Opinion

CellPress

An integrated parasitology: revealing the elephant through tradition and invention

Eric P. Hoberg[1], Salvatore J. Agosta[2], Walter A. Boeger[3], and Daniel R. Brooks[3]

[1] US National Parasite Collection, US Department of Agriculture, Agricultural Research Service, BARC East No. 1180, Beltsville, MD 20705, USA
[2] Center for Environmental Studies and Department of Biology, Virginia Commonwealth University, Richmond, VA 23284, USA
[3] Laboratório de Ecologia Molecular e Parasitologia Evolutiva, Universidade Federal do Paraná, Caixa Postal 19073, Curitiba, PR 81531-980, Brazil

The field of parasitology contributes to the elucidation of patterns and processes in evolution, ecology, and biogeography that are of fundamental importance across the biosphere, leading to a thorough understanding of biodiversity and varied responses to global change. Foundations from taxonomic and systematic information drive biodiversity discovery and foster considerable infrastructure and integration of research programs. Morphological, physiological, behavioral, life-history, and molecular data can be synthesized to discover and describe global parasite diversity, in a timely manner. In fully incorporating parasitology in policies for adaptation to global change, parasites and their hosts should be archived and studied within a newly emergent conceptual universe (the 'Stockholm Paradigm'), embracing the inherent complexity of host–parasite systems and improved explanatory power to understand biodiversity past, present, and future.

Describing the elephant

How we adapt to accelerating disruption of the biosphere, including variation in the distribution, abundance, and emergence of pathogens and diseases (most often old diseases in new hosts), depends critically on our ability to identify and anticipate responses to perturbation of global ecosystems. Effective strategies require a thorough grounding in ecology and evolution [1]. Taxonomy provides the names that make it possible for informed discourse about the biosphere irrespective of concerns in conservation, disease ecology, agriculture and food production, and security [2]. A key observation of many biodiversity initiatives has been 'no name= no information, wrong name = wrong information' [3]. Systematics and taxonomy link evolution, ecology, and biogeography in a rich and integrated tapestry describing global diversity. The dynamics of biodiversity cannot be explained in a comprehensive manner without a systematic foundation. Coping with the challenges of a changing biosphere is not only about systematics, but that systematics is also essential to the explanatory adequacy of the evolutionary and ecological framework that we use to interpret patterns and processes affecting biodiversity [4–7].

We have an opportunity to develop a relevant and integrated parasitology, from which success emerges through broad disciplinary support of systematic biologists and the collections on which they are dependent [7,8], and which are critical for research groups investigating climate change, biodiversity dynamics, and emerging disease [9–12]. However, few programs extend biodiversity information beyond the basics of taxonomic identification related to monitoring and surveillance. Although there are many rationales for wildlife parasitology, here we suggest a more general and integrated framework, bridging taxonomy, systematics, and historical ecology, contributing to powerful explanations and predictions about change in the biosphere [13–15]. A generation ago, Brooks and McLennan [16] applied that framework specifically to parasitology, but only a few research groups have explored these approaches. Research efforts are isolated in a manner consistent with the analogy of 'the blind men and the elephant'. We remain balkanized across disciplines within parasitology, failing to 'connect the dots' across diverse expertise and divergent interests and, as a consequence, the explanatory tapestry is woven too slowly [17]. Parasitology progresses into increasingly narrow avenues, while aging scientific lineages are only inconsistently transferring traditional knowledge and skills. Furthermore in this maelstrom of reductionism, we are increasingly losing our basic capacities to pursue complex taxonomic questions because practitioners in this arena appear to be diminishing over time.

We can no longer afford this state of affairs. Parasitology can, and must, contribute appropriately as a general model system elucidating patterns and processes in evolution, ecology, and biogeography of fundamental importance across the biosphere. In addition, incorporation of parasitology in the development of policies for adapting to climate change, biodiversity alterations, and emerging disease,

must bring together important capacities in a meaningful way. How we choose to address wildlife parasitology reflects larger options for the future and relevance of the discipline.

Systematics and the scope of the challenge

Brooks and Hoberg [18] detailed the compelling need to expand parasite systematics capacity, an exigency that remains to be realized. Systematics is the cornerstone for understanding past, present, and future patterns and processes across global biological communities. It provides the foundation for biodiversity knowledge that is needed to tackle a range of increasingly urgent and applied environmental challenges. The development and use of biodiversity knowledge by parasitologists, which to a great extent has encompassed free-living taxa [e.g., *Encyclopedia of Life* (www.eol.org) and *Global Biodiversity Information Facility* – http://www.gbif.org], have yet to become a global priority, despite decades of discussion at national and international levels. These resources could facilitate broad dissemination of critical parasite biodiversity information through use of common reference points and resources. As a result of research by the past generation, we recognize, document, and understand better the consequences of interacting crises for biodiversity perturbation and extinction, climate warming, and emerging infectious disease [3,7]. However, the scope of the problems facing humanity outstrips the knowledge gained by largely independent and competitive, rather than integrative and cooperative, efforts.

The taxonomic impediment [18,19] remains the single greatest obstacle for parasitology to contribute meaningfully to efforts dealing with climate change, biodiversity alteration, and emerging disease. Contrary arguments, and the idea that sufficient taxonomic infrastructure exists, are based on skewed species estimates from the Catalogue of Life that do not include macro- and microparasites in any meaningful way [20,21]. These estimates may disregard as much as 50% of the species on this planet [17,22]. A more accurate accounting of biodiversity would emphasize the significance of parasites as drivers and mediators of interactions that shape ecosystems, food webs, host demographics, and behavior [23–25], affecting ecosystem assembly across the expanse of Earth history [4,26,27].

We estimate that no more than 10% of global pathogens have been documented [3]. As well, we have elucidated critical elements of evolution and ecology for a minority of those species that have been named. For example, approximately 75% of all named parasitic platyhelminthes are known only from their original descriptions, meaning one host, one place, one time [22]). Thus, in most situations, we cannot anticipate capacities for host switching, the primary source of disease emergence [6]. Human–wildlife interfaces expand through occupation of new habitats, the translocation and/or introduction of species for conservation, alteration and fragmentation of ecosystems under natural and anthropogenic forcing, and the cascading influence of climate change. These factors combine to create a geographic arena of pathogen emergence [3,11,28] that has been likened to an evolutionary minefield of potential emerging diseases [29].

We must reverse the diminishing emphasis on proficiency in comparative biology that underlies all applications of systematics and/or phylogenetic data. Morphological, physiological, behavioral, and life-history data can be integrated with molecular data to characterize species, and to discover and describe global parasite diversity in a timely manner. Those efforts provide essential data for understanding ecological and evolutionary frameworks and the temporal and spatial partitions that influence diversity [2,7,30]. Molecular toolkits, initially informed by authoritative identification of specimens, provide a relatively rapid means for assessment of parasite–host assemblages emphasizing, for example, the potential for intensive landscape sampling across large geographic scales necessary to identify range shifts in real time [31–33]. Relatively few individuals are proficient in more than a few of these areas, underscoring the need for cooperative networks of research groups with diverse interests and capacities [30,34]. We need collaborations to build and apply fundamental skills, develop capacity for producing synoptic morphological and molecular data, as well as analytical models applied in areas such as phylogeography and epidemiology of disease [35–39].

Cryptic diversity and its implications

Sorting biodiversity into morphospecies remains an essential bridge to higher systematics, measures of species richness, and expanding views of diversity. Morphology provides substantial insights into phylogeny, and resulting phylogenetic trees and historical hypotheses often share considerable congruence with molecular-based assessments [40,41]. By contrast, morphology can also confound [42], highlighting the importance of detecting and delimiting cryptic species for understanding responses to perturbation related to variation in physiological tolerances and resilience that may determine geographic distributions, potential host associations, and patterns of disease [2,43]. Molecular characterization of biodiversity does not constitute formal description, a process requiring considerable expertise and comparative resources usually linked to archival specimen collections. Although providing an avenue to address landscape-scale phenomena that are critical to understanding temporal and spatial distributions and transmission of pathogens [7], barcoding is not a panacea. Knowing the players in the biosphere is an initial step in exploring the mechanisms determining the panoply of biodiversity in this world [30,42] and is fundamental to many applications, including drug discovery and biological control [44].

Cryptic species are ubiquitous among parasitic groups. Their discovery has been bolstered by large-scale surveys and inventories specifically designed to explore limits of diversity [45–47]. Notable examples among helminth parasites include: anoplocephalid, catenotaeniid, and hymenolepidid cestodes of rodents and lagomorphs [48–54]; *Taenia* spp. cestodes in carnivorans [55,56]; hookworms and anisakine nematodes in marine mammals [57–59]; lungworms (Protostrongylidae) in ungulates [31]; and *Trichinella* spp. nematodes in mammals [60,61] (for comprehensive discussion, see [62]).

Discovery of cryptic diversity stems from observations of: (i) considerable morphological variation in a nominal species that (in the case of parasites) is not immediately

linked to a host, host group, or specific locality; (ii) broad host range, often involving multiple families; and (iii) geographically broad occurrence, often intercontinental in scope. Further study almost always demonstrates that the single putative species is a species complex [2]. Sometimes, we discover that the putative variable species is a composite, having been formed artificially by taxonomists lumping taxa together. A fundamental contribution of molecular systematics has been to demonstrate that taxonomic 'splitters' have almost always been more correct than taxonomic 'lumpers.' As a result, some 'newly discovered' cryptic complexes comprise species for which names have been proposed in the past.

We need considerable global exploration to document the true dimensions of diversity in host–parasite systems. In some cases, this reflects host groups that have received minimal attention and, surprisingly, this is not limited to vast oceanic marine systems or even the tropics, but is a chronic issue across reasonably accessible terrestrial and aquatic habitats in temperate and boreal latitudes. By contrast, for instances in which survey and inventory were thought reasonably complete, the timeframes of original work unfolded before the advent of current integrative approaches; this is apparent across many host groups and geographic regions where cryptic diversity is now being revealed [31,54,62].

Inventory, collections, archives and biodiversity informatics

Species exploration requires field-based, hypothesis-driven inventory of expanded scope and depth, completed in a time- and cost-effective manner [2,7]. Biodiversity inventory encompasses: (i) collecting geographically extensive assemblages of hosts and parasites with field data and voucher specimens deposited in archival repositories [34] (e.g., a primary exemplar is the Beringian Coevolution Project and broader global programs at http://arctos.database.museum/SpecimenSearch.cfm); (ii) concurrent comparative morphological and molecular analyses on which to base taxonomic decisions [54]; (iii) molecular–phylogeographic approaches [35]; and (iv) historical ecological and biogeographic studies establishing deep-time evolutionary contexts for contemporaneous diversity ([15,27,45] and references therein). In this regard, Bernardo [2] noted that 'discovering localized, cryptic, evolutionarily distinctive lineages relies upon unbiased genealogical and geographic sampling, which generally entails high-intensity sampling.' Furthermore, comprehensive delimitation of the geographic distributions of members of phylogenetic groups is intimately related to sampling intensity and dispersion across the landscape.

Although many of our comments focus on high-latitude systems, such as the exemplar of Beringia, inventories emphasizing integrated methods exploring micro- and macroparasites are increasingly evident across all environments and scales that link landscapes, ecosystems, and global communities. As an example, explorations are addressing marine, aquatic, and terrestrial systems of Mexico [63], vertebrates of Mongolia (http://lamarck.unl.edu/mongolia/) [64], birds of Amazonia (http://www.fieldmuseum.org/science/microsites/southernamazonian.birds),

reptiles in New Guinea [65], and stickleback fishes from estuarine and freshwater habitats throughout the world (http://www.nrel.colostate.edu/projects/lboy/whatandwhere.html#stickleback). We can identify the prototype for vertebrate parasitology that codified concepts for integrated inventor, and anticipated these approaches in the All Taxon Biodiversity Inventory centered in the topical systems of the Area de Conservacion Guanacaste (ACG) of northwestern Costa Rica that extended over a decade from 1996 to 2006 (http://hwml.unl.edu/index.php/resources/database-68) [66]. More broadly, the development of ideas about inventory of complex systems and conservation is best exemplified by the innovative paths involving parataxonomists, barcoding, and informatics exploring caterpillars, food plants, and parasitoids in the ACG over the past 35 years [67].

Synoptic historical baselines with authoritative identification across the full range of environments are necessary to recognize patterns of environmental change over time [46,47]. Articulation of specimen, genetic (direct linkage to GenBank), genomic, and informatics archives (georeferenced data, GIS environmental interpretations, niche modeling, phylogenies, and ecological and historical context) in digital formats contributing to these baselines leads to maximum flexibility in characterization of biodiversity. Archives available as online resources of museums and other permanent repositories can provide vital information to biologists, managers, conservationists, and the veterinary and biomedical communities helping to anticipate emerging wildlife diseases. Development and applications of such resources promotes examination of concepts about the nature of mosaic faunas and ephemeral emergence of disease in space and time [45,68,69]. Nuanced and data-rich pathways are leading to increasingly robust insights into the abiotic and biotic factors that are converge during emergence. Collectively, these serve to highlight the understanding that the distribution of a parasite is always broader than its associated disease [70].

Surveillance and monitoring are vital strategic components of wildlife parasitology, epidemiology, and disease studies. Molecular protocols provide potential epidemiological tools for shifting from geographically and numerically restricted assessments to near-simultaneous sampling across large interconnected or isolated host populations and regions [3,36]. Accumulation of basic field survey collections and archival submission of tissues and parasites from cases or outbreaks of mortality and disease under investigation across wildlife health networks at the local, regional, and national level, can also provide insights into faunal structure and patterns of change. Irrespective of the scope and depth of collections, complete data must be assembled and archived, and extensive series of specimens (hosts, parasites, and tissues) and DNA products preserved (cryopreservation and ethanol preservation), or prepared to maximize later development of information and the possibility of re-evaluation. Pathways for voucher specimens and digitized information become self-correcting records for identity and biodiversity [46,47,71]. Maximizing critical resources to explore biodiversity and to recognize and anticipate change requires a culture in parasitology that develops, uses, and supports archives and collections held in museum repositories rather than in personal collections [8,71].

Evolving conceptual arenas

Biodiversity information is only as useful as the conceptual universe in which it is explained. Parasitology has, for more than a century, been immersed in a version of coevolutionary thought in which host switching should be rare; a corollary is that emerging diseases related to host jumps ought be infrequent events. Increasingly, insights into host colonization, diversification, and ecological structure across Earth history highlight the need to explore novel developments in the pattern and process of faunal assembly [4,5], specifically what is termed the 'parasite paradox' [6]. The parasite paradox arises from the observations that: (i) parasites are considered extreme ecological specialists, especially with respect to co-adaptive relations with a small range of hosts and, thus, should rarely switch hosts; and (ii) host switching among related or unrelated hosts is a common finding in phylogenetic studies [4,6]. The paradox is significant because it relates directly to faunal assembly and outcomes for episodic ecological collision, invasion, and mixing, including the origins of emergent pathogens in space and time [4,5].

An alternative view more completely accommodates and describes empirical findings, and the relation between cospeciation and host colonization. Elements of this framework have existed within parasitology for 35 years, when the term 'cospeciation' was first used [72], but a comprehensive description has only recently been articulated [5,6] and named the 'Stockholm Paradigm' [33].

The Stockholm Paradigm integrates: (i) Ecological Fitting (EF) [73]; (ii) the Oscillation Hypothesis (OH) [74]; (iii) the Geographic Mosaic Theory of Coevolution (GMC) [68]; and (iv) the Taxon Pulse Hypothesis (TP) [75]. EF refers to the ability of ecological specialists to host switch easily and without prior evolution of novel host-use capabilities, if the host resource upon which they are specialized is phylogenetically conservative and widespread. The OH postulates that large-scale evolutionary diversification of interspecific ecological associations involves an initial phase (permitted by EF) in which host-range increases, setting the stage for the parasite to become an ecological generalist, which in turn sets the stage for the generalist parasite to become fragmented into new specialists. The GMC describes the microevolutionary co-adaptive dynamics among new combinations of interacting species, explaining the emergence of new specialists from ancestral generalists. The relative ease with which host switches, oscillations, and new co-adapted associations can arise, reflects that even ecological specialists exist in a 'sloppy' rather than a tightly optimized fitness space [6,76,77]. The TP dynamic postulates that species-level biodiversity results from alternating episodes of biotic expansion and biotic isolation. This appears to be largely responsible for altering geographic and trophic ecological contexts, leading to opportunity for new arrays of associations to arise often manifested in mosaic structure that relates to faunal assembly over space and time [45]. In conjunction with EF, host colonization is maximized during phases of biotic expansion (disruption), whereas stasis promotes emergence of new specialists during episodes of geographic isolation [4,5].

The Stockholm Paradigm provides a new way to understand emerging pathogens and diseases of wildlife, including a shift in emphasis from reactive to proactive and anticipatory policies of management. We believe that adopting the Stockholm Paradigm can promote more sustainable and cost-effective approaches to anticipating and managing emergent diseases in space and time. Evolutionary risk assessment becomes a proactive stance contrasting with reactive modes characterized by current epidemiology. Basic tenets of the Stockholm Paradigm direct attention to emerging infectious diseases, before they happen, in the context of ecological perturbation, using knowledge of biodiversity, past environments, and equivalence of biological processes to anticipate the future in a world of rapid change.

A new way

Proposals for an integrated parasitology are not new, yet interconnected resources for biodiversity information have not been realized. Parasitology remains disconnected from broader concerns in biodiversity, ecology, and conservation, including a burgeoning disease ecology community. Host switching and emergence do not occur in an ecological and/or historical vacuum, but are linked to specific processes, most predictably to breakdown in ecological isolation and increasing opportunity. Central to understanding the implications of global change is a firm foundation based on biodiversity discovery, emphasizing the need to re-engage a considerable infrastructure and history of integrative research in parasitology. A recent proposal for such a pathway, termed 'DAMA' for 'documentation–assessment–monitoring–action', would serve to build biodiversity informatics and capacity in parasitology to understand, anticipate, and respond to the outcomes of accelerating environmental change [7]. We would advocate transboundary informatics explicitly emphasizing and building multidisciplinary foundations and pathways for big data. Such a path would lead to synergy linking museums and their broad-based biodiversity data, genomics, and geographic systems in descriptions of a biosphere in transition.

Sources and solutions for the biodiversity crisis, encompassing pervasive anthropogenic extinction and ecosystem disruption of global extent [78,79], emphasize disconnect for parasitology. We suggest, for example, that proposals for translocations and (re)introductions of potential hosts to restore diversity, ecological equivalence, and integrity [80] in a world historically dominated by geographic colonization, host switching, and emergence of pathogens, is misguided. Furthermore, that such proposals can be made seriously, indicates the degree to which parasitology has been overlooked, when, instead, it should be seen as a primary source of input for policy-making. Wildlife parasitologists have a responsibility to engage and inform a broader community about outcomes for the biosphere under a regime of accelerating perturbation and transformation. We can apply our unique insights and tools in leading and contributing to understanding, mitigating, and resolving the challenges now quickly dominating our horizons.

References

1 Dawson, T.P. *et al.* (2011) Beyond predictions: biodiversity conservation in a changing climate. *Science* 332, 53–58
2 Bernardo, J. (2011) A critical appraisal of the meaning of diagnosibility of cryptic evolutionary diversity, and its implications for conservation

in the face of climate change. In *Climate Change, Ecology and Systematics* (Hodkinson, T.R. *et al.*, eds), pp. 380–438, Cambridge University Press

3 Brooks, D.R. and Hoberg, E.P. (2013) The emerging infectious disease crisis and pathogen pollution: A question of ecology and evolution. In *The Balance of Nature and Human Impact* (Rohde, K., ed.), pp. 215–229, Cambridge University Press

4 Hoberg, E.P. and Brooks, D.R. (2008) A macroevolutionary mosaic: episodic host-switching, geographic colonization, and diversification in complex host-parasite systems. *J. Biogeogr.* 35, 1533–1550

5 Hoberg, E.P. and Brooks, D.R. (2010) Beyond vicariance: Integrating taxon pulses, ecological fitting and oscillation in historical biogeography and evolution. In *The Geography of Host-Parasite Interactions* (Morand, S. and Krasnov, B., eds), pp. 7–20, Oxford University Press

6 Agosta, S.J. *et al.* (2010) How specialists can be generalists: resolving the 'parasite paradox' and implications for emerging infectious disease. *Zoologia* 27, 151–162

7 Brooks, D.R. *et al.* (2014) Finding them before they find us: informatics, parasites and environments in accelerating climate change. *Comp. Parasitol.* 81, 155–164

8 Hoberg, E.P. (2002) Foundations for an integrative parasitology: collections archives and biodiversity informatics. *Comp. Parasitol.* 69, 124–131

9 Dobson, A.P. and Carper, R. (1992) Global warming and potential changes in host-parasite and disease vector relationships. In *Global Warming and Biological Diversity* (Peters, R.L. and Lovejoy, T., eds), pp. 201–220, Yale University Press

10 Hoberg, E.P. *et al.* (2008) Pathogens of domestic and free-ranging ungulates: global climate change in temperate to boreal latitudes across North America. *Rev. Sci. Tech.* 27, 511–528

11 Altizer, S. *et al.* (2013) Climate change and infectious diseases: from evidence to a predictive framework. *Science* 341, 514–519

12 Kutz, S.J. *et al.* (2014) A walk on the tundra: host-parasite interactions in an extreme environment. *Int. J. Parasitol. Parasites Wldl.* 3, 198–208

13 Brooks, D.R. (1985) Historical ecology: a new approach to studying the evolution of ecological associations. *Ann. Missouri Bot. Garden* 72, 660–680

14 Brooks, D.R. and McLennan, D.A. (1991) *Phylogeny, Ecology and Behavior: A Research Program in Comparative Biology*, University of Chicago Press

15 Brooks, D.R. and McLennan, D.A. (2002) *The Nature of Diversity: An Evolutionary Voyage of Discovery*, University of Chicago Press

16 Brooks, D.R. and McLennan, D.A. (1993) *Parascript: Parasites and the Language of Evolution*, Smithsonian Institution Press

17 Dobson, A. *et al.* (2008) Homage to Linnaeus: how many parasites? How many hosts? *PNAS* 105, 11482–11489

18 Brooks, D.R. and Hoberg, E.P. (2001) Parasite systematics in the 21st century: opportunities and obstacles. *Trends Parasitol.* 17, 273–275

19 Blackmore, S. (1996) Knowing the earth's biodiversity: challenges for the infrastructure of systematic biology. *Science* 274, 63–64

20 Costello, M.J. *et al.* (2012) Predicting total global species richness using rates of species description and estimates of taxonomic effort. *Syst. Biol.* 61, 871–883

21 Costello, M.J. *et al.* (2013) Can we name Earth's species before they go extinct? *Science* 339, 413–416

22 Poulin, R. and Morand, S. (2004) *Parasite Biodiversity*, Smithsonian Institution Press

23 Hudson, P.J. *et al.* (2006) Is a healthy ecosystem one that is rich in parasites? *Trends Ecol. Syst.* 21, 381–385

24 Lafferty, K.D. *et al.* (2006) Parasites dominate food web links. *PNAS* 103, 11211–11216

25 Kuris, A.M. *et al.* (2008) Ecosystem energetic implications of parasite and free-living biomass in three estuaries. *Nature* 454, 515–518

26 Hoberg, E.P. (1997) Phylogeny and historical reconstruction: host parasite systems as keystones in biogeography and ecology. In *Biodiversity II: Understanding and Protecting Our Resources* (Reaka-Kudla, M. *et al.*, eds), pp. 243–261, Joseph Henry Press

27 Hoberg, E.P. and Brooks, D.R. (2013) Episodic processes, invasion, and faunal mosaics in evolutionary and ecological time. In *The Balance of Nature and Human Impact* (Rohde, K., ed.), pp. 199–213, Cambridge University Press

28 Daszak, P. *et al.* (2000) Emerging infectious diseases of wildlife: threats to biodiversity and human health. *Science* 287, 443–449

29 Brooks, D.R. and Ferrao, A.L. (2005) The historical biogeography of coevolution: emerging infectious diseases are evolutionary accidents waiting to happen. *J. Biogeogr.* 32, 1291–1299

30 Janzen, D.H. *et al.* (2012) What happens to traditional taxonomy when a well-known tropical saturinid moth fauna is DNA barcoded? *Invert. Syst.* 26, 478–505

31 Kutz, S.J. *et al.* (2007) Serendipitous discovery of a novel prostostrongylid (Nematoda: Metastrongyloidea) associated with caribou (*Rangifer tarandus*), muskoxen (*Ovibos moschatus*) and moose (*Alces alces*) from high latitudes of North America based on DNA sequence comparisons. *Can. J. Zool.* 85, 1143–1156

32 Kutz, S.J. *et al.* (2013) Invasion, establishment, and range expansion of two parasitic nematodes in the Canadian Arctic. *Globle Change Biol.* 19, 3254–3262

33 Hoberg, E.P. and Brooks, D.R. (2014) Evolution in action: climate change, biodiversity dynamics and emerging infectious disease. *Philos. Trans. R. Soc. Lond. B* (in press)

34 Cook, J.A. *et al.* (2005) Beringia: intercontinental exchange and diversification of high latitude mammals and their parasites during the Pliocene and Quaternary. *Mammal Study* 30, S33–S44

35 Avise, J.C. (2000) *Phylogeography: The History and Formation of Species*, Harvard University Press

36 Archie, E.A. *et al.* (2008) Infecting epidemiology with genetics: a new frontier in disease ecology. *TREE* 24, 21–30

37 Polley, L. and Thompson, R.C.A. (2009) Parasite zoonoses and climate change: molecular tools for tracking shifting boundaries. *Trends Parasitol.* 25, 285–291

38 Herbreteau, V. (2010) When geography of health meets health ecology. In *The Geography of Host-Parasite Interactions* (Morand, S. and Krasnov, B., eds), pp. 247–266, Oxford University Press

39 Morgan, E.R. *et al.* (2012) Parasite epidemiology in a changing world: can molecular phylogeography help us tell the wood from the trees. *Parasitology* 139, 1924–1938

40 Patterson, C. *et al.* (1993) Congruence between molecular and morphological phylogenies. *Ann. Rev. Ecol. Syst.* 24, 153–188

41 Brooks, D.R. *et al.* (2007) Quantitative phylogenetic analysis: progress and prognosis. *Rev. Mex. Biodiv.* 78, 225–252

42 Hebert, P.N. *et al.* (2004) Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. *PNAS* 101, 14812–14817

43 Bickford, D. *et al.* (2006) Cryptic species as a window on diversity and conservation. *TREE* 22, 148–155

44 Krug, P.J. *et al.* (2013) Integrative species delimitation in photosynthetic sea slugs reveals twenty candidate species in three nominal taxa studied for drug discovery, plastid symbiosis or biological control. *Mol. Phylogenet. Evol.* 69, 1101–1119

45 Hoberg, E.P. *et al.* (2012) Northern host-parasite assemblages: history and biogeography on the borderlands of episodic climate and environmental transition. *Adv. Parasitol.* 79, 1–97

46 Hoberg, E.P. *et al.* (2013) Parasites in terrestrial, freshwater and marine systems. In *Arctic Biodiversity Assessment: Status and Trends in Arctic Biodiversity* (Meltofte, H., ed.), pp. 476–505, Conservation of Arctic Floral and Fauna, Arctic Council

47 Cook, J. *et al.* (2013) Genetics. In *Arctic Biodiversity Assessment: Status and Trends in Arctic Biodiversity* (Meltofte, H., ed.), pp. 514–539, Conservation of Arctic Floral and Fauna, Arctic Council

48 Haukisalmi, V. *et al.* (2004) Molecular and morphological evidence for multiple species within *Paranoplocephala omphalodes* (Cestoda, Anoplocephalidae) in *Microtus* voles (Arvicolinae). *Zool. Scripta* 33, 277–290

49 Haukisalmi, V. *et al.* (2009) Molecular systematics and morphometrics of *Anoplocephaloides dentata* (Cestoda, Anoplocephalidae) and related species in voles and lemmings. *Zool. Scripta* 38, 199–220

50 Haukisalmi, V. *et al.* (2010) Taxonomic review of cestodes of the genus Catenotaenia Janicki, 1904 in Eurasia and molecular phylogeny of the Catenotaeniidae (Cyclophyllidea). *Zootaxa* 2489, 1–33

51 Wickström, L.M. *et al.* (2003) Phylogeography of the circumpolar *Paranoplocephala arctica* species complex (Cestoda: Anoplocephalidae) parasitizing collared lemmings (*Dicrostonyx* spp.). *Mol. Ecol.* 12, 3359–3371

52 Makarikov, A.A. *et al.* (2012) New species of *Arostrilepis* (Cyclophyllidea: Hymenolepididae) in members of Cricetidae and Geomyidae (Rodentia) from the western Nearctic. *J. Parasitol.* 98, 617–626

53 Makarikov, A.A. *et al.* (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

54 Galbreath, K.E. and Hoberg, E.P. (2012) Return to Beringia: parasites reveal cryptic biogeographic history of North American pikas. *Proc. R. Soc. B.* 279, 371–378

55 Lavikainen, A. *et al.* (2010) Mitochondrial DNA data reveal cryptic species within *Taenia krabbei*. *Parasitol. Int.* 59, 290–293

56 Haukisalmi, V. *et al.* (2011) *Taenia arctos* n. sp. (Cestoda: Cyclophyllidea: Taeniidae) from its definitive (brown bear *Ursus arctos* Linnaeus) and intermediate (moose/elk *Alces* spp.) hosts. *Syst. Parasitol.* 80, 217–230

57 Mattiucci, S. and Nascetti, G. (2008) Advances and trends in the molecular systematics of anisakid nematodes, with implications for their evolutionary ecology and host-parasite coevolutionary processes. *Adv. Parasitol.* 66, 47–148

58 Mattiucci, S. *et al.* (2014) Genetic and morphological approaches distinguish the three sibling species of the *Anisakis simplex* species complex, with a species designation as *Anisakis berlandi* n. sp. for *A. simplex* sp. C (Nematoda: Anisakidae). *J. Parasitol.* 100, 199–214

59 Nadler, S.L. *et al.* (2013) Molecular systematics of pinniped hookworms (Nematoda: *Uncinaria*): species delimitation, host associations, and host-induced morphometric variation. *Int. J. Parasitol.* 43, 1119–1132

60 Zarlenga, D.S. *et al.* (2006) Post-Miocene expansion, colonization, and host switching drove speciation among extant nematodes of the archaic genus *Trichinella*. *PNAS* 103, 7354–7359

61 Pozio, E. *et al.* (2009) Molecular taxonomy and phylogeny of nematodes of the genus *Trichinella*. *Infect. Genet. Evol.* 9, 606–616

62 Pérez-Ponce de León, G. and Nadler, S.L. (2010) What we don't recognize can hurt us: a plea for awareness about cryptic species. *J. Parasitol.* 96, 453–464

63 Pérez-Ponce de León, G. *et al.* (2011) Describing parasite biodiversity: The case of the helminth fauna of wildlife vertebrates in Mexico. In *Changing Diversity in Changing Environment* (Grillo, O., ed.), pp. 33–54, InTech

64 Tinnin, D.S. *et al.* (2011) Helminths of small mammals (Erinaceomorpha, Soricicomorpha, Chiroptera, Rodentia, and Lagomorpha) of Mongolia. *Spec. Publ. Museum Texas Tech Univ.* 59, 1–50

65 Austin, C.C. and Perkins, S.L. (2006) Parasites in a biodiversity hotspot: a survey of avian hematozoa and a molecular phylogenetic analysis of *Plasmodium* in New Guinea skinks. *J. Parasitol.* 92, 770–777

66 Brooks, D.R. and Hoberg, E.P. (2000) Triage for the biosphere: the need and rationale for taxonomic inventories and phylogenetic studies of parasites. *Comp. Parasitol.* 6, 1–25

67 Janzen, D.H. and Hallwachs, W. (2011) Joining inventory by parataxonomists with DNA barcoding of a large complex tropical conserved wildland in northwestern Costa Rica. *PLoS ONE* 6, e18123

68 Thompson, J.N. (2005) *The Geographical Mosaic of Coevolution*, University of Chicago Press

69 Hoberg, E.P. (2010) Invasive processes, mosaics and the structure of helminth parasite faunas. *Rev. Sci. Tech.* 29, 255–272

70 Audy, J.R. (1958) The localization of disease with special reference of the zoonoses. *Trans. R. Soc. Trop. Med. Hyg.* 52, 309–328

71 Hoberg, E.P. *et al.* (2009) Why museums matter: a tale of pinworms (Oxyuroidea: Heteroxynematidae) among pikas (*Ochotona princeps* and *O. collaris*) in the American west. *J. Parasitol.* 95, 490–501

72 Brooks, D.R. (1979) Testing the context and extent of host-parasite coevolution. *Syst. Zool.* 28, 299–307

73 Janzen, D.H. (1985) On ecological fitting. *Oikos* 45, 308–310

74 Janz, N. and Nylin, S. (2008) The oscillation hypothesis of host plant-range and speciation. In *Specialization, Speciation, and Radiation: The Evolutionary Biology of Herbivorous Insects* (Tilmon, K.J., ed.), pp. 203–215, University of California Press

75 Erwin, T.L. (1985) The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. In *Taxonomy, Phylogeny and Biogeography of Beetles and Ants* (Ball, G., ed.), pp. 437–472, W. Junk

76 Agosta, S.J. (2006) On ecological fitting, plant-insect associations, herbivore host shifts, and host plant selection. *Oikos* 114, 556–565

77 Agosta, S.J. and Klemens, S.A. (2008) Ecological fitting by phenotypically flexible genotypes: implications for species associations, community assembly and evolution. *Ecol. Lett.* 11, 1123–1134

78 Vignieri, S. (2014) Vanishing fauna. *Science* 345, 392–395

79 Dirzo, R. *et al.* (2014) Defaunation in the Anthropocene. *Science* 345, 401–406

80 Seddon, P.J. *et al.* (2014) Reversing defaunation: restoring species in a changing world. *Science* 345, 406–412