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Evolution and Biogeography of *Haemonchus contortus*: Linking Faunal Dynamics in Space and Time

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Abstract

History is the foundation that informs about the nuances of faunal assembly that are essential in understanding the dynamic nature of the host–parasite interface. All of our knowledge begins and ends with evolution, ecology and biogeography, as these interacting facets determine the history of biodiverse systems. These components, relating to *Haemonchus*, can inform about the complex history of geographical distribution, host association and the intricacies of host–parasite associations that are played out in physiological and behavioural processes that influence the potential for disease and our capacity for effective control in a rapidly changing world. Origins and evolutionary diversification among species of the genus *Haemonchus* and *Haemonchus contortus* occurred in a complex crucible defined by shifts in environmental structure emerging from cycles of climate change and ecological perturbation during the late Tertiary and through the Quaternary. A history of sequential host colonization

associated with waves of dispersal bringing assemblages of ungulates from Eurasia into Africa and processes emerging from ecosystems in collision and faunal turnover defined the arena for radiation among 12 recognized species of *Haemonchus*. Among congeners, the host range for *H. contortus* is exceptionally broad, including species among artiodactyls of 40 genera representing 5 families (and within 12 tribes of Bovidae). Broad host range is dramatically reflected in the degree to which translocation, introduction and invasion with host switching, has characterized an expanding distribution over time in North America, South America, southern Eurasia, Australia and New Zealand, coincidental with agriculture, husbandry and global colonization by human populations driven particularly by European exploration after the 1500s. African origins in xeric to mesic habitats of the African savannah suggest that historical constraints linked to ecological adaptations (tolerances and developmental thresholds defined by temperature and humidity for larval stages) will be substantial determinants in the potential outcomes for widespread geographical and host colonization which are predicted to unfold over the coming century. Insights about deeper evolutionary events, ecology and biogeography are critical as understanding history informs us about the possible range of responses in complex systems under new regimes of environmental forcing, especially, in this case, ecological perturbation linked to climate change. A deeper history of perturbation is relevant in understanding contemporary systems that are now strongly structured by events of invasion and colonization. The relaxation of abiotic and biotic controls on the occurrence of *H. contortus*, coincidental with inception and dissemination of anthelmintic resistance may be synergistic, serving to exacerbate challenges to control parasites or to limit the socioeconomic impacts of infection that can influence food security and availability. Studies of haemonchine nematodes contribute directly to an expanding model about the nature of diversity and the evolutionary trajectories for faunal assembly among complex host–parasite systems across considerable spatial and temporal scales.



1. INTRODUCTION

Biodiversity information is a cornerstone for developing a nuanced understanding and picture of the distribution and history of complex host–parasite associations (eg, Brooks and Hoberg, 2000; Brooks and McLennan, 1993, 2002; Brooks et al., 2014; Hoberg, 1997; Poulin, 1998; Poulin and Morand, 2004). The current regime of extensive environmental perturbation across biodiverse assemblages globally, including the recognized convergence of accelerating climate change, new or altered patterns of land use, and extensive globalization drive ecosystems in collision with anticipated cascading effects on the distribution of animal pathogens and emergence of diseases (eg, Brooks and Hoberg, 2013; Harvell et al., 2002; Hoberg, 2010; Hoberg et al., 2008; van Dijk et al., 2009). History, encompassing phylogeny, explorations of host–parasite coevolution, ecology and

biogeography (with phylogeographical approaches) provide a foundation to recognize or identify the drivers and responses to perturbation. Historical insights also provide a pathway for anticipating and mitigating the outcomes of accelerating change at regional to landscape scales.



2. HAEMONCHUS: HISTORY AND BIODIVERSITY

Species of the genus *Haemonchus* Cobb, 1898 occur in this complex intersection of history, ecology and biogeography (Cerutti et al., 2010; Giudici et al., 1999; Hoberg et al., 2004; Jacquet et al., 1995; Troell et al., 2006). Comparative morphological studies initially served to define a framework for the recognition of nine species in the genus (Gibbons, 1979). Although some species were defined based on relatively few specimens, consistent structural differences were apparent especially in attributes of the spicule tips and dorsal ray among male nematodes. Subsequently, evaluation of the synlophe (a system of longitudinal cuticular ridges present in male and female nematodes; eg, Durette-Desset, 1983) served to provide separation of species based on female specimens, provided the possibility of linking male and female conspecifics in mixed infections and recognition of hybrids between *Haemonchus contortus* and *Haemonchus placei* (Lichtenfels et al., 1986, 1994, 2002). These studies also were essential in validating prior conclusions regarding the inadequacy of variation in the morphology of vulval flaps as a defining character in the genus and among proposed subspecies and varieties of *H. contortus* (eg, Gibbons, 1979).

Expanding knowledge of structural characters and application of molecular methods to establish and explore species criteria have further resolved limits among 12 species-level taxa currently regarded as valid (Hoberg et al., 2004). Within this assemblage, most species can be separated and distinguished by unequivocal structural attributes among adult male and female nematodes (eg, Gibbons, 1979; Giudici et al., 1999; Jacquet et al., 1995, 1997; Lichtenfels et al., 1994, 2001, 2002). Species limits based initially on partitions derived from comparative morphology have been confirmed in those situations where genetic diversity has been explored, and especially for example in the differentiation of *H. contortus* and *H. placei* (chapter: The identification of *Haemonchus* Species and Diagnosis of Haemonchosis by Zarlenga et al., 2016, in this volume). Although considerable genetic diversity has been demonstrated among global populations of *H. contortus* at varying spatial scales, an indication of an unrecognized assemblage of cryptic species

has not been revealed (eg, Cerutti et al., 2010; Jacquet et al., 1995; Morrison and Höglund, 2005; Troell et al., 2006). There remains, however, a need to expand the development of synoptic information about population genetic diversity and possible genetic partitions at landscape to regional scales beyond those taxa [*H. contortus* (Rudolphi, 1803), *H. placei* (Place, 1893) *Haemonchus similis* Travassos, 1914 and *Haemonchus longistipes* Railliet and Henry, 1909] that most often circulate among domesticated ruminants (eg, chapter: The Identification of *Haemonchus* Species and Diagnosis of Haemonchosis by Zarlenga et al., 2016, in this volume). Collectively these species remain among the most economically significant on the global stage. Patterns of circulation for these species often cross ecotones or the interface between managed and natural ecosystems, with consequences for domesticated and free-ranging ungulates (eg, Hoberg, 2010; Hoberg et al., 2001, 2008).

Defining the parameters responsible for faunal assembly and species diversity on varying temporal and spatial scales remains critical for demonstrating the pathways and directionality for parasite transmission among assemblages of ungulates occurring in sympatry or in temporal overlap (Brooks et al., 2014; Cerutti et al., 2010; Haydon et al., 2002; Hoberg, 2010). Multispecies infections attributable to *Haemonchus* in single hosts are not uncommon, particularly in Africa, denoting complexity in evolutionary history, ecological structure and factors influencing circulation (Budischak et al., 2015; Hoberg et al., 2004; Jacquet et al., 1998). For example, 8 of 12 species of *Haemonchus* have been reported in impala [*Aepyceros melampus* (Lichtenstein)] from the African savannahs (Boomker, 1990). Emphasized by these interactions is the importance of ecotones and transmission among domestic and free-ranging wild ungulates for *H. contortus* and other species. On a global scale, elucidating an intersection for processes of invasion and colonization in evolutionary and ecological time addresses contemporary challenges transcending interactions for responses to accelerating climate change, potential geographical colonization, and the origins, routes of dissemination and persistence of drug-resistance genes at the intra-specific level in *H. contortus* and within species assemblages of *Haemonchus* (Chaudhry et al., 2015).



3. PHYLOGENY AND BIOGEOGRAPHY: OUT OF AFRICA

Haemonchines (species of *Haemonchus*, *Mecistocirrus* Railliet and Henry, 1912 and *Ashworthius* Le Roux, 1930) had origins among Eurasian

and African ungulates during the Miocene (Durette-Desset et al., 1999), although radiation among species of *Haemonchus* was subsequently limited to Africa. Diversification among species of *Haemonchus* demonstrates a geographically restricted history in sub-Saharan Africa, highlighted by the absence of endemic faunas in the Western Hemisphere (Nearctic and Neotropical regions) and the Palearctic encompassing Eurasia and the Indian Subcontinent. Substantial climatological controls on species radiation and geographical distribution are apparent (chapter: The Pathophysiology, Ecology and Epidemiology of *Haemonchus contortus* Infection in Small Ruminants by Besier et al., 2016, in this volume; Hoberg et al., 2002, 2004; O'Connor et al., 2006).

Phylogeny, biogeography and host distribution are consistent with African origins for species of *Haemonchus*, initial radiation associated with colonization among grazing and browsing antelopes (in the absence of cospeciation), and a downstream history of sequential host switching to artiodactyls among the Caprinae, Bovinae, Giraffidae and Camelidae (Fig. 1). Radiation occurred against a backdrop of climatological variation, shifting structure for habitats, pulses of ecological transition in sub-Saharan environments and independent episodes of biotic expansion/isolation (Hoberg et al., 2004). Faunal turnover, circumscribed in time, influenced recurrent zones of contact and defined opportunities for chronological and sequential geographical and host colonization. Episodes of colonization represent differential times for arrival from Eurasia and establishment of respective ungulate groups, extending from the Middle Miocene (14–15 MYBP) through the Pliocene (3–2.5 MYBP) and Quaternary (after 2.6 MYBP) (Hernández Fernández and Vrba, 2005; Vrba, 1985, 1995; Vrba and Schaller, 2000). The history for *H. contortus* is complex, and although recognized globally as a dominant nematode pathogen of domestic sheep and goats (tribe Caprini), the origin of this species is linked to an assemblage of antelopes in Africa during the late Tertiary.

The complexity of radiation for species of *Haemonchus* among ungulates demonstrates interacting and episodic mechanisms in evolution and biogeography that drive development and assembly of *Macroevolutionary Mosaic Faunas* (eg, Araujo et al., 2015; Hoberg, 2005, 2010; Hoberg and Brooks, 2008; Hoberg et al., 2008, 2012). At a minimal level of simplicity, mosaics in ecological time represent admixtures of endemic (indigenous) and introduced species (often invasive exotic taxa) or populations resulting from anthropogenic introduction and establishment. Mosaic structure is also manifested as a macroevolutionary process involving parasite assemblages on continental,

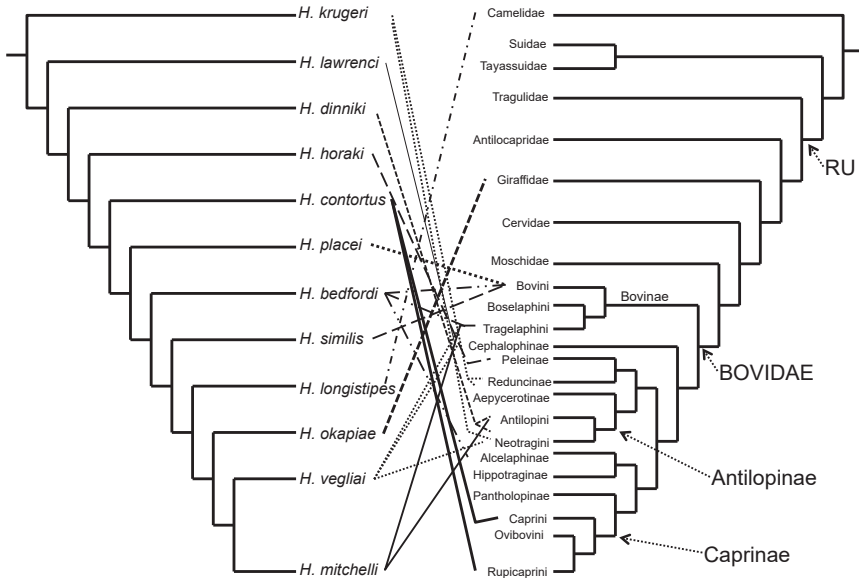


Figure 1 Phylogenetic perspective for host-group distribution and coevolutionary history for species of the genus *Haemonchus* among ungulates. Initial diversification among all *Haemonchus* species was associated with antelopes among Cephalophinae, Peleinae, Reduncinae and Antilopinae; secondarily radiation and faunal assembly was driven by sequential host colonization among ruminants (=RU) and other artiodactyles including Camelidae (Hoberg et al., 2004). Relationships are shown for species assemblages linked to putative 'core' hosts based on empirical data for prevalence and abundance; incidental associations representing postulated contemporary host-switching events since European colonization are not shown (Hoberg et al., 2004). Phylogeny for species of *Haemonchus* is from Hoberg et al. (2004). Ungulate and ruminant phylogeny is derived and modified from currently available sources (Hassanin and Douzery, 2003; Hernández Fernández and Vrba, 2005; Vrba and Schaller, 2000). Host taxonomy among ungulates is consistent with Grubb (2005).

regional and landscape scales, resulting from episodic dispersal and geographical colonization in deeper evolutionary time, encompassing populations, species and faunas (eg, Hoberg and Brooks, 2008, 2010, 2013; Hoberg et al., 2012). The dynamics of episodic environmental perturbation, recurrent invasion, geographical colonization, isolation and faunal radiation are described in the *Taxon Pulse* which provides a macroevolutionary perspective for evolution of complex systems (Araujo et al., 2015; Erwin, 1985; Halas et al., 2005; Hoberg and Brooks, 2008, 2010). Among species of *Haemonchus*, African origins and radiation in xeric to mesic habitats of the African savannah suggest that historical constraints linked to ecological adaptations (tolerances and developmental thresholds defined by temperature and humidity) will

be substantial determinants in the potential outcomes for widespread geographical and host colonization which are predicted to unfold over the coming century (chapter: The Pathophysiology, Ecology and Epidemiology of *Haemonchus contortus* Infection in Small Ruminants by [Besier et al., 2016](#), in this volume). As a consequence, insights about deeper evolutionary events, ecology and biogeography are critical as understanding history informs us about the possible range of responses in complex systems under new regimes of environmental forcing, particularly, in this case, ecological perturbation linked to climate change (eg, [Hoberg et al., 2008](#)).



4. DOMESTICATION, GEOGRAPHICAL EXPANSION AND INVASION

Considering *H. contortus*, *H. placei* and *H. similis*, the broad assemblage of hosts has resulted from initial diversification in Africa and subsequent events of colonization in ecological time. Introduction, establishment and dissemination in new ecological situations were coincidental with jump and long-range dispersal as mechanisms for breakdown in ecological isolation ([Capinha et al., 2015](#); [Hoberg, 2010](#); [Hoberg and Brooks, 2013](#); [Hoberg et al., 2004](#); [Wilson et al., 2009](#)). Thus, cosmopolitan distribution is a consequence of recurrent anthropogenic invasion, leading to the development of complex mosaic faunas and populations. As a generality for *Haemonchus*, these assemblages have not involved admixtures of endemic and introduced species (relative to source and recipient regions), but may involve genetic structuring and partitions in local populations among conspecifics ([Cerutti et al., 2010](#); [Giudici et al., 1999](#); [Hoberg, 2010](#); [Hoberg et al., 2004, 2012](#); [Thompson, 1994, 2005](#); [Troell et al., 2006](#)).

Diversification among species of *Haemonchus* was not associated with the process of domestication for sheep, goats or cattle, and these economically dominant ungulates were absent from sub-Saharan Africa during the history of radiation for these nematodes (eg, [Caramelli, 2006](#); [Chessa et al., 2009](#); [Hanotte et al., 2002](#)). The development of currently recognized breeds or lineages of domestic sheep has a complex history initially focused in southwestern Asia about 11,000 years before present (KYBP); sheep and goats expanded with agriculture into Africa by at least 8 KYBP. Considering cattle, initial domestication occurred in isolated centres of southwestern Asia and the Indian subcontinent reflecting the origins, respectively, of taurine and zebu lineages about 10 KYBP ([Caramelli, 2006](#); [Loftus et al., 1994](#)). Taurine cattle were established in Africa from sources in southwestern

Asia and possibly via exchange with Europe, whereas zebu (along with camels, *Camelus dromaderius* Linnaeus) appear associated with Arabian expansion and possibly development of early sea routes and trade (Caramelli, 2006). Near 10 to 6 KYBP, expansion of pastoralists and Neolithic agricultural systems led to a widening distribution for isolated domesticated breeds extending from Scandinavia in the north to the region of North Africa, suggesting the potential for early patterns of exchange and dissemination of *H. contortus*, *H. placei*, *H. similis* and *H. longistipes* among free-ranging and domestic ungulates (eg, Balter, 2014; Chessa et al., 2009).

A signature for human-mediated invasion for *H. contortus*, *H. placei* and *H. similis* is well established, reflecting the history of early trade routes following ungulate domestication, later European colonization and exploration after the 1500s, and accelerating globalization over the past two centuries (Brooks and Hoberg, 2013; Giudici et al., 1999; Hoberg, 2010; Morrison and Höglund, 2005; Rosenthal, 2009; Troell et al., 2006; Zarlenga et al., 2014). Patterns of genetic diversity at intercontinental scales, and possibly extending to local landscapes, are consistent with recurring episodes of geographical invasion often involving limited founding populations and varying levels of gene flow (eg, Hunt et al., 2008; Jacquet et al., 1995; Troell et al., 2006). It has been suggested that, once established in a new continental arena, intercontinental gene flow has been minimal for *H. contortus* (and perhaps other nematodes in domestic ungulates). Reflected is a history of anthropogenic introductions that influence distribution for parasites, dependent on hosts for dispersal relative to otherwise impermeable geographical barriers (eg, Leignel and Humbert, 2001; Poulin, 1998; Troell et al., 2006). In contrast, at landscape scales, where populations have been explored in regions of sympatry for domestic sheep, free-ranging caprines and cervids, evidence of extensive cross-transmission has been revealed, and raises substantial questions and implications about the nature of parasite circulation in zones of contact (Cerutti et al., 2010). Contemporary (and near-time) introductions at global, regional and landscape scales for species of *Haemonchus* are largely dependent on human-facilitated movement of domestic caprines and cattle, or in some situations free-ranging artiodactyls, as a function of vagility and permissive environments (Troell et al., 2006). The dynamics of transmission following establishment, however, may often involve host colonization and circulation in novel (and endemic) ungulates associated with particular regional ecosystems (eg, host colonization and circulation among cervids). For example, *H. contortus* is now a dominant nematode established in species of *Odocoileus* Rafinesque and particularly in

white-tailed deer, *O. virginianus* (Zimmermann), across the southern latitudes of North America, where it is a significant pathogen (Hoberg et al., 2001; Prestwood and Pursglove, 1981).

Defining specific parameters for the development of single and multiple species of *Haemonchus* and other nematodes in an array of disparate host taxa, for example, relative to fecundity, longevity and fitness for parasites and demographics and density for hosts, are essential in establishing the role of different ungulates as sources or sinks for population persistence on local to regional scales (eg, Fenton et al., 2015; Holt et al., 2003; Jacquiet et al., 1998). Among species of *Haemonchus*, including *H. contortus*, in multi-host assemblages, it is apparent that differential contributions to population persistence and circulation are often attributable to a limited spectrum of host species across a larger array of ungulates in sympatry (eg, Boomker, 1990; Jacquiet et al., 1998). In a historical perspective, susceptibility and competence for hosts as well as capacity and opportunity for parasites are essential components in establishing lineage persistence and evolutionary trajectories that are associated with downstream patterns of diversification (Hoberg and Brooks, 2008, 2013; Hoberg et al., 2004). In this arena, climate and abiotic controls determining the availability of infective larval nematodes, and the potential for infections, interface with multispecies host assemblages as well as aspects of parasite ontogeny and selection, to determine the limits for diversity and distribution (eg, Jacquiet et al., 1998). Thus, the potential for population bottlenecks for parasites across space and time emerges from interactions with host vagility, competence and demographics in an arena defined by environmental permissiveness, the latter which may shift incrementally in the long term, or be strongly influenced by extreme and ephemeral events associated with accelerating climate warming (Hoberg and Brooks, 2015; Hoberg et al., 2008; van Dijk et al., 2008).



5. HOST RANGE FOR *HAEMONCHUS CONTORTUS*

Understanding the limits of host range for *H. contortus* prior to the 1990s was confounded by our abilities for accurate identification and prevailing taxonomy (Gibbons, 1979). This understanding also may have been conflated with respect to reports that were undocumented by voucher specimens and which now cannot be validated (Hoberg et al., 2009). Although clear morphological and molecular attributes for female and male conspecifics have been developed and have been available for the past 25 years, these

have not always been applied in the process of identification (chapter: The Identification of *Haemonchus* Species and Diagnosis of Haemonchosis by Zarlenga et al., 2016, in this volume). In reports published prior to the advent of reliable morphological or molecular-based identification, those that ‘document’ *H. contortus* in various host species need to be carefully considered. Many appear to be correct based on ecological context; however, other records may be in error, representing known taxa such as *H. placei*, nominal taxa reduced as synonyms, or cryptic diversity that had not been previously distinguished from *H. contortus*. For example, the ‘long-spicule’ form of *H. contortus* reported from South Africa (Boomker et al., 1983) was later shown to be a distinct species, *H. horaki* Lichtenfels, Pilitt, Gibbons and Boomker, 2001, with an apparently restricted host range in grey rhebuck, *Pelea capreolus* (Forster) (Lichtenfels et al., 2001). Similarly, *H. okapiae* van den Berghe, 1937 in African giraffids was resurrected from synonymy with *H. contortus* based on structural attributes (Lichtenfels et al., 2002). These latter taxonomic revisions would not have been possible in the absence of type specimens and vouchers that were historically archived in museum repositories. Such also highlights the critical importance of integrated methods in systematics that incorporate comparative morphology and specific sequence data derived from archival specimen collections (vouchers with authoritative identification) as the foundation to define species limits and the distribution of global diversity (eg, Hoberg et al., 1999, 2001). Caveats aside, and correcting for these modifications in taxonomy, the host range for *H. contortus* is recognizably broad, including species among artiodactyls of 40 genera across 5 families (and within 12 tribes of Bovidae) (summarized in Hoberg et al., 2004) (Fig. 2).

An expansive host range for *H. contortus* is observed in endemic regions of Africa, encompassing ungulate species among 23 host genera, including domestic sheep, goats and cattle. The broad host range is further dramatically reflected in the degree to which translocation, introduction and invasion with host switching, among 20 additional host genera, in North America, South America, southern Eurasia, Australia and New Zealand has characterized an expanding distribution over time, coincidental with agriculture, husbandry and global colonization by human populations (Fig. 2) (Hoberg, 2010; Hoberg and Brooks, 2013; Hoberg et al., 2004, 2008; Wilson et al., 2009; Zarlenga et al., 2014). In comparison, other species of *Haemonchus* are characterized by considerably less variation in host associations (Gibbons, 1979; Hoberg et al., 2004), with 5 of 12 species having three or fewer recognized hosts in Africa (eg, *H. dinniki* Sachs, Gibbons and Lweno, 1973, *H. horaki*, *H. kruegeri* Ortlepp, 1964, *H. laurenci* Sandground, 1933, and *H. okapiae*).

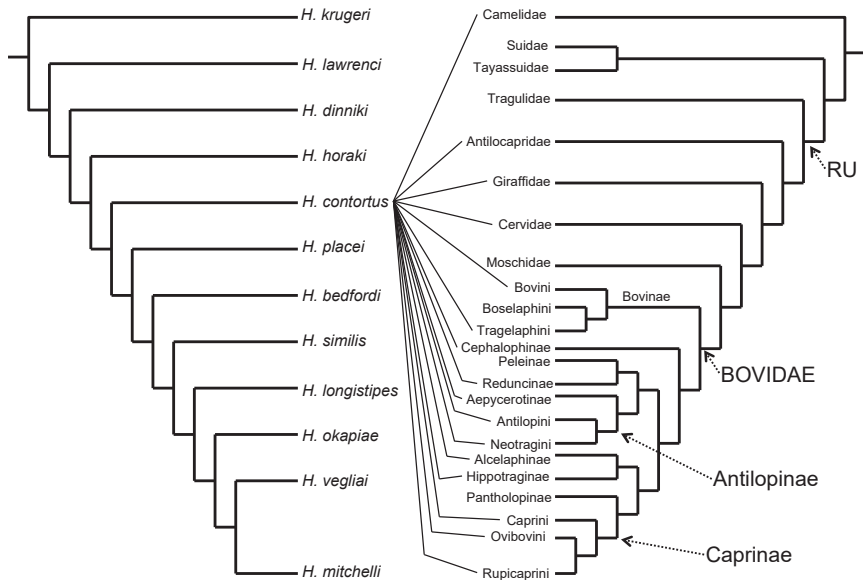


Figure 2 Phylogenetic perspective of host-group distribution for *H. contortus* among ungulates. Associations for *H. contortus* encompass a considerable array of ungulate families, subfamilies, tribes, genera and species denoting a complex history of natural expansion and anthropogenic events of global translocation, introduction and establishment with geographical and host colonization. Translocations of domestic caprines with global introduction, for example, were the drivers of host colonization among Cervidae, Antilocapridae and free-ranging Caprinae in the Western Hemisphere and Camelidae and Cervidae across Eurasia and South America. Dissemination out of Africa and globally reflects events tracking early routes of cultural interchange and later European colonization, exploration and trade. Phylogeny for species of *Haemonchus* is from [Hoberg et al. \(2004\)](#). Ungulate and ruminant phylogeny is derived and modified from currently available sources ([Gatesy and Arctander, 2000](#); [Hassanin and Douzery, 2003](#); [Hernández Fernández and Vrba, 2005](#); [Vrba and Schaller, 2000](#)). Host taxonomy among ungulates is consistent with [Grubb \(2005\)](#).

Further, *H. longistipes* occurs in six species of ungulates, including camelids, and less often in cattle, sheep, goats and antelopes. *Haemonchus mitchelli* Le Roux, 1929 occurs in six species of bovids, especially antelopes, and *H. vegliai* Le Roux, 1929 occurs in nine hosts, particularly antelopes, tragelaphines and cephalophines. Only *H. bedfordi* Le Roux, 1929 occurs among a diverse assemblage of 19 bovids or giraffids; however, host ranges of all congeners do not approach that seen for *H. contortus* (see [Hoberg et al., 2004](#)). *Haemonchus contortus* is one of three haemonchines, including *H. placei* (seven host species, primarily among Bovinae) and *H. similis* (nine host species primarily among Bovinae), which have been widely translocated, introduced and

established globally, coinciding with the expansion of trade routes and movement of domestic stock since the 1500s. The distribution of *H. longisittipes*, although influenced by anthropogenic translocation out of Africa, remains relatively limited to Eurasia and India.

In this arena, *H. contortus* might be considered as a generalist parasite, whereas congeners exhibiting varying degrees of apparent restriction to a more limited spectrum of host species or host groups would be regarded as specialists among the ungulates (eg, Walker and Morgan, 2014). In this conventional definition, generalists contrast with specialists relative to the apparent number of hosts in which parasites may successfully develop. Understanding the spectrum of hosts involved in persistence of *H. contortus* is essential, particularly in defining the competence of free-ranging artiodactyls to maintain viable populations in the absence of sheep and cattle, and thus to serve as significant reservoirs for infection of domestic stock. Among nematodes of ungulates, including *H. contortus*, the structure of host assemblages and dynamics for transmission are essential drivers for persistence and the potential for emergence when suitable conditions are conducive relative to a basic reproductive number of $R_{0,tot} > 1$ across the community (Dobson, 2004; Fenton and Pedersen, 2005; Fenton et al., 2015; Haydon et al., 2002). Although the basic reproductive number does represent the potential for establishment and persistence, relying on this measure is nondimensional and substantially changes the focus to outcomes, in contrast to process. Designations as generalist or specialist parasites based on convention, or an $R_{0,tot} > 1$, serve to diminish the adequacy of explanations reflecting the dynamic complexity of temporal, spatial, evolutionary and ecological processes, and mechanisms that determine host range in deep and shallow time (Agosta et al., 2010; Araujo et al., 2015; Brooks and McLennan, 2002; Hoberg and Brooks, 2008; Jacquet et al., 1995, 1998).

5.1 Host colonization, ecological fitting and sloppy fitness space

Colonization requires a convergence of opportunity and compatibility, or capacity, on the part of parasites to successfully infect, establish and be maintained in a novel host species or host group (see Combes, 2001). In a simplistic sense, opportunity is established through ecological perturbation and the disruption or breakdown of physical, biological or historical barriers (on a range of temporal and spatial scales) that previously limited exposure to infection or were the determinants for ecological isolation of populations, species, faunas and biotas in space and time (eg, Araujo

et al., 2015; Elton, 1958; Hoberg, 2010; Hoberg and Brooks, 2008). For example, intercontinental and regional barriers have historically limited dissemination and establishment for *H. contortus*. Breakdown in ecological isolation has emerged secondarily from anthropogenic events of translocation and introduction with domestic sheep and potentially other ungulates for conservation and game ranching that have established opportunity in new regional settings beyond Africa.

Opportunity converging with capacity in the context of *Ecological Fitting* defines events of colonization through the interaction of potential and realized host range, determined by a capability to utilize phylogenetically conserved resources by parasites (Brooks and McLennan, 2002; Janzen, 1985). Ecological fitting may be manifested by host colonization through resource tracking where similar attributes are presented by ancestral and novel hosts (Agosta and Klemens, 2008; Agosta et al., 2010). For example, sequential host-group acquisition and radiation demonstrated for species of *Haemonchus* among ungulates in Africa from the Miocene into the Quaternary appears consistent with this pathway. Alternatively, ecological fitting in 'sloppy fitness space' facilitates colonization through the exploitation of novel host-based resources that are beyond or outside of the range of conditions in which the species evolved, but may be characterized by a range in positive fitness encompassing suboptimal to optimal associations (Agosta and Klemens, 2008; Agosta et al., 2010; Araujo et al., 2015). *H. contortus* may occur in this variable or sloppy fitness space as reflected in the considerable array of ungulate hosts in which the parasite species may persist and which have been acquired through colonization in distant ecological settings following a history of translocation and introduction. Highlighted is the variation in competence across a broad spectrum of potential artiodactyl hosts and in host groups, which have been documented for *H. contortus* and other species of *Haemonchus* (eg, Boomker, 1990). Also apparent are the interrelationships for phenotypic plasticity, correlated trait evolution and phylogenetic conservatism that contribute to potential host-switching abilities of parasites, irrespective of the degree of specialization or specificity (Agosta and Klemens, 2008; Agosta et al., 2010; Araujo et al., 2015). Ecological fitting in broad sloppy fitness space facilitates translocation (geographical colonization and invasion), introduction and host switching, and has been an essential characteristic of faunal assembly on evolutionary and ecological time-scales (Agosta and Klemens, 2008; Agosta et al., 2010; Hoberg and Brooks, 2008, 2010, 2013).

The contemporary host range for species of *Haemonchus* contrasts the widespread versus restricted or narrow distributions for infections among

ungulates (Figs 1 and 2). An apparently extensive fitness space for *H. contortus*, coinciding with opportunity and capacity to infect a broad spectrum of endemic and introduced ungulates (with divergent trajectories on all continents, except Antarctica) has facilitated anthropogenic dissemination out of Africa. Congeners, including those that have been translocated, such as *H. similis* and *H. placei*, however, appear to be characterized by a smaller fitness space associated with a reduced assemblage of hosts; among African endemics, limited host range appears to be typical. Thus, a pertinent question is whether this assemblage of species has not had opportunity through breakdown in ecological isolation to utilize a broader spectrum of hosts, or if they are actually limited relative to the host groups in which they occur. Considered from a parallel perspective, how broad or narrow is the fitness space in which species other than *H. contortus* exist? A discussion of fitness space and ecological fitting appropriately changes the focus from explicit determination of generalists or specialists to an increasingly integrated view of ecology and evolution in the dynamics of host association and faunal assembly (eg, Brooks and McLennan, 2002).

5.2 Generalists and specialists: an obsolete nomenclature

Brooks and McLennan (2002) proposed that ecological fitting, in conjunction with the stochastic nature of opportunity would eliminate host range as a reliable indicator of whether a parasite is a specialist or generalist. Parasites are ecological specialists, irrespective of host range, as demonstrated by specific microhabitat preferences, conservative life cycles and transmission dynamics. Ecological fitting provides the mechanism that accounts for extensive host range and host switching, even in situations of specialization, and resolves these contrasting or conflicting relationships that are at the core of the *Parasitological Paradox* (Agosta et al., 2010; Araujo et al., 2015; Brooks and McLennan, 2002). Further, a property of parasites is considerable conservation in the degree of phylogenetic relatedness among hosts, although a clear relationship for host range and ecological specialization is equivocal. According to convention in these circumstances, parasites with a single or narrowly defined spectrum of hosts are considered as specialists, whereas those with multiple hosts are regarded as generalists (eg, Walker and Morgan, 2014) — an observation that is nondimensional in the context of evolutionary time. Consequently, applying restrictive nomenclature, such as generalist or specialist, is obsolete, and does not adequately reflect the evolutionary and ecological dynamics involved in the origins of faunal structure among complex assemblages of parasites in

multi-host associations, including species of *Haemonchus* (Brooks and McLennan, 2002).

Not all hosts are equivalent or optimal, and thus may represent different contributions to the maintenance and persistence of parasites among sympatric and multispecies assemblages, as exemplified among species of *Haemonchus* (eg, Achi et al., 2003; Fenton et al., 2015; Jacquet et al., 1998). Domestic sheep and goats, however, are the source of *H. contortus* globally through introduction, establishment and host colonization (eg, in cervids, particularly *Odocoileus* in North America and also camelids in South America). Persistence and maintenance often in suboptimal hosts (irrespective of introduced versus endemic populations) are indicated by patterns of prevalence and abundance (Boomker, 1990; Hoberg et al., 2004; Jacquet et al., 1998). Critically, these relationships determine the potential circulation of *H. contortus* in wild free-ranging ungulate hosts and the degree of 'threat' to domestic stock in ecotones involving overlap in managed and wild systems. As a function of ecological context, deer or pronghorn [*Antilocapra americana* (Ord)] can represent a source for colonization of domestic stock in southwestern North America; for example, putative circulation of *H. contortus* in cattle in the absence of sheep (E.P. Hoberg, P.A. Pilitt and D.S. Zarlenga, unpublished field data). Concurrently, expanding degrees of environmental perturbation that alter the field of ecological isolation and thus constitute emergent opportunity would be anticipated to drive bouts or events of switching among species of *Haemonchus* and ungulate host assemblages globally where conditions are suitable for transmission (chapter: The Pathophysiology, Ecology and Epidemiology of *Haemonchus contortus* Infection in Small Ruminants by Besier et al., 2016, in this volume).

Observations of contemporary host associations are most often viewed through a lens established by a slice of ecological time, rather than as a comprehensive picture across the expanse of evolutionary history. Such a perspective arises in discussions of specificity and host range, and has consequences for our understanding of the temporal definition and processes that determine host associations. An application of prevailing and convenient labels of generalist or specialist (based on the number of recognized hosts) to particular parasites reflects a limited temporal view or a window in time (eg, Walker and Morgan, 2014). Essentially, these designations depict a static snapshot of otherwise long-term and dynamic processes, extending across evolutionary into ecological time, and a misconception about the nature of host–parasite relationships (Araujo et al., 2015; Brooks and McLennan, 2002; Hoberg and Brooks, 2008, 2015).

Alternating trends for generalization and specialization emerge in the context of the *Oscillation Hypothesis* (Janz and Nylin, 2008), which has only been applied over during the past decade and less to systems of parasites and vertebrate hosts (eg, Hoberg and Brooks, 2008). Oscillation interacts with ecological fitting and constitutes the continuum for capacity that determines the limits for host exploitation. A temporally restricted snapshot, consequently, will reveal variation in the capacity to utilize hosts as fitness space changes over time (an intrinsic capacity of parasites) and interacts with local ecological structure. Such variation in observed associations is reflected in the existence of ‘faux generalists’ and ‘faux specialists’, where relationships are influenced by ecological context, further emphasizing that we cannot rely on host range even of the snapshot (Brooks and McLennan, 2002). Concurrently, oscillation tells us that specialists can produce generalists through alternating trends in relative specialization.

Oscillation embodies the dynamic nature of microevolutionary aspects of coevolution represented by co-accommodation (or coadaptation) (Brooks, 1979) that influences the degree of specialization (or specificity) demonstrated by parasites through reciprocal adaptation in associated lineages at any point in time. Trends in specialization/generalization interact with changing opportunities that are influenced by spatial/ecological dynamics, or the temporal and geographical arena for relative/apparent ecological isolation (Araujo et al., 2015; Hoberg and Brooks, 2008). Thus, opportunity and capacity determine host range at any point in time (constituting the limited temporal snapshot). Dynamics across evolutionary time, however, controls outcomes downstream, irrespective of the apparent picture or perspective within a particular temporal window, and are influenced at local scales by *Geographic Coevolutionary Mosaics* (Thompson, 2005) that determine the complexity of evolutionary interactions linking hosts and parasites through co-accommodation and cospeciation (Brooks, 1979). A focus on limited or nondimensional concepts in isolation, such as specificity, host range or even population parameters and fitness, provides an incomplete view of interactions and dynamics involved in multi-host associations and masks the considerable complexity resulting in faunal structure (eg, Fenton et al., 2015; Walker and Morgan, 2014). Each component alone is insufficient in providing broad explanatory power about diversification and faunal assembly, and is analogous to descriptions of the world that focus on a limited spectrum of mechanisms (eg, Hoberg et al., 2015).

Static snapshots or pictures of diversity in a contemporary arena do not accommodate historical processes; that is, the dynamic nature of change,

perturbation and episodic events that have structured faunal assemblages. Furthermore, this static picture results in the conceptual problem of generalists and specialists and host distribution within a temporally narrow context. It neither accounts for past change nor does it accommodate future dynamic change (how ecological fitting, sloppy fitness space and oscillation play out over time), but provides an inappropriate basis for interpretation of host associations that emerge from spatially and temporally discrete inventories. What we observe, or think we observe, is determined by the lens or perspective of spatial and temporal scale.

Current and widely held concepts of specificity or narrow host range (these terms are not synonymous) imply stasis and a static association or end point in host–parasite relationships. Specificity and stability/stasis are linked in the wider paradigm of cospeciation that does not adequately represent or account for the origins of complexity through ecological, biogeographical and evolutionary dynamics (eg, [Hoberg and Brooks, 2008, 2010, 2013](#)). Specificity in this realm becomes an observation about static phenomena, with implications that host switching and dispersal are rare. A paradigm view over the past century is apparent in the context of cospeciation, where diversification was most often linked to modification by descent in co-associated lineages occurring in a biosphere in relative stability governed by gradual change (reviewed in [Brooks, 1979](#); [Brooks and McLennan, 1993, 2002](#); [Klassen, 1992](#)). As a corollary, these assumptions conceptually established the parasitological paradox about the apparent enigma of the pervasive nature of host switching in associations dominated by host-specific parasites (see [Agosta et al., 2010](#)). This view of the biosphere is countered by considerable empirical observations and the nature of episodic perturbation, dispersal and host switching as factors central to diversification and assembly (eg, [Araujo et al., 2015](#); [Hoberg and Brooks, 2008, 2015](#)). Recognizing the importance of complexity in the biosphere has considerable implications for anticipating and managing/mitigating responses related to invasion and emergence of disease among intricate assemblages of hosts and parasites, including species of *Haemonchus* in ungulates, across environments under increasing change.



6. HOST AND GEOGRAPHICAL COLONIZATION IN FAUNAL ASSEMBLY

The history of radiation among species of *Haemonchus* and the development of expansive host associations for *H. contortus* are broadly consistent

with processes defined in the *Stockholm Paradigm*, which constitutes a synthesis and formal integration of macro- and microevolutionary dynamics, ecology and biogeography involved in diversification and faunal assembly (Araujo et al., 2015; Galbreath and Hoberg, 2015; Hoberg and Brooks, 2015). A synoptic approach or view of host range and specificity, and the central significance of geographical and host colonization emerges from this perspective, being one that is fundamental in understanding invasion and emergent disease (eg, Agosta et al., 2010; Brooks and Hoberg, 2013; Brooks and McLennan, 2002; Hoberg and Brooks, 2008, 2015).

Considered for diversification among species of *Haemonchus*, four primary and interrelated drivers, as interacting components of the *Stockholm Paradigm*, are involved as outlined in the previous sections: (1) opportunity and drivers of sequential (or episodic) geographical colonization and subsequent isolation in Africa connecting events, initiated during the Miocene and extending to the Quaternary, that are consistent with the *Taxon Pulse* that defines the ecological context and faunal outcomes of environmental perturbation/stability; (2) a capacity for host switching is established by *Ecological Fitting* and the potential for exploitation of phylogenetically conserved resources, and is seen in shifts to arrays of novel ungulate host groups arriving in Africa from Eurasia; (3) alternating trends for broadening (generalization) and narrowing (specialization) of host range in evolutionary time, associated with the potential for switching, occurs as a function of *Oscillation*; and (4) specificity may emerge downstream as a narrowing of host range during periods of relative stability and arises through co-accommodation (reciprocal co-adaptation in associated lineages) as specified in development of *Geographic Coevolutionary Mosaics*. Host colonization and a stepping-stone dynamic during diversification for species of *Haemonchus* are also evident among a considerable assemblage of ungulates in evolutionary time (eg, Araujo et al., 2015).

A deep history of sequential host colonization associated with waves of biotic expansion, bringing assemblages of ungulates from Eurasia into Africa, processes emerging from ecosystems in collision and faunal turnover defined the arena for radiation of *Haemonchus* (Hernández Fernández and Vrba, 2005; Vrba, 1995). Secondly, episodic waves of dispersal associated with human activities of agriculture, exploration and globalization, linking Africa, Europe, Eurasia, the Americas, Australia and New Zealand, only over the past 500 years demonstrate the importance of anthropogenic forces as determinants of distribution and invasion (eg, Capinha et al., 2015). This history is relevant in contemporary systems that are increasingly structured by events of invasion and colonization, which reveals the significance of

perturbation and ecological fitting as drivers of faunal assembly across all temporal and spatial scales. It is evident that these invasion processes are, to a large degree, equivalent, and that history informs about the potential range of responses that may be anticipated in contemporary systems across managed and natural habitats (Hoberg, 2010). Ecological fitting with respect to *H. contortus* accounts for what must be considered an extraordinary range of contemporary hosts. As such, this system, for species of *Haemonchus*, strongly validates the process and mechanisms outlined for faunal assembly by Hoberg and Brooks (2008, 2010, 2013), and also instructs about the emerging generality for the role of expansion and geographical colonization relating to the development and structure of chronological and spatial mosaics (Hoberg et al., 2012).



7. CLIMATE IMPACTS INTEGRATING HISTORICAL PERSPECTIVES

The origin of the assemblage of *Haemonchus* species provides historical context for environmental/ecological regimes and selective arenas for evolution and radiation in Africa over the late Tertiary and through the Quaternary. It is apparent that *H. contortus* initially emerged in association with antelopes in relatively xeric to mesic savannah habitats of Africa, emphasizing the importance of selection and adaptations for persistence in subtropical environments (Hoberg et al., 2004). Conversely, radiation under tropical regimes would pose historical constraints for development and expansion into Temperate/Boreal and Sub-Arctic regions, serving to explain the absence of endemic species of *Haemonchus* in the Western Hemisphere. Faunal continuity at high latitudes was strongly influenced by climate and cold-based filter bridges such as that across Beringia, linking the Nearctic and Eurasia, that limited the potential for dispersal during glacial–interglacial stages of the late Pliocene and Pleistocene (Hoberg et al., 2012). Host switching among and dissemination within now domestic caprines, bovids and camelids occurred secondarily. Sequential introductions out of Africa, and among the continents where considerable animal husbandry has expanded, now serve to define the global distribution for these nematodes (Fig. 2).

Broad geographical patterns of occurrence suggest that the constraints posed by temperature (resilience, tolerances, metabolic upper and lower thresholds for development of third-stage infective larvae) and moisture are critical to geographical persistence, and as determinants of distribution

and emergence (chapter: The Pathophysiology, Ecology and Epidemiology of *Haemonchus contortus* Infection in Small Ruminants by [Besier et al., 2016](#), in this volume; [O'Connor et al., 2006](#); [Troell et al., 2005](#); [van Dijk et al., 2008, 2009](#)). Limitations created by variation in moisture, humidity and pulses of precipitation (seasonally, and at finer temporal and spatial scales) could be decisive in establishing permissive conditions conducive for introduction/invasion, establishment and population amplification on the peripheries of current core distributions (eg, in Eurasia, North America and South America). Precipitation rather than elevated temperature may be a primary constraint on the distribution of *H. contortus* and other gastrointestinal nematodes in circulation among domestic ungulates, at least in some regions ([Beck et al., 2015](#); [Wang et al., 2014](#)). Scenarios and models for substantial alteration in patterns of temperature and precipitation encompassing incremental and extreme events emerging from accelerated climate warming suggest complex responses (expansion/retraction, local extinction) with respect to geographical range occupied by *Haemonchus* nematodes (eg, chapter: The Pathophysiology, Ecology and Epidemiology of *Haemonchus contortus* Infection in Small Ruminants by [Besier et al., 2016](#), in this volume; [Hoberg et al., 2008](#); [IPCC, 2013, 2014](#); [van Dijk et al., 2008, 2009](#)). In Europe, climate-driven increases in infection pressure are predicted for *H. contortus*, shifting from the south to north in response to environmental change related to increasing temperature and decreasing moisture over this century ([Rose et al., 2015](#)). An expanded window for transmission in northern Europe by 2–3 months is also predicted, which is consistent with general expectations for altered patterns and extension of seasonal dynamics for development and transmission of ungulate nematodes in the Temperate and Boreal zones (eg, [Hoberg et al., 2001, 2008](#)).

Aside from direct environmental forcing, [Waller et al. \(2004\)](#) demonstrated that the establishment and persistence of *H. contortus* in sheep at high latitudes of Sweden, above the Arctic Circle near 66°N, were dependent on apparent selection, resulting in a prolonged period of arrested development that may be of 7 months duration. Interactions across biotic and abiotic mechanisms result in populations of *H. contortus* sequestered as early fourth-stage larvae in overwintering ewes. Behavioural patterns of parasites led to a shift towards a single parasitic generation per year associated with peri-parturient emergence, subsequent pasture contamination and infection of lambs in the spring cycle. Epidemiology is consistent with absence of winter survival for eggs or larval stages at Swedish latitudes, although genetic signatures for selection and adaptations related to new life history pathways

could not be recognized (Troell et al., 2005). In these environments, characterized by extreme cold temperature, persistence is currently associated with populations that undergo long-term inhibition that carries each parasitic generation through extended periods of adverse ambient temperature. Changing temperature regimes, however, can alter the potential for survival of larval stages of *H. contortus* across northern environments as a consequence of incremental warming (chapter: The Pathophysiology, Ecology and Epidemiology of *Haemonchus contortus* Infection in Small Ruminants by Besier et al., 2016, in this volume; Hoberg et al., 2008; O'Connor et al., 2006). Coincidental with environmental shifts driven by warming, seasonally defined bimodal peaks for transmission, characteristic of core distributions in temperate environments, may be reestablished and influence expansion and population amplification at increasingly high latitudes (Rose et al., 2015). Shifting epidemiological trajectories for *H. contortus* are expected and further demonstrate the considerable phenotypic plasticity and capacity for selection leading to persistence in the dual adverse environments represented by hosts and the external environment (chapter: The Pathophysiology, Ecology and Epidemiology of *Haemonchus contortus* Infection in Small Ruminants by Besier et al., 2016, in this volume; Crofton et al., 1965).

Persistence of *H. contortus* in xeric environments and under historically elevated temperatures characteristic of Africa represents a contrast to conditions in the Temperate and Boreal zones (eg, Jacquet et al., 1998). Seasonal effects such as strongly defined wet and dry periods and variation in the distribution and degree of sympatry for assemblages of domestic ungulates through the annual cycle (sheep, goats, zebu cattle and dromedary camels) result in selection pressures that may determine circulation of different species of *Haemonchus* nematodes. Persistence appears linked to extended time frames (8–9 months) for arrested development spanning the duration of a 6-month dry season (*H. placei* and *H. longistipes*) or is associated with increased longevity or perhaps delayed senescence of adult parasites (*H. contortus*). Either trajectory provides a capacity for survival and circulation in otherwise harsh environmental conditions, and parallels observations from the Northern Hemisphere that may involve extension of seasonal hypobiosis, when conditions would directly limit the longevity of developing and infective larval stages.

Apparently rapid selection within small effective populations and at fine geographical scales leading to measurable genetic and phenotypic divergence demonstrates the potential for development of considerable population heterogeneity across landscapes (Hunt et al., 2008). Recognition of

such population mosaics has implications for patterns of potential emergence of disease conditions and should be considered in decisions about management and husbandry at local scales. These dynamics are consistent with local effects and the mosaic occurrence of disease in space and time that may result from selection and adaptation on landscape scales in convergence with changing environmental conditions for temperature and moisture (eg, [Hoberg and Brooks, 2008](#); [Hunt et al., 2008](#); [Thompson, 2005](#)).

Regimes of perturbation driving origins of new ecotones, sympatry among domestic and free-ranging wild ungulates, and dissolution of mechanisms for ecological isolation in combination with expansion of permissive environments can be associated with amplification of populations, emergence and disease ([Brooks and Hoberg, 2007](#); [Hoberg and Brooks, 2015](#); [Hoberg et al., 2008](#); [Mas Coma et al., 2008](#)). Relaxation of abiotic and biotic controls on the occurrence of *H. contortus*, coincidental with inception and dissemination of anthelmintic resistance may be synergistic, serving to exacerbate challenges to control expansion of parasite populations or to limit the socioeconomic impacts of infection that can influence the security and availability of food (eg, [Hoberg et al., 2008](#); [Rose et al., 2015](#)).



8. UNDERSTANDING DIVERSITY: SOME RECOMMENDATIONS

Although considerable advances have been achieved in recognizing the global extent of *Haemonchus* diversity and distribution, a definitive understanding of biogeography and host association remains complicated by several interacting factors: (1) a considerable morphological homogeneity has led to often superficial or incorrect identification when unequivocal structural or molecular criteria are not applied and where assumptions about host association drive concepts for elucidation of species diversity; (2) an occurrence of unrecognized cryptic diversity and incompletely defined limits for morphological variation conflate species identities that can only be revealed through integrated morphological/molecular approaches; (3) an uneven sampling across host taxa and geography may lead to biased or incomplete assumptions about diversity and distribution, demonstrating a justification for continued survey and inventory, especially in poorly known areas of the Neotropical region, Eurasia and North America; (4) an absence of broad-based landscape level assessments of genetic diversity, population structure and gene flow hinders the recognition of relationships or linkages for local and regional faunas; and (5) an ambiguity about transmission

pathways results from patchy information about the genetic structure of *H. contortus* and other species in multi-host assemblages in circulation among domestic and free-ranging ungulates. Such ambiguity is heightened in zones of sympatry or across ecotones, and among wild artiodactyls in isolation from managed systems. Additional conflation over the identity of *H. contortus* and related species of *Haemonchus* has also been introduced by a culture in parasitology and disease ecology that has not developed and applied a uniform strategy for archival deposition of voucher specimens in museum repositories (eg, Brooks et al., 2014; Hoberg et al., 2009). Absence of an unequivocal picture of diversity confounds the identification of routes and pathways for the dissemination of drug resistance, and in establishing robust models for species responses to environmental perturbation and accelerating climate change.

Proactive assessments of diversity are necessary and a proposal for broad-based capacities to assess and understand diversity of complex host–parasite systems was outlined in the *Documentation-Assessment-Monitoring-Action* (DAMA) protocols (reviewed in Brooks and Hoberg, 2000; Brooks et al., 2014; Hoberg et al., 2015). DAMA is a proposal which codifies articulation of a proactive and collaborative capacity for biodiversity informatics, linking field collections, archived specimens, morphology and sequence data in museum resources, to understand, anticipate and respond to the outcomes of accelerating environmental change and globalization. Envisioned is an expansive platform to develop and provide essential information addressing ecology, evolution and epidemiology for hosts and parasites linked across temporal and spatial scales, which codifies an ongoing discussion of the nature of diversity and biodiversity information that extends into the 1990s (eg, Hoberg, 1997). Relevant to *Haemonchus* and more generally across host–parasite systems, the past decades have demonstrated the nature of critical information emanating from biodiversity inventories that establishes the evolutionary/ecological context necessary to recognize and document (baselines) the cascading influence of climate change and emerging disease (Brooks et al., 2014). Inventories at regional scales provide the mechanism to identify new or continuing pathways for anthropogenic invasion and climate-driven modifications, and to monitor host and geographical associations through shifting spatial and ecological boundaries and expanding (or contracting) distributions. Informatics emerging from inventory processes is an essential key that links evolutionary and ecological history. The development of timely and effective responses that mitigate emergent parasitic infections will directly depend on integrating knowledge across

the past, present and the future of systems in dynamic change (chapter: The Pathophysiology, Ecology and Epidemiology of *Haemonchus contortus* Infection in Small Ruminants by [Besier et al., 2016](#), in this volume; [Brooks et al., 2014](#); [Hoberg and Brooks, 2013](#)).

Understanding diversity remains important. Translocation, establishment and invasion of otherwise exotic parasites continue in a regime of globalization ([Brooks and Hoberg, 2013](#); [Hoberg, 2010](#); [Hulme, 2014](#)). Habitat perturbation, transitions, and shifting distributions due to accelerating climate warming are analogous (or equivalent) to historical episodes of climate fluctuation and environmental disruption in Africa during the Miocene, Pliocene and Quaternary, which had influential contributions to the distribution and radiation among species of *Haemonchus* in ungulates ([Hoberg and Brooks, 2010, 2013](#); [Hoberg et al., 2004](#)). Species of *Haemonchus* radiated in savannah environments of sub-Saharan Africa under relatively xeric conditions and elevated temperatures. Controls on current distributions, for example in South America and North America, may reflect this evolutionary and ecological trajectory with thresholds for development, tolerances and resilience as conservative constraints linked to particular regimes of temperature and moisture. Consequently, climate, manifested in long-term incremental change and short-term extreme events for temperature and precipitation ([IPCC, 2013, 2014](#)), must be accounted for in anticipating responses in complex host–parasite systems that can influence patterns of persistence, emergence and disease across a broad spectrum of ungulate hosts (eg, [Hoberg et al., 2008](#); [Mas Coma et al., 2008](#); [van Dijk et al., 2009](#)). All of our knowledge starts with evolution, ecology and biogeography, as these interacting facets determine the history of biodiverse systems. These components, relating to *Haemonchus*, can inform about the nuanced history of geographical distribution, host association and the intricacies of the host–parasite interface that are played out in physiological and behavioural processes that influence the potential for disease and our capacity for effective control in a rapidly changing world.

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