Biodiversity and Host–Parasite (Co)Extinction

Chapter · December 2021

DOI: 10.1007/978-3-030-52233-9_3

2 authors:

Jeroen van Dijk
Wageningen University & Research
10 PUBLICATIONS **69** CITATIONS

Kenneth De Baets
University of Warsaw
154 PUBLICATIONS **2,041** CITATIONS

Chapter 3
Biodiversity and Host–Parasite (Co)Extinction

Jeroen van Dijk and Kenneth De Baets

Abstract Parasitism is one of the most common modes of life, and yet it is often disregarded or ignored in nature conservation. We are at the brink of the sixth mass extinction and in order to assess the extinction risk of both parasites and their hosts, we first need to fully understand the role and function of parasites in ecosystems. Parasites might play an active role in their host's extinction, and coextinction has been postulated to be the most common mode of extinction. However, parasites may be able to survive their host's extinction through host switching, perhaps to a more abundant host, for example. The dilution effect has been described as an important natural defense mechanism for the host: higher biodiversity is associated with lower infection risk. Discussed here is the importance of biodiversity and host–parasite associations and (co)extinction, and the role the fossil record has in filling the knowledge gap regarding deep-time host–parasite interactions.

Keywords Biodiversity · Co-extinction · Dilution effect · Host–parasite associations · Fossil record · Host switching

3.1 Introduction

We are currently witnessing the sixth mass extinction or at least its beginning, as became clear in the last decades (Wake and Vredenburg 2008; Barnosky et al. 2011; Payne et al. 2016). The Earth's biodiversity is decreasing, with more and more species disappearing. Even more worrying though is that a large portion of the estimated number of existing species today are still awaiting description (Mora et al. 2011). There is some bias in human pity: it seems dramatic when wild cats and rhinoceroses disappear, but who will cry for mites, fleas, and lice? Costello et al.

J. van Dijk (✉) · K. De Baets
Friedrich–Alexander University Erlangen–Nürnberg, Faculty of Science, GeoZentrum Nordbayern, Erlangen, Germany
e-mail: joendijk@gmail.com; kenneth.debaets@fau.de

K. De Baets, J. W. Huntley (eds.), *The Evolution and Fossil Record of Parasitism*, Topics in Geobiology 50, https://doi.org/10.1007/978-3-030-52233-9_3

(2013) famously asked whether we can name all species before they go extinct. The question raised is not trivial: Is naming every single species necessary, or is the cessation of some groups a loss that we can easily bear? Parasites, for example, are more or less considered species *non gratae* in nature conservation (Strona 2015; Dougherty et al. 2016; Carlson et al. 2020).

The macroevolutionary point of view defends parasites, arguing that they might fulfill an important stabilizing function for maintaining the balance of ecosystems (Seilacher et al. 2007; Lafferty 2012), a balance that might shift during mass extinctions (Seilacher et al. 2007). Dougherty et al. (2016) and Carlson et al. (2020) suggested to include parasites into nature conservation, but this requires a framework that tests for the viability of host–parasite assemblages within a population in order to assess extinction risk. And here is where we come to some quite important and interesting questions: How important are parasites to an ecosystem (beyond being a nuisance to their hosts)? And, if they are important, what is their role? More importantly, how does parasite diversity and extinction relate to host diversity and what happens to parasite diversity during mass extinctions?

3.2 Host–Parasite Biodiversity

Parasitism is one of the most common modes of life on Earth (Poulin and Morand 2000), which has independently evolved at least 223 times within metazoa (Weinstein and Kuris 2016), but also throughout the entire tree of life (Bass et al. 2015). Parasites can be highly abundant in ecosystems, and not only reach high diversity levels, but also take up a substantial part of an ecosystem's biomass (Kuris et al. 2008). Indeed, ecosystem functioning seems to improve with increased diversity of parasite species (Hudson et al. 2006).

Nonetheless, parasites are often seen as disgusting, associated with diseases and low hygienic conditions, and are therefore probably the most ignored group of organisms in nature conservation (see Dougherty et al. 2016). When it comes to protecting the natural world, parasites are often overlooked (e.g., biodiversity counts), because they do not come to mind (e.g., too small), or because they simply lack charisma (Dunn et al. 2009). Instead, they are often seen as part of the problem: a threat to wildlife, and should therefore be eradicated. Medical and veterinary sciences attempt to remove parasites from both human and animals by all means necessary, as evidenced by the tragic fate of the condor louse (*Colpocephalum californici*) that went extinct during the captive breeding program of its host, the highly endangered California condor, *Gymnogyps californianus* (Pizzi 2009). This example demonstrates that we care more for the hosts than for their parasites, and that hosts may survive with the help of our conservation programs, while their parasites go extinct.

Emiliani (1993) and also Vredenburg et al. (2010) have postulated that, potentially, parasites and viruses could even drive their host to extinction during particular conditions. A strong decline has been observed in the total number of adult and subadult frogs in three metapopulations after the detection of amphibian chytrid fungus, *Batrachochytrium dendrobatidis* (Fig. 3.1; Vredenburg et al. 2010).

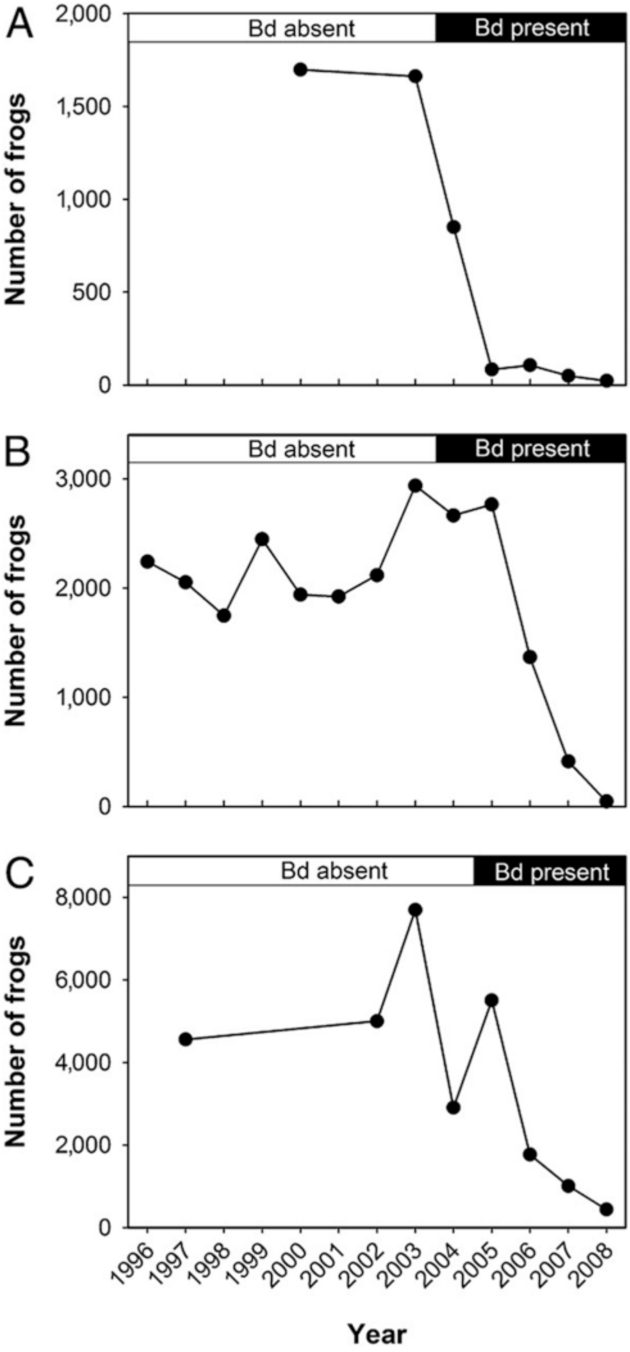

Fig. 3.1 The number of adult and subadult frogs in the different metapopulations before and after detection of Bd. Studied sites: Milestone Basin (**a**), Lake Basin (**b**), and Barrett Lake Basin (**c**). Image from Vredenburg et al. (2010)

However, the evidence for this dynamic is lacking from deep time, and the total exclusion of a species by another species is considered rare in nature (Vermeij 2004).

Traditionally, disease models suggest that parasites driving their host to extinction are highly unlikely to nearly impossible, and often the parasites go extinct before the hosts (De Castro and Bolker 2005). Some conditions, however, may allow for parasite-driven extinctions of a host, for example, a parasite which significantly reduces the reproductive capacity of infected hosts (Boots and Sasaki 2002), or the evolution of costly host defense that is limited by resource availability (Boots 2011).

However, resource availability and cost of resistance may actually play a more important role in the so-called killing the winner motifs (Våge et al. 2013; Våge et al. 2018). In this particular motif, the parasite (or virus) selectively attacks the "winner" (i.e., superior competitor or abundant) populations, preventing any single host from dominating a community and thereby promoting diversity (Thingstad and Lignell 1997). Empirical examples are few and far between, but they have been observed in land snails (Cunningham and Daszak 1998), and the red flour beetle, *Tribolium castaneum* (Rafaluk et al. 2015).

It is safe to assume that parasites and pathogens must have played an important and active role in past extinctions as evidenced by the global decline of amphibians caused by virulence, which is here defined as the parasite-induced reduction in host lifetime reproductive success (Herre 1993), and the emerging infectious disease chytridiomycosis, which was likely spread through the introduction of exotic species, and was enhanced by climate change and habitat destruction (Wake and Vredenburg 2008).

While plausible in theory, it is challenging to track host–parasite relationships empirically in the fossil record. It is reasonable to assume that parasitism has existed in one form or another since the beginning of early life. However, most parasites are small, and their soft bodies hardly fossilize (Leung 2017). However, some types of host–parasite collections allow us to track parasitic infestation in deep time (De Baets and Littlewood 2015; De Baets et al. 2021a, b; Wood et al. 2017). Parasites can leave traces in their host's remains, which can be studied, as well as traces and (resistant) propagules in coprolites, the host's fecal remains. Yet it is difficult to gather enough evidence to precisely identify host and parasite. In some cases, it is possible to track hosts and their associated parasites and/or characteristic pathologies, as with platyceratid gastropods in the fossil record (Baumiller and Gahn 2002).

3.3 Co-extinction

Global change is expected to typically lead to co-extinction of hosts and their specific parasites (Dunn et al. 2009; Carlson et al. 2017; but see Strona 2015). Some models that account for host-driven co-extinctions predict that up to 30% of the parasites go extinct in the form of such secondary extinctions (Fig. 3.2; Carlson et al. 2017). However, such a perspective would strongly depend on to what degree

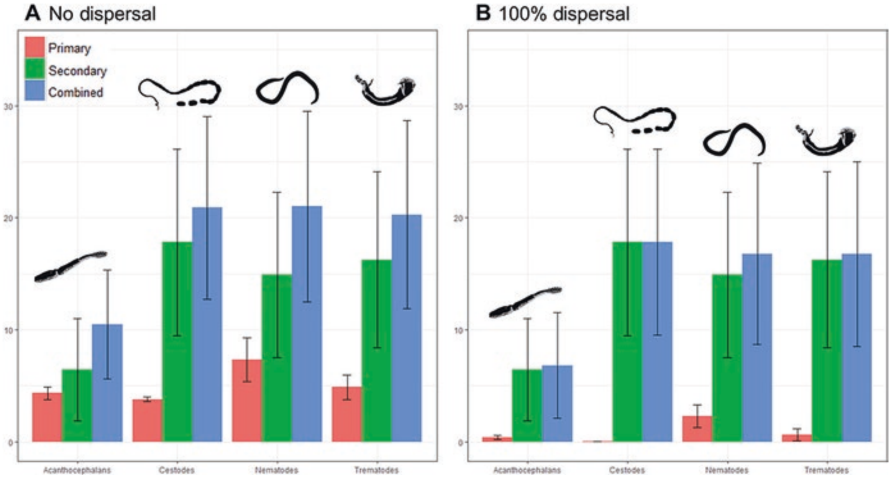

Fig. 3.2 Dispersal (**a**) and no dispersal (**b**) scenarios and the effects on the primary (due to climate change), secondary (co-extinction with hosts), and combined (total) extinction rates for major helminth clades. Figure from Carlson et al. (2017)

parasites specialize on niche specialists or top predators (Lafferty 2012). Models of parasite co-extinction with host decline differ from models that are based on host extinction alone. Such models of co-extinction only focus on the outcome after complete host extinction, but a species will generally show a significant decline in abundance and range size well before it finally goes extinct (Farrell et al. 2015).

Parasite survival has often been closely linked to the survival of its host; it can therefore be expected that when the host goes extinct, so will the parasite (Koh et al. 2004). Many tick species, for example, are endangered (Mihalca et al. 2011). Dunn et al. (2009) rightly posit that with current species' declines and extinctions, the most endangered species will actually be parasites and mutualists. This is because all species with a symbiotic lifestyle naturally depend on the availability of a host. Additionally, each host species likely harbors just as many, if not more, in symbiosis living species: from the mutualistic bacteria in our intestinal tract, the ones on our skin (e.g., lice and ticks), to parasitic flatworms and viruses.

Endoparasites are especially vulnerable to host-driven co-extinction (Carlson et al. 2017). Some are specialists, being highly host species specific, and thus potentially more prone to co-extinction, while others are generalists that may be able to adapt to the change in host availability. Co-extinction has a high chance to occur when the parasites are specialized on niche specialists or hosts higher on food chains (Lafferty 2012). However, this does not need to be the case when the host has a wide distribution and high abundance (Strona et al. 2013; Strona 2015). Highly specific parasites predominantly use low-vulnerability hosts (Fig. 3.3), and thereby reduce the risk of a co-extinction (Strona et al. 2013). Parasite and host co-extinction are often overlooked, but may have occurred throughout Earth's history, especially during mass extinction events (e.g., Seilacher 2007).

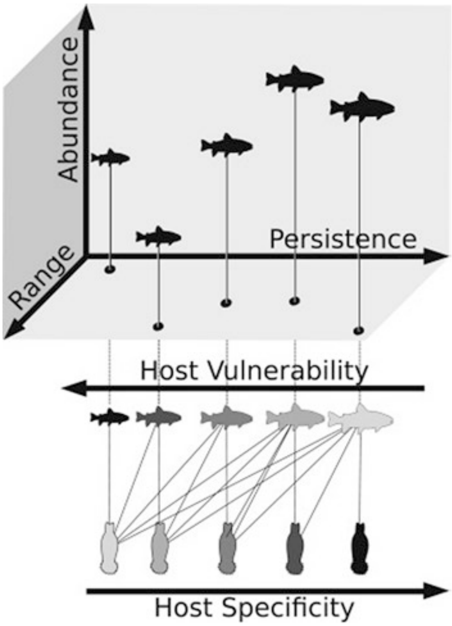

Fig. 3.3 3D representation of the relation between host vulnerability and host specificity. Image reproduced from Strona (2015)

Co-extinctions can be expected at a much broader scale and are not only restricted to host–parasite relationships, but concern all types of species that depend on one or more species in general: from the many forms of symbiosis to predators and their prey, to key species in an ecosystem. In a predator-prey relationship, for example, where the predator is highly specialized on just one type of prey, the predator has a high risk of co-extinction if it does not change its diet, but also herbivores with a very specific diet can fall victim to co-extinction (Labandeira et al. 2002).

Another, highly relevant, coevolutionary relationship is that between plants and pollinators. One-third of Europe's crop plants depend on pollinators (Kearns and Inouye 1997). Local extinctions of bee populations and the parallel decline of insect-pollinated plants due to anthropogenically modified landscapes have been observed in several parts of Europe and are of much concern (Biesmeijer et al. 2006). Co-extinctions of plants and their pollinators is nothing new and has happened in the deep past as well (Bascompte and Jordano 2007). Thus, co-extinction may be the most common form of species loss (Koh et al. 2004; Dunn et al. 2009).

The disappearance of key species should thus be our main concern as that could result in a cascade of secondary extinctions and co-extinctions of the parasites and others that depend on them (Stork and Lyal 1993). The assumption has been that threatened hosts have relative fewer single-host parasites (Dunn et al. 2009; Lafferty 2012), but host extinction may vary across groups of hosts. Threatened ungulates were found to have a higher proportion of single-host parasites compared to non-threatened ungulates, a result related to a disproportionate decrease in richness of multi-host parasites, but among carnivores this relation does not exist (Farrell et al. 2015).

3.4 Dilution Effect

The current biodiversity loss and disease emergence have become two of the most challenging issues confronting science and society (Johnson et al. 2008). Different authors have found a strong correlation between parasite success in ecosystems and biodiversity of their ecological communities (Johnson et al. 2013; Lagrue and Poulin 2015), and many of them underline that the rapid loss of populations and biodiversity significantly increases overall disease risk. Studies concerning the causal relationship between biodiversity and disease emergence in a particular environment are focused on testing the "dilution effect" model (Ostfeld and Keesing 2000), which parasitologists refer to as the "decoy-effect" hypothesis (Combes and Moné 1987; Johnson and Thieltges 2010). According to these researchers, the mechanisms of the decoy effect, as observed in the case of high biodiversity in ecological communities, concern (1) the physical degeneration of parasite life history stages infecting a nontarget host, (2) the encounter reduction caused by infecting a nontarget host, and (3) the stimulation of defense mechanisms in nontarget hosts against the infectious stages of the parasite. Regardless of the mechanism, the nontarget host becomes a dead-end host, which is the real factor reducing the emergence of parasitic disease (Mehlhorn 2008). Essentially, this is in the same line of thought as Keesing et al. (2006), who propose that the term "dilution effect" should be interpreted as "the net effect of increased species diversity reducing disease risk."

The dilution hypothesis has been in particular investigated for zoonotic diseases, like Lyme disease, but has also been reported to be more widespread (Civitello et al. 2015), and has even been reported for zooplankton (Hall et al. 2009). However, a meta-analysis of classical studies with new approaches has demonstrated that research is heavily biased towards studies presenting the dilution hypothesis, which yield biased results (Young et al. 2013). When correcting for this, a meta-analysis could not find strong evidence for the dilution hypothesis (Salkeld et al. 2013). Further analyses suggest that there is a slight publication bias towards negative relationships between biodiversity and disease risk (Fig. 3.4; Salkeld et al. 2013).

The generality of the dilution hypothesis is still debated and might be context dependent. It might particularly work on local scales, while large-scale analyses usually find a positive correlation between host and parasite diversity (Wood and Lafferty 2013). In that sense, it is mostly a matter of scale whether one observes a dilution effect or not (Fig. 3.5; Hopkins 2013), and may further depend on the characteristics of host communities (Halliday et al. 2020) and species interactions, such as predation (Su et al. 2020). Large-scale studies show mostly the traditional patterns, and this is potentially also the dominant relationship we might find on longer evolutionary patterns observed in the fossil record. Preliminary data compiled by Baumiller and Gahn (2002) on the prevalence of parasitic pathologies in marine invertebrates are very reminiscent of the traditional perception of metazoan diversity (the so-called Sepkoski (1981) curve). A similar positive relationship also exists between infested species of crinoids and crinoid diversity (Fig. 3.6; compare Baumiller and Gahn 2002; Baumiller et al. 2004). Irrespective of the presence of the

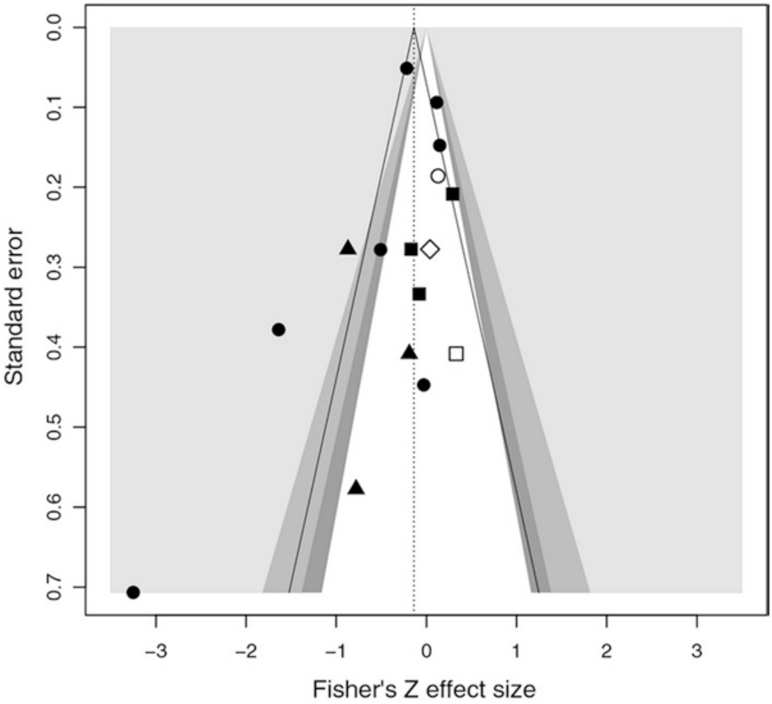

Fig. 3.4 Funnel plot of the relation between the Fisher's Z effect size and the standard error for studies on biodiversity and disease risk. Adapted from Salkeld et al. (2013)

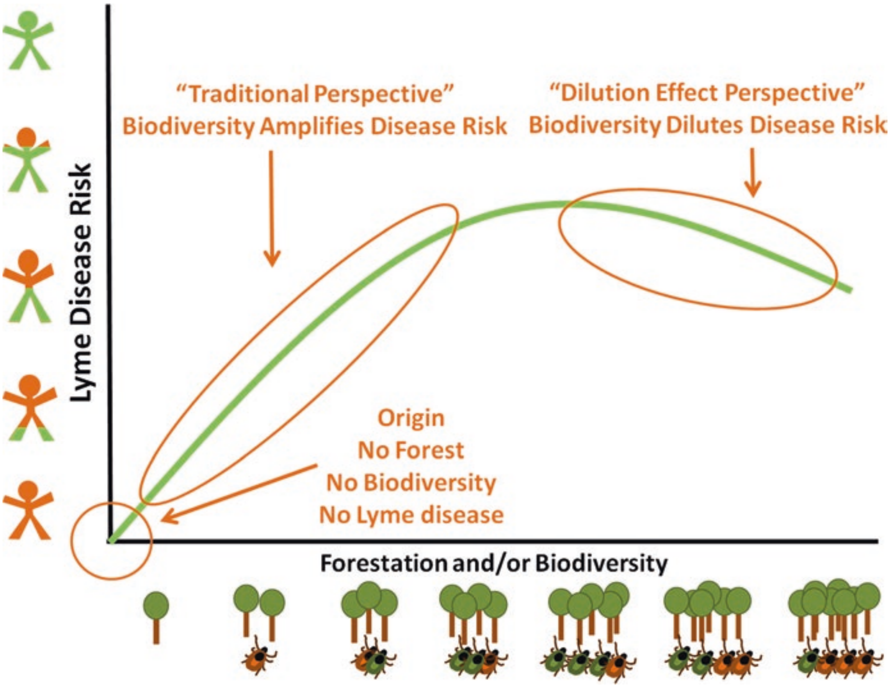

Fig. 3.5 As forest area increases, tick density will increase, but less fragmentation will lead to a decrease of infection prevalence. Lime green is used to indicate Lyme infection. Figure by Hopkins (2013)

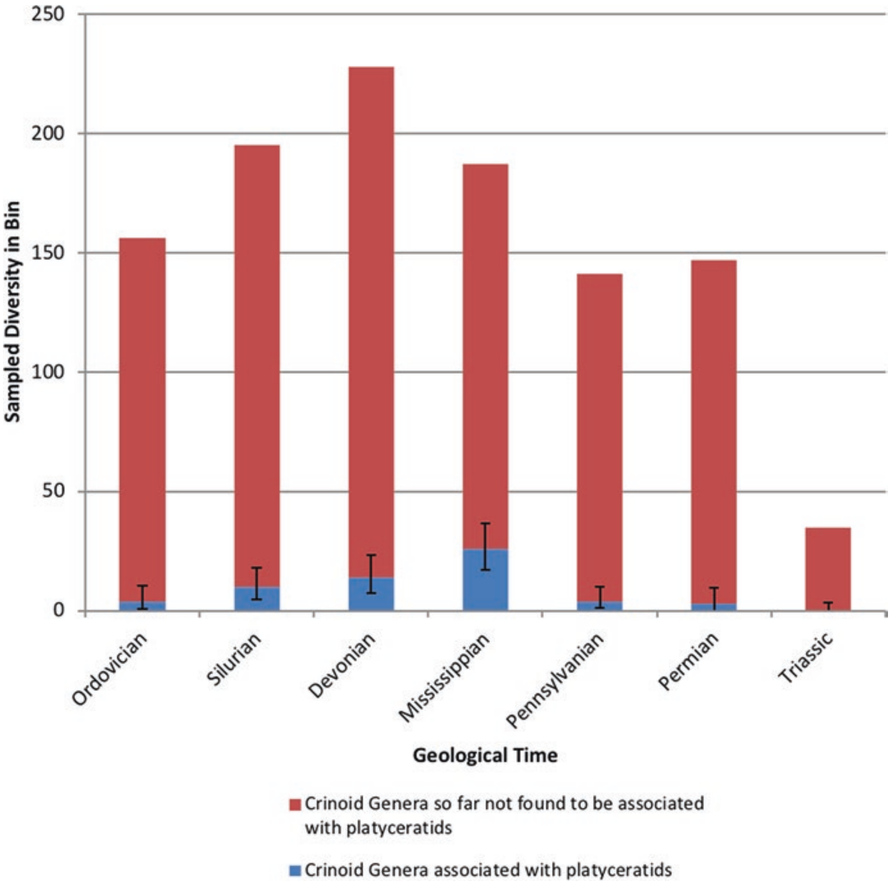

Fig. 3.6 Crinoid genera parasitized by platyceratids during the Paleozoic. Entire bars show the crinoid generic diversity based on sampled-in-bin diversity downloaded from the Paleobiology Database (PBDB, accessed in 14/11/2019). Co-occurrences of crinoids and platyceratids are shown in the solid blue part with error bars for 95% confidence levels. Based on data from Baumiller and Gahn (2002)

dilution effect or opposite patterns—this context dependency is still of great interest on larger timescales.

How can we extrapolate anything like the dilution effect to deep time, especially when there is no general consensus on the dilution effect occurring in the modern world? In fact, some workers even question how effective a dilution effect actually is in reducing disease risk. Critique on the dilution effect model concerns the issue that it may only work if the parasite is (more or less) a host specialist, and increasing host diversity will also increase infection prevalence; thus the addition of host species may actually increase parasite abundance (Randolph and Dobson 2012; Wood and Lafferty 2013). The mechanisms behind the dilution effect are complicated, even if some aspects of it might be applicable to the fossil record, e.g., trace fossils that indicate a parasite with host preference, and high vs. low variation in potential hosts; but these findings will first and foremost indicate density dependence. Let us not forget that the dilution effect itself refers to the reduced *disease risk* for a vulnerable focal host at higher biodiversity due to the presence of more diluter species (Keesing et al. 2006). These diluter species can in several ways decrease transmission: they can affect focal host behavior, reduce focal host population density so it may become fragmented, or may feed on the disease vectors, e.g., the parasites (Keesing et al. 2006; Keesing et al. 2010). Thus, parasites do play a role here as a vector transmitting the disease (e.g., ticks spreading Lyme disease), but the transmitting-part is hardly observed in the fossil record, if at all. To actually observe this in the fossil record we would need to investigate three things: (1) an indication that the mortality of selected fossils was caused by disease, (2) the prevalence of parasite traces, and (3) whether 1 and 2 are related, or not. Morphological studies of fossil remains could be one approach, as disease may affect morphology as well as size. Infected organisms may compromise with reduced growth (Ruiz 1991), a phenomenon reminiscent of the "Lilliput effect," which was observed in the context of mass extinctions (Urbanek 1993). However the opposite may also have happened in some cases, in the form of pathological gigantism, possibly caused by parasitic castration (Manger et al. 1999; but see De Baets et al. 2015). Modern studies show that skeletal pathologies observed in helminth-infested frogs are inversely correlated with survival (Johnson et al. 2011). The number of malformed amphibians has markedly risen (Fig. 3.7, Johnson and Chase 2004)—making it tempting to attribute this to anthropogenically induced factors (Johnson and Chase 2004).

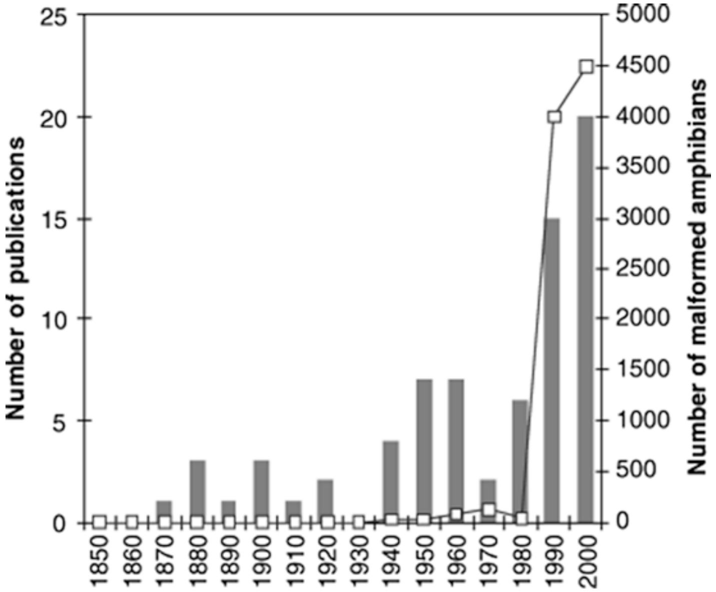

Fig. 3.7 The number of articles published on, and the number observed in (line), malformed amphibians in wild populations in North America (USA and Canada). Figure from Johnson and Chase (2004)

An observed dilution effect may well be a “chicken or the egg” causality dilemma, and in fact, there may be more a “killing the winner” dynamic going on, than an actual dilution effect. Indeed, it may be a matter of scale as some workers have pointed out, but it may also depend on the moment in (long-term) time. Much like the “Red Queen” dynamics in predator-prey interactions, populations of hosts will likely follow a sinusoidal pattern through time. In turn, Red Queen dynamics might be one mechanism that promotes host switching (Rabajante et al. 2016). A highly successful and abundant species may attract more parasites, and then decline because of parasite load, which then allows the host’s competitors to rise. As a result, parasite density may fall and/or the parasites may switch to a new host, which, in turn, would allow the original host population to strengthen and increase again. The presence of competition may in fact be beneficial to the host, driving rapid evolution of hosts with high phenotypic variation and may thereby “rescue” the host’s population densities despite larger epidemics (Strauss et al. 2017).

The notion that diverse communities inhibit the proliferation of parasites (Civitello et al. 2015) is in that sense incorrect, because in reality it is more likely that parasites inhibit the proliferation of any single (or multiple) host species. Much like the “paradox of the plankton,” which addresses the situation where a number of phytoplankton species are able to coexist in the same environment while competing for the same resources (Hutchinson 1961). Here, the parasites play an important role in facilitating diversity by allowing multiple species to exploit a certain niche (Våge et al. 2018). The deep-time fossil record could well play an important part here if only we could find an effective way to reconstruct these dynamics.

A complicating factor here might be that an increase of host pathologies in the fossil record could relate to an increase in parasitized specimens, but could also reflect an increase in abundance of hosts that can better cope with being parasitized, or at least with the developing pathologies. A positive relationship between sampling opportunity and finding pathologies might also affect such a relationship (cf.) as it has been suggested for predation prevalence (Huntley and Kowalewski 2007). However, by looking at larger samples of hosts from various localities and time intervals one could get an idea about the relationship between host population structure and prevalence of pathology changes through time. Such a larger sampling would also avoid the pitfalls of small sample size.

3.5 Host Switching

Host switching, e.g., parasites “jumping” from one species to the other, broadly speaking, occurs naturally as part of the life cycle of many species of parasites. On evolutionary timescales this usually refers to events where parasites switched host, which is usually inferred from coevolution patterns in phylogenies (Page 2003; Martínez-Aquino 2016). However, these phylogenies might be hard to resolve and not entirely equivalent (e.g., De Vienne et al. 2013; Poisot 2015). The biology of host switching revolves around three factors: (1) the rate of exposure of the new host to the parasite, (2) the compatibility of the pathogen towards the new host, and (3) whether the pathogen is sufficiently transmissible between individuals within the new host population (Woolhouse et al. 2005).

Host switching has played an important role in the evolution of many parasite groups, but most of these host-switch events have been inferred solely from molecular phylogenies of extant taxa (e.g., Badets et al. 2011). Fossil parasites may help us to calibrate molecular clocks in such trees, as well as confirm past host-switching events (De Baets and Littlewood 2015; Leung 2017; Warnock and Engelstädter 2021). The fossil record has also revealed various combinations of parasite and host (e.g., arthropod and their pathogens) that have no extant equivalents (see De Baets and Littlewood 2015; Leung 2017, 2021 for reviews).

Ticks (order Ixodida) are known to have switched hosts many times during their evolution. It is therefore likely that host specificity is merely temporal and determined by biogeography and ecology (Klompen et al. 1996). One example is *Nuttalliella namaqua*, a monotypic tick species (the only representative of its genus). Phylogenetic analysis placed *N. namaqua* basal to the Ixodida, and can therefore be considered a "living fossil," with its ancestors originating in the Late Carboniferous to Early Permian (Mans et al. 2011; Mans et al. 2012). These ancestors must have parasitized early reptiles and evidently changed host preference to mammals and lizards (Mans et al. 2014; but see Dunlop 2021).

Traces of host switches can also be identified via horizontal gene transfers (HGT) or horizontal transfers of retrotransposons (HTT) in the genomes of hosts and parasite species. For example, lymphatic filariasis and loiasis are two widespread human diseases caused by insect-borne filarial nematodes *Brugia spp.*, *Wuchereria bancrofti*, and *Loa loa*. These nematodes were likely endoparasites of tropical birds during the Oligocene/Miocene epochs (Suh et al. 2016; Suh 2021)—both of these groups were at least present at the same time in the same regions, as evidenced by amber records (Poinar et al. 2007; Poinar 2010, 2011a, b). Evidence was found that the genomes of these nematode species share the retrotransposon AviRTE with seven lineages of tropic birds, which must have come from two waves of horizontal gene transfer (Suh et al. 2016).

3.6 Parasites as Drivers and Regulators

Parasites have various ways to affect the lives of their host. They can, for example, deteriorate the host's health, or influence the host's reproductivity or even host behavior, as seen in rats and mice. The common brain parasite, *Toxoplasma gondii*, influences the behavior of rats and mice (the intermediate hosts) to become easier prey for cats (the target host). Infected intermediate hosts show more exploratory behavior and are less fearful of cats. Humans can also be infected, but normally serve as a dead end, although it is interesting to hypothesize how *T. gondii* may have influenced our behavior and culture in the long term, after centuries of exposure.

Climate change and biotic invasions of disease vectors promote the transfer of novel diseases and parasites to native species (Tylianakis et al. 2008). Higher temperatures can both enhance host susceptibility to parasites and reduce host survival and fertility (Traill et al. 2010). The most optimal parasite and host phenotype, in terms of infectivity and resistance, respectively, vary from one time point to the next leading to fluctuating selection dynamics (Hall et al. 2011). In turn, this may result in fluctuating "Red Queen" coevolutionary interactions, where the parasite is locally adapted to infect sympatric host species, but has trouble infecting allopatric hosts (Brockhurst et al. 2014). In natural systems this leads to negative frequency-dependent selection, where the parasite follows the most common host over time (Decaestecker et al. 2007; Wolinska and Spaak 2009). Parasite diversity can then be maintained through negative frequency-dependent selection and multiple-niche polymorphism (Radolf and Samuels 2010; Strona et al. 2013; Strona 2015).

The occurrence of diverse natural populations of asexual organisms can be explained by the presence of parasites, which seem to play an important role in maintaining host genetic diversity (Turko et al. 2018). Sexual reproduction may exist for the same reason: instead of clonal reproduction where each generation is basically a copy of the previous, sexual reproduction creates diversity, which enables populations to cope with parasite infection (Jokela et al. 2009). Competition and defense could be central structuring factors in some microbial communities (Våge et al. 2018). This may also lead to diversification of both host and parasite, even in a homogenous environment, such as with the prey and predator leading to the paradox of the plankton (Hutchinson 1961). This process has also been termed "killing the winner," where a parasite or virus prevents a susceptible competitive host (the winner) from monopolizing a limiting resource (Thingstad and Lignell 1997). This in turn allows the coexistence of resistant hosts, even when their defense is associated with a cost in the form of reduced competitiveness.

While competitive hosts tend to be infected by virulent specialists, less virulent generalists infect more hosts with higher resistance. Species that have found a way to reduce the costs of defense against parasitism without losing too much in competitive ability may reach the highest abundances (Våge et al. 2018), although other factors such as predation may still prevent this. The resistant hosts may be resource controlled, disappearing at low resource levels and dominating at high resource levels (Våge et al. 2018). Highest diversity would then be found around intermediate resource levels, which seems to be a general pattern found in both microbial and macroorganism ecosystems (Smith 2007). Lower amounts of remaining resources will likely slow down the Red Queen arms race based on the reduced probability that resistant hosts can successfully exploit them. Over geological time, these arms races may have played an important role in structuring the food webs with its major functional groups (Våge et al. 2018).

3.7 What Can the Fossil Record Tell Us?

Host–parasite associations in the fossil record can be studied by comparing trait variation through time of the host, and whether or not they show signs of having been parasitized. The host may have reached adulthood, but compensated with decreased growth, abnormal growth response, or some visible pathology, for example (Hengsbach 1990; Rothschild and Martin 1993; Dittmar et al. 2012). Certain defensive traits may have come about as a response to parasitism as well, as is the case with the tubed crinoids that evolved in response to parasitization by platyceratids (Baumiller and Gahn 2002). In some cases, targetting of parasites by predators might also induce changes in the hosts such as spinosity in crinoids as a defense mechanisms against predation on platyceratid gastropods (Syverson et al. 2018).

Traces of parasites have also been found in coprolites, in the form of tapeworm eggs in ancient shark coprolites, for example (Dentzien-Dias et al. 2013). New methods such as using the synchrotron phase-contrast microtomography and high-quality virtual 3D reconstructions of coprolite inclusions may reveal ancient trophic relations (Qvarnstrom et al. 2017). An integrated approach of scanning combined with dissolving coprolites might be the most effective way forward (but see Wood and Wilmshurst 2016). Each of these systems has its own challenges.

The direct fossil record of viruses and unicellular pathogens is very limited, making it hard-to-test hypotheses about their origins and coevolution directly (Hayward 2017; Leung 2017)—other than by attribution of changes in diversity and/or abundance without recorded environmental perturbations. Nonetheless, viruses, and in particular retroviruses, have been found to leave endogenous viral elements (EVEs) behind in the genomes of hosts and previous (ancestral) hosts (Katzourakis and Gifford 2010; Holmes 2011). These EVEs can be used to explore ancient viral evolution and trace their origins (Aiewsakun and Katzourakis 2015; Aiewsakun and Katzourakis 2017).

Some of the more spectacular data involve ancient DNA, or aDNA (Lafferty and Hopkins 2018). Ancient DNA (aDNA) extracted from moa coprolites found in New Zealand revealed that some species of parasites survived the extinction of their hosts (Table 3.1), and still exist today (Wood et al. 2013; Boast et al. 2018). This dataset could indicate that since the extinction of moas, as much as 19 species of parasites

Table 3.1 Chart showing the distribution of parasite taxa across extinct species of moa, modern birds, and mammals, and the total number that appears, persists, or disappears

	Taxon	L. Bush Moa	Giant Moa	Upland Moa	H.-footed Moa	Kakapo	Modern birds	Mammals	Appear	Persist	Disappear
Apicomplexa	Eimeriidae[a]	1	3	9	3	0	3	0	0	3	6
	Emeria	0	0	0	0	0	0	1	1	0	0
	Sarcocystidae	1	0	1	1	1	0	0	0	0	1
Ciliophora	Balantiididae	0	0	0	0	0	4	0	4	0	0
Nematoda	Ascaridida[b]	0	1	0	0	0	0	0	0	0	1
	Heterakoidea	6	6	7	0	0	0	0	0	0	9
	Seuratidae	1	1	1	0	0	0	0	0	0	1
	Panagrolamoidea	0	0	0	0	0	0	2	2	0	0
	Strongylida	0	0	1	0	0	0	11	10	1	0
Platyhelminthes	Notocotylidae	0	1	1	1	0	0	0	0	0	1

Color fill illustrates presence (green) and absence (red)

[a] Eimeriidae: excluding *Eimeria*

[b] Ascaridida: unidentified species, excluding Heterakoidea and Seuratidae. Based on data from Boast et al. (2018), *SI Appendix*, Fig. S20

went extinct, while as little as 3 species might have survived and up to 4 might have newly appeared in birds. For example, three upland moa's eimeriid coccidia are still found parasitizing extant kiwis. On the other hand, up to 9 heterakoid nematode species that had coevolved to specialize on moas have disappeared since their host's extinction. Moreover, the disappearance of moas led to the secondary extinction of their predator and a cascade of secondary extinctions of host-specific parasites of both predator and prey.

The extinctions might however be overestimated as in modern birds only one (captive) kiwi and two (non-native) ostriches could be investigated, while the number of survivors and newly appeared species may have been underestimated for the same reasons. This is also supported by the fact that only 18 species of parasites went extinct when modern mammal samples are also included, while as few as 4 and as many as 17 species might have survived or appeared in the modern fauna investigated. Even though this approach might be suitable for investigating extinctions during relatively recent extinction events, it is limited when going further back in time. It does demonstrate that a significant proportion of parasite species can disappear when their hosts go extinct.

In more ancient (lithified) coprolite samples, identifying the parasites using aDNA is limited (Chin 2021; De Baets et al. 2021a; Greenwalt et al. 2021). This means eggs themselves can rarely be assigned on the species or genus level, but are usually only attributable to higher taxonomic ranks. Also, precisely identifying the hosts is difficult—especially when found isolated from their producers. This is not an issue per se, as one can still study the diversity and relative abundance of propagules and their relationship/dominance in coprolites assignable to larger groups. However, further work (e.g., Camacho et al. 2018) is necessary to understand the abundance of propagules and their relationship with parasite abundance in hosts as well as loss through preparation. More important, although sampled, their record is still comparatively patchy. Coprolites need to be more systematically investigated for parasitic remains throughout the Phanerozoic (Chin 2021)—ideally covering major climatic and/or extinction events. As it is difficult to assign coprolites precisely to their hosts, their precise relationship with host species might be limited.

Although the precise identification of the culprit of a particular pathology will be a challenge, the host can, in most cases, be identified up to genus or species level depending on the state of preservation. Moreover, the expression of the disease (paleopathology) can be precisely measured, and its prevalence in populations can be quantified. Through cost-benefit analysis and population studies it is even possible to establish their impact on growth and fitness of particular host samples (Baumiller 2003; Huntley and Scarponi 2012; Baumiller and Gahn 2018; Klompmaker et al. 2021; Zhang et al. 2020). Such an approach is necessary to understand the negative impact of parasites on their hosts. If we have densely spaced samples through time and/or space, we could even track how disease or infestation prevalence relates to characteristics of the hosts, such as abundance, evolutionary persistence, geographic range, mode of life, or degree of specialization. Particularly interesting systems are those that have modern analogues, like the isopod swellings in decapods (Klompmaker et al. 2014, 2021; Robins and Klompmaker 2019), and trematode-induced traces in bivalves (Ruiz and Lindberg 1989; Huntley and De Baets 2015; Rogers et al. 2018; Huntley et al. 2021), which can at least be traced back to the Mesozoic. However, such studies are even more important when parasites have a higher preservation potential—like platyceratid gastropods shown to be parasitic on crinoids (Gahn and Baumiller 2003).

Considering that remains of shelled invertebrate hosts are more widespread—they do allow us to investigate the precise contribution of shifts in pathology prevalence, environmental perturbations, diversity fluctuations and mass extinctions. More importantly, the relationship between specificity, or the prevalence of pathologies and host characteristics, can be investigated. This could be used to investigate whether the perception holds true that parasites tend to specialize on a specific host or rather on a number of resistant hosts. A better idea of this on longer timescales would also be crucial to understand the future of parasite diversity, as well as disease prevalence, in their hosts. Climate change for example, and in particular sea-level rise, has been linked to an increased prevalence of trematode infestations in bivalves (Huntley et al. 2014; Scarponi et al. 2017).

Cost-benefit analysis and modelling can help to establish the nature of this association (Baumiller 2003; Baumiller and Gahn 2018). Furthermore, the relationship between diseased species (specificity) and infested individuals within samples (prevalence) could be investigated. This, in principle, allows us to investigate how these properties relate to host persistence, abundance, and/or geographic range.

In the case of amber inclusions, novel techniques, such as phase-contrast synchrotron X-ray tomography (Dunlop et al. 2011; Dunlop et al. 2016), may allow the precise identification of the host, and the identification of the parasite to genus, or (at least) family level, might well be within grasp. However, more quantitative studies of amber inclusions are necessary to establish the prevalence of such associations. Due to a limited number of characters, it is still not that straightforward without knowledge about the life cycle of modern relatives and their host associations, to precisely identify particular parasites with limited external characters such as nematodes (Poinar 2011a, 2011b). Research has, at least, revealed potential new extinct, or rare, host associations (Peñalver et al. 2017), as well as tracked ancient host associations back in time (Haug et al. 2021; Labandeira and Li 2021). Another factor which needs to be considered when using amber deposits remains the debate concerning the age of many deposits, their patchiness in time, and the selectivity of trapping and preserving hosts (McCoy et al. 2018; Solórzano-Kraemer et al. 2018; De Baets et al. 2021a).

Despite these limitations, we are convinced that studying these model systems would advance our understanding of host–parasite evolution in deep time, as well as further constrain the modern baseline. Amber inclusions would be particularly good to understand the evolution and extinction of arthropod parasites and vectors, while invertebrate pathologies and propagules in vertebrate coprolites might be the only way to cover the impact of mass extinctions on parasitic disease and their link with host diversity. Before we can fully exploit the fossil record for this purpose, more data needs to be collected still, before such studies become feasible. Currently, most of these systems are incompletely studied—larger samples in particular are rare, and reports of prevalence of certain pathogens or impact on host population are still limited or restricted to particular time intervals (e.g., De Baets et al. 2021b). Systematic screening of museum collections yielding large samples of well-determined hosts from particular localities might help considerably in such an endeavor (Harmon et al. 2019), as well as considering these constraints when sampling and describing new host remains.

Acknowledgements The authors would like to thank Carl J. Reddin and Tatjana E. Döbeling for comments on earlier versions of this chapter. The authors would also like to thank John W. Huntley for reviewing this chapter.

References

Aiewsakun P, Katzourakis A (2015) Endogenous viruses: connecting recent and ancient viral evolution. Virology 479:26–37

Aiewsakun P, Katzourakis A (2017) Marine origin of retroviruses in the early Paleozoic era. Nat Commun 8:13954

Badets M, Whittington I, Lalubin F, Allienne JF, Maspimby JL, Bentz S, Du Preez LH, Barton D, Hasegawa H, Tandon V, Imkongwapang R (2011) Correlating early evolution of parasitic platyhelminths to Gondwana breakup. Syst Biol 60(6):762–781

Barnosky AD, Matzke N, Tomiya S, Wogan GO, Swartz B, Quental TB, Marshall C, McGuire JL, Lindsey EL, Maguire KC (2011) Has the Earth's sixth mass extinction already arrived? Nature 471(7336):51

Bascompte J, Jordano P (2007) Plant-animal mutualistic networks: the architecture of biodiversity. Annu Rev Ecol Evol Syst 38:567–593

Bass D, Stentiford GD, Littlewood D, Hartikainen H (2015) Diverse applications of environmental DNA methods in parasitology. Trends Parasitol 31(10):499–513

Baumiller TK (2003) Evaluating the interaction between platyceratid gastropods and crinoids: a cost–benefit approach. Palaeogeogr Palaeoclimatol Palaeoecol 201(3–4):199–209

Baumiller TK, Gahn FJ (2002) Fossil record of parasitism on marine invertebrates with special emphasis on the platyceratid-crinoid interaction. Paleontol Soc Pap 8:195–210

Baumiller TK, Gahn FJ (2018) The nature of the platyceratid–crinoid association as revealed by cross-sectional data from the Carboniferous of Alabama (USA). Swiss J Palaeontol 137(2):177–187

Baumiller TK, Gahn FJ, Savill J (2004) New data and interpretations of the crinoid-platyceratid interaction. In: Heinzeller J, Nebelsick JH (eds) Echinoderms: München. Taylor and Francis, London.

Biesmeijer JC, Roberts SPM, Reemer M, Ohlemuller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J, Kunin WE (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313(5785):351–354. https://doi.org/10.1126/science.1127863

Boast AP, Weyrich LS, Wood JR, Metcalf JL, Knight R, Cooper A (2018) Coprolites reveal ecological interactions lost with the extinction of New Zealand birds. Proc Natl Acad Sci U S A 115:1546–1551

Boots M (2011) The evolution of resistance to a parasite is determined by resources. Am Nat 178(2):214–220

Boots M, Sasaki A (2002) Parasite-driven extinction in spatially explicit host-parasite systems. Am Nat 159(6):706–713

Brockhurst MA, Chapman T, King KC, Mank JE, Paterson S, Hurst GD (2014) Running with the Red Queen: the role of biotic conflicts in evolution. Proc R Soc Lond B Biol Sci 281(1797):20141382

Camacho M, Araújo A, Morrow J, Buikstra J, Reinhard K (2018) Recovering parasites from mummies and coprolites: an epidemiological approach. Parasit Vectors 11(1):248

Carlson CJ, Burgio KR, Dougherty ER, Phillips AJ, Bueno VM, Clements CF, Castaldo G, Dallas TA, Cizauskas CA, Cumming GS (2017) Parasite biodiversity faces extinction and redistribution in a changing climate. Sci Adv 3(9):e1602422

Carlson, C. J., Hopkins, S., Bell, K. C., Doña, J., Godfrey, S. S., Kwak, M. L., ... & Wood, C. L. (2020). A global parasite conservation plan. Biological Conservation, 250, 108596.

Chin K (2021) Gastrointestinal parasites of ancient nonhuman vertebrates: evidence from coprolites and other materials. In: De Baets K, Huntley JW (eds) The evolution and fossil record of parasitism: coevolution and paleoparasitological techniques. Topics in Geobiology 50. Springer

Civitello DJ, Cohen J, Fatima H, Halstead NT, Liriano J, McMahon TA, Ortega CN, Sauer EL, Sehgal T, Young S (2015) Biodiversity inhibits parasites: broad evidence for the dilution effect. Proc Natl Acad Sci 112(28):8667–8671

Combes C, Moné H (1987) Possible mechanisms of the decoy effect in Schistosoma mansoni transmission. Int J Parasitol 17(4):971–975

Costello MJ, May RM, Stork NE (2013) Can we name Earth's species before they go extinct? science 339 (6118):413-416

Cunningham AA, Daszak P (1998) Extinction of a species of land snail due to infection with a microsporidian parasite. Conserv Biol 12(5):1139–1141

De Baets K, Huntley JW, Klompmaker AA, Schiffbauer JD, Muscente AD (2021a) The fossil record of parasitism: Its extent and taphonomic constraints. In: De Baets K, Huntley JW (eds) The evolution and fossil record of parasitism: Coevolution and paleoparasitological techniques. Topics in Geobiology 50

De Baets, K., Huntley, J. W., Scarponi, D., Klompmaker, A. A., & Skawina, A. (2021b). Phanerozoic parasitism and marine metazoan diversity: dilution versus amplification. Philosophical Transactions of the Royal Society B, 376(1837), 20200366.

De Baets K, Littlewood DTJ (2015) The importance of fossils in understanding the evolution of parasites and their vectors. Adv Parasitol 90:1–51

De Baets K, Keupp H, Klug C (2015) Parasites of ammonoids. In: Klug C, Korn D, De Baets K, Kruta I, Mapes RH (eds) Ammonoid Paleobiology: From anatomy to paleoecology, Topics in Geobiology 43. Springer, Dordrecht, pp 837–875

De Castro F, Bolker B (2005) Mechanisms of disease-induced extinction. Ecol Lett 8(1):117–126

De Vienne DM, Refrégier G, López Villavicencio M, Tellier A, Hood ME, Giraud T (2013) Cospeciation vs. host shift speciation: methods for testing, evidence from natural associations and relation to coevolution. New Phytol 198(2):347–385

Decaestecker E, Gaba S, Raeymaekers JA, Stoks R, Van Kerckhoven L, Ebert D, De Meester L (2007) Host–parasite 'Red Queen' dynamics archived in pond sediment. Nature 450(7171):870

Dentzien-Dias PC, Poinar G, de Figueiredo AEQ, Pacheco ACL, Horn BLD, Schultz CL (2013) Tapeworm eggs in a 270 million-year-old shark coprolite. PLoS One 8(1):e55007. https://doi.org/10.1371/journal.pone.0055007

Dittmar K, Araújo A, Reinhard KJ (2012). The study of parasites through time: archaeoparasitology and paleoparasitology. In: A companion to paleopathology. Oxford, UK. Blackwell Publishing Co, pp 170–190

Dougherty ER, Carlson CJ, Bueno VM, Burgio KR, Cizauskas CA, Clements CF, Seidel DP, Harris NC (2016) Paradigms for parasite conservation. Conserv Biol 30(4):724–733. https://doi.org/10.1111/cobi.12634

Dunlop JA (2021) Chelicerates as parasites. In: De Baets K, Huntley JW (eds) The evolution and fossil record of parasitism. Topics in geobiology 49. Springer, Cham. https://doi.org/10.1007/978-3-030-42484-8_9

Dunlop JA, Wirth S, Penney D, McNeil A, Bradley RS, Withers PJ, Preziosi RF (2011) A minute fossil phoretic mite recovered by phase-contrast X-ray computed tomography. Biol Lett 8(3):457–460

Dunlop JA, Apanaskevich DA, Lehmann J, Hoffmann R, Fusseis F, Ehlke M, Zachow S, Xiao X (2016) Microtomography of the Baltic amber tick Ixodes succineus reveals affinities with the modern Asian disease vector Ixodes ovatus. BMC Evol Biol 16(1):203

Dunn RR, Harris NC, Colwell RK, Koh LP, Sodhi NS (2009) The sixth mass coextinction: are most endangered species parasites and mutualists? Proc R Soc Lond B Biol Sci 276(1670):3037–3045

Emiliani C (1993) Extinction and viruses. Biosystems 31(2–3):155–159

Farrell MJ, Stephens PR, Berrang-Ford L, Gittleman JL, Davies TJ (2015) The path to host extinction can lead to loss of generalist parasites. J Anim Ecol 84(4):978–984

Gahn FJ, Baumiller TK (2003) Infestation of Middle Devonian (Givetian) camerate crinoids by platyceratid gastropods and its implications for the nature of their biotic interaction. Lethaia 36(2):71–82

Greenwalt D (2021) The fossil record of blood and its constituents. Topics in geobiology 50. Springer, Cham. https://doi.org/10.1007/978-3-030-52233-9_12

Hall SR, Becker CR, Simonis JL, Duffy MA, Tessier AJ, Cáceres CE (2009) Friendly competition: evidence for a dilution effect among competitors in a planktonic host–parasite system. Ecology 90(3):791–801

Hall AR, Scanlan PD, Morgan AD, Buckling A (2011) Host–parasite coevolutionary arms races give way to fluctuating selection. Ecol Lett 14(7):635–642

Halliday FW, Rohr JR, Laine AL (2020) Biodiversity loss underlies the dilution effect of biodiversity. Ecology letters 23(11):1611–1622

Hengsbach R (1990). Die Paläoparasitologie, eine Arbeitsrichtung der Paläobiologie. Senckenbergiana lethaea 70:439–461

Harmon A, Littlewood DTJ, Wood CL (2019) Parasites lost: using natural history collections to track disease change across deep time. Front Ecol Environ 17(3):157–166

Hayward A (2017) Origin of the retroviruses: when, where, and how? Curr Opin Virol 25:23–27

Herre EA (1993) Population structure and the evolution of virulence in nematode parasites of fig wasps. Science 259(5100):1442–1445

Holmes EC (2011) The evolution of endogenous viral elements. Cell Host Microbe 10(4):368–377

Hopkins SR (2013) The dilution effect debates. Parasite ecology blog. https://parasiteecology.wordpress.com/

Hudson PJ, Dobson AP, Lafferty KD (2006) Is a healthy ecosystem one that is rich in parasites? Trends Ecol Evol 21(7):381–385

Huntley JW, De Baets K (2015) Trace fossil evidence of trematode—bivalve parasite—host interactions in deep time. Adv Parasitol 90:201–231. Academic Press

Huntley JW, Scarponi D (2012). Evolutionary and ecological implications of trematode parasitism of modern and fossil northern Adriatic bivalves. Paleobiology 38(1):40–51

Huntley JW, Kowalewski M (2007) Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. Proc Natl Acad Sci 104(38):15,006–15,010

Huntley JW, Fürsich FT, Alberti M, Hethke M, Liu C (2014) A complete Holocene record of trematode–bivalve infection and implications for the response of parasitism to climate change. Proc Natl Acad Sci 111(51):18,150–18,155

Huntley JW, De Baets K, Scarponi D, Linehan LC, Epa YR, Jacobs GS, Todd JA (2021) Bivalve mollusks as hosts in the fossil record. In: De Baets K, Huntley JW (eds) The evolution and fossil record of parasitism: coevolution and paleoparasitological techniques. Topics in Geobiology 50. Springer

Hutchinson GE (1961) The paradox of the plankton. Am Nat 95(882):137–145

Johnson PT, Chase JM (2004) Parasites in the food web: linking amphibian malformations and aquatic eutrophication. Ecol Lett 7(7):521–526

Johnson P, Thieltges D (2010) Diversity, decoys and the dilution effect: how ecological communities affect disease risk. J Exp Biol 213(6):961–970

Johnson PT, Hartson RB, Larson DJ, Sutherland DR (2008) Diversity and disease: community structure drives parasite transmission and host fitness. Ecol Lett 11(10):1017–1026

Johnson PT, Kellermanns E, Bowerman J (2011) Critical windows of disease risk: amphibian pathology driven by developmental changes in host resistance and tolerance. Funct Ecol 25(3):726–734

Johnson PT, Preston DL, Hoverman JT, LaFonte BE (2013) Host and parasite diversity jointly control disease risk in complex communities. Proc Natl Acad Sci U S A 110:16,916–16,921

Jokela J, Dybdahl MF, Lively CM (2009) The maintenance of sex, clonal dynamics, and host-parasite coevolution in a mixed population of sexual and asexual snails. Am Nat 174(S1):S43–S53

Katzourakis A, Gifford RJ (2010) Endogenous viral elements in animal genomes. PLoS Genet 6(11):e1001191

Kearns CA, Inouye DS (1997) Pollinators, flowering plants, and conservation biology—much remains to be learned about pollinators and plants. Bioscience 47(5):297–307. https://doi.org/10.2307/1313191

Keesing F, Holt RD, Ostfeld RS (2006) Effects of species diversity on disease risk. Ecol Lett 9(4):485–498

Keesing F, Belden LK, Daszak P, Dobson A, Harvell CD, Holt RD, Hudson P, Jolles A, Jones KE, Mitchell CE (2010) Impacts of biodiversity on the emergence and transmission of infectious diseases. Nature 468(7324):647

Klompen J, Black WC, Keirans J, Oliver J Jr (1996) Evolution of ticks. Annu Rev Entomol 41(1):141–161

Klompmaker AA, Artal P, van Bakel BW, Fraaije RH, Jagt JW (2014) Parasites in the fossil record: a Cretaceous fauna with isopod-infested decapod crustaceans, infestation patterns through time, and a new ichnotaxon. PLoS One 9(3):e92551

Klompmaker AA, Robins CM, Portell RW, De Angeli A (2021) Crustaceans as hosts of parasites throughout the phanerozoic. In: De Baets K, Huntley JW (eds) The evolution and fossil record of parasitism: coevolution and paleoparasitological techniques. Topics in Geobiology 50. Springer

Koh LP, Dunn RR, Sodhi NS, Colwell RK, Proctor HC, Smith VS (2004) Species coextinctions and the biodiversity crisis. Science 305(5690):1632–1634

Kuris AM, Hechinger RF, Shaw JC, Whitney KL, Aguirre-Macedo L, Boch CA, Dobson AP, Dunham EJ, Fredensborg BL, Huspeni TC (2008) Ecosystem energetic implications of parasite and free-living biomass in three estuaries. Nature 454(7203):515

Labandeira CC, Li L (2021) The history of insect parasitism and the Mid-Mesozoic parasitoid revolution. In: De Baets K., Huntley J.W. (eds) The evolution and fossil record of parasitism. Topics in Geobiology 49. Springer, Cham. https://doi.org/10.1007/978-3-030-42484-8_11

Labandeira CC, Johnson KR, Wilf P (2002) Impact of the terminal cretaceous event on plant–insect associations. Proc Natl Acad Sci 99(4):2061–2066

Lafferty KD (2012) Biodiversity loss decreases parasite diversity: theory and patterns. Philos Trans R Soc Lond B Biol Sci 367(1604):2814–2827

Lafferty KD, Hopkins SR (2018) Unique parasite aDNA in moa coprolites from New Zealand suggests mass parasite extinctions followed human-induced megafauna extinctions. Proc Natl Acad Sci 115(7):1411–1413

Lagrue C, Poulin R (2015) Local diversity reduces infection risk across multiple freshwater host-parasite associations. Freshw Biol 60(11):2445–2454

Leung TL (2017) Fossils of parasites: what can the fossil record tell us about the evolution of parasitism? Biol Rev 92(1):410–430

Leung TLF (2021) Parasites of Fossil Vertebrates: What We Know and What Can We Expect from the Fossil Record? In: De Baets K, Huntley JW (eds) The evolution and fossil record of parasitism: coevolution and paleoparasitological techniques. Topics in Geobiology 49. Springer

Manger WL, Meeks LK, Stephen DA (1999) Pathologic gigantism in Middle carboniferous cephalopods, Southern Midcontinent, United States. In: Oloriz F, Rodriguez-Tovar FJ (eds) Advancing research on living and fossil cephalopods. Springer, Boston, MA. https://doi.org/10.1007/978-1-4615-4837-9_7

Mans BJ, De Klerk D, Pienaar R, Latif AA (2011) Nuttalliella namaqua: a living fossil and closest relative to the ancestral tick lineage: implications for the evolution of blood-feeding in ticks. PLoS One 6(8):e23675

Mans BJ, de Klerk D, Pienaar R, de Castro MH, Latif AA (2012) The mitochondrial genomes of Nuttalliella namaqua (Ixodoidea: Nuttalliellidae) and Argas africolumbae (Ixodoidae: Argasidae): estimation of divergence dates for the major tick lineages and reconstruction of ancestral blood-feeding characters. PLoS One 7(11):e49461

Mans BJ, De Klerk DG, Pienaar R, Latif AA (2014) The host preferences of Nuttalliella namaqua (Ixodoidea: Nuttalliellidae): a generalist approach to surviving multiple host-switches. Exp Appl Acarol 62(2):233–240

Martínez-Aquino A (2016) Phylogenetic framework for coevolutionary studies: a compass for exploring jungles of tangled trees. Curr Zool 62(4):393–403

McCoy VE, Soriano C, Pegoraro M, Luo T, Boom A, Foxman B, Gabbott SE (2018) Unlocking preservation bias in the amber insect fossil record through experimental decay. PLoS One 13:e0195482

Mehlhorn H (2008) Encyclopedia of parasitology: AM, vol 1. Springer Science & Business Media, New York

Mihalca AD, Gherman CM, Cozma V (2011) Coendangered hard-ticks: threatened or threatening? Parasit Vectors 4(1):71

Mora C, Tittensor DP, Adl S, Simpson AG, Worm B (2011) How many species are there on earth and in the ocean? PLoS Biol 9(8):e1001127

Ostfeld RS, Keesing F (2000) Biodiversity and disease risk: the case of Lyme disease. Conserv Biol 14(3):722–728

Page RD (ed) (2003) Tangled trees: phylogeny, cospeciation, and coevolution. University of Chicago Press, Chicago, IL

Payne JL, Bush AM, Heim NA, Knope ML, McCauley DJ (2016) Ecological selectivity of the emerging mass extinction in the oceans. Science 353(6305):1284–1286

Peñalver E, Arillo A, Delclòs X, Peris D, Grimaldi DA, Anderson SR, Nascimbene PC, Pérez-de la Fuente R (2017) Ticks parasitised feathered dinosaurs as revealed by cretaceous amber assemblages. Nat Commun 8(1):1924

Pizzi R (2009) Veterinarians and taxonomic chauvinism: the dilemma of parasite conservation. J Exot Pet Med 18(4):279–282

Poinar GO (2011a) Vetufebrus ovatus n. gen., n. sp. (Haemospororida: Plasmodiidae) vectored by a streblid bat fly (Diptera: Streblidae) in Dominican amber. Parasit Vectors 4(1):229

Poinar GO (2011b) The evolutionary history of nematodes: as revealed in stone, amber and mummies. Brill, Nematology Monographs and Perspectives, Leiden, The Netherlands

Poinar G (2010) Palaeoecological perspectives in Dominican amber. Ann Soc Entomol France 46(1–2):23–52. Taylor & Francis Group

Poinar G, Voisin C, Voisin JF (2007) Bird eggshell in Dominican amber. Palaeontology 50(6):1381–1383

Poisot T (2015) Chapter 23. When is co-phylogeny evidence of coevolution? In: Morand S, Krasnov BR, Littlewood DTJ (eds) Parasite diversity and diversification: evolutionary ecology meets phylogenetics, vol 420. Cambridge University Press, Cambridge, UK

Poulin R, Morand S (2000) The diversity of parasites. Q Rev Biol 75(3):277–293

Qvarnstrom M, Niedzwiedzki G, Tafforeau P, Zigaite Z, Ahlberg PE (2017) Synchrotron phase-contrast microtomography of coprolites generates novel palaeobiological data. Sci Rep 7:2723. https://doi.org/10.1038/s41598-017-02893-9

Rabajante JF, Tubay JM, Ito H, Uehara T, Kakishima S, Morita S, Yoshimura J, Ebert D (2016) Host-parasite red queen dynamics with phase-locked rare genotypes. Sci Adv 2(3):e1501548

Radolf JD, Samuels DS (2010) Borrelia: molecular biology, host interaction and pathogenesis. Horizon Scientific Press, Norwich, UK

Rafaluk C, Gildenhard M, Mitschke A, Telschow A, Schulenburg H, Joop G (2015) Rapid evolution of virulence leading to host extinction under host-parasite coevolution. BMC Evol Biol 15(1):112

Randolph SE, Dobson A (2012) Pangloss revisited: a critique of the dilution effect and the biodiversity-buffers-disease paradigm. Parasitology 139(7):847–863

Robins CM, Klompmaker AA (2019) Extreme diversity and parasitism of Late Jurassic squat lobsters (Decapoda: Galatheoidea) and the oldest records of porcellanids and galatheids. Zool J Linnean Soc 187(4):1131–1154

Rogers RR, Curry Rogers KA, Bagley BC, Goodin JJ, Hartman JH, Thole JT, Zatoń M (2018) Pushing the record of trematode parasitism of bivalves upstream and back to the cretaceous. Geology 46(5):431–434

Rothschild BM, Martin LD (1993) Paleopathology disease in the fossil record. CRC Press, Boca Raton

Ruiz GM (1991) Consequences of parasitism to marine invertebrates: host evolution? Am Zool 31(6):831–839

Ruiz GM, Lindberg DR (1989) A fossil record for trematodes: extent and potential uses. Lethaia 22(4):431–438

Salkeld DJ, Padgett KA, Jones JH (2013) A meta-analysis suggesting that the relationship between biodiversity and risk of zoonotic pathogen transmission is idiosyncratic. Ecol Lett 16(5):679–686

Scarponi D, Azzarone M, Kowalewski M, Huntley JW (2017) Surges in trematode prevalence linked to centennial-scale flooding events in the Adriatic. Sci Rep 7(1):5732

Seilacher A, Reif WE, Wenk P (2007) The parasite connection in ecosystems and macroevolution. Naturwissenschaften 94(3):155–169

Smith VH (2007) Microbial diversity-productivity relationships in aquatic ecosystems. FEMS Microbiol Ecol 62(2):181–186. https://doi.org/10.1111/j.1574-6941.2007.00381.x

Solórzano-Kraemer MM, Delclòs X, Clapham ME, Arillo A, Peris D, Jäger P, Stebner F, Peñalver E (2018) Arthropods in modern resins reveal if amber accurately recorded forest arthropod communities. Proceedings of the National Academy of Sciences 115:6739–6744

Stork NE, Lyal CH (1993) Extinction or 'co-extinction' rates? Nature 366(6453):307

Strauss AT, Hite JL, Shocket MS, Cáceres CE, Duffy MA, Hall SR (2017) Rapid evolution rescues hosts from competition and disease but—despite a dilution effect—increases the density of infected hosts. Proc R Soc B 284:20171970

Strona G (2015) Past, present and future of host–parasite co-extinctions. Int J Parasitol Parasites Wildl 4(3):431–441

Strona G, Galli P, Fattorini S (2013) Fish parasites resolve the paradox of missing coextinctions. Nat Commun 4:1718

Su M, Yang Y, Hui C (2020) How intraguild predation affects the host diversity-disease relationship in a multihost community. Journal of theoretical biology 490:110174

Suh A (2021) Horizontal transfer of transposons as genomic fossils of host-parasite interactions. In: De Baets K, Huntley JW (eds) The evolution and fossil record of parasitism: coevolution and paleoparasitological techniques. Topics in Geobiology 50. Springer

Suh A, Witt CC, Menger J, Sadanandan KR, Podsiadlowski L, Gerth M, Weigert A, McGuire JA, Mudge J, Edwards SV (2016) Ancient horizontal transfers of retrotransposons between birds and ancestors of human pathogenic nematodes. Nat Commun 7:11396

Syverson VJ, Brett CE, Gahn FJ, Baumiller TK (2018) Spinosity, regeneration, and targeting among Paleozoic crinoids and their predators. Paleobiology 44:290–305

Thingstad T, Lignell R (1997) Theoretical models for the control of bacterial growth rate, abundance, diversity and carbon demand. Aquat Microb Ecol 13(1):19–27

Traill LW, Lim ML, Sodhi NS, Bradshaw CJ (2010) Mechanisms driving change: altered species interactions and ecosystem function through global warming. J Anim Ecol 79(5):937–947

Turko P, Tellenbach C, Keller E, Tardent N, Keller B, Spaak P, Wolinska J (2018) Parasites driving host diversity: incidence of disease correlated with Daphnia clonal turnover. Evolution 72(3):619–629

Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. Ecol Lett 11(12):1351–1363

Urbanek A (1993) Biotic crises in the history of upper Silurian graptoloids: a palaeobiological model. Hist Biol 7(1):29–50

Våge S, Storesund JE, Thingstad TF (2013) Adding a cost of resistance description extends the ability of virus–host model to explain observed patterns in structure and function of pelagic microbial communities. Environ Microbiol 15(6):1842–1852

Våge S, Bratbak G, Egge J, Heldal M, Larsen A, Norland S, Paulsen ML, Pree B, Sandaa RA, Skjoldal EF, Tsagaraki TM, Ovreas L, Thingstad TF (2018) Simple models combining competition, defence and resource availability have broad implications in pelagic microbial food webs. Ecol Lett 21(9):1440–1452. https://doi.org/10.1111/ele.13122

Vermeij GJ (2004) Ecological avalanches and the two kinds of extinction. Evol Ecol Res 6(3):315–337

Vredenburg VT, Knapp RA, Tunstall TS, Briggs CJ (2010) Dynamics of an emerging disease drive large-scale amphibian population extinctions. P Natl Acad Sci U S A 107(21):9689–9694. https://doi.org/10.1073/pnas.0914111107

Wake DB, Vredenburg VT (2008) Are we in the midst of the sixth mass extinction? A view from the world of amphibians. Proc Natl Acad Sci 105:11466

Warnock RCM, Engelstädter J (2021) The Molecular Clock as a Tool for Understanding Host-Parasite Evolution. In: De Baets K, Huntley JW (eds) The Evolution and Fossil Record of Parasitism: Coevolution and Paleoparasitological Techniques. Topics in Geobiology 50. Springer

Weinstein SB, Kuris AM (2016) Independent origins of parasitism in Animalia. Biol Lett 12(7):20160324

Wolinska J, Spaak P (2009) The cost of being common: evidence from natural Daphnia populations. Evolution 63(7):1893–1901

Wood CL, Lafferty KD (2013) Biodiversity and disease: a synthesis of ecological perspectives on Lyme disease transmission. Trends Ecol Evol 28(4):239–247

Wood JR, Wilmshurst JM (2016) A protocol for subsampling Late Quaternary coprolites for multi-proxy analysis. Quat Sci Rev 138:1–5

Wood JR, Wilmshurst JM, Rawlence NJ, Bonner KI, Worthy TH, et al. (2013) A megafauna's microfauna: gastrointestinal parasites of New Zealand's extinct moa (Aves: Dinornithiformes). (Aves: Dinornithiformes). PLoS ONE 8(2):e57315. https://doi.org/10.1371/journal.pone.0057315

Wood JR, Perry GL, Wilmshurst JM (2017) Using palaeoecology to determine baseline ecological requirements and interaction networks for de-extinction candidate species. Funct Ecol 31(5):1012–1020

Woolhouse ME, Haydon DT, Antia R (2005) Emerging pathogens: the epidemiology and evolution of species jumps. Trends Ecol Evol 20(5):238–244

Young H, Griffin RH, Wood CL, Nunn CL (2013) Does habitat disturbance increase infectious disease risk for primates? Ecol Lett 16(5):656–663

Zhang Z, Strotz LC, Topper TP, Chen F, Chen Y, Liang Y, Zhang Z, Skovsted CV, Brock GA (2020) An encrusting kleptoparasite-host interaction from the early Cambrian. Nat Commun 11:2625. https://doi.org/10.1038/s41467-020-16332-3