

Finding Them Before They Find Us: Informatics, Parasites, and Environments in Accelerating Climate Change

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ABSTRACT: Parasites are agents of disease in humans, livestock, crops, and wildlife and are powerful representations of the ecological and historical context of the diseases they cause. Recognizing a nexus of professional opportunities and global public need, we gathered at the Cedar Point Biological Station of the University of Nebraska in September 2012 to formulate a cooperative and broad platform for providing essential information about the evolution, ecology, and epidemiology of parasites across host groups, parasite groups, geographical regions, and ecosystem types. A general protocol, documentation–assessment–monitoring–action (DAMA), suggests an integrated proposal to build a proactive capacity to understand, anticipate, and respond to the outcomes of accelerating environmental change. We seek to catalyze discussion and mobilize action within the parasitological community and, more widely, among zoologists and disease ecologists at a time of expanding environmental perturbation.

KEY WORDS: documentation–assessment–monitoring–action, climate change, biodiversity, emerging infectious disease, parasites, hosts, epidemiology, ecology, evolution.

STOCKHOLM PARADIGM

Parasitology finds itself in a time of exciting possibilities. During the past generation, parasites have become recognized as significant components of both biological diversity and as excellent model systems for general evolutionary (Brooks and McLennan, 1993) and ecological (Poulin, 1997; Poulin and Morand, 2004) studies. At this time, there is growing interest in parasites as we begin to understand more and more that there are direct connections among climate change, biodiversity dynamics, and emerging infectious disease (EID). Parasites occupy a central role in efforts to develop proactive protocols for monitoring changes in ecosystem structure and for detecting the potential for emerging disease in resident and colonizing host species, be they human, livestock, or wildlife (Daszak et al., 2000; Brooks and Hoberg, 2006, 2008, 2013;

Patz et al., 2008; Agosta et al., 2010; Hoberg, 2010; Weaver et al., 2010; Hartigan et al., 2012; Altizer et al., 2013; Hoberg and Brooks, 2013). Parasites, especially those with specialized transmission dynamics, including complex life cycles, are not only agents of disease in humans, food-animal resources, crops, and wildlife, they are also powerful representations of the ecological and historical context of the diseases they cause (Dobson and Hudson, 1986; Dobson and May, 1986a, b; Dobson and Carper, 1992; Hoberg, 1997; Dobson and Foufopoulos, 2001; Marcogliese, 2001, 2005; Nieberding and Olivieri, 2007; Hoberg and Brooks, 2008; Hoberg et al., 2008; Rosenthal, 2008; Lafferty, 2009; Kilpatrick, 2011; Kuris, 2012). This is especially true for eukaryotic parasites.

Recognizing this nexus of professional opportunities and global public need, we gathered at the Cedar Point Biological Station of the University of Nebraska in September 2012 for a workshop to discuss the possibility of developing a cooperative

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platform for providing essential information about the evolution, ecology, and epidemiology of parasites broadly across host groups, parasite groups, geographical regions, and ecosystem types. Here we summarize our discussions and make some recommendations. We seek to catalyze discussion and mobilize action within the parasitological community and, more widely, among zoologists and disease ecologists, conservation biologists, and those in the policy arena at a time of expanding environmental perturbation.

Parasites are primary components of environmental change and, concurrently, contribute to developing a nuanced understanding of ecosystems in transition because they allow the incorporation of biological insights across considerable spatial and temporal scales. Parasites and parasitologists reside at the expanding nexus of interacting crises of biodiversity, climate stability and change, and emerging infectious diseases (Brooks and Hoberg, 2013; Mora and Zapata, 2013). Clearly, a substantial and potentially irreversible challenge to the distribution and continuity of biodiversity, ecosystem integrity and sustainability, and socioeconomic stability, through changing interfaces and ecotones, influencing patterns of disease, emerges directly from the footprint of accelerating climate warming and its attendant environmental perturbation (e.g., Parmesan and Yohe, 2003; Lovejoy and Hannah, 2005; Patz et al., 2005; Lawler et al., 2009; Post et al., 2009; Weaver et al., 2010; IPCC, 2007a, b, 2013; Meltote et al., 2013). Equally clearly, the nature, scope, and scale of anthropogenic climate warming are pervasive, and anticipating unprecedented perturbation across the biosphere necessitates both the incorporation of historical and contemporary insights regarding the structure and distribution of biodiverse systems as well as the development of novel integrative approaches to serve as a framework in which to understand the impacts and effects of such change.

In this arena, we increasingly recognize that faunal assembly (structure and diversification) among hosts, parasites, and pathogens has often been associated with ecological perturbation as a driver of geographic and host colonization at varying spatial and temporal scales over Earth's history (e.g., reviewed in Hoberg and Brooks, 2008, 2010). In short, parasite diversification has unfolded (in part) through episodic shifts in climate and environmental settings in conjunction with both ecological mechanisms and host switching (e.g., Hoberg and Klassen, 2002; Nieberding et al., 2008; Hoberg et al., 2012; Hoberg and Brooks,

2013). Such an ecocentric view of parasite diversification, tied to considerable complexity in ecological processes, counters more than a century of coevolutionary thinking about the nature of the development of host-parasite assemblages (for comprehensive reviews, see Brooks and McLennan, 1993, 2002; Janz, 2011). Further, the apparent significance of host colonization in diversification poses a "parasite paradox" (Agosta et al., 2010) that stems from 2 observations: (1) Parasites demonstrate specificity (restricted and apparently specialized host ranges) and are resource specialists; and (2) such specialization occurs even though shifts onto relatively unrelated hosts are common in the phylogenetic diversification of parasite lineages and are even often directly observable in ecological time.

The articulation of what we herein refer to as the "Stockholm paradigm" serves as a conceptual foundation for resolution of the parasite paradox and provides a new integrative view of complex associations grounded in both a considerable body of experimental observations and in core principles emanating from 4 academic generations of researchers at Stockholm University (for a review, see Brooks and McLennan, 2002; Agosta et al., 2010; Janz, 2011, and references therein). In this paradigm, the resolution of the parasite paradox emerges through integration of 4 key ecological and historical concepts: ecological fitting; the oscillation hypothesis; the geographic mosaic theory of coevolution; and taxon pulses. Ecological fitting (Janzen, 1985) drives substantial opportunities for accelerated host colonization, prior to the evolution of a novel spectrum of capabilities for host exploitation, and is a function of both phenotypic flexibility and phylogenetic conservatism in traits related to the use of broad-based resources. Consequently, specialists may be involved in host-range expansion through shifts under a dynamic of ecological fitting. The oscillation hypothesis describes events downstream, setting the stage for alternating trends in the evolution of generalists and subsequent new specialists (Janz and Nylin, 2008; Nylin et al., 2014). More generally, and over time, novel combinations of interacting species emerge through processes defined within the geographic mosaic theory of coevolution (Thompson, 2005). Whether referring to helminths of vertebrates or phytophagous insects, such symbiotic assemblages originate, exist, and persist in a crucible of accelerating change that serves to demonstrate the equivalence of processes for faunal assembly, including host and geographic colonization across spatial scales and

through evolutionary and ecological time (Hoberg and Brooks, 2008, 2010; Hoberg, 2010). Thus, considerable complexity arising from taxon pulses (Erwin, 1985; Halas et al., 2005) driven by climate change and large-scale ecological perturbation lead to extensive biotic mixing (and mosaics) and further serve as the antecedents for episodes of rapid host switching, including outbreaks of emerging infectious diseases (Brooks and Hoberg, 2007, 2013; Hoberg and Brooks, 2008, 2013; Agosta et al., 2010).

A contrast of the Stockholm paradigm with the more traditional paradigm of coevolution in defining the nature of complex host–parasite associations is apparent. As noted above, classical coevolutionary models predict that host colonization becomes less likely as the intensity of co-adaptive responses (microevolutionary phenomena) increase across the time frame of an association (i.e., parasites become more specialized to their hosts). Thus, in this context, it is assumed that the process of coevolution itself should provide a high degree of protection against emerging diseases because it becomes more and more difficult for increasingly specialized parasites to jump hosts. Two logical conclusions from this classical view emerge: (1) Host switches should be rare at all scales; and (2) when events of host colonization occur, there must be an underlying genetic change in the parasite that is its precursor, and this change determines the capacity to be associated with a novel host (e.g., Kilpatrick, 2011). This immediately shifts the focus of discussions about climate change and emerging diseases to center on the possible mechanisms by which climate forcing can influence the origins of novel genetic variation (and the conditions or environmental regime to try them out in, where the latter, but not the former, is consistent with the Stockholm paradigm). As a consequence, the expectation remains that because novel genetic innovations must lead the way, emerging diseases will be rare under the classical paradigm.

Counter to this relatively simple scenario for coevolution, the Stockholm paradigm, by contrast, predicts that emerging diseases—in the form of parasites of humans, livestock, crops (we include novel phytophagous pest insects and insect parasitoids of beneficial insects), and wildlife—will be common rather than rare events during episodes of climate change. Colonization is based on those genetic capacities historically retained within a particular system that provide the potential for switching related to ecological fitting. An implicit feature is the assumption of a large sloppy fitness

space (Agosta, 2006; Agosta and Klemens, 2008, 2009; Agosta et al., 2010) represented by an array of potential hosts from which most pathogens had been historically precluded by circumstances of time, space, and origin. Exposure of that space, and a concomitant increase in the rate and frequency of host colonization, cascades from accelerating climate change and associated events of biotic expansion. Concurrently, heightened rates of host switching are also predicted under this paradigm as habitats are disrupted and restricted and as patterns of sympatry among species are modified through range contraction and compression into increasingly reduced biogeographic areas.

The Stockholm paradigm also suggests an alternative pathway for addressing the implications of emerging disease. Over the past century, our expanding understanding of epidemiological processes has, for the most part, led to attempts to mitigate the damage posed by emergent diseases, with humanity tending to react to specific events as they occurred. Reactive management policies, however, are not economically sustainable, especially in the context of the Stockholm paradigm reflecting a fundamentally correct explanation of the evolution of interspecific associations. Thus, our largely reactionary mode for addressing outbreaks and ecological disruption could be supplanted by an additional strategy based on a proactive stance and tactics. In a mode defined as evolutionary risk assessment, we can use our knowledge of diversity, past environments, and biological processes in the context of the paradigm to aid in anticipating the future in a world of rapid change. While, like climate change, we cannot stop emerging diseases, we believe and suggest that a path to proactive risk management is less expensive, and thus more effective, than responding in the aftermath of an emerging crisis.

Parasitologists have 3 major contributions to offer in what we hope will become a more inclusive discussion of the relationships among climate change, emerging disease, and biodiversity dynamics. First, some of our organisms, much like the bacteria and viruses that occupy so much press attention and reporting on emerging diseases, cause acute and chronic diseases in humans, livestock, crops, and wildlife. Second, our organisms track broadly through ecosystems and, as such, reveal much about the trophic structural context of disease transmission. Finally, though there is still much to learn, we know a lot about our organisms, their evolution, and their

ecology. Clearly, this is a complex phenomenon, but a combination of technical advances, empirical experience, and a strong recognition of the need for, and importance of, baseline data to understand the structure and history of the biosphere has given us an integrative approach by which we as parasitologists can contribute in a proactive and adaptive manner towards a solution.

WHERE TO BEGIN

Proper valuation of biodiversity on scales from local to global depends on information derived from systematics. Biologists implicitly acknowledge that an understanding of systematics is the underpinning of all of the life sciences whenever they attach a species name to the organisms they are studying. Systematics is the branch of biology charged with the responsibility of making certain that every biologist who uses a particular name actually refers to “the same thing.” Since Darwin, the assignment of a specific epithet to a group of organisms has been the proposal of a hypothesis that those organisms belong to what Darwin (1872) termed “communities of descent.” That is, they are members of a diagnosably inclusive and mutually exclusive hereditary information system. As a result, the names we assign to the organisms we study are indices of information—not just about unique identity, but about an array of characteristics ranging from their reproductive biology to their development, ecology, and behavior, e.g., all the traits that, when combined, characterize their life and lifestyle. This gives rise to the adage “No name, no information; wrong name, wrong information.” The seemingly inexhaustible potential of evolutionary diversification means that each species is marked by always amazing, often surprising, and sometimes extremely subtle, diagnostic differences requiring considerable taxonomic expertise to recognize and distinguish (e.g., Makarikov et al., 2013). Because no 2 species are the same, no matter how closely related, it is therefore essential to know with what you are dealing. The crucial nature of proper identification has been underscored for research as disparate as the study of parasites and sexual selection (e.g., McLennan and Brooks, 1991), of parasites as bio-indicators (e.g., Frank et al., 2013), and of parasites as biodiversity probes (Gardner and Campbell, 1992).

A second function of systematics is generating phylogenies, which are fundamental for all comparative evolutionary studies (Brooks and McLennan, 1991, 1993, 2002). Darwin’s insight that all commu-

nities of descent are related to each other in a tree (in part a reticulating network) of life led to his dictum that the most likely explanation for similarity is inheritance from a common ancestor and not existence in common environments. This explains the massive evidence indicating that most aspects of the biology of parasites, including their ecology and behavior, are phylogenetically conservative, something anticipated by Harold Manter (1966) when he coined the term “parascript” (see Brooks and McLennan, 1993).

Parasitology, like most disciplines, suffers from the “taxonomic impediment,” the global shortage of professional taxonomists and systematists (GTI, 1999), and it cannot be clearer that the need for expert taxonomists is now greater than ever in the past. In parallel, recognition of the taxonomic impediment emphasizes not just the need to develop and use our increasingly valuable existing archival collections of voucher specimens of hosts and parasites at all spatial scales, but also the need for a concomitant expansion of informatics resources to describe the biosphere. Although we encourage all countries and institutions to train and hire more taxonomists and to support museum infrastructure, we are realistic. In the short term, at least, we cannot assume that additional resources will be allocated for this important purpose. As a consequence, it becomes even more imperative that existing taxonomists cooperate both with each other and with other biodiversity specialists (for an extensive discussion of the benefits of such cooperation, see Brooks and McLennan, 2002).

In the following, we propose a general protocol, with the acronym DAMA, which we believe can be a blueprint for many different cooperative efforts. DAMA is our name and rationale for documentation–assessment–monitoring–action, an integrated proposal and rationale to build a proactive capacity to understand, anticipate, and respond to the outcomes of accelerating environmental change.

Document

For all biodiversity inventories, including those for parasites, the more we look, the more species we find. Moreover, the more we find, the more information about these species we discover. To make significant progress in understanding complex biological interactions globally, we need to know what parasites exist in as many different parts of the planet as possible (Hoberg, 1997; Brooks and Hoberg, 2000; Hoberg et al., 2013). This will require comprehensive taxonomic inventories. Importantly, and to maximize information content, each species name used in any

such inventory needs to be linked to voucher specimens available in properly maintained state-of-the-art archival collections with direct links to informatics resources describing specimen-associated ecological, phylogenetic, and population-level data (Frey et al., 1992; Haverkost et al., 2010; Cook et al., 2013). We cannot emphasize enough the need for a major sea change in the parasitological tradition of maintaining private collections, as these limit data information and sharing during a time of decreasing resource availability and change.

In addition to knowing what parasites occur in any given area, we also need to know how to find specimens of each particular parasite species when needed. As well, we need to know as much as possible about the natural history of each parasite species, especially with respect to its geographic origin, transmission dynamics, microhabitat preferences, and host range (e.g., what parasite species are present, when they are there, in what hosts, and in what parts of the hosts they are found in, and how they are transmitted).

It appears now that 1 of the most efficient ways to summarize this globally available species-specific data is through the construction of digital home pages for each species, as envisioned in the international initiative called the *Encyclopedia of Life* (www.eol.org). In order for inventory information to be maximally useful, all cooperating research groups must agree to share such information, and, ideally, all such inventory information should be stored in a form that can be updated in real time and that is freely and readily available on the internet, as embodied in the *Global Biodiversity Information Facility* (www.gbif.org).

Assess

Every species has a story to tell, and that story is fundamentally a story of descent with modification, meaning common ancestry, in the context of the selective crucible of a multivariate and changing set of environmental conditions through which each hereditary lineage passes. Species-specific information about ecology, behavior, and geographic distributions, examined in an evolutionary (i.e., phylogenetic) context, provides far more information than a simple list of species and their known properties (Brooks and McLennan, 2002), and this fundamentally Darwinian perspective is amplified in the case of parasites. Manter (1966) stated that parasites always tell not just the stories of their own ecology, but also that of their hosts and of the geographic distributions and complex ecosystems in which they live and evolve. He called

for a research program integrating systematics, ecology, and biogeography, which he termed parascript. Parasite phylogenies began to appear in the late 1970s, and many of the initial studies integrating phylogeny, ecology, and biogeography used parasite systems as exemplars (Brooks, 1985; see summaries in Brooks and McLennan, 1991, 1993, 2002; Hoberg and Klassen, 2002). The coherent research program for Parascript that emerged in the early 1990s (Brooks and McLennan, 1993) has catalyzed, and continues to catalyze, significant basic research in this field.

In the past 15 yr, a case has been made that significantly greater information relevant to climate change, biodiversity dynamics, and emerging disease, that is, the critical information needed for making proactive, anticipatory policies, results when parasite biodiversity inventories are placed in an evolutionary context (Gardner and Campbell, 1992; Hoberg, 1997; Brooks and Hoberg, 2000, 2013; Hoberg et al., 2008). For this reason, we need a relevant and powerful paradigm—one that explains not only the dynamics of maintaining a pathogen in association with a particular host in a particular ecosystem, but one that also explains historical origins and how such associations can change rapidly in response to rapidly changing environments. The Stockholm paradigm provides such a foundation (see, e.g., Agosta et al., 2010, and references therein).

Monitor

We want to develop proactive and anticipatory policies for using basic information about parasites in climate change, biodiversity, and emerging disease. This approach will require that we monitor the parasite diversity documented in our inventories. Moreover, we must also be able to recognize distributional and ecological changes as soon as they occur, and we must know if those changes are unusual. This means we need to document not just parasite diversity in each area inventoried through time, but that inventories also need to be large scale across both time and space. Such an approach emphasizes that basic inventory work needs to be an ongoing process—it is not enough to collect parasites in 1 place at 1 time, as patterns can only be detected by sampling over wide geographic areas (Gardner and Campbell, 1992; Hoberg et al., 2008). Such an approach will allow us to compare findings within and among given places over time, and we envision a network of information growing in space and time that will be capable of alerting us to not just shifting spatial and ecological boundaries but also to

the critical changes in 1 place that will allow us to anticipate similar changes in other areas (e.g., Polley and Thompson, 2009).

Documentation, surveillance, and the monitoring of parasite biodiversity can encompass a continuum that collectively contributes to informatics resources of the highest quality (e.g., Hoberg et al., 2013). Across this spectrum are: (1) targeted taxonomic studies of single species of parasites; (2) limited surveys in single host species, perhaps at a restricted number of localities; (3) surveys and inventories at the ecosystem level based on standardized and comprehensive sampling protocols; and (4) fully integrated inventories of hosts and parasites and the application of population genetics/phylogeography to explore associations on both fine temporal and spatial scales. Ecosystem approaches and geographic coverage from landscape to regional scales feed into archival collections (parasites, hosts, and tissues) held in museum repositories and become the cornerstone for establishing baselines for parasite faunal diversity, abundance, epidemiological, populational, and spatial patterns, and disease emergence over time. Linked with phylogeny and biogeography on varying spatial and temporal scales, these provide a window into change in the biosphere across both evolutionary and ecological time (Hoberg, 1997; Brooks and Hoberg, 2000). Further, such essential inventory information can provide the data required for the development of modeling protocols to examine various scenarios for both environmental change and the distribution of disease (Waltari and Perkins, 2010) and can serve to validate predictions about biological outcomes, including events of ongoing geographic colonization and host switching (e.g., Hoberg et al., 2013; Kutz et al., 2013).

To maximize the efficient use of limited resources, parasite monitoring programs should be fully integrated with efforts to document and archive host diversity. Those of us who conduct parasite inventories have often had the frustrating experience of dealing with people who very much want information from us about the parasites of the hosts they are studying, and who are incredulous when we tell them such information, in most cases, does not exist. Those same investigators often refuse to allow destructive sampling of "their" organisms in order to provide the information they desire. Similarly, parasitologists who discard host carcasses after extracting the parasites waste critical data regarding the ecological and evolutionary context within which the parasites exist. They miss the opportunity to maximize the impact of their efforts and the value of their data. In short, increased

cooperation between parasitologists and those who study host taxa has the potential to enhance the productivity of both realms of investigation, as well as to foster and open new paths of inquiry.

The appropriate application of molecular tools offers an important way in which to facilitate the description of complex parasite communities, though this approach does not stand alone. For example, the technique popularly known as genetic or DNA barcoding offers the possibility of performing nondestructive monitoring of hosts for parasites. This creates the potential to shift from logistically challenging field collections, necropsy, and morphological characterization based on assessments of a few hosts to more geographically extensive, site-intensive, and near-simultaneous sampling across ecosystems, thus linking landscape to regional scales for assemblages of host species and populations (e.g., Jenkins et al., 2005; Kutz et al., 2007). This means we now have or can develop the capacity to more readily assess parasite impacts on host species that are rare or endangered. As well, barcoding provides a quick and cost-effective means of establishing transmission patterns, since larvae and juveniles of any given species of parasite in a particular place will have the same barcode profile. Clearly, an understanding of transmission dynamics is a critical element of assessing the ecological context of parasites in their environments.

Barcoding alone, however, is inadequate for documenting and assessing parasite diversity; among some groups of flatworms, for example, barcoding applications remain challenging (Vanhove et al., 2013). There are 2 reasons for this inadequacy. First, barcodes by themselves do not provide a direct link to a species name, and it is only when a particular barcode, or set of barcodes, is validated relative to a physical morphospecies already linked to a name that it can be used to index the information about the species it represents. In short, it is only at that point that barcodes can become useful tools in assessment and monitoring. Importantly, there may also be significant issues associated with determining the precise number and identity of species represented by a set of barcodes that are obtained without reference to the specimens from which they have been derived.

While barcoding is thus an excellent alternative to destructive sampling for assessing transmission dynamics and for monitoring parasite diversity, it does not eliminate the need for some destructive sampling during the basic documentation phase of inventorying. This means that we as parasitologists

must continue to cooperate with host specialists in order to minimize destructive sampling—even in some cases foregoing any destructive sampling of particular host species. On a positive note, however, such destructive sampling can provide a means for making barcoding more time- and cost-effective. If, for example, 1,000 pinworms occur in the rectum of a *Chauna marina* (cane toad), a barcoder working alone would need to analyze all 1,000 worms to determine how many species were present. Working in concert with a parasite taxonomist, who can recognize that all 1,000 worms belonged to a single species, would enable the barcoder to save both considerable time and expense. Some of the most spectacular successes of barcoding have occurred when a systematist or ecologist had presorted a collection of specimens in this manner (e.g., Burns et al., 2008).

Looping back and reassessing: Monitoring is not just about redocumenting. It is also about reassessing. When ongoing documentation and monitoring produce new findings, we must ask important reassessment questions, such as: What is missing? What is new? What transmission dynamics need to be determined? Are new transmission dynamics implied by new host records? Does anything need to be redetermined? How has the environment changed or shifted over time? Significantly, those regions of the world where monitoring for EIDs is most badly needed are precisely where such reassessment should immediately take place. For example, high-latitude systems are under rapidly accelerating change and are among the most sensitive environments on the planet and thus require continued reassessment, and the ongoing work to survey and inventory complex host–parasite systems has already demonstrated substantial ecological perturbation in both marine and terrestrial habitats (e.g., Hoberg et al., 2013; Kutz et al., 2013; Melfo et al., 2013). Thus, collaborative reassessment efforts across boundaries should be made in order to enable research groups to maintain already ongoing monitoring programs and in order to offer uninterrupted continuity during the development of basic research on the parasite diseases of both humans and wildlife. Decidedly, this will not happen if efforts are dispersed and not focused on precise aims.

Act

“To be forewarned is to be forearmed.” —Robert Greene, 1592 (or earlier)

Our call to action asks parasitologists to propose and implement policies for dealing with the inter-

twined crises of climate change, biodiversity, and emerging diseases based upon basic and sound biological principles. Those policies necessarily involve matters of socioeconomic development. More than most other biologists, parasitologists live in a research milieu in which basic and applied research programs are inextricably linked, so we should all have a deep understanding of this perspective and its importance. We believe that the most at-risk part of the biosphere is the source of our scientific infrastructure—technological humanity.

We also believe that the development of effective action plans for coping with the complexity of climate change, biodiversity, and emerging diseases begins with accepting that there is a critical need and that time is short. To the extent that we cannot stop or reverse climate change, we also cannot stop diseases from emerging. Clearly, the accumulation of pathogen pollution creates an increasing economic burden for humanity, and we know that preventing or anticipating problems is cheaper than crisis response. Therefore, if we do not want EIDs to become an unsustainable economic burden, we need to be proactive. We are not suggesting that humanity stop responding to crises as they occur, but we believe that there are economic reasons to attempt to anticipate problems, to mitigate them when possible, and to only respond rapidly to them when such mitigation fails. We cannot stop or reverse the climate change events that are occurring, but we can mitigate circumstances or adapt to them, at least in some situations (IPCC, 2007a, b, 2013).

Human knowledge is the basis of human adaptation. Phylogenetic conservatism—stored information about past evolutionary successes—is the primary source of evolutionary adaptability. This is the reason assessments need to tie inventory information to as much as is known about the evolutionary history of each parasite species and its closest relatives. The action plan implied in this proposal requires integrated knowledge of the past, present, and future. What *were* the drivers of emerging disease in the past, and how can we learn from them? What *is* happening now, and what factors are currently inhibiting or driving such changes? We simply must know more about the world in which we live. Finally, what future events *may* we anticipate that will be similar to what we know about the past and present?

We do not think our proposal is the only way to proceed, nor do we think that in all cases it will prove to be either feasible or the best pathway forward. We do, however, believe our proposal has merit,

especially in terms of linking human activities with basic evolutionary principles. As well, our proposal provides a framework for cooperation among many specialists and their institutions throughout the world, and it is based on the recognition of a common need. If we do not cooperate now, we will surely face far fewer options for mitigating or alleviating the impacts of global environmental change in the future.

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LITERATURE CITED

- Agosta, S. J.** 2006. On ecological fitting, plant–insect associations, herbivore host shifts, and host plant selection. *Oikos* 114:556–565.
- Agosta, S. J., N. Janz, and D. R. Brooks.** 2010. How generalists can be specialists: resolving the “parasite paradox” and implications for emerging disease. *Zoologia* 27:151–162.
- Agosta, S. J., and J. A. Klemens.** 2008. Ecological fitting by phenotypically flexible genotypes: implications for species associations, community assembly and evolution. *Ecology Letters* 11:1123–1134.
- Agosta, S. J., and J. A. Klemens.** 2009. Resource specialization in a phytophagous insect: no evidence for genetically based performance tradeoffs across hosts in the field or laboratory. *Journal of Evolutionary Biology* 22:907–912.
- Altizer, S., R. S. Ostefeld, P. T. J. Johnson, S. Kutz, and C. D. Harvell.** 2013. Climate change and infectious diseases: from evidence to a predictive framework. *Science* 341:514–519.
- Brooks, D. R.** 1985. Historical ecology: A new approach to studying the evolution of ecological associations. *Annals of the Missouri Botanical Garden* 72:660–680.
- Brooks, D. R., and E. P. Hoberg.** 2000. Triage for the biosphere: the need and rationale for taxonomic inventories and phylogenetic studies of parasites. *Comparative Parasitology* 68:1–25.
- Brooks, D. R., and E. P. Hoberg.** 2006. Systematics and emerging infectious diseases: from management to solution. *Journal of Parasitology* 92:426–429.
- Brooks, D. R., and E. P. Hoberg.** 2007. How will global climate change affect parasite–host assemblages? *Trends in Parasitology* 23:571–574.
- Brooks, D. R., and E. P. Hoberg.** 2008. Darwin’s necessary misfit and the sloshing bucket: the evolutionary biology of emerging infectious diseases. *Evolution Education and Outreach* 1:2–9.
- Brooks, D. R., and E. P. Hoberg.** 2013. The emerging infectious disease crisis and pathogen pollution: a question of ecology and evolution. Pages 215–229 in K. Rohde, ed. *The Balance of Nature and Human Impact*. Cambridge University Press, Cambridge, UK.
- Brooks, D. R., and D. A. McLennan.** 1991. *Phylogeny, Ecology and Behavior: A Research Program in Comparative Biology*. University of Chicago Press, Chicago, Illinois. 441 pp.
- Brooks, D. R., and D. A. McLennan.** 1993. *Parascript: Parasites and the Language of Evolution*. Smithsonian Institution Press, Washington, DC. 429 pp.
- Brooks, D. R., and D. A. McLennan.** 2002. *The Nature of Diversity: An Evolutionary Voyage of Discovery*. University of Chicago Press, Chicago, Illinois. 668 pp.
- Burns, J. M., D. H. Janzen, M. Hajibabaei, W. Hallwachs, and P. D. N. Hebert.** 2008. DNA barcodes and cryptic species of skipper butterflies in the genus *Perichares* in Area de Conservación Guanacaste, Costa Rica. *Proceedings of the National Academy of Sciences* 105:6350–6355.
- Cook, J., C. Brochman, S. L. Talbot, V. Fedorov, E. Taylor, R. Väinölä, E. P. Hoberg, M. Kholodova, and M. Magnuson.** 2013. Genetics. Pages 514–539 in H. Meltotte, ed. *Arctic Biodiversity Assessment—Status and Trends in Arctic Biodiversity*. Conservation of Arctic Flora and Fauna, Arctic Council, Akureyri, Iceland.
- Daszak, P., A. A. Cunningham, and A. D. Hyatt.** 2000. Emerging infectious diseases of wildlife—threats to biodiversity and human health. *Science* 287:443–449.
- Darwin, C.** 1872. *The Origin of Species*, 6th ed. John Murray, London, U.K. 492 pp.
- Dobson, A., and R. Carper.** 1992. Global warming and potential changes in host–parasite and disease vector relationships. Pages 201–220 in R. L. Peters and T. E. Lovejoy, eds. *Global Warming and Biological Diversity*. Yale University Press, New Haven, Connecticut.
- Dobson, A., and J. Foufopoulos.** 2001. Emerging infectious pathogens of wildlife. *Philosophical Transactions of the Royal Society of London, Series B* 356:1001–1012.
- Dobson, A. P., and P. J. Hudson.** 1986. Parasites, disease and the structure of ecological communities. *Trends in Ecology and Evolution* 1:11–15.
- Dobson, A. P., and R. M. May.** 1986a. Disease and conservation. Pages 345–365 in M. E. Soulé, ed. *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, Massachusetts.
- Dobson, A. P., and R. M. May.** 1986b. Patterns of invasions by pathogens and parasites. Pages 58–76 in H. A. Moore and J. A. Drake, eds. *Ecology of Biological Invasions of North America and Hawaii*. Ecological Studies 58. Springer-Verlag, New York, New York.

- Erwin, T. L.** 1985. The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. Pages 437–472 in G. E. Ball, ed. *Taxonomy, Phylogeny, and Biogeography of Beetles and Ants*. W. Junk, Dordrecht, Netherlands.
- Frank, S. N., S. Godehardt, M. Nachev, A. Trubiroha, W. Kloas, and B. Sures.** 2013. Influence of the cestode *Ligula intestinalis* and the acanthocephalan *Polymorphus minutus* on levels of heat shock proteins (HSP70) and metallothioneins in their fish and crustacean intermediate hosts. *Environmental Pollution* 180:173–179.
- Frey, J. K., D. W. Duszynski, W. L. Gannon, T. L. Yates, and S. L. Gardner.** 1992. Designation and curatorial management of type host specimens (symbiotypes) for new parasite species. *Journal of Parasitology* 78:930–932.
- Gardner, S. L., and M. Campbell.** 1992. Parasites as probes for biodiversity. *Journal of Parasitology* 78: 596–600.
- GTI (Global Taxonomy Initiative).** 1999. Using Systematic Inventories to Meet Country and Regional Needs. A Report of the DIVERSITAS/Systematics Agenda 2000 International Workshop, 17–19 September 1998, American Museum of Natural History. The Center for Biodiversity and Conservation, American Museum of Natural History, New York, New York. 34 pp.
- Halas, D., D. Zamparo, and D. R. Brooks.** 2005. A historical biogeographical protocol for studying diversification by taxon pulses. *Journal of Biogeography* 32: 249–260.
- Hartigan, A. L., A. Peacock, A. Rosenwax, D. N. Phalen, and J. Šlapeta.** 2012. Emerging myxosporean parasites of Australian frogs take a ride with fresh fruit transport. *Parasites & Vectors* 5:208–211.
- Haverkost, T. R., S. L. Gardner, and A. T. Peterson.** 2010. Predicting the distribution of a parasite using the ecological niche model, GARP. *Revista Mexicana de Biodiversidad* 81:895–902.
- Hoberg, E. P.** 1997. Phylogeny and historical reconstruction: host–parasite systems as keystones in biogeography and ecology. Pages 243–261 in M. Reaka-Kudla, D. E. Wilson, and E. O. Wilson, eds. *Biodiversity II: Understanding and Protecting Our Biological Resources*. Joseph Henry Press, Washington, D.C.
- Hoberg, E. P.** 2010. Invasive processes, mosaics and the structure of helminth parasite faunas. *Revue Scientifique et Technique Office International des Épizooties* 29:255–272.
- Hoberg, E. P., and D. R. Brooks.** 2008. A macroevolutionary mosaic: episodic host-switching, geographical colonization and diversification in complex host–parasite systems. *Journal of Biogeography* 35:1533–1550.
- Hoberg, E. P., and D. R. Brooks.** 2010. Beyond vicariance: integrating taxon pulses, ecological fitting and oscillation in evolution and historical biogeography. Pages 7–10 in S. Morand and B. Kransow, eds. *The Geography of Host–Parasite Interactions*. Oxford University Press, Oxford, U.K.
- Hoberg, E. P., and D. R. Brooks.** 2013. Episodic processes, invasion and faunal mosaics in evolutionary and ecological time. Pages 199–213 in K. Rhode, ed. *The Balance of Nature and Human Impact*. Cambridge University Press, Cambridge, U.K.
- Hoberg, E. P., K. E. Galbreath, J. A. Cook, S. J. Kutz, and L. Polley.** 2012. Northern host–parasite assemblages: history and biogeography on the borderlands of episodic climate and environmental transition. *Advances in Parasitology* 79:1–97.
- Hoberg, E. P., and G. J. Klassen.** 2002. Revealing the faunal tapestry: coevolution and historical biogeography of hosts and parasites in marine systems. *Parasitology* 124:S3–S22.
- Hoberg, E. P., S. J. Kutz, J. A. Cook, K. Galaktionov, V. Haukisalmi, H. Henttonen, S. Laaksonen, A. Makarikov, and D. M. Marcogliese.** 2013. Parasites. Pages 477–505 in H. Meltofte, ed. *Arctic Biodiversity Assessment—Status and Trends in Arctic Biodiversity*. Conservation of Arctic Flora and Fauna, Arctic Council, Akureyri, Iceland.
- Hoberg, E. P., L. Polley, E. M. Jenkins, and S. J. Kutz.** 2008. Pathogens of domestic and free-ranging ungulates: global climate change in temperate to boreal latitudes across North America. *Revue Scientifique et Technique Office International des Épizooties* 27:511–528.
- IPCC.** 2007a. *Climate Change 2007. Synthesis Report. Contribution of Working Groups I, II, and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Core Writing Team (R. K. Pachauri and A. Reisinger, eds.). IPCC, Geneva, Switzerland. 104 pp.
- IPCC.** 2007b. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden, and C. E. Hanson, eds.). Cambridge University Press, Cambridge, U.K. 976 pp.
- IPCC.** 2013. Summary for policymakers. Pages 1–27 in T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, eds. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, U.K.
- Janz, N.** 2011. Ehrlich and Raven revisited: mechanisms underlying codiversification of plants and enemies. *Annual Review of Ecology, Evolution and Systematics* 42:71–89.
- Janz, N., and S. Nylin.** 2008. The oscillation hypothesis of host plant-range and speciation. Pages 203–215 in K. J. Tilmon, ed. *Specialization, Speciation, and Radiation: The Evolutionary Biology of Herbivorous Insects*. University of California Press, Berkeley, California.
- Janzen, D. H.** 1985. On ecological fitting. *Oikos* 45:308–310.
- Jenkins, E. J., G. D. Appleyard, E. P. Hoberg, B. M. Rosenthal, S. J. Kutz, A. M. Veitch, H. M. Schwantje, B. T. Elkin, and L. Polley.** 2005. Geographic distribution of the muscle-dwelling nematode *Parelaphostrongylus odocoilei* in North America, using molecular identification of first stage larvae. *Journal of Parasitology* 91:574–584.
- Kilpatrick, A. M.** 2011. Globalization, land use, and the invasion of West Nile Virus. *Science* 334:323–327.

- Kuris, A. M.** 2012. The global burden of human parasites: who and where are they? How are they transmitted. *Journal of Parasitology* 98:1056–1064.
- Kutz, S. J., I. Asmundsson, E. P. Hoberg, G. D. Appleyard, E. J. Jenkins, K. Beckmen, M. Branigan, L. Butler, N. B. Chilton, D. Cooley, B. Elkin, F. Huby-Chilton, D. Johnson, A. Kuchboev, J. Nagy, M. Oakley, B. Olsen, R. Popko, A. Scheer, and A. Veitch.** 2007. Serendipitous discovery of a novel protostrongylid (Nematoda: Metastrongyloidea) in caribou (*Rangifer tarandus*), muskoxen (*Ovibos moschatus*) and moose (*Alces alces*) from high latitudes of North America based on DNA sequence comparisons. *Canadian Journal of Zoology* 85:1143–1156.
- Kutz, S. J., S. Checkley, G. G. Verocai, M. Dumond, E. P. Hoberg, R. Peacock, J. Wu, K. Orsel, K. Seegers, A. Warren, and A. Abrams.** 2013. Invasion, establishment, and range expansion of two protostrongylid nematodes in the Canadian Arctic. *Global Change Biology* 19:3254–3262.
- Lafferty, K. D.** 2009. The ecology of climate change and infectious diseases. *Ecology* 90:888–900.
- Lawler, J. J., S. L. Shafer, D. White, P. Karieva, E. P. Maurer, A. R. Blaustein, and P. J. Bartlein.** 2009. Projected climate-induced faunal change in the Western Hemisphere. *Ecology* 90:588–597.
- Lovejoy, T. E., and L. Hannah, eds.** 2005. *Climate Change and Biodiversity*. Yale University Press, New Haven, Connecticut. 418 pp.
- Makarikov, A. A., K. E. Galbreath, and E. P. Hoberg.** 2013. Parasite diversity at the Holarctic nexus: species of *Arostrilepis* (Eucestoda: Hymenolepididae) in voles and lemmings (Cricetidae: Arvicolinae) from greater Beringia. *Zootaxa* 3608:401–439.
- Manter, H. W.** 1966. Parasites of fishes as biological indicators of recent and ancient conditions. Pages 59–71 in J. E. McCauley, ed. *Host-Parasite Relationships*. Oregon State University Press, Corvallis, Oregon.
- Marcogliese, D. J.** 2001. Implications of climate change for parasitism of animals in the aquatic environment. *Canadian Journal of Zoology* 79:1331–1352.
- Marcogliese, D. J.** 2005. Parasites of the superorganism: are they indicators of ecosystem health? *International Journal of Parasitology* 35:705–716.
- McLennan, D. A., and D. R. Brooks.** 1991. Parasites and sexual selection: a macroevolutionary perspective. *Quarterly Review of Biology* 66:255–286.
- Meltofte, H., T. Barry, D. Berteaux, H. Buelmann, J. S. Christiansen, J. A. Cook, F. J. A. Daniëls, A. Dahlberg, F. Friðriksson, B. Ganter, A. J. Gaston, L. Gillespie, L. Grenoble, G. Henry, E. P. Hoberg, I. Hodkinson, H. P. Huntington, R. A. Ims, A. B. Josefson, S. J. Kutz, S. A. Kuzmin, K. Laidre, D. R. Lassuy, P. N. Lewis, C. Lovejoy, C. Michel, V. Mokievskiy, D. Payer, D. Reid, J. Reist, D. Tessler, and F. Wrona.** 2013. Status and trends in Arctic biodiversity—Synthesis: implications for conservation. Pages 21–66 in H. Meltofte, ed. *Arctic Biodiversity Assessment—Status and Trends in Arctic Biodiversity*. Conservation of Arctic Flora and Fauna, Arctic Council, Akureyri, Iceland.
- Mora, C., and F. A. Zapata.** 2013. Anthropogenic footprints on biodiversity. Pages 239–258 in K. Rhode, ed. *The Balance of Nature and Human Impact*. Cambridge University Press, Cambridge, U.K.
- Nieberding, C., M.-C. Durette-Desset, A. Vanderpoorten, J. C. Casanova, A. Ribas, V. Deffontaine, C. Feliu, S. Morand, R. Libios, and J. R. Michaux.** 2008. Geography and host biogeography matter in understanding the phylogeography of a parasite. *Molecular Phylogenetics and Evolution* 47:538–554.
- Nieberding, C., and I. Olivieri.** 2007. Parasites: proxies for host genealogy and ecology? *Trends in Ecology and Evolution* 22:156–165.
- Nylin, S., J. Slove, and N. Janz.** 2014. Host plant utilization, host range oscillations and diversification in nymphalid butterflies: a phylogenetic investigation. *Evolution* 68:105–124.
- Parmesan, C., and G. Yohe.** 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37–42.
- Patz, J. A., D. Campbell-Lendrum, T. Holloway, and J. A. Foley.** 2005. Impact of regional climate change on human health. *Nature* 438:310–317.
- Patz, J. A., S. H. Olson, C. K. Uejio, and H. K. Gibbs.** 2008. Disease emergence from global and land use change. *Medical Clinics of North America* 92:1473–1491.
- Polley, L., and R. C. A. Thompson.** 2009. Parasite zoonoses and climate change: molecular tools for tracking shifting boundaries. *Trends in Parasitology* 25:285–291.
- Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. V. Callaghan, T. R. Christensen, B. Elberling, A. D. Fox, O. Gilg, D. S. Hik, T. T. Hoye, R. A. Ims, E. Jeppesen, D. R. Klein, J. Madsen, A. D. McGuire, S. Rysgaard, D. E. Schindler, I. Stirling, M. P. Tamstorf, N. J. C. Tyler, R. van der Wal, J. Welker, P. A. Wookey, N. M. Schmidt, and P. Aastrup.** 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science* 325:1355–1358.
- Poulin, R.** 1997. *Evolutionary Ecology of Parasites*. Princeton University Press, Princeton, New Jersey. 332 pp.
- Poulin, R., and S. Morand.** 2004. *Parasite Biodiversity*. Smithsonian Institution Press, Washington, D.C., 216 pp.
- Rosenthal, B. M.** 2008. How has agriculture influenced the geography and genetics of animal parasites? *Trends in Parasitology* 25:67–70.
- Thompson, J. N.** 2005. *The Geographic Mosaic of Coevolution*. University of Chicago Press, Chicago, Illinois. 400 pp.
- Vanhove, M. P. M., B. Tessen, C. Schoelink, U. Jondelius, D. T. J. Littlewood, T. Artois, and T. Huyse.** 2013. Problematic barcoding in flatworms: a case study on monogeneans and rhabdocoels (Platyhelminthes). *Zookeys* 365:355–379.
- Waltari, E., and S. L. Perkins.** 2010. In the hosts footsteps? Ecological niche modeling and its utility in predicting parasite distributions. Pages 145–155 in S. Morand and B. Krasnow, eds. *The Geography of Host-Parasite Interactions*. Oxford University Press, Oxford, U.K.
- Weaver, H. J., J. M. Hawdon, and E. P. Hoberg.** 2010. Soil-transmitted helminthiases: implications of climate change and human behavior. *Trends in Parasitology* 26:574–581.