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Invited Review

The rise of ecological parasitology: twelve landmark advances that changed its history

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ABSTRACT

In the five decades since the first publication of the International Journal for Parasitology, ecological parasitology has grown from modest beginnings to become a modern discipline with a strong theoretical foundation, a diverse toolkit, and a multidisciplinary approach. In this review, I highlight 12 advances in the field that have spurred its growth over the past 50 years. Where relevant, I identify pivotal contributions that have altered the course of research, as well as the influence of developments in other fields such as mainstream ecology and molecular biology. The 12 key advances discussed are in areas including parasite population dynamics and community assembly, the regulation of host population abundance and food web structure, parasites as agents of natural selection, the impacts of biodiversity and anthropogenic changes on host-parasite interactions, the biogeography of parasite diversity, and the evolutionary genetics of parasites. I conclude by identifying some challenges and opportunities lying ahead, which need to be met for the future growth of ecological research on host-parasite interactions.

1. Introduction

Toward the end of the 1960s and the beginning of the 1970s, ecology entered a period of rapid growth. A combination of classical field experiments and theoretical models established a general framework to explain spatial and temporal variation in the structure, diversity and stability of natural ecosystems (Paine, 1966; MacArthur and Wilson, 1967; MacArthur, 1972; May, 1973). This formed the platform for a boom in ecological research that has continued to the present. For much of the past five decades, this research in 'mainstream' ecology has focused almost entirely on free-living organisms, that is, plants, animals, and more recently microbes. The ecological study of parasitic organisms has developed somewhat independently, with its theoretical framework built upon the particular biology of parasites, although often borrowing concepts from mainstream ecology.

Where was 'parasite ecology' going in the 1970s? Here, I define parasite ecology (or ecological parasitology) as the study of intra- and interspecific interactions and environmental influences that determine the behaviour, abundance, spatial distribution and diversity of parasites (parasite-centric perspective), as well as the effects of parasites on the behaviour, abundance, spatial distribution and diversity of hosts (host-centric perspective). It would be fair to say that it consisted still mostly of old-school 'natural history'. Its practitioners occupied themselves mainly with descriptive surveys of the parasite fauna in wildlife hosts, the discovery and description of new parasite species, and the elucidation of their life cycles. Parasite ecology lacked any real theoretical foundation. Some rules had been proposed to explain patterns of host-parasite associations, i.e., why a particular parasite species infected a particular host species and not others (Fahrenholz's rule, Manter's rule; see Brooks and McLennan, 1993), but these had not been subjected to robust empirical testing. Dogiel (1961, 1964; English translations of work published many years earlier in Russian) was the first to attempt to rationalise patterns in parasite occurrence and abundance as a function of environmental factors and biological characteristics of their host. His work marked the birth of the new discipline of ecological parasitology, but the field did not progress much further until several years later. The 1960s also saw the refinement of experimental methods, including the development of laboratory infection protocols and suitable culture media, that would allow the establishment of key model species for parasitological research. These included the cestodes *Hymenolepis diminuta* (Read and Voge, 1954) and *Schistocephalus solidus* (Smyth, 1946), the digenean *Echinostoma revolutum* (Fried et al., 1968), and the nematode *Heligmosomoides polygyrus* (formerly *Nematospiroides dubius*) (Dobson, 1961). The availability of these and other laboratory models would later pave the way for important experimental studies in parasite ecology.

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From this starting point, parasite ecology has developed rapidly over the last 50 years, from a mostly descriptive science grounded in natural history and influenced by biomedical research, to a rigorous and quantitative discipline driven by hypothesis testing and drawing on mainstream ecological theory. In spite of Price's (1980) influential and thought-provoking monograph which expanded the definition of parasites to include herbivorous insects and other organisms traditionally studied by ecologists, ecological parasitology has continued to progress in parallel with, rather than as a part of, mainstream ecology. Here, I review 12 advances in the field that have fuelled its growth over the past five decades, from the time when the first issue of the International Journal of Parasitology was published to the present. As much as possible, I attempt to place them within the broader temporal context of developments in mainstream ecology and evolutionary biology (Fig. 1). Each major advance has either been triggered by one or a few related seminal, game-changing contributions, or progressed more continuously in a stepwise manner. Instead of a comprehensive review of the literature, I focus on the pivotal articles or research trends, using only a few selected case studies as examples and instead referring readers to key syntheses. The order in which the 12 advances are presented does not reflect their relative importance, but is instead an attempt to sort them out by scale (from individuals to populations to communities, from parasite ecology to host-parasite ecology) as well as by approximate chronology. Since ecology defines the setting for evolution, and evolution in turn shapes the ecology of organisms, I also touch on aspects of parasite evolutionary biology that pertain to their ecology. No one can do justice, in such a short article, to the rich history of parasite ecology and to the many scientists who contributed to its growth.

GENERAL BIOLOGY AND ECOLOGY	ECOLOGICAL PARASITOLOGY
	1971 – First issue of *International Journal for Parasitology*
	1971 – Crofton identifies aggregation as a key parasite population feature
Publication of *Geographical Ecology*, by MacArthur – 1972	1972 – Holmes and Bethel establish host manipulation by parasites
Tinbergen, von Frisch and Lorenz share Nobel Prize as pioneers of animal behaviour research – 1973	
Publication of *Ecology and Evolution of Communities*, by Cody and Diamond – 1975	
	1977 – Brooks conducts the first host-parasite cophylogenetic study
	1978/79 – Anderson and May's host-parasite population models
	1980 – Publication of *Evolutionary Biology of Parasites*, by Price
Publication of *The Extended Phenotype*, by Dawkins – 1982	1982 – Hamilton and Zuk hypothesis of parasite-mediated sexual selection
Invention of the polymerase chain reaction, by Mullis – 1983	1982/83 – Anderson, May and Ewald redefine the evolution of virulence
Publication of *Ecological Communities*, by Strong et al. – 1984	
First commercial use of Sanger DNA sequencing – 1986	1986 – Holmes and Price rationalise parasite community ecology
	1988 – Hafner and Nadler conduct the first molecular cophylogenetic study
Publication of *Macroecology*, by Brown – 1995	1995 – First integration of parasites in a food web analysis
Enemy Release Hypothesis proposed for invasive plants – 1997	
Critical look at general laws in ecology, by Lawton – 1999	1998 – Publication of *Evolutionary Ecology of Parasites*, 1st edition, by Poulin
Publication of *Phylogeography*, by Avise – 2000	2000 – Ostfeld and Keesing propose the 'diversity dilutes disease' hypothesis
	2001/02 – First serious warnings that climate change will affect host-parasite interactions
	2002 – Publication of the first genome of a parasite, *Plasmodium falciparum*
Completion of the Human Genome Project – 2003	
Brown proposes the metabolic theory of ecology – 2004	2004 – Publication of the first genome of a helminth parasite, *Brugia malayi*
First commercial use of massively parallel (or next-generation) DNA sequencing – 2005	2005 – First use of network analysis to study host-parasite interactions
	2005 – NHM's Host-Parasite Database is made publicly available online
	2008 – Kuris et al. quantify parasite biomass at ecosystem level
	2015– Campbell, Ōmura and Tu share Nobel Prize for their discovery of anti-parasite drugs
	2017 – Launch of the Parasite Microbiome Project

Fig. 1. Timeline (vertical arrow of time), from 1970 (top) to present (bottom), with some key milestones in general biology and ecology on the left, and some key milestones in ecological parasitology on the right. These lists are not meant to be exhaustive.

Therefore, not every reader will agree that the key advances summarised here were the 12 most important of the past five decades in the field of parasite ecology, but hopefully most readers would come up with a list that shares many of the ones presented here.

2. Parasites as host manipulators

The realisation that parasites, far from being simple and morphologically degenerate creatures, were in fact wonderfully well adapted to the particular challenges they encountered, took quite some time. No other parasite adaptation has captivated scientists in other spheres of biology, as well as the public at large, as much as the ability of parasites to alter the behaviour or appearance of their hosts in ways that enhance their probability of transmission and the completion of their life cycle. There had been earlier anecdotal reports that infected prey looked and behaved differently from uninfected ones, and might be more susceptible to predation by their parasite's definitive host (e.g., Zeller, 1874; van Dobben, 1952). However, it was Holmes and Bethel (1972) who first formalised the notion that this phenomenon was the product of natural selection, and likely to have evolved in a range of parasite taxa facing similar transmission challenges. Their landmark paper spawned an entire research enterprise lasting to this day, resulting in hundreds of studies and the identification of hundreds of host-parasite associations in which manipulation of host behaviour by the parasite can be seen (Moore, 2002; Poulin, 2010; Poulin and Maure, 2015). The most active area of research nowadays focuses on the molecular mechanisms through which parasites manipulate host behaviour, with the black box slowly yielding its secrets to researchers (see Herbison, 2017).

The wide recognition that parasites alter host behaviour for their own benefit has had huge ramifications across multiple disciplines within biology. In ecology, a large body of literature has explored how parasite-manipulated hosts can alter predator–prey interactions and the flow of energy through ecosystems (e.g., Sato et al., 2008), and even the structure and diversity of entire communities (Lefèvre et al., 2009). In evolutionary biology, host manipulation by parasites was used as a key supporting example by Dawkins (1982) in his influential book on the extended phenotype, i.e., the idea that genes in one organism can have phenotypic effects in a different organism. Even in psychology, classical studies on how the parasite *Toxoplasma gondii* alters the risk-taking behaviour of its rodent intermediate host (Berdoy et al., 2000) have sparked huge interest into how it may affect human behaviour and personality (e.g., Flegr, 2013; Johnson et al., 2018), given its high prevalence in many human populations. The host manipulation concept is therefore one of the most, if not the most, influential ideas in parasitology, whose impact has gone well beyond ecological parasitology, its subdiscipline of origin.

3. The dawn of parasite population ecology

It took some time for parasitologists to start thinking like ecologists, and recognise that the number of parasites in an individual host represents not only a parasite load with pathological consequences (host-centric view), but also a subset of a larger parasite population patchily distributed among suitable host habitats (parasite-centric view). Parasite population biology had its true beginning with Crofton's (1971) influential paper demonstrating that metazoan parasites of all kinds are almost universally overdispersed in their hosts' population. In other words, a few host individuals harbour large numbers of parasites, whereas most hosts harbour few or none. From the parasites' perspective, this means that the parasite population is mostly aggregated in only a subset of available hosts. This distributional pattern has since been confirmed by empirical data compiled from hundreds of natural host-parasite systems (Shaw and Dobson, 1995; Poulin, 2013) and has been identified as the only universal law of parasite ecology (Poulin, 2007). Combined with the earlier observation that the 'crowding' of many parasite individuals within the same host decreases their average survival, growth and/or fecundity (Read, 1951), aggregation hinted at an important role for density dependence in regulating parasite populations, an idea that was later validated (Keymer, 1982; Shostak and Scott, 1993; Churcher et al., 2005).

Building on Crofton's (1971) work, the real pivotal moment in the history of parasite population biology came in the form of mathematical models developed by Roy Anderson and Robert May (Anderson and May, 1978; Anderson and May, 1979; May and Anderson, 1978; May and Anderson, 1979). Their modelling framework was soon validated empirically (e.g., Scott and Anderson, 1984) and thereafter became an essential tool to integrate the processes driving parasite population dynamics. They established host population density (i.e., the availability of susceptible hosts) as a key parameter determining transmission rates and therefore temporal variation in parasite population size, and predicted that for each parasite species there exists a threshold host density below which the parasite population goes extinct. The Anderson and May models heralded the use of the parasite's basic reproductive number, or R_0, in ecological parasitology, which for metazoan parasites represents the average lifetime number of offspring produced per adult individual that will themselves survive to reproduce. This fundamental parameter is now the standard benchmark used in parasitology and epidemiology to forecast the spread of an infection through a host population.

In parallel with the growth of the theoretical foundation of parasite population biology, several pioneering field studies, including some long-term studies, linked the temporal dynamics of parasite populations with local environmental factors and seasonal host abundance cycles (e.g., Kennedy, 1975; Aho and Kennedy, 1984; Lemly and Esch, 1984; Riggs and Esch, 1987; see review in Marcogliese and Goater, 2016). Data on natural parasite populations could be analysed at different hierarchical levels; one could focus on the average size of parasite populations within individual hosts, on the size of the parasite population across all individual hosts of a given species, or (in the case of generalist parasites) across all host species in the local community. To make sense of this complexity and avoid confusion, Margolis et al. (1982) formalised the terminology of ecological parasitology still used today, to distinguish between different parameters and levels of organisation. Thus, terms such as infrapopulation and suprapopulation became part of the ecological parasitologist's vocabulary. The distinction between levels of organisation allowed the identification of distinct factors regulating parasite populations at different levels. In the end, the combination of Anderson and May's modelling work and those early empirical field studies provided the basis for our modern understanding of how parasite populations rise and fall.

4. Parasite communities as model systems

Within mainstream ecology, community ecology aims to describe and understand the spatio-temporal structure and dynamics of natural communities of plants and animals. In its early years, progress in community ecology was catalysed by a debate regarding the role of assembly rules in shaping communities and how to test them against null hypotheses (Cody and Diamond, 1975; Strong et al., 1984). Later, after being criticised by prominent ecologist John Lawton (1999) for being a messy discipline where contingency ruled and generalisations were hard to find, the field matured rapidly and is now guided by unifying theoretical frameworks (Vellend, 2016; Leibold and Chase, 2018).

Parasite community ecology has developed in parallel, mostly ignored by mainstream ecologists. In the 1970s, the focus of parasitologists shifted from purely single-species studies to whole parasite communities, i.e., assemblages of all parasite species exploiting a host individual or host population. Holmes (1973), Holmes and Price (1986) and Rohde (1979) deserve credit for building the first conceptual framework allowing some order to emerge from the findings that had accumulated since Holmes (1961) demonstrated experimentally that co-infecting parasite species can compete for resources. They proposed a continuum of parasite communities ranging from species-rich communities structured by interactions among parasites within the host (interactive communities), to species-poor communities with little interaction, empty niches and subject to stochastic processes (isolationist communities). As with parasite populations, parasite communities can be studied at various hierarchical scales: they may be defined as all parasites within an individual host, within a host population, or within a host community. This Russian doll arrangement of parasite communities provides replicate units of study at the lowest scales; this makes them ideal model systems for tests of scale-dependent drivers of community structure (e.g., Bolnick et al., 2020). To establish a common ground for the growing number of results and hypotheses, a new terminology was proposed and adopted, giving us terms such as infracommunity (all parasites in an individual host) and component community (all parasites in a host population) (Bush et al., 1997). Because scientific disciplines are often ensconced in their particular jargon, Bush et al.'s (1997) paper and the earlier one by Margolis et al. (1982) served to give ecological parasitology its own identity, distinct from mainstream ecology. In recent years, a range of other terms (e.g., co-infections, polyparasitism, etc.) have also been used to refer to the simultaneous infection of a host by more than one parasite species, however the terminology proposed by Bush et al. (1997) remains the standard one.

The interactive-isolationist classification paved the way for important empirical studies at all hierarchical levels (e.g., Bush and Holmes, 1986; Esch et al., 1990) and held sway over the field for many years. From the 1990s to the present, under the influence of ideas from mainstream ecology, the emphasis has shifted toward rigorous testing of patterns in parasite community structure. In particular, a central question has been whether the parasite species harboured by a host individual (infracommunity) represent a non-random or predictable subset of the pool of parasite species present locally (component community). This has been explored with a range of approaches involving comparisons of the observed composition of parasite infracommunities with that predicted by randomizations based on null models. These comparisons have been used to test patterns expected from processes ranging from nested community assembly (Guégan and Hugheny, 1994; Rohde et al., 1998) to deterministic succession (Espinola-Novelo et al., 2020).

Three other approaches have also contributed to advances in parasite community ecology in the past 20 years. First, extensive field datasets combined with modelling have revealed complex patterns of positive or negative associations among co-infecting parasites as varied as viruses, bacteria and helminths, suggesting previously unsuspected pathways of interaction (e.g., Jolles et al., 2008; Telfer et al., 2010; Johnson et al., 2015a; Johnson et al., 2015b). Secondly, the recently renewed interest in the use of experimental infections to identify the proximate mechanisms, such as interspecific competition or priority effects, responsible for structuring infracommunities (e.g., Benesh and Kalbe, 2016; Budischak et al., 2016) has strengthened inferences derived from studies on natural parasite communities. Finally, at a higher hierarchical level, considering all parasite species and all host species in the same habitat (parasite supracommunity), network analysis has proven a powerful tool to investigate the structure of complex multi-species webs of host-parasite associations. First applied to parasites and their hosts in the mid-2000s, network analysis has rapidly become the approach of choice to unravel their associations and shed light on underlying processes (Runghen et al., 2021).

In parallel with these more fundamental advances in parasite community ecology, the growing understanding of the intrinsic and external forces shaping parasite communities has empowered their use in applied ecology as well. For example, differences in parasite community composition between host samples collected at different points in time or space have been widely used in the past few decades to track animal migrations (e.g., Alarcos and Timi, 2013; Sheehan et al., 2016), discriminate between fishing stocks (MacKenzie, 1987; Lester and MacKenzie, 2009) or measure the success of protected conservation areas (e.g., Braicovich et al., 2021).

5. Parasites as drivers of host population, community and food web dynamics

Because they are small and mostly invisible, parasites were long ignored by ecologists as a potential force modulating the abundance of animals in nature, and by extension the structure and functioning of natural communities and ecosystems. Again, it was the theoretical models of Anderson and May (Anderson, 1978; Anderson and May, 1978; Anderson and May, 1979; May and Anderson, 1978; May and Anderson, 1979) that served as the catalyst that changed how ecologists viewed parasites. Their work showed that, based on realistic parameter values, the presence of a moderately pathogenic parasite in a host population could result in either fluctuations in host abundance over time or, more likely, a reduction in the equilibrium abundance of hosts compared with what they would achieve in the absence of parasites. The role of parasites in host population dynamics was later demonstrated empirically in both free-running laboratory host populations (Keymer, 1981; Scott, 1987) and wild host populations (Scott and Lewis, 1987; Hudson et al., 1998).

The realisation that parasites can regulate host populations marked their arrival into mainstream ecology, where their importance has been increasingly acknowledged in the past two decades. From their impact on host populations, it was only a small step to consider their effects on interactions between different animal species (Hudson and Greenman, 1998), all the way to their effects on entire communities and ecosystems (Thomas et al., 2005). A large body of empirical and theoretical research has revealed the many direct and indirect effects of parasitism on interactions among host species, either through density-mediated or trait-mediated processes (Hatcher and Dunn, 2011; Buck, 2019). More recently, the non-consumptive effects of parasites, manifested by hosts simply altering their behaviour or niche in response to the 'fear' of infection, have also been shown to impact community structure and diversity (Buck et al., 2018; Buck, 2019). The many ramifications of parasitism are now well integrated in community ecology research, and widely accepted by mainstream ecologists.

In parallel with the more classical community ecology research, one of the most holistic approaches to the study of communities is the use of food web analysis, as it encompasses not just the species present in the system, but the trophic interactions among them that reveal the routes of energy flow through the system. On the heels of a pioneering study by Huxham et al. (1995), an appeal to include parasites in food web analyses was made to ecologists (Marcogliese and Cone, 1997). It was eventually followed by a string of field studies that highlighted not only that parasites are involved as consumers or even resources in a high proportion of energy transfer links, but also that they modify the topology of food webs and challenge some of the earlier models proposed to explain patterns in food web structure (Thompson et al., 2005; Lafferty et al., 2006; Dunne et al., 2013). The notion that parasites account for a trivial proportion of the biomass in natural systems was also dismissed, reinforcing their importance for ecosystem productivity and energetics (Kuris et al., 2008). These pioneering studies have paved the way for the acceptance by mainstream ecologists of parasitism as an important regulatory force in nature, with parasite diversity being a sign of ecosystem health (Marcogliese, 2005; Hudson et al., 2006); this recognition was almost unthinkable 30 years ago.

6. Parasites, host sex, and host sexual selection

The realisation that parasites can regulate host populations was also a watershed moment for the acceptance of parasites as agents of natural selection. Parasites were already recognised as driving forces in the evolution of particular host traits, ranging from the immune system to specialised behavioural adaptations such as self-medication, grooming, and cleaning symbioses. However, no one believed they could have played a greater role and shaped the evolution of more fundamental animal features.

All this changed in the span of just a few years, mostly through the work of evolutionary biologist William Hamilton. Firstly, building on an earlier suggestion by Jaenike (1978), Hamilton (1980) demonstrated that parasites were likely to have played a key role in the evolution and maintenance of sex, i.e. sexual as opposed to asexual reproduction, across animals and plants. Sex represented a conundrum for evolutionary biologists (Maynard Smith, 1978). All else being equal, if sexually and asexually reproducing individuals occurred in a population and were allowed to reproduce without constraints, the asexuals would multiply twice as fast as the sexuals and eventually outcompete them into extinction. This two-fold cost of sex is due to the need for males. In sexual systems, about half of all resources spent on reproduction goes toward making males; the latter represent half of the sexual population, but they produce no offspring themselves. Asexual reproduction does not involve such a waste of resources. Therefore, why is sexual reproduction maintained across practically all plant and animal taxa? Hamilton (1980) provided a solution, by proposing that sex allows recombination and the production of genetically heterogeneous offspring, a clear advantage in the coevolutionary arms race against fast-evolving parasites. This explanation applied universally, since all species have parasites of one type or another. Following landmark empirical demonstrations of a link between parasitism and the maintenance of sexual reproduction (e.g. Lively, 1987), the hypothesis gained broad acceptance. It is now integrated within the broader Red Queen hypothesis, which explains how parasites maintain sexual reproduction in their hosts through frequency-dependent selection in any system where parasites are specialised on the most common host genotypes (Clay and Kover, 1996). Hamilton's (1980) original idea is now regarded as a likely solution to the sex conundrum.

Secondly, picking up on an idea put forward by Freeland (1976), Hamilton and Zuk (1982) published a seminal paper proposing parasites as central players in the evolution of mate choice and secondary sexual characteristics such as the peacock's tail. Their hypothesis assumes that females choose to mate with males of the highest genetic quality, and that this quality is reflected in the expression of bright colours, elaborate courtship displays or other secondary sexual traits. The Hamilton–Zuk hypothesis postulates that males with genes for resistance against the most common or virulent parasites will be more likely to be uninfected and develop showier traits, and that females mating with those males can secure good resistance genes for their offspring. Crucially, because parasites evolve rapidly, the most common parasite genotypes change through time, preventing the erosion of genetic variation in the male population and maintaining the benefits of female choice across generations. Since its proposal, the hypothesis has been a major focus of theoretical, comparative and experimental research: the Hamilton and Zuk (1982) paper has been cited thousands of times and has become one of the most influential in behavioural ecology (Balenger and Zuk, 2014). Today, thanks to Hamilton and Zuk (1982), the role of parasites is now well entrenched in sexual selection theory.

7. Virulence and host-parasite coevolution

Reciprocal selection pressures shape the ecological traits of both hosts and their parasites. One of these traits, parasite virulence, is of fundamental importance for both host and parasite population dynamics. Virulence was long thought to inevitably decrease over evolutionary time, with the end point being a relationship in which the parasite imposed very little fitness cost on its host. Once again, theoretical work by Anderson and May (1982), supported by strong arguments from Ewald (1983), played a pivotal role in disproving this one-size-fits-all scenario. They showed that host-parasite coevolution can follow a broad range of trajectories, depending on the interplay between virulence and transmission success, and that virulence can either increase or decrease over time as parasites evolve for their own good, not that of their host. Key experimental studies supported this theoretical prediction shortly afterward using fast evolving pathogens (Bull et al., 1991), laying the foundation for our modern understanding of the evolution of parasite virulence.

More broadly, coevolutionary theory initially developed in mainstream ecology (Thompson, 1994) was applied to host-parasite interactions shortly after this landmark shift in our thinking on parasite virulence. Local adaptation of parasites was first confirmed with simple reciprocal infection experiments, in which parasites were shown to be more successful at infecting sympatric hosts than allopatric hosts of the same species (e.g., Lively, 1989; Ballabeni and Ward, 1993). These studies demonstrated that there is substantial variation within a parasite species among individuals from geographically distinct populations. Local host genotypes as well as local biotic and abiotic conditions impose different selection pressures, leading to parasites of the same species but from different populations displaying differences in host preferences, infectivity, virulence, etc. Parasites were shown to perform disproportionately well against host genotypes that were locally common, with local adaptation resulting from parasites in different geographical localities tracking the most frequent host genotypes in their locality, or the most locally abundant host species in the case of generalist parasites (Morand et al., 1996; Lively and Dybdahl, 2000). Seen from the host's perspective, resistance against parasites, i.e. the ability to prevent infection, was traditionally seen as the main host defence in their coevolutionary arms race with parasites. In the past 10–15 years, our understanding of the host coevolutionary response has broadened to include tolerance, or the ability to limit the fitness impacts of parasites without preventing their infection (Råberg, 2014). Together with the shift in our understanding of virulence evolution stimulated by Anderson and May (1982), this recent research on local adaptation and the resistance-versus-tolerance components of host defence have formed our current conceptual basis for host-parasite coevolution.

8. Parasite transmission among connected hosts

From the early 20th century, epidemiological models have been fundamental tools to understand the spread of parasitic infections through host populations (Hudson et al., 2002). For many directly-transmitted parasitic diseases, SIR models have proven particularly useful. These models assign host individuals to three compartments: susceptible (S) individuals, infectious (I) individuals, and recovered (R) individuals that are now resistant through acquired immunity. As individuals move from one compartment to another, they are assumed to be mostly homogeneous within each category. One of the great advances in ecological parasitology has been the growing recognition that differences in individual host characteristics can matter to parasite transmission.

One of the key moments came with the broad acceptance in the mid-1990s that in most host species, especially in higher vertebrates such as birds and mammals, there were consistent differences in infection risk and infection levels between male and female hosts (Poulin, 1996; Zuk and McKean, 1996; Schalk and Forbes, 1997). Males are very often more severely infected than females, due to their larger size, differences in behaviour, or the immunosuppressive effect of androgenic hormones. Later studies showed that in wild host populations, the small fraction of host individuals, often about 20% of individuals, that harboured most of the parasites tended to be older males (Perkins et al., 2003; Ferrari et al., 2004). This small subset of individuals was not only central to the persistence of the parasite population, but also acted as the source of infection for the rest of the host population. The emphasis was therefore shifting to acknowledge individual-level heterogeneity in basic traits such as sex and age as important determinants of a host's importance in transmission dynamics.

However, the pivotal moment was the inclusion of host behavioural interactions as transmission routes using social network analysis, dating back only about 15 years ago. In these days of the COVID-19 pandemic, we all understand the importance of social interactions for disease transmission (Stockmaier et al., 2021). In gregarious host species, many ectoparasites, several endoparasites, as well as a large number of pathogenic microbes, are transmitted either by physical contact or close proximity between an infected and a susceptible host. The application of social network analysis provides a useful framework to not only disentangle patterns of parasite transmission within groups of hosts, but also identify superspreaders or subsets of individuals more likely to transmit or acquire parasites (see Godfrey, 2013; Grear et al., 2013; White et al., 2017). Social networks capture the ensemble of pairwise interactions among individual hosts in a group, accounting for the frequency, duration, intensity and directionality of interactions. They thus provide a map of possible transmission routes for contagious parasites transmitted directly by physical contact or close proximity. Since its first application to the study of parasite transmission, social network analysis has become the method of choice to explore within-group parasite transmission dynamics.

9. Host-parasite interactions in the anthropocene

Following in the footsteps of mainstream ecology, in the early 2000s research on ecological parasitology began to pay attention to the consequences that global environmental changes arising from anthropogenic impact might have on host-parasite interactions.

Two areas in particular have generated much interest. First, human activities have led to the transport and introduction of multiple plant and animal species to parts of the world where they were previously absent. In some cases, introduced species have flourished and spread to the detriment of native species. The enemy release hypothesis provides an explanation for the success of these invaders. First proposed in the context of invasive plant species (Williamson, 1996; Crawley, 1997), the enemy release hypothesis postulates that introduced species have left their natural enemies, including parasites, back in their area of origin, and are now proliferating in enemy-free space. This hypothesis has sparked much interest among parasite ecologists and formed the basis of multiple studies, which together have produced strong but not universal support for its role in the success of invasive species (Torchin et al., 2003; Roy et al., 2011). The introduction of alien species into novel ecosystems can also alter the transmission dynamics of parasites, both native parasites and alien parasites brought in by the introduced species. Parasite species introduced along with their invasive host may infect native hosts (parasite spillover), sometimes with devastating consequences (Prenter et al., 2004). In parallel, native parasites may infect introduced hosts, and if the latter prove to be suitable, they may amplify local parasite abundance and increase infection risk for native hosts (parasite spillback) (Kelly et al., 2009). The related concepts of enemy release, spillover and spillback have fuelled a large number of studies in ecological parasitology (Poulin, 2017), and proven instrumental in guiding efforts to manage infectious disease risk resulting from biological invasions.

Second, human activities also cause the release into the environment of various chemical compounds that change the abiotic component of our world. After an important call to arms (see Marcogliese, 2001), research on the impact of global climate change on host-parasite ecology has blossomed in the past 20 years, with a particular focus on the potential effect of global warming on the geographic distribution of parasites and their local abundance (Harvell et al., 2002; Lafferty, 2009; Byers, 2020). Research on the interactions between parasitism and other facets of global change has also grown rapidly in the past two decades; these include eutrophication, ocean acidification, and pollution by various toxic chemicals (see Blanar et al., 2009; Vidal-Martinez et al., 2010). The findings from these studies reveal that some parasite taxa may be particularly sensitive to abiotic conditions; their abundance may drop in the early stages of local environmental changes well before the host population shows any signs of being affected. The emerging field of 'environmental parasitology' focuses on the role of parasites as sentinels of environmental change and reliable early-warning indicators of environmental degradation (Vidal-Martinez et al., 2010; MacLeod and Poulin, 2012; Sures et al., 2017). Overall, whether in the context of biological invasions or as potential canaries in the coal mine for environmental change, studies on parasites in the face of anthropogenic impacts have become a major research direction in ecological parasitology.

10. Biodiversity and infection risk

The other human impact on nature that has influenced research in ecological parasitology is the loss of biodiversity occurring at both local and global scales, across all ecosystems on Earth. In addition to co-extinctions of parasites, reductions in local biodiversity may have other impacts on parasite ecology. Lower diversity may affect the dynamics of transmission for particular host-parasite associations. First proposed two decades ago, the dilution hypothesis postulates that high host diversity reduces the risk of parasite acquisition for a focal host species, because a high number of unsuitable hosts provide more dead-end targets for parasites (Ostfeld and Keesing, 2000). The hypothesis was originally formulated to account for infection patterns in tick-borne Lyme disease: a high diversity of small mammals in local communities caused fewer ticks to feed on the mouse species that is the most competent reservoir of Lyme disease, resulting in reduced transmission of the disease to humans. The idea that 'diversity dilutes disease' has been quite influential and has inspired multiple studies in a variety of other host-parasite systems. Recent reviews and meta-analyses of this large body of research have concluded that a negative diversity-disease relationship, while far from universal, does appear across a broad range of ecosystems and host and parasite taxa (Ostfeld and Keesing, 2012; Civitello et al., 2015; Johnson et al., 2015a; Johnson et al., 2015b; Huang et al., 2016). In fact, the dilution effect is much stronger in cases where disturbances cause losses in biodiversity, than among systems spanning a natural gradient of biodiversity (Halliday et al., 2020).

In parallel to testing for dilution effects, parasite ecologists have also made great efforts to explore the various mechanisms through which the presence of multiple non-host species in the local environment can impair parasite transmission and lower the risk of infection for a focal host species. For example, in aquatic habitats, filter-feeding organisms and invertebrate predators feeding on small prey can reduce the densities of parasite infective stages from the surrounding water, thus indirectly protecting these parasites' target hosts from infection (e.g., Welsh et al., 2014). In addition to preying on infective stages, the ambient fauna may include organisms capable of physically or chemically interfering with parasite transmission, or acting as unsuitable decoys in which parasites reach a transmission dead end (Thieltges et al., 2008; Johnson and Thieltges, 2010). The growing research on the mechanisms by which non-host organisms affect transmission success highlights the tight connection between biodiversity and disease risk, and the impact that biodiversity loss can have on host-parasite interactions.

11. The rise of parasite biogeography and biodiversity studies

Beginning with the publication of the theory of island biogeography (MacArthur and Wilson, 1967), mainstream ecologists began to lay the theoretical foundation for large-scale ecology and biogeography. From the outset, research in this area aimed to link observed patterns in the distribution of plant and animal diversity, such as latitudinal diversity gradients or species-area relationships, with the underlying processes generating them (MacArthur, 1972; Brown and Gibson, 1983). Later, the emerging field of macroecology (Brown, 1995) expanded this approach to tackle patterns in the distribution of species properties, such as body size and population density, across taxa or space. More recently, this line of research has culminated in the metabolic theory of ecology (Brown et al., 2004), which posits that the metabolic rate of organisms underpins most large-scale patterns in life history traits, population dynamics, ecosystem productivity, and biodiversity.

Influenced by these developments in mainstream ecology, ecological parasitology first turned its attention toward large-scale patterns in parasite diversity in the 1980s. Following the pioneering study by Price and Clancy (1983), a vast number of studies have sought to explain why certain host species have more parasites than others. Borrowing ideas from biogeography, macroecology and epidemiology, these studies have identified several host properties that generally correlate with parasite species richness across host species, such as host body size, population density, and geographical range size (see Poulin, 2004; Kamiya et al., 2014; Morand, 2015). We now have a much better understanding of the factors that shape the distribution of parasite diversity across host species. Metabolic theory has even been used to predict how much parasite biomass can be supported by a host, and the energy flux between host and parasite (Poulin and George-Nascimento, 2007; Hechinger, 2013).

The study of parasite biogeography has often been applied to the reconstruction of the evolutionary history of their hosts; for instance, the associations of cestodes and nematodes with their avian or mammalian hosts can act as signatures of past events and explain the post-Pleistocene colonisation and geographical distribution of these hosts in the Holarctic (Hoberg, 1992; Nieberding et al., 2004). At the same time, in line with mainstream biogeographical studies that aim to explain the global distribution of biodiversity, parasite ecologists have begun in the last couple of decades to investigate why certain geographical areas harbour richer parasite faunas than others (e.g., Guernier et al., 2004; Stephens et al., 2016). Mapping parasite biodiversity is an essential step to forecast the risk of emerging disease, as well as predicting shifts in geographical hotspots of parasite richness in response to environmental change. Research on parasite biogeography has also focused on the species composition of local parasite assemblages and how it changes over geographical space. The turnover in parasite species from locality to locality, or beta diversity, results in dissimilarity among parasite assemblages. From the starting point that this dissimilarity generally increases exponentially with increasing distance among localities (Poulin, 2003), understanding of parasite beta diversity has progressed toward more complex explanatory spatial models also including differences between localities in their biotic (host communities) and abiotic components (e.g., Williamson et al., 2019; Krasnov et al., 2020).

Parasite biogeography and macroecology are now thriving subdisciplines of ecological parasitology (Morand and Krasnov, 2010; Stephens et al., 2016), that have grown from nothing in the past three decades. Nowadays, large and growing public databases on host-parasite interactions, such as the Natural History Museum's Host-Parasite Database (Gibson, D.I., Bray, R.A., Harris, E.A., 2005. https://www.nhm.ac.uk/research-curation/scientific-resources/taxonomy-systematics/host-parasites/), FishPEST (Strona and Lafferty, 2012) or the Global Mammal Parasite Database (Stephens et al., 2017), provide the basis for powerful tests of large-scale patterns in parasite diversity and distribution. In this age of 'big data' and rapidly growing computational capabilities, parasite biogeography and macroecology are likely to reach new heights.

12. Parasite ecology into the molecular age

If parasite biogeography and macroecology started from scratch in the past few decades, so did parasite molecular ecology, in large part because there were no tools available prior to the late 1970s to even contemplate using genetic information to explore parasite ecology. The advent of the molecular era in ecological research initially involved protein electrophoresis; later, this was superseded by Sanger DNA sequencing, which has been more recently followed by next-generation sequencing methodologies. These have provided increasingly more sophisticated tools to investigate parasite evolutionary ecology by seeking the signature of ecological processes within parasite genomes. Although molecular genetic tools have not always been embraced by parasite ecologists as swiftly as by mainstream ecologists (Selbach et al., 2019), they have opened up multiple new avenues for research; here, I only focus on three of the most important.

Firstly, in the wake of Avise's (2000) founding of phylogeography, multiple studies started using gene markers to unveil evidence of genetic structure among conspecific parasite populations (e.g., Wickström et al., 2003; Criscione and Blouin, 2004). These early studies and those that followed allowed recent or ancient gene flow among populations to be quantified, thus enabling rigorous testing of hypotheses about historical events and contemporary dispersal shaping parasite movements (see

Mazé-Guilmo et al., 2016). In addition, these phylogeographic studies provided support for some local adaptation patterns identified prior to the molecular era, as well as uncovering incipient parasite speciation events.

Secondly, genetic markers have provided a huge boost for parasite biodiversity studies, by allowing cryptic species that are difficult to distinguish based on morphology to be detected and counted (Nadler and Pérez-Ponce de León, 2011). The use of genetic markers to characterise parasite samples and prospect for new species has blossomed in the past 15 years (Pérez-Ponce de León and Poulin, 2018). This has not only led to more accurate estimates of parasite diversity and host specificity, but also indirectly allowed the resolution of many parasite life cycles (e.g., Jensen and Bullard, 2010; Blasco-Costa and Poulin, 2017). The morphologically very different larval and adult stages of helminths with complex life cycles are increasingly being matched with gene sequences, shedding light on transmission routes and uncovering new trophic links in food webs.

Thirdly, the growing application of genomics and transcriptomics in parasitology is informing our understanding of parasite ecology. The genomes of many parasite species have now been fully sequenced and annotated (Zarowiecki and Berriman, 2015), allowing tracking of the evolution of ecological traits. Powerful genomic tools also facilitate the study of eco-evolutionary dynamics (Hendry, 2017), or in this case, the co-evolutionary feedback between hosts, parasites and their environment. Already much progress is being made toward identifying the genomic signature of key traits such as parasite virulence and host resistance, and the gene expression profiles of either antagonist under different environmental conditions (e.g., Brunner et al., 2017; Ebert and Fields, 2020). The next few years are likely to see great advances in the application of '-omics' technologies to understand the mechanisms that link genes, ecological traits, and their coevolution.

13. Host-parasite cophylogeny

Also benefiting from the advent of molecular genetics, cophylogenetic studies of parasites and their hosts have proliferated in the molecular era. A look at associations between parasites and hosts in nature raises several questions. Why are parasite species found in particular host species? Why do certain parasites infect multiple host species, whereas others infect only one? What factors favour low or high host specificity? Fahrenholz's rule provided a baseline to address these questions; it postulated that parasites track their hosts over evolutionary time, i.e. they cospeciate with their hosts, resulting in the phylogeny of a group of related parasites being a mirror image of that of their respective hosts (see Brooks and McLennan, 1993). Even the first attempt to test this rule (Brooks, 1977) revealed that host-parasite cophylogenetic patterns can be more complex, with a range of evolutionary events, such as host-switching or extinctions, acting to create incongruence between host and parasite phylogenetic trees, and leading to some parasites being found in more than one host species.

The advent of molecular methods to reconstruct phylogenies stimulated research in this area, from the earliest study based on protein electrophoresis data (Hafner and Nadler, 1988) to the myriad modern ones using genomic information. The other key innovation that gave impetus to this research was the development of software packages such as TreeMap (Page, 1994), ParaFit (Legendre et al., 2002) and PACo (Balbuena et al., 2013), that allow the congruence between host and parasite phylogenetic trees to be tested statistically. In other words, these analytical methods allow one to determine whether the parasite tree is more similar to the host tree than expected by chance, and to identify incongruent branches in a tree that may indicate host-switching, extinction, or some other event.

The vast body of research that followed the implementation of these methods suggests that some degree of cospeciation is generally detectable across a broad range of host and parasite taxonomic groups. However, the signature of cospeciation is often weak and indicative of the complexity of evolutionary pathways by which parasites have come to infect hosts in the present (de Vienne et al., 2013; Hayward et al., 2021). Through this research, we now have a clearer idea of what parasite properties (life cycle complexity, mode of transmission, virulence, etc.) can favour tighter cospeciation as opposed to rampant host-switching.

14. Conclusions and future outlook

From its modest beginnings rooted in natural history and influenced by the medical side of parasitology, parasite ecology has matured into a rigorous discipline, adopting ideas from other fields when appropriate but also following its own traditions and pursuing its own goals. Although it initially borrowed and adapted many ideas from mainstream ecology, parasite ecology is returning the favour, as some of its concepts are now influencing mainstream ecology. Much progress has been made toward answering questions first posed in the 1970s, while along the way new questions have come up that could not even have been imagined in those early days. From the dynamics of parasite populations and communities to their impact on host individuals and populations, from host manipulation to host-parasite coevolution, our understanding of parasite ecology has grown by leaps and bounds. Many studies, including some important advances, have been published in the pages of International Journal for Parasitology since its first issue in 1971 (Fig. 2). Articles on parasite population biology dominated in the early years, however other research areas, notably studies on parasite molecular ecology, biodiversity and biogeography, and anthropogenic impacts have grown in importance in the past three decades. Overall, the proportion of all articles in the journal that can be considered as addressing parasite ecology has increased over time (Fig. 2). Despite how much has been achieved, there are challenges on the horizon for parasite ecology; here, I briefly highlight five of them.

First, although the number of new parasite species discovered and formally described annually has been rising steadily in past decades (Poulin, 2014), we are still a long way from a full inventory of parasite species on Earth. To understand ecological processes in natural systems, one must first know the players involved. Yet our knowledge of parasite biodiversity is lagging well behind our knowledge for most major groups of free-living animals serving as their hosts. The search for new parasite species has been plagued by a lack of coordination and an inefficient deployment of effort (Jorge and Poulin, 2018). Calls have been made for a global strategic approach to parasite discovery (Carlson et al., 2020a), and now is the time for action.

Second, even before we have discovered and described many parasite species, they are becoming extinct. This is happening via co-extinction, as parasites also vanish when their hosts go extinct (Dunn et al., 2009). Alternatively, parasites may become extinct when their host populations dwindle below the threshold density necessary for transmission, even if the hosts themselves persist. Parasite ecologists need to implement a global strategy for parasite conservation (Carlson et al., 2020b), using a combination of action and advocacy to engage with the broader conservation biology movement.

Third, it is now clear that microbial communities living within animals, i.e. the animals' microbiomes, play fundamental roles in their biology (Zilber-Rosenberg and Rosenberg, 2008; Lynch and

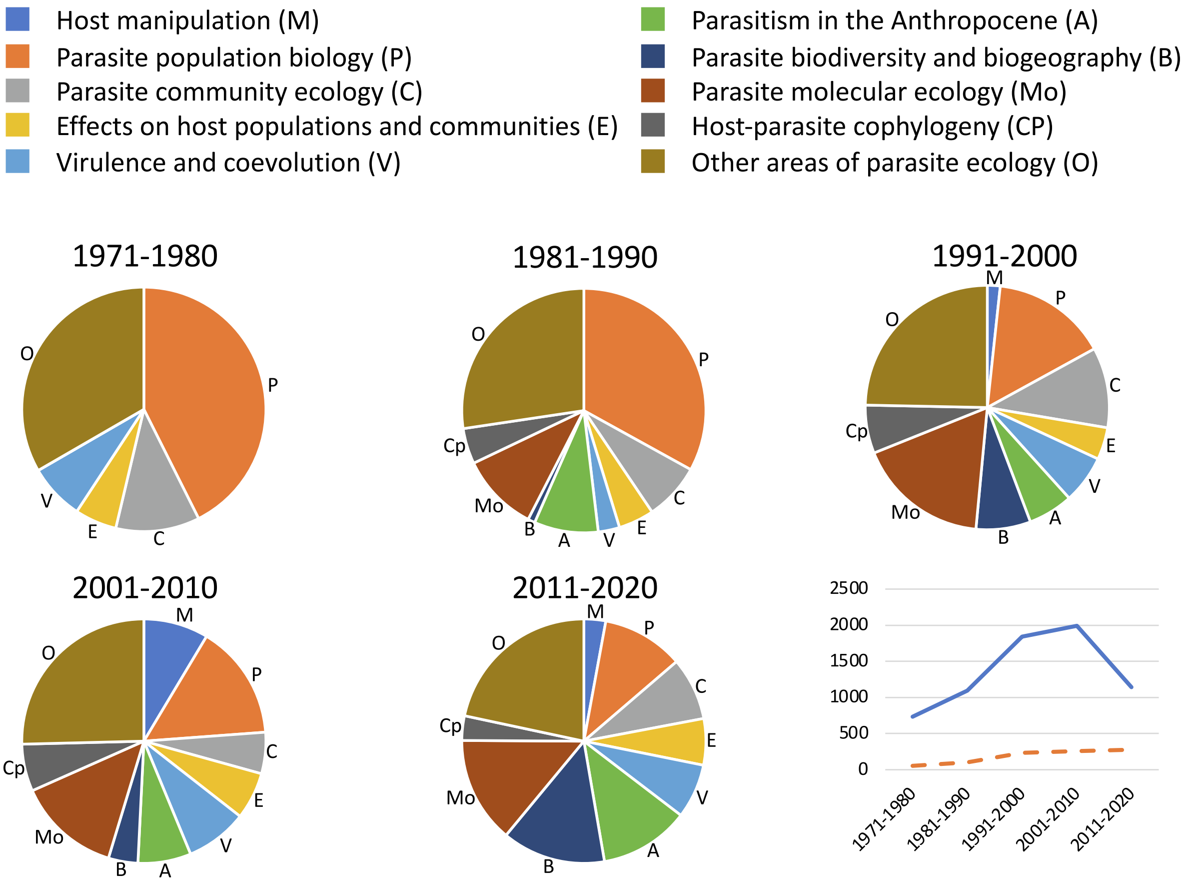

Fig. 2. Summary of research on ecological parasitology published in the International Journal for Parasitology in the five decades since it was first published. Assignment of articles to each category was done by the author following consistent and conservative criteria. Ecological parasitology was defined narrowly; for instance, articles on veterinary parasitology were excluded even if touching on themes that could be interpreted as ecological. Of the 12 research areas considered in the present review, only the nine most frequently represented are shown separately; all other articles on any aspect of ecological parasitology are grouped as "Other areas". The graph shows the rise in the number of articles on ecological parasitology (broken line) published in the journal over the five decades, relative to the total number of articles (solid line) of all types published in the journal, according to the Web of Science. The dip in the total number of articles published in the last decade represents a genuine drop in total output in the journal.

Hsiao, 2019). Microbial communities within hosts can determine how resistant they are to infection (Koch and Schmid-Hempel, 2012; Dheilly et al., 2015). Parasites too harbour their own microbiomes (Ben-Yosef et al., 2017; Sinnathamby et al., 2018; Jorge et al., 2020). We can no longer view the host-parasite interaction as a simple two-player interaction; the roles of microbes living within the host or within the parasite need to be integrated into our studies of host-parasite ecological interactions. The recent launch of the Parasite Microbiome Project (Dheilly et al., 2017) provides a solid platform to achieve this more inclusive perspective, one that parasite ecologists should take advantage of.

Fourth, 'disease ecology' has arisen out of mainstream ecology in the 1990s, as a new and growing field of research (Real, 1996). Although its focus has been mainly on microbial pathogens and the drivers of epidemics and epizootics, the main themes of disease ecology clearly overlap with those of ecological parasitology (Koprivnikar and Johnson, 2016). Researchers who associate with one or the other discipline often attend different conferences and publish in different journals. Yet they would all benefit from greater interactions and exchanges, as they have shared interests and complementary approaches (Koprivnikar and Johnson, 2016). Ecological parasitologists have much to gain by building bridges with their disease ecology colleagues, and should be encouraged to do so. For example, disease ecologists have been quick to embrace the One Health framework, a holistic approach that considers environmental, wildlife and human factors associated with the threat of infectious disease (Cunningham et al., 2017); ecological parasitologists have much to offer in this area.

Fifth, research into the impact of climate change on host-parasite interactions is more pressing than ever. Despite early calls that climate-related impacts needed urgent attention (Marcogliese, 2001), and later appeals for greater interdisciplinary collaboration and improvements in data collection for use in predictive models (Rohr et al., 2011), research in this area is still very much piecemeal and poorly integrated. Just as 'global change biology' has emerged as a separate field within mainstream ecology (with its own, highly successful journal), there is a need to establish 'global change parasitology' as a sub-discipline of parasite ecology. This is urgently needed to achieve greater forecasting power regarding changes in parasite geographic distribution or infection levels, shifting hotspots of emerging diseases, etc., in the face of environmental and climate change. This is possibly the greatest challenge facing ecological parasitology. However, we may instead think of it as an opportunity, a catalyst to bring parasite ecologists together with colleagues from other disciplines. Progress in this as well as other areas of ecological parasitology will not happen if research is conducted in silos. Multidisciplinary collaboration would not only create mutually beneficial exchanges of ideas and approaches, but also raise the profile of ecological parasitology in the eyes of other biologists who have for a long time considered parasites as unworthy of attention.

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