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THE RISE OF DISEASE ECOLOGY AND ITS IMPLICATIONS FOR PARASITOLOGY

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?1 ABSTRACT: Many fields in the biological sciences have witnessed a shift away from organism- or taxon-focused research and teaching in favor of more conceptual and process-driven paradigms. The field of parasitology is no exception, despite the diversity of topics and taxa it encompasses. Concurrently, however, interest in disease ecology has increased dramatically, suggesting new opportunities that merit exploration, as well as the need for parasitology to promote its long history of ecological research to do so. Here we undertake a quantitative analysis of metrics relating to publications, research funding, career opportunities, and undergraduate teaching to comprehensively illustrate the rising prominence of disease ecology. While we distinguish generally between the fields of parasitology and disease ecology, we also emphasize the common interests and complementary approaches that enhanced integration could offer. To illustrate why enhanced integration between these 2 fields is increasingly critical, we highlight 2 successful areas in which parasitology and disease ecology have intersected (community assembly and scale, and the effects of natural enemies on life history traits). We conclude by identifying "frontier topics" that will benefit from greater cooperation and interaction between these currently relatively separate areas and the need for principal investigators to identify and communicate changes in their discipline to students and trainees, which will collectively result in many possible new benefits and prospects for current and future researchers.

Research and teaching in organism-focused fields has rapidly changed over the past 3 decades, with broad conceptual approaches increasingly favored over more taxon-specific specialties (Greene, 2005; Cheesman et al., 2007). The field of parasitology is no exception, despite its long history (see Worboys, 1983, for a review), the wide diversity of organisms that fall under its domain, and the growing awareness of just how little we know about parasite biology, ecology, and evolutionary history. For instance, while the American Society of Parasitology was established in 1924, with a recent long-time member (Dr. William C. Campbell) receiving the 2015 Nobel Prize in Medicine, only 25% of the top 25 life science-ranked universities in the United States currently either have a full-time faculty member identified as a parasitologist on staff for general undergraduate programs in the life sciences or offer a dedicated course in parasitology (see teaching subsection below). Changes in foci are inherent in science, with fields constantly evolving, including that of parasitology (Warren and Purcell, 1981; Worboys, 1983). Nevertheless, other associated disciplines—in particular that of disease ecology—have recently gained momentum. In recognition of these patterns, here we discuss the increasing prominence of disease ecology as a discipline that offers parasitologists opportunities that have been largely overlooked thus far to promote teaching in parasitology, engage in novel collaborative opportunities, achieve greater funding success, and enhance student recruitment while ensuring that trainees acquire the skills necessary for future career accomplishments.

What are the differences between parasitology and disease ecology as disciplines? After all, parasitologists have a long history of engaging in ecologically-themed research. For example, the mutual regulation of host and parasite populations (Anderson and May, 1978; May and Anderson, 1979) is a classic illustration of using parasites to demonstrate broader ecological principles. However, ecologically-themed research involving parasites does not directly translate to the focal areas often associated with disease ecology, or more critically, has not been perceived and promoted as such when it does. This may be partially attributable to the historical focus on drivers of epidemics and epizootics by the latter (for reviews, see Wilcox and Gubler, 2005; Granter et al., 2014; Ostfeld, 2014), i.e., the "disease" aspect has been critical, whereas many parasitologists study hosts and/or parasites not intimately linked to known diseases, or pursue ecological and evolutionary questions that do not pertain to disease dynamics in an obvious way. Although disease ecology is not a new discipline, its prominence rapidly grew in the early 1990s (Real, 1996), due to both (1) increasing recognition of the importance of ecological interactions in understanding emerging infections, and (2) the realization that parasites and disease-causing organisms had greater potential to affect population- and ecosystem-level processes than previously assumed. Stated another way, ecology was important for the study of disease just as disease was relevant for understanding ecology (Johnson et al., 2015a).

The field of disease ecology can be defined in different ways, but certain re-occurring points are often emphasized. Kilpatrick and Altizer (2010) define disease ecology as, "the ecological study of host–pathogen interactions within the context of their environment and evolution." They further emphasize the discipline's primary goals of understanding the spatial and temporal transmission of pathogens, as well as how they affect host populations, whereas parasitology has been perceived to have a greater focus on taxonomy and parasite life cycles (Kilpatrick and Altizer, 2010). Others have defined disease ecology as a growing sub-discipline in ecology that "combines field studies, epidemiology, molecular approaches, and modeling to understand interactions among wildlife hosts, vectors, and pathogens, and to better forecast risk of disease" (Stapp, 2007), or as a field devoted to the study of "complex interactions between disease incidence in some host and various environmental/ecological processes influencing such incidence" (Waller, 2008). Waller (2008) particularly highlighted the multi-disciplinary nature of disease ecology: "including (but not limited to) entomology, climate change, veterinary medicine, microbiology, immunology, epidemiology, mathematical biology, and public health surveillance."

So what then defines parasitology as a discipline? The definition of parasitism itself still lacks broad consensus, but it is widely recognized as an ecological or functional characterization of lifestyle that evolved independently in organisms from many taxa, and could simply be 1 system in a general consumer–resource model (Zelmer, 1998; Poulin, 2007; Lafferty et al., 2015). Because of this, parasitology encompasses a variety of approaches and

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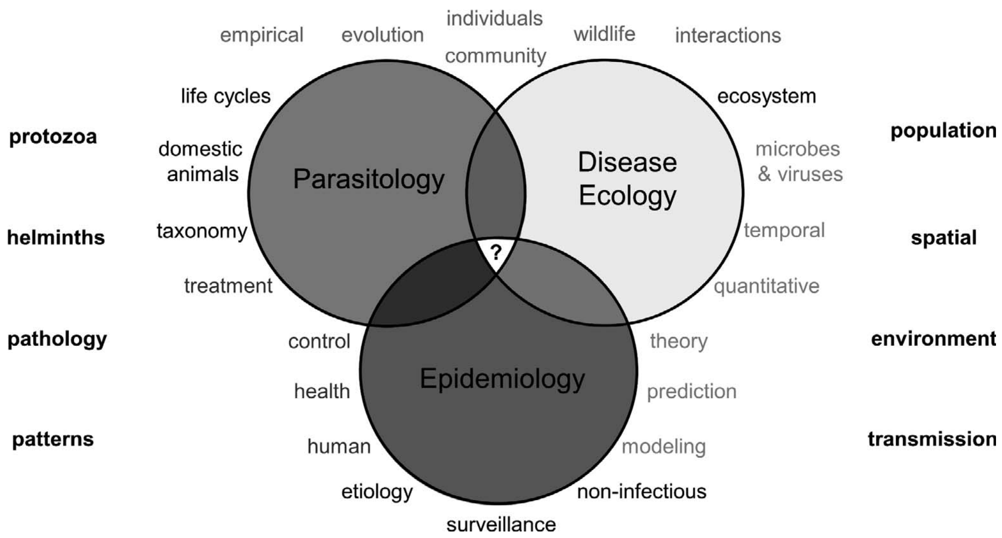

FIGURE 1. Overlap among the fields of disease ecology, epidemiology, and parasitology. Bold terms indicate similar interests among all 3 disciplines, with colored terms representing particularly high levels of overlap between 2 fields. Areas of relative specialization are denoted beside each field, although these are not mutually exclusive.

questions and is difficult to define. Indeed, even the member site for the American Society of Parasitologists lacks a clear definition of the field, but notes the breadth of research with parasites (http://amsocparasit.org/). The descriptions of select parasitological journals reveal the problems inherent with defining this discipline and the problems with its perception by those within and outside of it. The *Journal of Parasitology* describes itself as a publication dedicated to, "basic or applied aspects of general, veterinary, or medical parasitology, and epidemiology" (http://www.journalofparasitology.org/page/author_instructions). The journal *Parasitology* publishes papers related to, " all aspects of parasitology and host-parasite relationships, including the latest discoveries in parasite biochemistry, molecular biology and genetics, ecology and epidemiology in the context of the biological, medical and veterinary sciences," (http://journals.cambridge.org/action/displayJournal?jid=PAR). Last, the *International Journal for Parasitology* covers, "all aspects of basic and applied parasitology, . . ., and ranging from parasites and host-parasite relationships of intrinsic biological interest to those of social and economic importance in human and veterinary medicine and agriculture," (http://www.journals.elsevier.com/international-journal-for-parasitology/). Based on these journal mission statements, the breadth of ecological and evolutionary research conducted with parasites seems largely overlooked.

Similar questions often emerge about how to differentiate parasitology and disease ecology from the field of epidemiology. Notably, a central focus of epidemiology is to identify determinants of disease events and their distributions (WHO, http://www.who.int/topics/epidemiology/en/), similar to commonly-stated goals of disease ecology. However, epidemiology has a greater human focus (demos = people), is more oriented toward population-level processes, and most importantly, includes non-infectious diseases, such as contaminants, injuries, and cancer (WHO). Disease ecologists generally conduct research on a range of infectious agents, which can include bacteria, fungi, viruses, protozoa, and helminths, whereas the field of parasitology began to distinguish itself as specializing in the latter 2 categories in the early 1900s (Worboys, 1983). In addition, while epidemiologists often examine environmental correlates associated with disease risk, disease ecology as a discipline seeks to be more mechanistic in identifying the direct and indirect pathways through which the environment influences infection (Waller, 2008; Kilpatrick and Altizer, 2010). As a generalization, disease ecology includes a wider range with respect to biological scales of inquiry (individual, population, community, and ecosystem-level dynamics) compared to epidemiology and traditional parasitological research.

There are clearly many common interests among the fields of disease ecology, epidemiology, and parasitology, or between 2 of these in many cases, but each discipline does tend to have certain areas of focus, be they real or perceived as such (Fig. 1). While we try to emphasize the commonalities between disease ecology and parasitology here to highlight the potential benefits of doing so, there are distinctions to be made, and these are important for many reasons. For instance, parasitologists and epidemiologists may be more inclined to apply for health-related funding, but disease ecologists perhaps would not. Conversely, parasitologists might not consider applying for funding under the umbrella of disease ecology, even though much parasite ecology could clearly be considered as such. Regardless of the overlaps among these 3 fields, and the many investigators who span them, separations that are self-imposed or result from a lack of communication among educators and researchers represent a serious impediment to future success.

THE INCREASING ROLE OF DISEASE ECOLOGY

The rising influence of disease ecology as a discipline can be seen by its increasingly large role in research, teaching, and career opportunities. Here we illustrate this phenomenon by examining trends related to journal publications, research funding, undergraduate teaching, and career opportunities, comparing the patterns between parasitology and disease ecology wherever possible.

FIGURE 2. Temporal patterns in the publication of disease- and parasite-related papers within the field of ecology. Depicted is the percentage of papers published between 1970 and 2014 that include terms in the title related to parasites and disease (solid line). As a comparison, we also show the percentage of papers with competition-related terms in the article title (dashed line). Searches were performed using the Web of Science database to identify all publications within the field of ecology (using the Web of Science category "ecology"), those within this search that included disease terms (TI = parasit* OR disease* OR pathog* OR infect*), and those that include competition terms (TI = compet*). A subsample of articles in each search (~5%) were checked to ensure the search terms were effective in identifying relevant articles.

Publications

To evaluate patterns of disease- and parasite-related publications within the field of ecology, we used the Web of Science database to search for papers within the "ecology" subcategory of journals that included words in the title related to parasit*, disease*, pathog*, or infect*. We restricted the analysis to papers published between 1970 and 2014. The use of title words—rather than all key words and the abstract—helps to maintain consistency over the search period given variable inclusion of abstracts and number of key words both over time and across journals (see Ward and Lafferty, 2004; Raffel et al., 2008; Johnson and Paull, 2011—although we acknowledge that temporal changes in length of titles could influence our results). We then completed a secondary search that extracted all papers in the "ecology" subcategory published over the same time horizon to allow us to assess how the proportion of papers with disease-related words in the title has changed. As a comparison, we also performed an analysis of the proportion of ecological publications that included title words associated with another form of ecological interaction: competition (compet*).

Our results indicate a clear trend of increased overall attention to infectious diseases and parasites within ecological publications since 1970 (Fig. 2). After correcting for research effort in terms of the total number of publications, the proportion of articles referencing disease or parasites has more than doubled since 1970 (GLM with Gaussian distribution, year coefficient = 0.048 ± 0.003, t = 16.53, $P < 0.00001$). Incorporating temporal autocorrelation did not improve model diagnostics. Combined with increased publication rates, this translates into an increase from 14 disease-related publications within ecological journals in 1970 to 470 published in 2014. This illustrates broad interest in disease-causing organisms, including parasites, outside of historical outlets for parasite-focused research, such as specialized parasitological journals. In contrast, we saw no such pattern for papers with competition in the title, the proportion of which has declined since 1970 (GLM with Gaussian distribution, year coefficient = –0.009 ± 0.002, t = –3.44, $P < 0.005$). This analysis yields results parallel to those of Raffel et al. (2008), who found a significant increase in the proportion of disease-related articles published within 12 ecological journals since 1991 with no such increase in articles focused on predator–prey interactions.

Funding

Several funding agencies have undertaken initiatives targeted toward supporting the study of disease ecology. In 1999, the National Science Foundation (NSF) and the National Institutes of Health (NIH) initiated a joint effort to fund research related to disease ecology, with the stated goal to, "support efforts to create a predictive understanding of the ecological and biological mechanisms that govern relationships among human-induced environmental changes and the emergence and transmission of infectious diseases," (http://www.nsf.gov/funding/pgm_summ.jsp?pims_id=5269). This led to the creation of the Ecology and Evolution of Infectious Diseases program (EEID), which is meant to support research on the ecological, evolutionary, and socio-ecological principles and processes that influence the transmission dynamics of infectious diseases, with a focus on quantitative or computational understanding of pathogen transmission dynamics. Projects funded by the EEID program can be at any scale from specific pathogens to ecosystems and are encouraged to be broad, interdisciplinary efforts with teams comprised of different sub-disciplines (Scheiner and Rosenthal, 2006). Similarly, the NSF-funded National Ecological Observatory Network (NEON), which intends to use standardized methods to monitor as many as 60 sites over 30 yr to understand the ecological responses of systems to global change, has emphasized the importance of surveillance of wildlife pathogens (Springer et al., in press). The Governing Board of the U.S. National Research Council, whose members are drawn from the councils of the National Academy of Sciences, the National Academy of Engineering, and the National Institute of Medicine, also recognized the growing importance of investigating pathogens in an ecological and evolutionary context, highlighting infectious diseases and the environment as 1 of the 4 areas of environmental science research most deserving of immediate research investment in a 2001 report (NRC, 2001).

To more quantitatively examine trends related to NSF-funded research that focuses on disease ecology, we used the NSF-search engine to query awards within the Division of Environmental Biology (DEB) since 1991, including both graduate student grants (Doctoral Dissertation Improvement Grants, DDIGs) and full proposals associated with any initiative within DEB. In total, this included 7,822 full grants totaling $2.8 billion U.S. and 2,120 DDIG grants totaling $24.8 million U.S. Similar to the publication search, we included a keyword search for any grants (active or expired) awarded between 1991 and 2014 that included parasit* or disease*. We then compared the annual fraction of awarded funding related to disease to the total funding amount, differentiating between DDIGs and full proposals. Our results suggest a long-term increase in the proportion of total funding

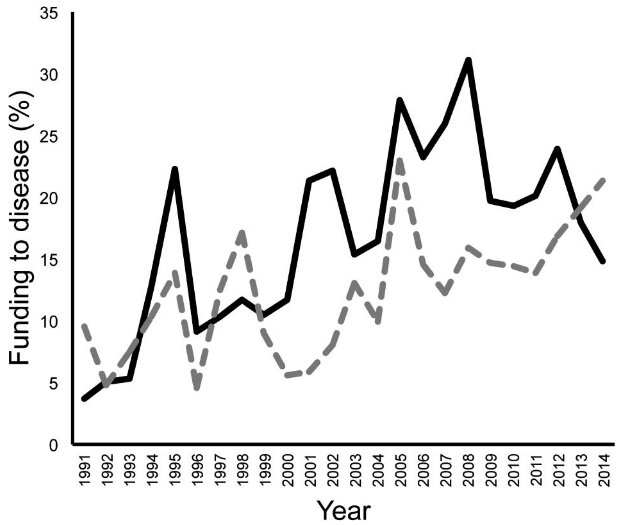

FIGURE 3. Temporal patterns in funding from the National Science Foundation allocated to disease- and parasite-related proposals within the Division of Environmental Biology (DEB). Depicted is the percentage of total funding in US dollars awarded between 1991 and 2014 to proposals that included keywords related to parasites or disease (parasit* or disease*), including current as well as expired awards. The solid line is used for "full proposals," whereas the dashed line is specific to graduate student grants (i.e., the Doctoral Dissertation Improvement Grant or DDIG program).

within DEB allocated toward proposals associated with parasites and disease, which roughly doubled for graduate student grants and more than tripled for full grants (GLMs with Gaussian distribution: graduate student proposals, year coefficient $= 0.472 \pm 0.115$, $t = 4.104$, $P < 0.0005$; major proposals, year coefficient $= 0.698 \pm 0.167$, $t = 4.18$, $P < 0.0005$) (Fig. 3). Whether this is indicative of an increased success rate of disease-related submissions or an increase total proportion of submissions in this area is unclear. While some of this pattern is certainly driven by the EEID program, the fact that the trend is also apparent for graduate student grants likely reflects a more widespread influence of disease ecology in proposals. These patterns indicate that research funding for projects involving infectious organisms is increasingly oriented toward inter- and multi-disciplinary approaches that undertake broad questions at multiple scales. Program descriptions also emphasize the critical need to include quantitative analysis, and the ability to forecast or predict outcomes are typically explicit goals.

Professional societies

New groups and meetings also demonstrate the increasing interest, and influence of, disease ecology. For example, the 13th annual "Ecology and Evolution of Infectious Disease" meeting was held in 2015 and had speakers from a range of sub-disciplines (http://eeidconference.org/2015/). Disease ecology groups have also been created within larger, well-established professional societies, such as the Disease Ecology Section that was founded in 2014 as part of the Ecological Society of America (http://esa.org/disease/) and the division of Ecoimmunology and Disease Ecology that was formed within the Society for Integrative Biology in the same year (see Martin et al., 2014). Similarly, the British Ecological Society has a number of "special interest" subgroups, including that for Parasite and Pathogen Ecology and Evolution (http://www.britishecologicalsociety.org/getting-involved/special-interest-groups/parasite-and-pathogen-ecology-and-evolution/). The formation of such groups reflects a strong interest in research with parasites outside of that conducted by self-identifying "parasitologists." There are likely many missed opportunities for collaboration by the continued overall separation of researchers in the fields of parasitology and disease ecology.

Teaching

Undergraduate teaching in the life sciences has changed profoundly over the last 3 decades (Greene, 2005; Cheesman et al., 2007), including a shift away from taxon-based courses toward more integrative studies with a greater focus on fundamental concepts, underlying tools, and emergent processes (Gil-Pérez, 1996; Pianka et al., 1998). Consequently, many programs historically offered courses that focused on particular groups of organisms (e.g., herpetology, ornithology, and entomology), which are no longer offered, or offered only occasionally. The pros and cons of this shift have been the subject of an intense debate that will no doubt continue, and we do not address these here, but rather simply recognize the current general state in undergraduate education and what it means for parasitology. Although parasitology courses cover many taxa and arguably a large fraction of global biodiversity, this field also falls under the auspices of taxon-based curricula and is subject to the same selection pressure.

We explored the extent to which undergraduate courses with "parasitology" in the title are currently offered relative to those in disease ecology or a comparable title (see below), as well as another taxon-focused course (entomology) for comparison. To do this, we surveyed the top 25 life science-ranked universities in the United States based on the 2013–2014 *Times Higher Education* world university rankings (https://www.timeshighereducation.com/world-university-rankings/2014/subject-ranking/life-sciences#!/page/0/length/25), as well as the top 25-ranked liberal arts colleges in the United States (http://colleges.usnews.rankingsandreviews.com/best-colleges/rankings/national-liberal-arts-colleges/data). We excluded courses that were not offered as part of a general undergraduate program in the life sciences, i.e., those in schools of public health or veterinary medicine, or similarly specialized programs. The official website of each of the 25 ranked institutions was used to determine whether courses in disease ecology, entomology, and parasitology were available, although these were not necessarily offered every term or academic year. We were able to gather information for 24/25 of the universities, with the following results: disease ecology/comparable = 15/24 (63%), entomology = 9/24 (37%), and parasitology = 6/24 (25%). Findings for the liberal arts colleges found a more even distribution of these courses: disease ecology/comparable = 7/25 (28%), entomology = 6/25 (24%), and parasitology = 6/25 (24%). Courses that included a large component of disease ecology had a variety of titles, including *Ecological and Epidemiological Control of Parasitic Diseases*; *Ecology and Evolution of Infectious Disease in a Changing World*; *Evolutionary Medicine*; *Disease Ecology, Economics, and Policy*; *Ecology and Epidemiology—Parasites and Diseases*; *Disease Ecology and Conservation*; *Seminar in Ecology and Evolution of Infectious Diseases*; *From Influenza A to Varicella*

TABLE I. Career opportunities in taxon- or discipline-specific areas.

Source	Range	"Parasite"	"Disease ecology"	"Bird"
Chronicle (U.S.)*	As of Oct. 14	3	9	2
Nature†	As of Oct. 14	5	6	0
ECOLOG-L‡	Since 2005	96	488	800
Science†	As of Oct. 14	5	18	0
New Scientist	As of Oct. 14	0	2	0
The Scientist	As of Oct. 14	0	0	0
Higher Ed Jobs†	As of Oct. 14	5	32	0

* Only faculty positions.
† Faculty, postdoc, and research associate positions.
‡ Faculty, postdoc, grad student positions (included "position" in search term).

Zoster—The Physiology, Ecology, and Evolution of Infectious Disease; *Infectious Disease in Ecology and Conservation*; *Wildlife Disease*; *The Ecology and Evolution of Infectious Diseases*; *Modeling Infectious Diseases*; *Health and Disease in Human*
?2 *Evolution*; and *Wildlife Disease Ecology*.

While it is likely that this examination missed certain course offerings, including those offered irregularly (e.g., special topics) or exclusively at field stations, it is clear that disease ecology is now widely taught at many institutions, particularly more so at universities than liberal arts colleges when compared to taxon-focused courses such as entomology and parasitology. This reflects changes in pedagogy, but we also acknowledge possible financial considerations given that parasitology courses tend to include a laboratory component, and these represent an added cost for institutions. Although on one hand this is a deficit in contemporary undergraduate education, with only a third of our surveyed schools offering a classical course in parasitology, we contend that the growing interest in infectious diseases presents an opportunity for parasitologists to still expose undergraduates to basic knowledge regarding parasites and reach out to the students who will become the next generation of researchers and policy-makers. To effectively do so, graduate students and post-doctoral researchers must ensure that they are adequately prepared to teach broad courses such as disease ecology that incorporate a wider range of pathogens than those typically studied by parasitologists and employ approaches from other fields such as epidemiology.

Career opportunities

Paralleling the trend in undergraduate course offerings discussed above, recruitment of new faculty has also emphasized wide-ranging or interdisciplinary subject areas compared to the taxon-specific expertise that was historically typical of life science departments. Although significant career opportunities for researchers focused on particular groups of organisms likely still exist, the shift away from taxon-specific professional paths has been noted for other fields such as herpetology (Pianka et al., 1998). Here we examined this pattern with respect to parasitology in 2 ways. We first determined whether there were parasitologists and disease ecologists on the faculty at the same 25 universities and departments evaluated above with respect to undergraduate courses, as well as the same 25 liberal arts colleges. To do so, we relied on faculty profiles from institution websites that used key words such as "parasite" and "disease," but excluded non-infectious diseases. Adjunct faculty and sessional/visiting faculty, or those with primary affiliations at associated institutes, research centers, etc., were also excluded. Although this approach might not precisely identify the research activities of all faculty, we obtained information for 23/25 of the universities and all 25 liberal arts colleges. In total, 6 universities had faculty identified as conducting research with parasites, while 13 had faculty who worked with infectious diseases in some manner corresponding to the definitions of disease ecology provided in the Introduction. Faculty in both fields co-occurred at 4/6 universities with "parasitologists," indicating that these are not necessarily mutually exclusive. There was 1 parasitologist identified among the 25 liberal arts colleges, and 5 disease ecologists. Because disease ecology spans a diverse array of sub-disciplines, with parasitology considered one of them, it is not necessarily surprising that more faculty would be potentially covered by this wide umbrella; however, our results demonstrate the strong presence of disease ecology in many life sciences departments and presumably institutional support for this type of research and teaching.

In addition to considering the current composition of faculty, we also searched commonly-used platforms such as *The Chronicle of Higher Education* for career opportunities, including faculty and postdoctoral positions, as well as graduate student openings where this information was available (see Table I). We used key words to compare those specific to "parasite" relative to "disease ecology," also including another other taxon-specific term ("bird"). To eliminate country- or region-specific priorities, we limited ourselves to U.S. data. We did not eliminate positions that were advertised with multiple key words, which may have resulted in double-counting in a few instances because it was not possible to discern whether these were intended to prioritize 1 field over another. Unfortunately, most sources were temporally limited and did not lend themselves to an examination of trends; however, we used a generalized linear model (GLM) with a Gaussian distribution and an identity link function to determine whether the number of positions ($\log_{10}$-transformed) advertised on ECOLOG-L increased with time (year as a covariate), and whether this differed for parasite-, bird-, and disease ecology–related positions (discipline as a categorical predictor). While the ECOLOG-L records dated back to 2005, we excluded that first year from our analysis given that only 12 positions total for our 3 disciplines were advertised (Fig. 4).

Although there was overlap in the current positions advertised, opportunities in disease ecology were approximately 3–4× more common than those specifically referring to parasites. This was also true for the other taxon-specific search term ("bird"), with the exception of graduate student positions (see Table I). Similar to the current faculty composition of life science departments, this likely reflects the wide range of topics that form part of disease ecology. Our overall GLM revealed a temporal increase in total number of positions advertised on ECOLOG-L since 2006 ($P < 0.001$), as well as a significant effect of discipline ($P < 0.001$) since there were more total opportunities available related to birds compared to disease ecology and parasites, but more for disease ecology relative to parasites (Fig. 4). This represents a true increase through time since there was no significant temporal autocorrelation of the residuals (Durbin Watson statistic = 2.833). There was also a significant interaction of year and discipline ($P <$

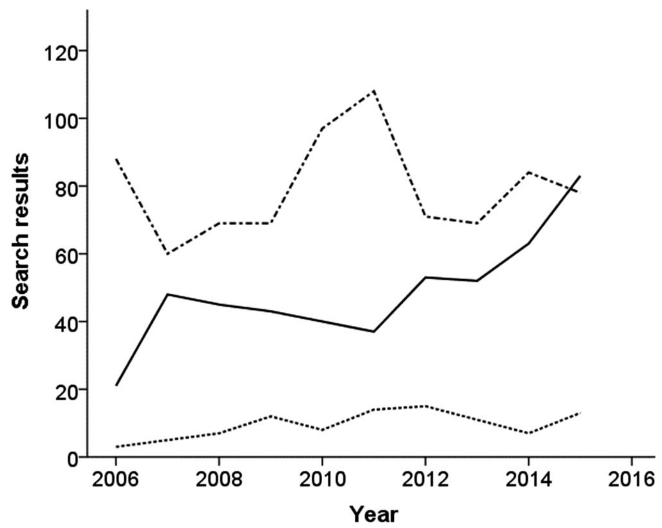

FIGURE 4. Positions advertised on the ECOLOG-L listserv since 2005, including faculty, postdoctoral, technician, and graduate student opportunities. Lines indicate key words used in search along with "position." Key: solid line = disease ecology, dashed line = parasite, dot and dash line = bird.

0.001) since the strength of the relationship between time and number of positions advertised differed for the 3 fields (disease ecology β coefficient = 0.804; parasite β coefficient = 0.662; bird β coefficient = 0.032). Notably, the total number of disease ecology positions advertised on ECOLOG-L in 2015 actually surpassed that for bird-related research for the first time. In practical terms, our results suggest that students working with parasites should be open to pursuing opportunities in academia outside of defined parasitology positions. Identifying such opportunities early on will help students to acquire the proper skill set to be competitive for broadly-advertised positions, ultimately helping to ensure continued research and teaching with parasites.

INTEGRATING PARASITOLOGY AND DISEASE ECOLOGY—CASE STUDIES

We advance that the natural intersections between the fields of parasitology and disease ecology provide many potential opportunities for broad, integrative research that builds on the overlapping and complementary strengths of each. An increased ability and willingness to view parasite-centered research through the lens of disease ecology will expand research possibilities, and there are many unrealized opportunities to incorporate parasitological knowledge into disease ecology research. Here we have chosen 2 examples of comprehensive topics that not only illustrate the interest of disease ecologists in using parasites to examine key principles, but also demonstrate the important contributions made by parasitologists and the potential to benefit from the rise of disease ecology by expanding beyond "traditional parasitology" as it is perceived by other disciplines (e.g., Kilpatrick and Altizer, 2010).

Natural enemies and host life history alterations

Background: Given the emphasis in disease ecology on examining host–pathogen interactions within the context of their environment and evolution (Kilpatrick and Altizer, 2010) and the key role of host life history for pathogen transmission and virulence (e.g., Nunn et al., 2014; Izhar and Ben-Ami, 2015), investigations of pathogen effects on host life history traits illustrate an area where parasitology has made important contributions and is poised to make more. Host life history is a major consideration in disease ecology because it encompasses critical parameters such as host population growth, body size, and lifespan, ultimately influencing investment into resistance and tolerance, i.e., "ecological immunity" (Sheldon and Verhulst, 1996; Zuk and Stoehr, 2002). Pathogen transmission and virulence are also influenced by host life history (e.g., Gandon et al., 2002). It has long been recognized that other natural enemies, such as predators, influence various aspects of prey life history. Under strong selection pressure by predators, prey may compensate for an expected loss of fitness by changes to their life history that represent individual phenotypic plasticity and/or population-level genetic differentiation. Documented and theoretical responses to predation include faster growth, earlier reproductive maturity, and smaller size at maturity (see Abrams and Rowe, 1996; Riessen, 1999; Benard, 2004 for reviews), although the coupling between predator and prey exerts a strong influence (Day et al., 2002). While there are certain distinctions between parasites and predators as natural enemies (see Lafferty and Kuris, 2002; Raffel et al., 2008), both meet the basic criteria typically identified as necessary to influence their victim's life history: namely, hosts/prey that are likely to have their future reproductive success eliminated or reduced by natural enemies are predicted to compensate through alterations of life history traits such as increased reproductive effort and earlier maturation (see Minchella, 1985; Hochberg et al., 1992; Michalakis and Hochberg,1994; Agnew et al., 2000 for overviews).

Past contributions of parasitology: Given the exceptional ability of certain parasites to eventually eliminate all host reproduction, particularly those that castrate their hosts (Lafferty and Kuris, 2009), this type of natural enemy was first suggested to affect host life history in a manner similar to predators (Minchella, 1985). Digenean trematodes are particularly well-known as castrators of their first intermediate mollusk hosts (Lafferty and Kuris, 2009) and were documented to cause compensatory life history shifts such as earlier sexual maturation and pre-patent increases in fecundity almost 30 yr ago (Minchella, 1985; Minchella et al., 1985; Lafferty, 1993). Since then, many studies have reported similar counter-adaptations displayed by a variety of mollusks that are parasitized by castrating trematodes (e.g., Jokela and Lively, 1995; Fredensborg and Poulin, 2006). Notably, these host life history shifts strongly correlate with risk of infection, exhibiting variation among populations and even microhabitats (Lafferty, 1993; Jokela and Lively, 1995; Krist, 2001) that suggests a primary role for parasite-mediated selection.

After these initial investigations focused on trematodes, subsequent studies have reported alterations of host life history traits related to infectious diseases in an incredibly diverse array of host and pathogen taxa, including fungi (Agnew and Koella, 1999), viruses (Gomariz-Zilber and Thomas-Orillard, 1993; Pontier et al., 1998), and nematodes (Kristan, 2004). Pathogen-induced life history changes have also been recently reported in vertebrates, sometimes with surprising speed (Jones et al., 2008a; Ohlberger et al., 2011). For instance, the infectious cancer responsible for facial tumor disease in Tasmanian Devils has caused a rapid shift from iteroparity toward single breeding events (Jones et al., 2008a), likely due its high virulence. Host life history shifts have also been reported in response to holoparasites (parasitic plants) and brood parasites such as cuckoos (Soler et al., 2001; Koskela, 2002), indicating this may be a widely-occurring compensatory strategy.

Future contributions of parasitology: Predators often exert a strong influence on prey life history (Day et al., 2002), and the same is likely for other natural enemies, but noted distinctions between parasites and predators may introduce additional, unique considerations for parasites such that disease ecologists cannot rely solely on empirical or theoretical work focused on predators (Lafferty and Kuris, 2002; Raffel et al., 2008). One such dichotomy is whether the enemy completely eliminates victim fitness—a criterion almost universally accepted as central to predation but not always true of parasites (Lafferty and Kuris, 2002). Given the vast range of pathology experienced by parasitized hosts, not all parasites may impose high enough costs on host reproductive success to drive life history shifts, or hosts may resist infection by other means (Minchella, 1985; Hochberg et al., 1992). Despite the inclusion of more host and pathogen taxa over time, a concerted effort to compare host life history alterations in different systems is warranted to determine the selective forces needed to cause shifts, and parasitologists can make major contributions to such data-gathering efforts. For example, it has been suggested that significant elimination of host fitness is needed, with relatively virulent parasites primarily driving substantive life history changes (Minchella, 1985; Michalakis and Hochberg, 1994); however, targeted comparative studies are lacking, even though there are examples where hosts do not adjust reproductive effort when confronted with lethal parasites or exhibit alterations even in the absence of an immediate impact on fitness (e.g., Agnew et al., 2000; Kolluru et al., 2002). The probability of host–parasite contact is another critical consideration (Minchella, 1985), and the chances of parasite encounter may be higher for many organisms relative to potential risk of predation (Raffel et al., 2008). Consequently, it is not clear whether the same life history traits can be altered by both types of natural enemy or which is generally the stronger driver. Indeed, parasites provide a study system that is advantageous in many ways, since they represent a wider spectrum and quality of fitness impacts, which might in turn provide a richer range of effects on host life history evolution, ranging from being equal to what is expected from predation to outcomes not predictable from a restrictive definition of natural enemies.

Incorporating host life history shifts into the forecasting models that form a major component of disease ecology is important and will require a comprehensive approach to generate rigorous predictions under various scenarios. Notably, the evolution of critical parasite features such as virulence and transmission has typically been modeled with an assumption of constant host life history traits (Gandon et al., 2002). Failure to account for host life history alterations, such as higher host reproductive efforts that lead to higher host death rates, is problematic, since these have been shown to have direct and indirect effects on the evolution of virulence (Gandon et al., 2002). In essence, many features, such as virulence, transmission, and susceptibility, are the product of host–parasite interactions that are dynamic in both ecological and evolutionary parameter space. In addition, changes to host life history can have significant effects on pathogen transmission. Agnew and Koella (1999) demonstrated that the propensity for horizontal or vertical transmission of microsporidia was largely dependent on the life history traits of their mosquito hosts, as well as their responses to different environmental conditions. A related study found that this, and parasite virulence, was based on the genetically-determined age at which the mosquitoes pupated: microsporidia from mosquitoes that developed quickly were benign and transmitted vertically, but those using slowly developing mosquitoes were more virulent and horizontally-transmitted (Koella and Agnew, 1999). Such considerations of host–parasite coevolution in the context of host life history shifts have yielded interesting and potentially significant predictions, including the bifurcation and coexistence of host strategies (Restif et al., 2001); however, many studies still focus on only the host or pathogen (Lambrechts et al., 2006), and empirical data are largely lacking.

Long-term experimental studies have been identified as vital to testing the host–parasite coevolutionary interactions predicted from models (Gandon et al., 2002). Parasitologists can play a key role in such efforts, identifying candidate host–parasite systems and optimizing their use based on intricate knowledge of parasite life cycles and practical considerations. Systems that allow control over the force of infection and experimental transfer of parasites would be particularly suited for such studies (Gandon et al., 2002). Unfortunately, this type of experimental study will not be possible with many host–parasite systems. As an alternative, and complement to, controlled manipulations, examinations of spatial and temporal covariation in host life history traits along with parasite traits such as virulence and modes of transmission should also be conducted across different environments (Gandon et al., 2002). Once again, parasitologists are positioned to make significant contributions through continued work on "traditional" aspects such as parasite life cycles and host pathology that can be applied within the larger context of disease ecology. Not only are there opportunities for ecologically-oriented parasitologists to explore potential applications and collaborations within the broader realm of disease ecology, but these are also there for other areas of specialization. For instance, although Michalakis and Hochberg (1994) identified the need to determine whether host life history alterations are mainly attributable to phenotypic plasticity or genetic differentiation given that both mechanisms occur in prey subject to predation pressure, this remains far from resolved.

Community assemblages and scale

Background: One of the most frequently cited challenges inherent to disease ecology is the involvement of multiple host species, multiple parasite species, and non-host members of the ecological community with the potential to alter host–parasite interactions (Johnson et al., 2015b). How do we more effectively manage diseases that are the product of multiple species or assemblages? While classical examples of disease control often feature highly host-specific infections with the potential for long-lived immunity (e.g., measles), many contemporary examples of disease emergence are much more complex from a management standpoint (e.g., Daszak et al., 2000; Lloyd-Smith et al., 2009). Most emerging infections involve multiple host species, including alternative hosts, intermediate hosts, and vectors, such that vaccination efforts alone are unlikely to control transmission (Taylor et al., 2001; Jones et al., 2008b; Johnson et al., 2015a).

Moreover, additional interactions both among parasites and with other members of the ecological community can affect parasite spread. Interactions between coinfecting parasites, whether involving direct effects or those mediated through the immune system, have been identified as important in the spread or evolution of several human and wildlife disease systems (Pedersen and Fenton, 2007; Graham, 2008; Ezenwa and Jolles, 2015). Concurrently, the introduction and loss of species from environments, such as predators, can lead to strong changes in infection and pathology (e.g., Packer et al., 2003; Ostfeld and Holt, 2004).

Collectively, these observations emphasize the importance of understanding the full ecological community within which host–parasite interactions are embedded. This topic—which is arguably at the core of disease ecology—is the product of intersections across a range of disciplines and topic areas, including species invasions, biodiversity loss, food webs, and community assembly/disassembly. Parasitological research has already made fundamental contributions to these topics, as we highlight below. However, as is perhaps unsurprising, these contributions have at times developed along independent trajectories from those in other disciplines, highlighting the need for greater integration and cross-application between fields. Stated another way, many findings from parasitology need to be communicated to a broader range of interested parties, while parasitology stands to benefit from enhanced integration of its research questions with those from other disciplines.

Past contributions of parasitology:

(1) Parasitology and scale: one of the most foundational concepts in community ecology is the importance of scale (Whittaker, 1960; Levin, 1992). How species interact with each other and the environment is strongly scale-dependent. This issue is arguably even more pronounced for parasites, which incur an "extra" scale in the form of the within-host level. Perhaps because of this natural nesting, the field of parasitology has long-embraced the importance of scale, specifically in the form of ecological level of organization. Building from Holmes and Price (1986), Bush et al. (1997) articulated the distinctions among the community of parasites within a single host (the infracommunity), the community of parasites within all hosts of a single species (the component community), and among all host species within the environment (the supracommunity). Importantly, however, these hierarchically nested levels of organization are linked through demographic and immigration-related processes—thus, the number and identity of parasite species at the regional scale will be a key determinant of what species are found locally, whereas the success of parasites within individual hosts and host populations can reciprocally influence the regional distribution of parasites. This potential for bi-directional linkages across scales is a key tenet of metacommunity theory in ecology (Leibold et al., 2004; Holyoak et al., 2005), which builds from metapopulation theory by recognizing the linked nature of species interactions in communities across the landscape.

(2) Ecological filters and emergence: a fundamental challenge in the study of emerging infections is understanding when a parasite will "jump" or "spillover" from 1 host into another. Depending on the type of parasite, host, and environment, this type of ecological event may be extremely rare or relatively frequent, but it has enormous implications for topics ranging from evolutionary diversification to forecasting pandemics. A consideration of the factors likely to influence parasite spread and establishment has long been central to parasitology. In his 2001 book, Claude Combes built upon earlier notions (Euzet and Combes, 1980) to develop what he termed the encounter and compatibility filters of host–parasite relationships. The encounter filter is the probability of a particular host and parasite species encountering one another, which is influenced by geographic distribution, behavior, and local habitat use. Thus, a host and parasite occurring on opposite sides of the globe would be less likely to encounter one another, just as a parasite with soil-borne infectious stages might be less likely to encounter a strictly arboreal host. The compatibility filter focuses on the likelihood of the host and parasite living together "durably" following contact; i.e., how likely is the parasite to be able to both infect a potential host and establish a persistent infection thereafter? Compatibility was hypothesized to be a function of both the host offering the necessary resources needed by a parasite while lacking highly effective defensive mechanisms against its establishment or persistence. The degree to which each filter is open or closed will determine whether infection can occur—a framework that is applicable both across different spatial scales and over variable temporal scales (ecological to evolutionary). These same issues form the foundation of much contemporary research focused on spillover and disease emergence (Power and Mitchell, 2004; Parker et al., 2015, Plowright et al., 2015), although the number of filters considered can be increased substantially.

(3) Decoy effect and the dilution effect: a current debate in disease ecology focuses on the role of host biodiversity in affecting parasite transmission and disease risk (e.g., Civitello et al., 2015). The dilution effect hypothesis posits that higher levels of host diversity will often reduce disease risk because of the progressive addition of less-suitable host species (Ostfeld and Keesing, 2012; Johnson et al., 2015b). While often framed as a relatively recent line of inquiry emerging from the literature on biodiversity and ecosystem function, parasitologists have studied a similar phenomenon for more than 50 yr. Termed the "decoy effect" by Chernin (1968), this field of study has examined the role of alternative hosts, predators, and physical obstructions in inhibiting the ability of parasites to get from 1 host to another. In particular, many of these studies have focused on the free-living infectious stages of macroparasites and their sensitivity to the abiotic and biotic environmental conditions, which may be especially important given the short life span of some of these stages (Thieltges et al., 2008). For instance, "decoy" snail species can dramatically reduce the ability of schistosome miracidia to find suitable host snails—a result that has been thoroughly demonstrated in both laboratory and field conditions (Johnson et al., 2009). Such findings have the potential to inform or complement applied management strategies, especially in light of species' losses (local extirpations) and additions (invasions). Research on the decoy effect has helped to illustrate the diverse range of mechanisms through which community changes can alter transmission (Johnson and Thieltges, 2010), often through experimental manipulations,

which represents an important complement to much of the field-based correlational studies on the dilution effect.

(4) Parasite communities and their potential for interaction: the potential for coinfecting parasites to interact is a topic of increasing prominence in many fields associated with disease research. Multi-pathogen interactions have recently been implicated as influential in a number of human and wildlife diseases, such as HIV and malaria in humans, colony collapse disorder in honeybees, and emerging infections in coral reefs (Bentwich et al., 1995; Cooney et al., 2002; Druilhe et al., 2005; Bromenshenk et al., 2010). Such interactions can be direct, as might occur when multiple parasites compete over a shared resource (e.g., red blood cells), or be indirect, typically mediated through changes in host immune function (apparent competition and apparent facilitation). Similarly, the topic of parasite competition has a well-established history within parasitology, often focusing on changes in the within-host distribution of a parasite in the presence of a second species (i.e., changes between the fundamental and realized niche) (Poulin, 2007). Notably, this research includes an extensive suite of experiments. While many past studies have focused on particular pairs of parasite species, Holmes and Price (1986) suggested that entire communities of parasites within hosts can be considered along a continuum between "isolationist" and "interactive" communities. Isolationist communities are characterized by low colonization rates, high beta diversity, and unsaturated communities, for which the importance of parasite interactions is expected to be low. In contrast, parasite interactions are a key feature of interactive communities, for which parasite populations are closer to capacity, resources are limiting, and alpha diversity is high (Dove and Cribb, 2006). Although the existence and utility of this proposed continuum has been debated within parasitology, this previous body of research has much to contribute to contemporary studies of coinfection, the microbiome, and the regulation of parasite communities.

Future contributions of parasitology: The potential for future contributions from the field of parasitology to the study of ecological communities is extensive. While such study will provide specific insights about the nature of parasite communities, it can also offer more general inference about communities generally. In many respects, interactions between hosts and parasites offer an ideal system in which to explore questions about metacommunity theory (Seabloom et al., 2015). Because of their natural hierarchy, with parasites nested within hosts that are themselves nested within host populations and communities, many of the challenges associated with artificial habitat delineation are avoided (see Zelmer and Seed, 2004; Richgels et al., 2013). Testing when and how interactions within a host (i.e., among parasites) are likely to have effects beyond the individual host, such as on transmission among hosts, is a key challenge for such research. Moreover, parasites offer great opportunities to more rigorously quantify the influence of forces such as dispersal and niche factors (e.g., host suitability, parasite interactions) against neutral processes (e.g., demographic and environmental stochasticity). Using experimental treatments to clear hosts of infection, which are well-established for many parasites, could also afford chances to look at patterns of parasite community re-assembly and the degree to which they are deterministic (and therefore predictable) versus more stochastic, for which random variation as well as "priority effects" can play important roles. ?3

Research in parasitology can also help to shed light on questions focused on hosts and their communities. Disease ecology has recently emphasized the importance of quantifying the separate yet related features of resistance, or the capacity of a host to resist infection given exposure, and tolerance, or the ability of a host to minimize pathology given infection (Råberg et al., 2009). Although often presented from a "host-centric" perspective, these processes represent the interaction between host and parasite and align with components of the ecological filters proposed by Combes. Such processes have relevance both at the scale of individual hosts and host species; considerable effort in disease ecology has recently focused on heterogeneity—why do some individual hosts (e.g., superspreaders) or host species (e.g., amplification hosts) have such disproportionate roles in transmission? Linking such topics within the resistance-tolerance framework might lead to characterization of "super-spreading" or "supershedding" individuals as hosts with low resistance but high tolerance, while "dilution" or "decoy" hosts might be those species with high resistance and a high encounter probability. The experimental tractability of some parasite systems for infection studies alongside opportunities to explicitly quantify processes such as initial infection success, establishment, parasite aggregation, and clearance is especially important in understanding this mechanism (Johnson et al., 2011; LaFonte et al., 2015). From a community standpoint, understanding how the addition or removal of particular hosts affects transmission remains a key challenge for biodiversity-disease theory. The long and successful history of parasitology in this regard could be therefore highly beneficial, particularly if combined with field-relevant data on how host communities assemble and disassemble (Johnson et al., 2013).

FUTURE MUTUALISMS BETWEEN PARASITOLOGY AND DISEASE ECOLOGY?

Given the emerging influence of disease ecology as detailed in earlier sections, as well as the past and future benefits of integration between the 2 fields, we emphasize the existence of important yet underutilized opportunities for parasitologists to bring their research to the forefront of this field. In Table II for instance, we highlight "frontier topics" that further demonstrate instances where cooperation and integration between the 2 disciplines may be mutually beneficial. These range from within-host to ecosystem scales and include both empirical and theoretical approaches. Looking forward, we advocate for increased interactions among researchers engaged in parasite-related research to facilitate and promote complementary and interdisciplinary approaches that maximize the strengths of all parties. For instance, there are likely host–parasite systems that would make ideal models for disease ecology–related questions or that can contribute existing data into larger conceptual frameworks, but these rely on communication and awareness to identify such opportunities. Realizing the full potential contributions of parasitological research to disease ecology requires a concerted effort by both fields to recognize the prospective benefits of increased interactions. We suggest better linkages among professional societies, such as joint meetings or special symposia, as 1 possible initiative. Notably, the mission statements of parasito-

TABLE II. Examples of parasite-related “frontier topics” of current focus in disease ecology.

Topic	Questions	Related study examples
Biodiversity and the dilution effect	How do realistic changes in ecological communities change parasite transmission and disease risk? Through what mechanisms? How are ongoing patterns of biodiversity loss and invasions likely to influence parasites and infectious diseases?	Johnson and Thieltges (2010); Wood and Lafferty (2013); Civitello et al. (2015)
Coinfection and multi-parasite communities	Can we predict when parasite interactions will affect both within-host processes (e.g., exposure, pathology) as well as among-host processes (e.g., population-level transmission)? How do we move beyond studying pairwise combinations of parasites to embrace the full complexity of symbiont assemblages?	Pedersen and Fenton (2007); Ezenwa and Jolles (2015)
Metabolic theory and parasites	Can the metabolic theory of ecology be used as a framework to understand changes in host–parasite interactions with climate shifts?	Hechinger et al. (2011); Altizer et al. (2013); Hechinger (2013); Molnár et al. (2013); Rohr et al. (2013)
Disease macroecology	To what extent do parasites and other symbionts follow the same macroecological “rules” associated with free-living organisms? Can this information be used to enhance our understanding of global parasite biodiversity and the identification of disease hotspots?	Morand and Krasnov (2008); Dunn et al. (2010); Kamiya et al. (2014); Poulin (2014); Smith et al. (2014); Torchin et al. (2015)
The interface between parasitology, community ecology, and ecosystem science	How do parasites and pathogens affect community- and ecosystem-scale processes, including nutrient cycling, disturbance regimes, primary production, and community composition?	Wood et al. (2007); Johnson et al. (2015a); Lafferty et al. (2015); Preston et al. (2016)

logical journals may largely overlook the many ecologically- and evolutionary-themed papers that they publish, and this quite likely acts as a deterrent to investigators outside of parasitology to consider these as outlets for their research in favor of ecological journals.

Despite our definitions of parasitology and disease ecology as separate fields, the case examples and frontier topics included here make it quite clear that there is considerable natural overlap between them. Importantly, the distinctions and separation may be largely artificial and somewhat self-imposed, as well as driven by a lack of communication and interaction. Basic conceptual differences and varying terminology also likely obscure commonalities while emphasizing differences. For instance, disease ecology has obviously historically focused on disease-causing organisms, with its recent emergence largely driven by the value of incorporating an ecological approach to understanding outbreaks of vectored pathogens in humans and domesticated animals (Wilcox and Gubler, 2005; Granter et al., 2014; Ostfeld, 2014), and does not necessarily consider the full suite of less harmful host–parasite interactions that might be studied by parasitologists in an ecological context. However, disease ecologists do study hosts and/or parasites not regularly associated with epidemics/epizootics, as well as processes not always related to disease per se. The use of different terms that are conceptually identical also poses a barrier to recognizing that the line between parasitologists and ecologists is often blurred, or marginal (see Bush et al., 1997). One might thus consider whether disease ecology is actually a sub-discipline of parasitology specializing in disease-causing parasites. Such difficulties in delineating these 2 fields illustrate the need for better integration and for parasitologists to consider the broader context of their activities.

However, the greatest impact on parasitology with respect to the emergence of disease ecology as a discipline will be on current and future students. With respect to undergraduate education, “hybrid” courses that span both disease ecology and parasitology could provide a creative strategy to maintain and promote traditional expertise, also providing disease ecologists with critical background and hands-on training, particularly if the popularity of such courses facilitates a laboratory component to promote skills ranging from dissections and microscopy to modeling and simulations. Trainees engaging in parasite-related research are well-positioned to take advantage of the growing interest in disease ecology and the resultant opportunities by marketing themselves more widely and considering how their skills fit into a broader context. In turn, principal investigators also bear a responsibility to identify changes in their discipline and communicate these to students and trainees along with more comprehensively training personnel and seeking opportunities for cross-fertilization. With such efforts, the field of parasitology will be well-poised to continue making important contributions for many years to come and to take a larger role in leading the critical questions that disease ecology must tackle.

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