. This event underscores the pivotal role of biotic interactions, particularly the metabolic activities of photosynthetic organisms, in shaping the course of planetary evolution and the biodiversity of life on Earth.

The second type of extinction, background extinction, refers to the average, standard rate of extinction during most of Earth's biological history (*i.e.*, during the long periods between two mass extinction events), occurring at a relatively steady pace due to natural selection, environmental changes, and ecological interactions (MacLeod, 2003). Gradual environmental changes, such as climate shifts or habitat alterations, can drive background extinctions by altering the availability of resources and living conditions. Species that cannot adapt to these changes may gradually decline and

eventually go extinct. However, biotic interactions play an important role in contributing to either the stability of ecosystems or to background extinctions.

In a stable environment, competitive exclusion can lead to background extinctions when one species or clade outcompetes another for resources. This gradual process can reduce biodiversity over time as dominant species monopolize ecological niches. Additionally, the evolution of more efficient predators or the decline of prey species can result in background extinctions. Natural selection pressures can favour predators that develop better hunting strategies, leading to the decline or extinction of prey species that cannot adapt quickly enough in this arm race. Disruptions in mutualistic relationships are another biotic interaction that can lead to background extinctions. For instance, the extinction of a pollinator species can result in the extinction of plant species that rely on it for reproduction (similarly, the disappearance of a host species has negative effects on its parasites). This interdependence means that the loss of one species can have cascading effects on others (Estes *et al.*, 2011).

The background extinction rate is estimated to be about 1–5 species per year, although this rate can vary depending on the taxa and environmental conditions considered (Raup & Sepkoski, 1982). Since the early Cambrian, there has been a noticeable decrease in the intensity of background extinctions, implying a trend towards optimizing biological fitness over evolutionary time (Raup & Sepkoski, 1982). This trend may also indicate stronger ecological stability mediated by biotic interactions. A substantial increase in this rate, whether accelerating gradually over a short period of geological time (1 to 3 million years) or abruptly (catastrophically) in ecological terms, leads to mass extinctions (De Renzi, 2009). There is substantial evidence supporting the idea of an accelerated rate of extinction caused by human activities (Ceballos *et al.*, 2015, 2017). This will probably result in the sixth major extinction event in the history of life on Earth, as noted before.

BIOTIC INTERACTIONS IN THE FOSSIL RECORD

Palaeontology studies the history of life on Earth, as documented by fossils, while Palaeobiology is the biological analysis and interpretation of the organisms that produced those fossils, their relationships (*e.g.*, ecological, biogeographic, phylogenetic, taxonomic), and the general dynamics of the biota through time (De Renzi, 1981, 2005). The fossil record holds a wealth of data about ancient ecosystems and the organisms that inhabited them. Moreover, we can also find evidence in the fossil record of past biotic interactions that will in turn provide pivotal information of ancient ecosystems, thus allowing both a better understanding of evolutionary dynamics and the drawing of parallels to modern ecological patterns (Palmqvist *et al.*, 2003). Some examples of these evidences are provided in Table 2.

Fossil evidence of competition for particular resources can be found by studying fossil assemblages and comparing α (intra-community), β (inter-community), and γ (geographic scale) biodiversity indexes, that is, by analysing ecospace utilisation by different modes of life (Servais *et al.*, 2010). Antagonistic interactions are very diverse. Both direct and indirect evidences can be found about predation (Tab. 2). Direct evidence of predation are trace fossils or praedichnia such as bite marks, drill holes, repair marks, even coprolite contents might be a good indicator of predatory behaviour on certain preys (Baumiller *et al.*, 2006; Bromley, 1996; Kowalewski, 2002; Shillito *et al.*, 2020; Espigares *et al.*, 2023). Indirect evidence can be found as an increase in biodiversity of certain morphological forms that are mechanically resistant to predation or based on biogeochemical markers (Palmqvist *et al.*, 2008; Vermeij, 1977). Parasites and pathogens can be found in all ecosystems, but it is not easy to find them in the fossil record because many of them are small and soft-bodied organisms, single celled individuals, or virus-like forms (De Baets & Huntley, 2021; Leung, 2017). Thus, other than whole parasite bodies, larvae, eggs, or single cell stages found in vector-borne parasites in amber, evidence can be found in host structural and functional attributes (*e.g.*, mouthparts, reproductive structures) affected by parasite activity as well as in trace fossils on host's skeletons and shells or in leaves, *e.g.*, bryozoans, serpulid worms, barnacles, leaf miners, etc. (Bromley, 1996; De Baets & Huntley, 2021; Leung, 2017; Littlewood & Donovan, 2003). Mutualistic interactions are more challenging to detect than other biotic interactions, such as predation or competition, but can be inferred from fossilised associations, specialised structures, and trace fossils (Tab. 2). There exist notable examples of these associations: the presence of mycorrhizae associated with land plants since the early Devonian (Remy *et al.*, 1994), the Triassic corals associated with photosynthetic zooxanthellae algae (Stanley & Swart, 1995), or the pollination of plants since Upper Jurassic (Peña-Kairath *et al.*, 2023). Detecting mutualism in the fossil record requires a multidisciplinary approach, combining morphological, isotopic, chemical, and ecological evidence. By carefully analysing these indicators and comparing them with modern analogues, palaeontologists can infer the presence and nature of mutualistic relationships in ancient ecosystems.

Fossilisation of biotic interactions, however, is biased towards certain types of interactions. Several factors contribute to this bias, including the nature of the interaction, the organisms involved, and the environmental conditions under which fossilisation occurred. For example, many interactions that affect hard parts such as shells, bones, and exoskeletons are more likely to be recorded as evidence of predation, parasitism, or mutualism (De Baets & Huntley, 2021; Kowalewski, 2002; Stanly & Swart, 1995; Taylor *et al.*, 1995). This bias can be facilitated by different factors:

Table 2. Evidence of biotic interactions in the fossil record. Some fossil evidences to identify the main biotic interactions with examples. References: **1,** Servais *et al.* (2010); **2,** Condamine *et al.* (2020); **3,** Bromley (1996); **4,** De Baets & Huntley (2021); **5,** Leung (2017); **6,** Littlewood & Donovan (2003); **7,** Nakajima & Izumi (2014); **8,** Peñalver & Grimaldi (2006); **9,** Vermeij (1977); **10,** Palmqvist *et al.* (2008); **11,** Chan *et al.* (2021); **12,** Stanley & Swart (2016); **13,** Weiblen & Treibe (2015); **14,** Taylor & Krings (2005); **15,** Peña-Kairath *et al.* (2023).

Interaction	Fossil evidence and examples	Ref.
Competition (-,-)	Fossil evidence for competition includes changes in species abundance, diversity, and morphological adaptations over time. *e.g.*, The Great Ordovician Biodiversification Event, or the rise of angiosperms outcompeting gymnosperms	1, 2
Antagonism (+,-)	Evidence of predation can be direct (bite marks on bones or shells) or indirect, inferred from morphological adaptations. *e.g.,* Mesozoic gastropods diversity, presence of animal parts in coprolites. *e.g.*, Inferences on predator–prey relationships in a community based on biogeochemical markers Evidence of parasitism can be found when finding the actual parasite, its structures, or in the form of trace fossils. *e.g.*, A wide diversity of parasites, parasitoids, vector borne parasites, and pathogens can be found conserved in amber: Arachnida (mites), diptera (midges), hemiptera, hymenoptera, protozoans, fungal structures…	3-10
Commensalism (+, 0)	These organisms can be challenging to detect but are inferred from consistent fossil associations such as burrows of commensal organisms within the shells of larger marine invertebrates from the Palaeozoic.	3, 11
Mutualism (+,+)	Certain morphological features can indicate mutualistic relationships, especially when they show specialized adaptations that suggest a close interaction between species (specialized structures, trace fossils, isotopic and chemical analysis, functional adaptations, …) *e.g.*, Late Triassic zooxanthellate scleractinian corals; plants and insects; plants and microorganisms	12-15

the tissue, the environmental conditions, and both the size and durability of the organism. Thus, fossilisation favours hard tissues (bones, shells, teeth, xylem, or even fungal hyphae) over soft tissues due to the higher preservation potential of skeletal parts. Therefore, interactions involving hard parts are more likely to be recorded (Behrensmeyer *et al.*, 2000). Rapid burial in sedimentary environments, anoxic conditions, and mineral-rich waters enhances preservation potential, thus biasing the fossil record of biotic interaction towards these conditions (Allison & Bottjer, 2011). Larger and more durable organisms or structures buried in suitable sedimentary environments (*e.g.*, vertebrate bones in basic soils of open habitat) are more likely to leave a fossil record. Smaller or more delicate interactions might be underrepresented, except in very particular situations, as noted above. Examples are the unicellular symbionts and parasites within insects in amber, or mycorrhizae in roots (Poinar, 2005; Taylor *et al.*, 1995; Wier *et al.*, 2002). In addition, taphonomic analysis can also provide valuable palaeobiological information about a species ecology and feeding behaviour (Palmqvist & Arribas, 2001).

Fossilisation of biotic interactions can suffer a temporal bias as well, due to factors such as changes in the Earth's environment, the evolution of organisms, and varying conditions conducive to fossilisation over geological time. Different geological periods experienced varying sedimentation rates and taphonomic conditions, which influenced the preservation potential of biotic interactions (Allison & Briggs, 1993; Behrensmeyer *et al.*, 2000); *e.g.*, the exceptional conservation of faunas during the Cambrian and Jurassic. Biological evolution can play a role in both facilitating the preservation of the interaction or biasing the fossil record. On the one hand, the development of hard parts such as shells and exoskeletons in many phyla during the rapid diversification of the Cambrian Explosion (~541 million years ago) led to an increase in the fossilisation potential of biotic interactions involving these organisms. On the other hand, some evolutionary dynamics through geological time had the potential to impact upon fossil preservation. For example, predator-prey dynamics led to developing more destructive crunching jaws to feed on shell-protected animals (Allison & Bottjer, 2011; Skinner, 2005). Another factor providing a temporal bias is the evolution of the complexity of ecosystems over time, because it has an effect on the types of interactions that could be preserved. For instance, the appearance of complex reef systems in the Silurian and Devonian periods led to a better preservation of symbiotic interactions in these environments (Copper, 2002).

LESSONS TO LEARN FROM THE BIOTIC INTERACTIONS AND THE FOSSIL RECORD

One important lesson learnt from the ideas exposed above is that any particular individual found in the fossil record was once an organism living and prospering in a particular ecosystem; and, thus, both exposed to, and exerting many, potential biotic interactions, as well as playing a role in shaping its own niche and ecosystem. A second lesson is the understanding that, while fossilization begins the moment an organism produces evidence suitable of being preserved in the record (*e.g.*, carcass, excrement, footprint, nest), not all biotic interactions occurring at that time will be recorded. For example, a predator will feed and leave; many parasites will flee as soon as they detect their host is dead (due

to changes in body temperature); a pollinator will seek a new fresh flower, and so on. Rare counterexamples can be found in amber (Peñalver *et al.*, 2023; Poinar & Buckley, 2011); or even in stone, like a *Velociraptor* fighting a *Protoceratops* (Hone *et al.*, 2010). These examples offer direct evidence of interactions that would otherwise be inferred indirectly, thus enriching our understanding of the evolutionary history of life on Earth.

A third lesson is that the interpretation of the presence of biotic interactions in the fossil record can differ significantly when viewed from a geological versus an ecological timescale. These differences arise due to the nature of the timescales, the types of data available, and the perspectives and goals of the studies involved. Thus, geological timescales encompass millions to billions of years, providing a broad view of the history of life and major evolutionary trends. When interpreting biotic interactions on this scale, the focus is on long-term patterns and processes, such as macroevolutionary trends, showing large-scale evolutionary patterns, such as the rise and fall of major groups, the radiation of species, and the impact of mass extinctions. Moreover, at the geological timescale we can understand how environmental and climate changes affected the taxonomic distribution and evolutionary dynamics, *e.g.*, because changes in sea levels and continental configurations have led to shifts in ecosystems and influenced biotic interactions over millions of years. The data is produced through taphonomic processes, and thus, factors like preservation potential, sedimentation rates, and diagenesis will determine which interactions are captured in the fossil record (Behrensmeyer *et al.*, 2000; Fraser *et al.*, 2021). At the geological timescale interpretations rely heavily on the fossil record, sedimentary layers, and isotopic data, which provide, most of the time, indirect evidence of interactions (*e.g.*, Hone *et al.*, 2010). However, ecological timescales are much shorter, ranging from years to centuries, offer high temporal resolution, and focus on the diversity composition and interactions within ecosystems and on population dynamics over short time periods (*e.g.*, Wing *et al.*, 1993).

Ecological studies examine how biotic interactions such as predation, competition, and symbiosis affect population sizes and community structure in the short term. Moreover, these studies can reveal how species interact and coexist in an ecosystem. Neontological analogues are a proxy to infer past interactions when analysing the structure and function of biological communities found in the fossil record. Palaeoecological analyses also provide clues on this (Jackson & Erwin, 2006). Then, while both geological and ecological timescales provide valuable insights into biotic interactions, they do so from different perspectives.

Geological interpretations highlight long-term trends and large-scale processes, whereas ecological interpretations focus on detailed, short-term dynamics and interactions. Integrating insights from both timescales can offer a more comprehensive understanding of the complexities of biotic interactions through time and allow to explore and verify, or falsify, microevolutionary theories, as well as to generate keys for the present (De Renzi, 2001; Jackson & Erwin, 2006; Palmqvist *et al.*, 2008; Simpson, 1944; Fitch & Ayala, 1995).

THE 21ST CENTURY PALAEONTOLOGIST

The classic idea of a palaeontologist solely dedicated to searching for new fossils as treasures to classify and use for dating the relative age of rock strata began to become obsolete following Simpson's synthesis (1944). However, classical stratigraphers still emphasise the importance of detailed sedimentological analyses to understand the context of fossil deposits. They contend that palaeontology should concentrate on its unique methodologies and datasets rather than integrating modern biological studies, which may dilute the discipline's distinct focus.

Today, amid the global biodiversity and climate crises, the new professional in palaeontology is a direct witness to phenomena such as species extinctions, shifts in species distributions, and changes in ecosystem dynamics and climate change through deep time. The effects of anthropogenically-driven climate change on ecosystem composition and organisation may echo those recorded in the fossil record from past periods of environmental change. They must be prepared to understand these events, integrate this knowledge, and help build resilience against 21st-century challenges. Indeed, integrating updated knowledge on the biology and ecology of living organisms (neontology) into the syllabus of palaeontological studies is pivotal for providing a comprehensive understanding of the biological and ecological processes that have shaped life on Earth (De Renzi, 1981; Jackson & Erwin, 2006). Thus, understanding developmental biology and genetic regulation in modern organisms can elucidate the evolutionary pathways of ancient species (De Renzi, 2009). This integrative approach not only enhances the accuracy of palaeontological reconstructions but also cultivates a holistic perspective necessary for addressing complex evolutionary questions (De Renzi, 1981, 2005).

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