

# Invasive processes, mosaics and the structure of helminth parasite faunas

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## **Summary**

The biosphere in evolutionary and ecological time has been structured by episodes of geographic and host colonisation that have determined distributions of complex assemblages of microparasites and macroparasites, including helminths circulating among vertebrates. Biological invasion is an intricate phenomenon often involving 'extra-range dispersal' and establishment of exotic (non-indigenous) species and populations substantially beyond their native range. Invasion may also involve the expansion or shifting of host and geographic distributions of an endemic (indigenous) species or fauna under changing environmental conditions. Invasions result in faunal interchange occurring under influences from both natural and anthropogenic forces where expansion on spatial/temporal continua bridges continents, regions and landscapes. Drivers for invasion are idiosyncratic, multifactorial, interactive, and opportunistic, with a powerful role for historical contingency. The life history patterns of helminths interact with invasion pathways to determine the potential for introduction. Human-mediated events, such as the global expansion of pathogens linked to development of agriculture, domestication of food animals, and European exploration have had a pervasive influence on the distribution of helminths. Globalisation, broad transport networks and environmental perturbation linked to climate change, along with other drivers, have accelerated these processes. A consequence of invasion and establishment of exotic species is that faunal structure will be a mosaic that includes admixtures of indigenous and non-indigenous species and populations; exemplified by helminth faunas among domestic and free-ranging ungulates and a diversity of host-parasite systems among vertebrates. Contemporary mosaics are evident where human-mediated events have brought assemblages of new invaders and relatively old endemic species into sympatry, highlighting interactions at ecotones, particularly those at borderlands between managed and natural ecosystems. Understanding the historical origins and complex components of mosaics is essential in formulating predictions about future responses to environmental change. Powerful tools are available which support the study of invasive species, the most important being systematics and our capacity to accurately identify parasites and to define evolutionary and biogeographic history. Faunal baselines derived from arrays of biological specimens, integrated surveys and informatics are a permanent record of the biosphere when archived in museum collections. The absence of comprehensive taxonomic inventories of parasites, including molecular-genetic data, limits our ability to recognise the introduction of non-indigenous parasites, and to document patterns of expansion for local faunas under a regime of environmental perturbation.

## **Keywords**

Anthropogenic event – Biodiversity – Helminth – Invasive species – Propagule – Vertebrate parasite.

## Introduction: defining invasions

Biological invasions have characterised much of earth history and have occurred on temporal and spatial scales that link evolutionary and ecological time (109, 110, 111, 113). Invasions involve faunal interchange and transition. This occurs when indigenous (endemic) and alien or exotic species and biotas are brought into proximity or contact, by either natural or anthropogenic forces, following the dissolution of a barrier to dispersal and establishment. Invasions may also involve the expansion or shifting of host or geographic distributions of an indigenous species or fauna under changing environmental conditions. Successful invasion results from initial introduction and establishment, with subsequent amplification and expansion, in a new environmental setting, of non-indigenous species, which may include both free-living and parasitic taxa (21, 101). Invasive processes have structured the biosphere, and episodes of geographic colonisation have served as a determinant of distributions of complex assemblages of hosts and pathogens and as the basis for emergent disease (8, 10, 40, 41). Invasion is a complex process. It is a phenomenon which unfolds in the context of ecosystems and faunas, with expansion on a spatial/temporal continuum which bridges continents, regions and landscapes.

Largely anthropogenic drivers increasingly influence the invasion, distribution and dissemination of invasive species, which have pervasive ecological and economic impacts on local (landscape), regional and global scales (82, 90, 101, 115). Although not discussed explicitly in the following context, invasive processes have been an unintended outcome of the history of the 'domestication of landscapes and ecosystems', as humans have modified the environment to enhance the availability and sustainability of food resources and to create living spaces (57).

In exploring animal and human pathogens, the character of invasion has evolved over time and has been influenced by a series of thresholds or tipping points in human history (4, 93). Thus, the accelerating human imprint on the biosphere and on the distribution of pathogens and host-pathogen systems has been driven by our initial expansion out of Africa 40,000 to 60,000 years ago, the advent of agriculture and animal husbandry nearly 11,000 years ago, the ensuing age of European exploration in the 1500s, and the industrial revolution (90, 115). Increasingly, humans became a pervasive force in evolution, with direct influence over an array of free-living organisms and a diverse assemblage of pathogens in both free-ranging and domesticated hosts (68, 78). Each of these thresholds was accompanied by a burgeoning human population and a continuing transition from a 'slow and large world', dominated by relative isolation and local effects, to a 'rapid and small world' associated with

extensive globalisation, homogenisation and integrated, but often fragmented, environmental networks.

Invasion as an essential foundation of the biodiversity crisis is not simply related to species loss or extinction (114), but emphasises the impact of globalisation and translocation for an array of pathogens in humans, domestic stock and free-ranging species (9, 18). Invasion unfolds through the continual interplay linking the dynamics of transmission, ecological structure, biodiversity and climate, in the balance represented by the intricacies of parasite webs and parasite flow (19, 83). Furthermore, invasive processes are evident in the emergent properties of contemporary biotic structure that emanate from a deeper historical backbone or framework of host-pathogen interactions (40, 116). These interacting phenomena determine the disruptive force or pressure exerted by exotic parasite species introduced and established in new regional and ecological settings (via geographic colonisation) or host associations (via host switching). Similar phenomena are in play for indigenous parasites under expansion owing to accelerating environmental change and ecological perturbation. The interface for parasite faunas among native and non-indigenous hosts can determine the outcomes of invasion for both vertebrate and invertebrate species and ultimately for ecological structure in space and time (21, 102).

Central to the process of invasion is the breakdown of ecological isolation, a fundamental mechanism recognised in seminal discussions on the impact of exotic species on ecosystem structure and in the dissemination of pathogens (3, 24, 89). Invasion, including both natural and human-mediated dispersal, can follow multiple pathways involving varying numbers of individuals (propagules) and time frames with varying outcomes for the establishment, subsequent expansion and genetic structure of the founding population (31, 75, 99, 101, 115). Across landscape, regional and global scales, we have disrupted the biosphere. New waves of perturbation and extinction, emerging from landscape modification and climate change, threaten biological diversity and ecological continuity in terrestrial, aquatic and marine systems (55). Landscapes in transition influence the proximity of wildlife, domestic animals and people, and ecotone effects at borderlands influence transmission, emergence and resurgence of pathogens (5, 18, 83).

A primary concern has emphasised the economic impact of invasion and invasive parasite species and zoonoses on domestic stock, primary food animals, and human health (101). Invasive species, however, have broader implications, manifested across ecosystems and wildland habitats among a diverse assemblage of free-ranging vertebrates. Additionally, much of the discussion about the invasion of pathogens has been from a host-centric viewpoint, exploring the impact of parasites on the

potential for successful establishment of exotic or alien free-ranging vertebrates or invertebrates (21, 102). In contrast, parasite-centric views can address the ecological and evolutionary factors associated with invasion, examining whether or not there are core characteristics of parasites that transcend taxa and are critical for successful establishment. There has been relatively little exploration of the implications of invasive processes for the population genetic structure of helminths, although predictions suggest that those associated with humans will more often undergo demographic expansions coinciding with regional translocation and exposure of naïve host populations (6, 75).

## Natural invasions

The structure of contemporary faunas and patterns of parasite diversity have to a large extent been strongly influenced by geographic colonisation in space and time. Large-scale historical invasions (or biotic expansion and faunal interchange) have established the deep historical backbone or framework for understanding the patterns and processes involved in the distribution of complex host-pathogen systems (9, 40, 41). These patterns provide an important analogue for how contemporary (but accelerated) processes determine faunal structure, parasite distribution and emergent disease relative to hosts and geography (2, 33, 90).

Natural invasions are perhaps best exemplified by expansion events and geographic colonisation, which have influenced terrestrial faunas in Africa, Eurasia and North America. The diversification and current global distribution for species of *Trichinella* was to a great extent determined by events after the mid-Tertiary and was strongly influenced by host switching and multiple independent invasions with an assemblage of mammalian carnivores and omnivores into Africa and North America from Eurasia (41, 85, 117). Biotic expansion out of Eurasia was also instrumental in determining the initial structure of nematode faunas, including genera and species of the Nematodirinae, Ostertagiinae, Haemonchinae, Cooperiinae and others, among free-ranging ungulates (35, 38, 45). (Notably both Cooperiinae and Haemonchinae do not appear to have endemic distributions in the Western Hemisphere [35]). Additionally, following apparent independent origins of human *Taenia* in Africa during the Pliocene (*T. solium* and *T. saginata*), expansion into Eurasia influenced subsequent diversification (*T. asiatica*) and potential for global dissemination (36, 39, 93). The history of these disparate faunal elements emphasises the importance of ecological linkages and interactions – through foraging guilds among definitive hosts – as determinants for diversification and geographic distribution (40). Episodes of invasion

involved differential timing for expansion events from Eurasia into Africa (and out of Africa) and into the Western Hemisphere coincidental with development of land connections and dispersal corridors that led to the breakdown of geographic isolation prior to the emergence of modern humans. Cyclical climatological and environmental perturbations were primary drivers which resulted in variable duration of periods of faunal colonisation, occupation and regional isolation (40). Invasive processes served to create the foundations for distributions of contemporary regional faunas, representing endemic or indigenous species, and were important in establishing the evolutionary context, potential and range of responses to human-mediated dispersal in ecological time (42, 45).

## Anthropogenic invasions

The advent of agriculture, the domestication of our primary food (e.g. cattle, sheep and goats, swine, poultry) and companion animals (dogs and cats) and the expansion (both numerically and geographically) of human populations (with an array of synanthropic mammals, including rats and other rodents) established thresholds over time that have had a profound influence on the distribution of helminth parasites and associated parasitic diseases (93). Domestication influenced the evolutionary trajectories for assemblages of parasites characteristic of ungulates and some carnivores in Eurasia (74, 75). Burgeoning human populations subsequently were mediators of landscape transformation across agricultural and urban environments, with encroachment on wildlands creating ecotones at the interface of managed and natural habitats; these processes have expanded and accelerated over the past 10,000 years. European colonisation and exploration from the 1500s onwards reshaped parasite faunas through extensive and recurrent patterns of translocation and introduction on a global scale, probably excluding only Antarctica (32, 101). Inadvertent invasion occurred without controls on the widespread dissemination and establishment of exotic faunas, including helminths circulating in humans, domestic animals, or introduced wild hosts. Trade, long-distance transport and globalisation continue this trend, which can maximise the potential for rapid and widespread invasion of pathogens (56, 97).

## Ungulate helminth faunas

Beyond Eurasia, nematode, digenean and cestode faunas associated with domesticated ungulates have been invading new geographic localities for the last 500 years. Thus, understanding the history and structure of faunal

diversity has implications for defining how assemblages of parasites (and hosts) will respond to environmental perturbation (49). Among the trichostrongyloid nematodes, haemonchines (species of *Haemonchus*, *Ashworthius*, and *Mecistocirrus*) diversified in Eurasia and Africa and a number of species, including *H. contortus*, *H. placei* and *H. similis*, are now regarded as characteristic invaders on a global scale, with their expansion largely coinciding with the distribution of sheep and cattle in North America, South America, Australia and New Zealand (27, 45, 105). Geographically widespread species of *Haemonchus* are typically associated with domestic stock. Secondary associations, however, among Cervidae, Antilocapridae, and wild Caprinae in the Nearctic, and among Cervidae and Camelidae in the Neotropics, have been a consequence of introductions and exchange of parasites at historical interfaces for managed and natural systems (42, 45), although the implications for population genetic structure remain unknown (105). *Mecistocirrus digitatus* was widely introduced with *Bubalis bubalis* and *Bos indicus* from source populations in Asia and is now widely distributed in South and Central America, where it has apparently displaced other haemonchines in bovid hosts (70). In contrast, *Ashworthius sidemi* has been disseminated by translocation with cervids (*Cervus nippon*) from Asia into western Europe, where expansion resulted in colonisation of *C. elaphus* and *Bison bonasus* and emergence of disease (20, 25); exotic species of *Ashworthius* have not apparently been introduced in the Western Hemisphere (37).

The apparent northern expansion and emergence of *H. contortus* in Sweden may indicate that the interaction of management practices and climate change has facilitated a broader distribution of this nematode at high latitudes in domestic sheep (112). Lengthened periods of arrested development, with early fourth-stage larvae surviving through the winter and a limited seasonally defined period of activity for adult nematodes in the abomasum, represent a significant shift in epidemiology, which could reflect local directional selection; however, adaptations related to the presence of *H. contortus* in cold climates have yet to be identified (107). In this situation the role of management may outweigh other factors which can serve as determinants of parasite distribution.

A diversity of other strongylate nematodes have extensive histories of long-range dispersal and introduction via human-mediated pathways linked to introductions of domestic or free-ranging ungulates (42, 91, 100), they include:

- Strongylina (e.g. species of *Chabertia* and *Oesophagostomum*)
- Metastrongylina (e.g. species of *Protostrongylus*, *Muellerius*; and species of *Dictyocaulus*)

- Trichostrongylina, including molineoids (e.g. species of *Nematodirus*) and trichostrongyloids, notably genera and species among the Ostertagiinae (e.g. *Camelostrongylus mentulatus*, *Longistrongylus* spp., *Ostertagia ostertagi*, *O. leptospicularis*, *Teladorsagia circumcincta*, *Spiculoptera* spp., *Sarwaria bubalis*), Cooperiinae (e.g. *Cooperia oncophora*, *C. punctata*) and Trichostrongylinae (e.g. *Trichostrongylus axei*, *T. vitrinus*).

Furthermore, Libyostromylinae, and species of *Libyostromylus*, have been widely disseminated globally with the movements of their ostrich hosts (species of *Struthio*), which are now established for farming in many regions beyond Africa (23, 46). The list is not exhaustive, but serves to demonstrate the continuing role of anthropogenic drivers as determinants of helminth distribution. It also reveals the lack of general controls on the transport of domestic, semi-domestic and wild stock, along with their characteristic parasites, on local to regional scales.

Among the bursate nematodes, the complex and often enigmatic history of *Nematodirus battus* is particularly instructive (32, 51, 76). Although initially recognised as a significant pathogen of domestic sheep in the border regions of Scotland (17), *N. battus* has subsequently been documented at numerous localities in western Europe, and most recently in North America and possibly Central and South America. The geographic distribution and history of *N. battus* is consistent with sequential translocation over the past 60 years, with establishment, amplification, subsequent emergence and outbreaks of significant disease at many, but not all, localities. Notably, apparent displacement of other species of *Nematodirus* typical of sheep in areas of sympatry has also been observed. The potential for seasonally defined emergence of disease appears controlled by local epidemiological factors (92) and now, increasingly, may be strongly influenced by changing patterns of temperature and weather interacting with the developmental thresholds and tolerances of larval parasites (108).

The population genetic structure of these assemblages of introduced species should be influenced by patterns of host translocation and movement interacting with the life history and differential mortality rates of parasites, and directional selection (7, 52, 75, 101). At large geographic (intercontinental) scales, diversity appears strongly partitioned for such species as *H. contortus*, probably reflecting a history of introductions and subsequent limited gene flow (105). Data remain limited, but owing to extensive inter- and intra-regional movements of domestic ungulates (and probably highly recurrent patterns of introductions over time), some trichostrongyloid nematodes maintain high levels of genetic diversity relative to that demonstrated for species in free-ranging hosts

(7, 47). However, this appears to contrast with *Dictyocaulus*: seasonally defined bottlenecks related to low winter survival may result in the maintenance of considerable genetic structure at local geographic scales (52).

Digenean parasites of ungulates have also undergone recurrent patterns of long-range dispersal and establishment. For example, introductions of *Fascioloides magna* have coincided with translocations of cervids from North America into Europe and Eurasia (87). Introductions have resulted in a patchy distribution of *F magna* in western Europe, where broad expansion has apparently been inhibited by populations of parasites encountering an assemblage of new molluscan and cervid hosts. Across the historical range in North America, the distribution of *F magna* is also heterogeneous. In these situations, thresholds for host-parasite populations that are necessary for successful establishment may not always be attained through natural dispersal of cervids (87). Such is suggested by the apparently limited and disjunct distribution of *F magna* in North America, although evidence for natural dispersal with *Cervus elaphus* has been observed in central Europe (53). Translocations of multiple animals provide a viable mechanism for relatively rapid and long-range dispersal, suggesting that management plans dealing with free-ranging or semi-domestic cervids must address the potential for introduction of helminth parasites and other pathogens (16, 53).

The typical liver fluke of cattle and sheep, *Fasciola hepatica*, has also undergone an extensive history of dissemination from an ancestral geographic range in the Palearctic, coincidental with movements of domestic stock and invasive snail intermediate hosts (101, 104). In this case pathways for successful global introduction and establishment initially paralleled major trade routes and the historical shipment of both cattle and sheep (101). Establishment has also been related to introductions of exotic and suitable lymnaeid snails as intermediate hosts, which in some situations preceded the arrival of parasitised definitive hosts. These processes serve as a model for the complex pathways involved in the broad dissemination of a single parasite species on global to local scales (101).

Among fasciolids, changing management practices for landscapes and host species are significant in determining invasion at local scales. For example, changing distributions and emergence may be associated with (i) expansion of farming into wilderness; and (ii) regeneration of natural habitats in regions of intensive farming. Both practices may lead to modification and development of microhabitats suitable for an array of intermediate hosts (consider *Fasciola* in restored wetlands) (86). Furthermore, overgrazing and drought can alter susceptibility and infection pressure, and management practices in some instances may outweigh the effects of climate change.

## *Trichinella spiralis*

The nine species of encapsulating *Trichinella* are distributed regionally among terrestrial carnivores across the globe, but only *T. spiralis* has an extensive history of human-mediated and long-range geographic introduction (85, 94). *Trichinella spiralis*, an archaic lineage that initially diversified in Asia among an assemblage of carnivores and omnivores, is now largely adapted to synanthropic circulation among domesticated swine and rats, with zoonotic emergence in people (117). Transition from an ancestral mode of circulation is related to the development and expansion of animal husbandry and domestication of swine (67). Origins of an association of recent populations of *T. spiralis* with domesticated swine in western Europe were followed by anthropogenic translocation initiated with European colonial exploration in the 1500s which disseminated the host-parasite assemblage globally (93, 94). Interestingly, an apparent absence of genetic diversity for introduced *T. spiralis* may contrast with predictions for signals demonstrating population expansion among invasive parasites under strong human-mediated control (75). Variance from this pattern for *T. spiralis* may indicate influences from life history (indirect versus direct cycle), or could reflect events in shallow ecological time for geographic introduction and establishment interacting with the structure (and historical bottlenecks) of source or founding populations in Europe (93).

## *Taenia* species

Species of *Taenia* have a complex temporal and geographic association with human hosts which involves multiple waves of dispersal and patterns of global introduction and isolation over an extended period spanning the Quaternary to contemporary time frames (13, 36, 39, 77). Obligate parasites of humans, *Taenia solium*, and *T. saginata* + *T. asiatica*, initially emerged from Africa, secondarily colonised swine and cattle, and were later translocated globally with people and an assemblage of primary food animals (36). Although eradicated to a large extent in Europe and North America, *T. solium* and *T. saginata* remain endemic in some regions of Asia, Africa and Latin America. Human dispersal and associated swine husbandry appear to be the primary mechanism in the distribution of *T. solium*. Contemporary populations of *T. solium* in Africa and Latin America were derived from European sources, through multiple introductions from diverse source populations over the past 500 years (13, 77). The current re-emergence of this pathogen, for example in North America, and increasing incidence of human neurocysticercosis are related to movements of immigrant populations and introductions of parasites from regions of endemism (98). Socio-economic factors and displacement of human populations, particularly with

immigration, are expected to drive the continuing emergence and resurgence of *T. solium*, along with other species of *Taenia*, in humans.

## Climate-mediated invasions

Environmental perturbation driven by climate change is emerging as a pervasive influence on the ecological structure and patterns of distribution of complex host-parasite systems and associated disease (28, 79, 80). Climate-mediated invasions, geographic and host colonisation, and emergence of a diversity of helminth species, including those circulating among domestic and free-ranging vertebrates and as zoonoses in people, have been identified or predicted (11, 49, 50, 59, 61, 62, 84). Directional climate change resulting in cumulative or incremental processes (years to decades) on regional scales may contrast or interact with extreme and idiosyncratic (short-term) events which determine the emergence of parasites and disease across landscapes (49, 63).

A range of consequences and predictions emerge for invasive species in a regime of climate change, which apply to both hosts and parasites (29):

- altered mechanisms of transport and introduction
- establishment of new invasive species
- altered impact of existing invasive species (e.g. tropically adapted nematode faunas)
- altered distribution of existing invasive species (relative to both geography and assemblages of hosts)
- altered effectiveness of control strategies.

For example, in North America, biotic expansion from south to north is predicted for tropically adapted nematode faunas in ungulates (currently limited by environmental tolerance and thresholds of development) including *Haemonchus*, *Mecistocirrus* and *Cooperia*, coinciding with altered patterns of temperature and rainfall (49). Northward expansion of free-ranging cervids may also be predicted to broaden helminth distribution, leading to new zones of sympatry for host-parasite assemblages (62). Among northern or cold-adapted faunas, including *N. battus* and other nematodirines, expansion is also predicted under changing regimes of temperature as parasite populations respond to directional selection, leading to adaptations which enhance survival and transmission (108).

Filarioid nematodes, which circulate through arthropod vectors, are particularly sensitive to changing climate. Expansion and emergence of *Setaria tundra* has been associated with cumulative changes in climate over the past 30 years interacting with extreme or anomalous

weather events (63). The process of geographic expansion and emergent disease in reindeer was mediated by distributional shifts for vectors and amplification of parasite populations under episodes of extreme conditions of humidity and temperature. Northern systems are currently undergoing dramatic ecological perturbation linked to climate change, with cascading effects for the geographic distributions and emergence of parasitic diseases (50, 61, 62).

Shifts in ecological and trophic structure driven by climate are also identified as factors influencing the process of invasion by helminths. Climate as a driver of expanding distributions of suitable mammalian hosts will serve to modify distributions of zoonotic assemblages involving *Echinococcus multilocularis* in Europe and species of *Trichinella* in many regions of the world (84).

Climate change is altering the dynamics of parasite transmission and the composition of assemblages of sympatric hosts on which a diversity of helminths are dependent. Modified ecological conditions driven by climate, along with geographic expansion, changing phenology in the context of specific tolerances, developmental rates and resilience, and establishment of new associations, may also lead to broadened distributions for some parasites, and unanticipated patterns of disease (41, 84). Shifting boundaries, expansion of historical assemblages, invasions of novel parasites, and exposure and acquisition of new arrays of hosts all contribute to broadened geographic distributions and ecological linkages. This view contrasts with the idea that such alterations may represent latitudinal range shifts (tracking zones of environmental tolerance for parasites) rather than actual expansion, development of fundamentally broader geographic ranges and origin of novel ecological assemblages (64). Complexity is indicated in how faunas respond to environmental change, and the downstream outcomes may not always be predictable; climate change may also lead to substantial reductions in range for pathogen assemblages. Furthermore, the diverse drivers involved in the breakdown of ecological isolation, expansion and invasion suggest that climate may not always be the most significant contributor to faunal change over time (88).

## Generalities of invasive processes

Processes of invasion are largely idiosyncratic, multifactorial, interactive and opportunistic; the role of historical contingency is essential. Although the ubiquitous nature of invasion is apparent, there remains an imprecise understanding of both host- and parasite-centric determinants. Analogue approaches and an exploration of

historical processes define the arena for invasion in space and time. Invasion has been a frequent phenomenon at diverse spatial and temporal scales but it is not taxonomically limited nor associated more frequently with particular patterns of life history among macroparasites. Invasion and emergence are possible in any assemblage, given convergence in key evolutionary and ecological factors (8). An understanding of the interaction between macroevolutionary and microevolutionary processes and how the potential for invasion may be either limited or enhanced remains elusive.

## Understanding invasion

Invasion is the process of 'extra-range dispersal', establishment, subsequent propagation (amplification) and dissemination (115). The character of invasion is determined by pathways interacting with spatial and temporal windows which may either enhance or limit the potential for successful introduction. The pattern and form of invasion associated with natural dispersal may reflect biotic expansion on broad fronts (phalanx or leading edge dispersal) or on isolated and heterogeneous trajectories (pioneer) involving both extensive geographic ranges or corridors, and may often represent recurrent, continuous or episodic processes (31, 35, 40, 115). Expansions across Beringia during the Tertiary and Quaternary, and those associated with responses to contemporary climate change, are primary examples. The temporal aspect of dispersal and establishment (geographic colonisation) is compatible with variation in the arrival and residence times of different host-parasite groups (faunal assemblages) and may later serve as a determinant of the degree of local adaptation (35).

In contrast, human-mediated events are characterised by patterns involving long-distance introductions often leading to highly disjunct, isolated and patchy ranges for host-parasite assemblages (jump dispersal, extreme long-distance dispersal, mass dispersal) (101, 115). The duration of expansion, frequency (recurrent events), and spatial extent of recipient area(s) influence patterns of establishment. Interacting factors for establishment of helminths include propagule size (numbers of individuals) and pressure (size of the invasion), frequency and duration of events, host density, vagility and social structure, and the specific form of the invasion pathway (26, 101, 115).

Parasite-centric factors operate in natural and human-mediated events. Life history, and direct (or attenuated) versus indirect life cycles may influence the potential for establishment (101, 103). Intrinsic mechanisms, including generation time, fecundity, duration of fecundity – all of which contribute to  $R_0$  (basic reproductive number for the parasite) – serve to influence invasion.

Longevity or survivorship and lifespan of helminths in the definitive (or intermediate) host is also a contributing factor, although it has seldom, if ever, been explored. Established here is the idea of 'temporal buffers' or phenomena linked to the extended survival of free-living stages in the environment or of parasitic stages in either intermediate or definitive hosts. A temporal buffer results in the potential for broad dissemination and amplification in space and time and is predicted to facilitate invasion. Extended survival (and presumed availability) of infective stages in the environment can result from environmental resistance manifested as resilience, broad tolerances for temperature and desiccation, dormancy, and specific developmental thresholds (107). Maintenance of infectivity in intermediate and paratenic hosts can also act as a buffer which may extend generation time over multiple seasons, thus contributing to a pool of infective propagules.

Among adult parasites, indeterminate growth and longevity, coinciding with the lifespan of long-lived and highly vagile definitive hosts, such as large carnivores and ungulates, promotes broad spatial dissemination over extended time frames and possibly across heterogeneous environments. Such patterns are exemplified by filarioid and metastrongyloid nematodes among vertebrate hosts. For example, protostrongylids including *Umingmakstrongylus*, *Parelaphostrongylus* and *Elaphostrongylus* exhibit indeterminate growth and maintain great fecundity over a period of years in highly mobile free-ranging ungulates (60). It is notable that *E. rangiferi*, like other protostrongylids and elaphostrongylines which require gastropod intermediate hosts, was translocated to Newfoundland with infected reindeer hosts (66). Furthermore, arrested development, or retention of inhibited life history stages prior to completion of development, as seen among the gastrointestinal nematodes of ungulates (112), may contribute to invasion success by extending the time frame for introduction(s) of an exotic species or fauna. All of this assumes an otherwise conducive environment in which host, parasites, habitat and abiotic determinants coincide. For example, *Fasciola hepatica* was not introduced to Iceland because the climate and mean annual temperature of less than 10°C (104) are not conducive to its survival.

The ecological arena influences invasion based on the suitability of native or exotic intermediate hosts or host assemblages. For example, invasion pathways can be established by introducing suitable intermediate hosts that can facilitate completion of a life cycle in a new geographic locality (73). Extensive introductions of *Fasciola hepatica* from the Palearctic into Australia, New Zealand, South America and South Africa were preceded by the translocation and establishment of exotic gastropod intermediate hosts (101). Emergence of *Angiostrongylus* in China was associated with invasion of an exotic snail

servicing as an intermediate host (71). The occurrence of *Echinococcus multilocularis* on the Svalbard islands in the high Arctic was mediated by inadvertent introduction of suitable arvicoline rodents (30). Geographic expansion and epidemic emergence of this zoonotic taeniid at lower latitudes in Europe has also been facilitated by the broadening ranges of primary definitive hosts, including foxes (which have invaded urban environments) and raccoon dogs (22, 84, 96).

Parasite specificity can influence the potential for invasion and subsequent history and outcomes for establishment and persistence in a new ecological setting or geographic area (101). The phenomenon of specificity is complex and must be viewed in a broader ecological context that addresses patterns of circulation for parasites among an assemblage of definitive hosts (1, 12) and that accounts for pervasive host-switching (40). The host, or the parasite, or the entire assemblage can be involved in invasion. Limiting factors for establishment and dissemination of the parasite are the potential for completion of transmission and the presence of all components (resources, but not necessarily specific hosts or host taxa) of the life history. This observation emphasises the interaction of historical (evolutionary) and ecological determinants of faunal structure and the capacity for host switching, and shifts the emphasis from individual hosts or host-taxa to that of 'host space' or resources, as defined in the concept of 'ecological fitting' (1). Thus, switching can often involve phylogenetically disparate groups of hosts and parasites associated through ecologically conservative guild dynamics rather than through co-evolutionary processes of association by descent (1, 12).

Ecological fitting has implications for understanding and predicting invasions. As a consequence of ecological fitting, parasites in introduced species may rapidly colonise indigenous hosts, even if the parasite appears to be highly host-specific within its native range, and introduced hosts may acquire resident parasites. Hosts under natural range expansion or that mediated by climate may encounter new parasites, some of which have specificity that is more apparent than real. For example, the host switch by the protostrongylid, *Protostrongylus stilesi*, from Dall's sheep (*Ovis dalli*) to musk oxen (*Ovibos moschatus*) (as a consequence of geographic expansion) is consistent with this concept (44). Additionally, native or non-indigenous parasites may persist in a colonised host following local extinction of the original host; or indigenous parasites may persist in a colonising host (12, 41). Taraschewski (101) suggests that geographic colonisation and acquisition of novel hosts is related to the phylogenetic affinities of the potential spectrum of hosts in source and recipient areas. This view is incomplete and based on assumptions about faunal structure driven by co-evolution and co-speciation and does not sufficiently address the complexity introduced by historical ecological processes (40, 41).

Faunal mosaics emerge when primary mechanisms which structure parasite biodiversity are ecological and driven by episodes of host colonisation rather than co-evolution.

## Exploring translocations

Human-mediated translocations involving the movement of threshold populations of definitive hosts into suitable habitats (i.e. those in which all components of a life cycle are present, and abiotic conditions are suitable for development) are expected to have the most immediate influence on changing patterns of distribution and invasion. Such long-range dispersal may have implications for genetic diversity (115), although few studies of parasites have explored this issue (52, 105). How genetic diversity is partitioned or maintained between source and recipient populations reflects the relative importance of dispersal pathways, propagule pressure and numbers of source populations in the native range (75). For example, minimal propagule pressure and long distance (with bottlenecks?) may be equated with low genetic diversity. In contrast, high propagule pressure, such as mass dispersal, is likely to capture larger portions of genetic diversity. Historical factors, however, such as refugial effects or a signature from human intervention in source populations prior to translocation, may substantially influence the structure of introduced populations (75, 94). Discrete genetic signatures for parasite populations and development of islands of diversity in new geographic localities may be a result of recurrent introductions over time from multiple source populations in the native range.

Suarez and Tsutsui (99) suggest that there is a fundamental difference between human-mediated and natural invasion, and that geographic colonisation and successful establishment associated with the former is facilitated by multiple introductions (often from multiple sources to multiple recipient areas distributed over time) (115). Hoberg (35) and Hoberg and Brooks (40) have suggested that there are no essential differences in the mechanisms of geographic colonisation in either evolutionary or ecological time, and that the processes are equivalent, although may differ in terms of scale. Ricciardi (90) contrasted historical and contemporary processes with respect to rates and frequency of invasion, temporal and spatial scales, and the relatively large numbers of propagules associated with human-mediated events, all of which contribute to homogenisation of the biosphere.

The emergence of helminth-based disease is related to invasive processes, although it has been suggested that the phenomenon is rare, because macroparasites have relatively long generation times and often complex life cycles involving multiple host species (14). Cleaveland *et al.* (14) further suggested that the dynamics of transmission may inhibit substantial changes in abundance

or host range. Emergence, where it does occur, is complex and often associated with lag times which temporally separate points of initial introduction and infection from later manifestation of disease conditions that may represent substantial demographic changes for parasites. This phenomenon is demonstrated in filarioid nematode infections that cause substantial morbidity and mortality in reindeer from Fennoscandia (63) and the history of *Nematodrius battus* in the United Kingdom and western Europe (32, 108). Invasion and emergence are inter-related processes, involving introduction, establishment, amplification, and expansion.

### Invasion mosaics in space and time

A consequence of invasive processes and the introduction and establishment of species exotic to particular ecosystems is that faunal structure will be a mosaic (35, 42, 47, 49, 74, 93). Mosaics will be manifested in the structure of helminth faunas (and other macro- and microparasites) on continental, regional and local or landscape scales where parasites are represented by admixtures of endemic (indigenous) and introduced species and populations. Invasive processes (dispersal) operating on varying temporal and spatial scales indicate that the formation, development and persistence of mosaics have been universal in both evolutionary and ecological time (40, 41). Contemporary mosaics are particularly evident in areas where human-mediated processes have brought into sympatry assemblages of new invaders and relatively old endemic species (47). Invasion mosaics emphasise the importance of population genetic structure and outcomes and the potential for local co-adaptation between hosts and pathogens (102). Geographic mosaic structure is further manifested in ephemeral and heterogeneous distribution of emergent disease against a broader background of the distribution of a parasite. The extent to which faunas are mosaics (as all are to some degree) is dependent on the scale and historical (temporal) processes involved in episodic biotic expansion and establishment (40). Mosaics further emphasise interactions at ecotones or borderlands between managed and natural ecosystems and the potential for interfaces for endemic and introduced faunas in free-ranging and domestic hosts or for faunas in free-ranging hosts under conservation management plans for relocation and reintroduction. The formation of these complex assemblages heightens the potential for, and impact of, adverse co-infections involving both macroparasites and microparasites.

Faunal or historical mosaics (macroevolutionary) are represented by assemblages of indigenous and introduced species, such as trichostrongyloid nematodes among ungulates in North America, Africa and other regions of the world (38, 49). Phylogenetically disparate genera and species of parasites comprise assemblages shared among

introduced (usually domesticated hosts) and endemic hosts on regional to local scales. In these situations arrays of congeneric parasite species may be involved which have independent evolutionary and historical trajectories (47); consider species of *Ostertagia* or *Teladorsagia*, among others in North America. A contrast between tropical and boreal-adapted faunas may also be apparent (49). Mosaic patterns are ubiquitous and demonstrated by species of *Trichinella* (85, 94), taeniid tapeworms (species of *Taenia*, *Echinococcus granulosus* and *E. multilocularis*) and a diverse assemblage of helminth groups distributed globally and regionally (101).

Population mosaics, in contrast or as a continuum, are an extension (microevolutionary) of faunal assemblages manifested by geographical or spatial heterogeneity of populations of single species. Population mosaics result from recurrent human-mediated introductions from multiple source areas over time and are nested within macroevolutionary mosaics. These are exemplified in global but localised distributions of gastrointestinal nematodes of ungulates (75, 105) and some digeneans such as *Fasciola hepatica* (101). Such mosaics provide the local potential for reciprocal co-adaptation in associated hosts and parasites and may constitute the drivers for emergence or ephemeral outbreaks of disease in space and time on landscape scales (40, 102). This is compatible with original observations that the distribution of a pathogen is wider than the distribution of disease attributable to that pathogen (3). Discrete genetic signatures characteristic of introduced populations provide a mechanism to identify sources and pathways of invasion (26).

Also at the population level, introduced species and resulting mosaics are expected to exhibit reduced genetic diversity relative to native or endemic counterparts as a function of domestication, synanthropic cycles, and temporally shallow geographic dissemination (75, 93). This prediction, however, is not always realised as historical factors influencing source populations and effective population size (on native range) may determine patterns of genetic diversity following introduction; similarly, historical mechanisms such as bottlenecks may limit diversity in endemic species. For example, *Teladorsagia boreoarcticus*, an endemic species, exhibits substantially lower genetic diversity than *T. circumcincta*, which has been widely introduced in North America (47). This contrast appears to reflect the impact of refugial isolation for the former and recurrent patterns of introduction and continual regional translocations for the latter (7).

In some specious or highly diverse parasite taxa (e.g. nematodes), invasions result in faunal mosaics distributed in space and time (35, 40, 41, 49). In some cases, congeneric cryptic species may be distributed in source and recipient localities (potential examples in

*Teladorsagia*, *Marshallagia* [42, 47]). Downstream effects emerge following the origin of mosaics:

- faunas remain discrete in respective endemic and introduced hosts
- parasite species remain discrete, but faunal exchange occurs with reciprocal or unidirectional exchange of parasites, often at ecotones
- hybridisation and introgression
- displacement of an endemic fauna (69, 101).

Outcomes in evolutionary and ecological contexts have a bearing on understanding patterns and mechanisms of diversification, geographic distribution, parasite behaviour and pathogenic potential (42), and specific responses to environmental perturbation and climate change (49). Manifested in the structure of parasite assemblages on continental, regional, local and landscape scales, mosaics encompass populations, species, and faunas.

Understanding the historical origins and dual (or complex) components of mosaics is critical in formulating predictions about future responses to environmental change. For example, faunas of gastrointestinal nematodes in ungulates distributed in North America have dual origins: some genera and species are endemic and other taxa were introduced following European colonisation after the 1500s (32); some trichostrongylines also include both introduced and endemic elements (e.g. species of *Ostertagia*, *Teladorsagia*, *Nematodirus*). A substantial component of the introduced fauna has origins in Africa (e.g. species of *Haemonchus* and *Cooperia*) and is thus strongly adapted to tropical and subtropical environments (45, 49). Thus, Arctic-boreal adapted endemics are predicted to respond in fundamentally different ways relative to introduced faunas of tropical origin.

Tropical versus boreal/temperate adaptations have particular consequences in the regime of global climate change and prevailing scenarios for temperature and precipitation in North America and elsewhere. Whether a parasite has tropical or Arctic origins is predicted to have an influence on the potential for responses to changing conditions through selection and adaptation (49, 106, 108). Apparent genetic differences reflecting putative adaptations to local conditions, however, have not been documented in *H. contortus* populations (105). Physiological mechanisms involving up or down regulation of genetically based pathways may result in differential responses to changing conditions by parasites. Additionally, genetic mechanisms associated with adaptation to environments of origin may limit the capacity of various species to effectively respond to changing climate (72). Consequently, tropical and boreal forms may expand (or not) relative to their resilience, tolerances, genetic potential and capacity to respond to directional selection.

Defining mosaic structures is difficult because of antiquated taxonomic concepts and arbitrary species limits and the probability of the presence of cryptic species (81). Thus, the challenge in recognising mosaics is in accurate identification and application of current taxonomy. For example, *Teladorsagia boreoarcticus* and *T. circumcincta* are components of a cryptic species complex that has not yet been completely characterised; concurrently in North America they are components of a mosaic fauna. Divergent evolutionary pathways in this group of species suggest that behaviour, developmental rates and life history in respective free-ranging and domesticated hosts may vary, and different expectations for responses to environmental change may be predicted (49). Morphological differentiation of these species remains problematic, thus driving the need for rapid and molecular-based means of identification. A further implication of mosaics is that relatively few species actually may be hypervariable and geographically widespread (47). It would appear that such species are most often those which have been widely disseminated through human-mediated invasion pathways involving either domesticated or, in the case of conservation management, free-ranging host species.

There is a need to identify the sources and histories of sequential and multiple introductions of parasites, and to have appropriate tools to explore interactions at the interface of managed and wild systems. These factors contribute to defining the trajectories for spread, mechanisms of success and underlying drivers for invasions and a context to identify how endemic and introduced faunas interact across space and time (26, 99). In combining fine-scale assessments of biodiversity and historical ecological processes, the past becomes the key to the present, contributing to an empirical framework on which to base future predictions about perturbation in dynamic systems that are often structured by invasion (2, 33).

## Tools to recognise and explore invasions

We have at our disposal, and should use, powerful tools to describe, limit and counter invasion by helminths and other pathogens (84). The basis of these tools is systematics and our capacity to accurately identify parasites and to understand evolutionary and biogeographic history, which is the primary foundation for defining faunal structure in space and time (10). We increasingly have the means to understand ecological and epidemiological changes and to define underlying evolutionary processes using molecular data at fine temporal and spatial scales. We also have the capacity to document and archive past and present environments and

the opportunity to predict future conditions based on foreseeable scenarios explored by ecological modelling (84). Integrated methods of detection and identification should combine morphological and molecular approaches, particularly where cryptic species may be involved (47, 81). Heightened collaboration and communication across disciplines and international borders, and a sense of urgency, will be necessary to effectively address this global challenge.

Faunal baselines established through survey and inventory of source and recipient regions (9, 32, 43, 49, 50) can become a component of a permanent record of the biosphere when archived in museum-based repositories (15, 34, 48). The absence of comprehensive taxonomic inventories of pathogens, including molecular-genetic data (9, 10, 11, 75), influences our ability to recognise the introduction of non-indigenous parasites and to document the patterns of expansion for local faunas (8). These faunal baselines can also contribute to our understanding of the distributions of potential intermediate hosts, and possibly of how trophic structure among hosts and within guilds at particular localities may either enhance or inhibit the introduction and establishment of exotic species (40, 65). Food-web or trophic dynamics and structure may be important controls on the distributions of helminths, the potential for colonisation processes and the acquisition of new and naïve arrays of host species.

Comprehensive field-based approaches for geographically extensive and site intensive surveys should increasingly rely on epizootiological probes (42, 54, 58). Rapid non-invasive methods are needed to assess the geographic and host distribution of parasites when morphological diagnosis is confounded by impenetrable morphological variation or uniformity in life history stages such as larvae (84). Molecular-based surveillance is also important for exploring the distribution of diversity and the appearance of exotic species through invasion (5, 95). Surveillance and monitoring activities, however, must be linked to permanent archives of definitively identified and validated specimens against which to assess change at ecosystem to population level (48).

Establishing historical foundations from phylogeny, historical ecology, biogeography, and phylogeography can substantially assist in developing predictions for faunal response based on analogues (2, 33, 40, 115). Current distributions are emergent from a deeper historical background, and understanding that backbone makes it easier to predict the responses of complex biotic systems. Understanding the impact of historical processes may be particularly important in areas related to climate change and ecological perturbation where environmental transitions can either enhance or limit the potential for

expansion or invasion (new hosts and geography) (2). Climate-related invasion mechanisms may most closely parallel those associated with natural dispersal and expansion, and specifically those that have influenced faunal structure during the Quaternary over the past three million years (40, 115). The scope, depth and rates for the current regime of human-mediated invasion, however, may fundamentally differ from past events in earth history (90). Specifically, differences may be seen with respect to recurrent translocations, often large numbers of propagules, sustained propagule pressure, long-distance dispersal, and synergy with varying environmental stressors. Such a conclusion is consistent with the accelerated impact of globalisation following the advent of agriculture and European colonisation as drivers for environmental homogenisation.

Understanding evolutionary and biogeographic history transcends mechanisms and is of further importance because of what we can learn about the particular range of environmental adaptations manifested by species or species assemblages. Thus, it is not simply a necessity to define the processes and mechanisms of invasion that have occurred in the past. It is important to also understand that there may have been historical constraints on species and faunas that have been introduced over 'long' time frames in human history. For example, many trichostrongyle nematodes in domesticated ungulates, which have been translocated throughout the world, have origins in tropical environments of Africa and have potentially been constrained by cooler temperatures and relatively xeric conditions from extensive expansion at northern boreal latitudes (35, 45, 49). Such constraints may now be released due to warming and increased precipitation under the accelerating environmental effects of climate change, or as a consequence of modified adaptive responses (108). This further suggests that modified environments at the interface of agricultural and wild systems can influence the potential expansion of helminths and switching between domesticated and wild ungulates (49, 50). Similarly, shifting urban environments and encroachment will enhance the continued invasion and dissemination of diverse assemblages of helminths circulating through wild and synanthropic pathways.

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## Processus d'invasion, mosaïques et structure des faunes d'helminthes parasites

E.P. Hoberg

### Résumé

Tout au long des temps écologiques et évolutifs, la biosphère a connu plusieurs épisodes structurants, marqués par des colonisations d'hôtes et de territoires géographiques, qui ont déterminé des distributions d'assemblages complexes de microparasites et de macroparasites, y compris chez les helminthes parasites des vertébrés. Les invasions biologiques sont des phénomènes complexes où les dispersions se déploient souvent hors de leur aire normale de répartition et où des populations et des espèces exotiques (non indigènes) parviennent à s'établir en des lieux très éloignés de leur distribution d'origine. Les invasions peuvent également se manifester comme un élargissement ou un déplacement de la distribution des hôtes ou de la distribution géographique de faunes ou d'espèces endémiques (indigènes), sous l'effet d'un changement environnemental. Les invasions se traduisent par des échanges entre différentes faunes, sous l'effet de facteurs aussi bien naturels qu'anthropiques ; les expansions qui en résultent, sur un continuum spatial ou temporel, créent des ponts reliant les continents, les régions et les paysages. Les facteurs d'invasions sont par nature idiosyncrasiques, multifactoriels, interactifs et opportunistes, et dépendent étroitement d'évènements historiques contingents. La structure du cycle biologique des helminthes interagit avec les voies d'invasion pour déterminer les possibilités d'introduction de ces espèces. Les facteurs anthropiques tels que la dissémination mondiale d'agents pathogènes due au développement de l'agriculture, la domestication des animaux destinés à la consommation et les grandes explorations européennes ont fortement influencé la distribution des helminthes. D'autres facteurs comme la mondialisation, la multiplication des réseaux de transport et le bouleversement environnemental induit par le changement climatique ont accéléré ce processus. L'invasion par des espèces exotiques et leur établissement ultérieur ont pour conséquence la formation de mosaïques, constituées par des mélanges d'espèces et de populations indigènes et non indigènes, comme l'illustrent les faunes d'helminthes présentes parmi les ongulés domestiques et en liberté, ainsi que la diversité de systèmes hôtes/parasites au sein des vertébrés. Les mosaïques de formation contemporaine sont perceptibles partout où l'intervention de l'homme a donné lieu à des combinaisons d'espèces envahissantes nouvelles et d'espèces endémiques relativement anciennes, coexistant en sympatrie, avec des interactions encore plus fortes dans les écotones, notamment les zones de passage entre des écosystèmes naturels et aménagés. Il est indispensable de bien comprendre l'origine historique et les composantes complexes des mosaïques si l'on veut anticiper les évolutions environnementales futures. Nous disposons d'outils puissants, dont le plus important est la systématique, qui nous permettent d'étudier les espèces envahissantes, d'identifier avec précision les parasites et de retracer l'histoire de l'évolution et de la géographie du vivant.

Grâce à la déduction des caractéristiques initiales des faunes à partir de faisceaux de spécimens biologiques, aux enquêtes intégrées et aux outils informatiques, les collections des muséums nous offrent un panorama continu de la biosphère. Toutefois, en l'absence d'un inventaire taxonomique exhaustif des parasites, intégrant toutes les données moléculaires et génétiques pertinentes, il est plus difficile de discerner l'introduction de parasites non indigènes et de reconnaître les structures d'expansion des faunes locales soumises à des perturbations environnementales.

**Mots-clés**

Biodiversité – Espèce envahissante – Évènement anthropique – Helminthe – Parasite de vertébré – Propagule.



## Invasiones, mosaicos y estructura de las faunas de helmintos parásitos

E.P. Hoberg

**Resumen**

Los episodios de colonización geográfica y de hospederos registrados a lo largo de la evolución y de los tiempos ecológicos estructuraron la biosfera y determinaron las distribuciones de microparásitos y macroparásitos de complejas estructuras, comprendidos los helmintos que parasitan vertebrados. Las invasiones biológicas son fenómenos intrincados que, con frecuencia, incluyen la dispersión fuera del área de distribución y el establecimiento de especies y poblaciones exóticas (no autóctonas) muy lejos de su región normal de repartición. En caso de alteración de las condiciones del entorno, las invasiones también pueden implicar una ampliación o una modificación de la distribución de los hospederos, así como de la distribución geográfica de especies o poblaciones endémicas (autóctonas). Las invasiones tienen como resultado intercambios fáunicos provocados tanto por factores naturales, como antropogénicos, y las consiguientes dispersiones en el espacio y el tiempo salvan distancias entre continentes, regiones y entornos. Si bien los factores que provocan invasiones son de naturaleza idiosincrásica, multifactorial, interactiva y oportunista, también dependen estrechamente de la cronología de los acontecimientos. A lo largo de su ciclo biológico, los helmintos interactúan con las vías de invasión para determinar sus posibilidades de introducción. Los factores debidos a las actividades humanas, como la expansión mundial de patógenos ocasionada por el desarrollo de la agricultura, la domesticación de animales destinados al consumo y las exploraciones europeas tuvieron una influencia decisiva en la distribución de los helmintos. Entre otros factores, la mundialización, las extensas redes de transporte y la alteración del medio ambiente fruto del cambio climático han acelerado las invasiones. A consecuencia de ello, y del establecimiento de especies exóticas, la estructura fáunica forma mosaicos compuestos por combinaciones de especies y poblaciones autóctonas y exóticas, como lo ilustran las comunidades de helmintos presentes en ungulados domésticos y en libertad, así como la gran variedad de sistemas de hospederos y parásitos en vertebrados. Los mosaicos contemporáneos se observan en las regiones donde las actividades humanas

dieron lugar a la coexistencia en simpatria de combinaciones de nuevas especies invasoras y de especies endémicas relativamente antiguas, multiplicando las interacciones en los ecotonos, especialmente en aquellos situados en el límite entre ecosistemas ordenados y naturales. El conocimiento de la cronología de la aparición de los mosaicos y de sus complejos componentes es de fundamental importancia para prever su futura evolución en el marco del cambio climático. La sistemática es la más importante de las poderosas herramientas existentes actualmente para estudiar las especies invasoras, identificar a los parásitos con precisión y establecer la cronología de su evolución y biogeografía. Gracias a los datos sobre las características iniciales de las poblaciones, establecidos mediante la clasificación de los especímenes biológicos, y a los estudios integrados, así como a los medios informáticos para su estudio, los archivos de los museos cuentan con registros permanentes de la biosfera. Pero la carencia de inventarios taxonómicos exhaustivos de los parásitos, que comprendan datos genéticos y moleculares, limita la capacidad para detectar la introducción de parásitos exóticos y documentar los modelos de expansión de las poblaciones locales sometidas a las alteraciones del entorno.

#### Palabras clave

Biodiversidad – Especie invasora – Factor antropogénico – Helminto – Parásito de vertebrado – Propágulo.



## References

1. Agosta S.J. & Klemens J.A. (2008). – Ecological fitting by phenotypically flexible genotypes: implications for species associations, community assembly and evolution. *Ecol. Letters*, **11**, 1-12.
2. Anderson N.J., Bugmann H., Dearing J.A. & Gaillard M.-J. (2006). – Linking paleoenvironmental data and models to understand the past and to predict the future. *Trends Ecol. Evol.*, **21**, 696-704.
3. Audy J.R. (1958). – The localization of disease with special reference to the zoonoses. *Trans. roy. Soc. trop. Med. Hyg.*, **52**, 309-328.
4. Avise J.C., Hubbell S.P. & Ayala F.J. (2008). – In light of evolution II: biodiversity and extinction. *Proc. natl Acad. Sci. USA*, **105**, 11453-11457.
5. Bengis R.G., Leighton F.A., Fischer J.R., Artois M., Mörner T. & Tate C.M. (2004). – The role of wildlife in emerging and re-emerging zoonoses. In *Emerging zoonoses and pathogens of public health concern* (L.J. King, ed.). *Rev. sci. tech. Off. int. Epiz.*, **23** (2), 497-511.
6. Blouin M.S., Yowell C.A., Courtney C.H. & Dame J.B. (1995). – Host movement and the genetic structure of populations of parasitic nematodes. *Genetics*, **141**, 1007-1014.
7. Blouin M.S., Yowell C.A., Courtney C.H. & Dame J.B. (1998). – Substitution bias, rapid saturation, and use of mtDNA for nematode systematics. *Molec. Biol. Evol.*, **15**, 1719-1727.
8. Brooks D.R. & Ferrao A. (2005). – The historical biogeography of coevolution: emerging infectious diseases are evolutionary accidents waiting to happen. *J. Biogeogr.*, **32**, 1291-1299.
9. Brooks D.R. & Hoberg E.P. (2000). – Triage for the biosphere: the need and rationale for taxonomic inventories and phylogenetic studies of parasites. *Comp. Parasitol.*, **67**, 1-25.
10. Brooks D.R. & Hoberg E.P. (2006). – Systematics and emerging infectious diseases: from management to solution. *J. Parasitol.*, **92**, 426-429.
11. Brooks D.R. & Hoberg E.P. (2007). – How will global climate change affect host-parasite assemblages? *Trends Parasitol.*, **23**, 571-574.
12. Brooks D.R., León Régagnon V., McLennan D.A. & Zelmer D. (2006). – Ecological fitting as a determinant of the community structure of platyhelminth parasites of anurans. *Ecology*, **87**, S76-S85.
13. Campbell G., Garcia H.H., Nakao M., Ito A. & Craig P.S. (2006). – Genetic variation in *Taenia solium*. *Parasitol. int.*, **55**, S121-S126.

14. Cleaveland S., Laurenson M.K. & Taylor L.H. (2001). – Diseases of humans and their domestic mammals: pathogen characteristics, host range and the risk of emergence. *Philos. Trans. roy. Soc. Lond., B, biol. Sci.*, **356**, 991-999.
15. Cook J.A., Hoberg E.P., Koehler A., Henttonen H., Wickström L., Haukisalmi V., Galbreath K., Chernyavski F., Dokuchaev N., Lahzuhkin A., MacDonald S.O., Hope A., Waltari E., Runck A., Veitch A., Popko R., Jenkins E., Kutz S. & Eckerlin R. (2005). – Beringia: intercontinental exchange and diversification of high latitude mammals and their parasites during the Pleistocene and Quaternary. *Mammal Study*, **30**, S33-S44.
16. Corn J.L. & Nettles V.F. (2001). – Health protocol for translocation of free-ranging elk. *J. Wildl. Dis.*, **37**, 413-426.
17. Crofton H.D. & Thomas R.J. (1951). – A new species of *Nematodirus* in sheep. *Nature*, **168**, 559.
18. Daszak P., Cunningham A.A. & Hyatt A.D. (2000). – Emerging infectious diseases of wildlife: threats to biodiversity and human health. *Science*, **287**, 443-449.
19. Daszak P., Cunningham A.A. & Hyatt A.D. (2001). – Anthropogenic environmental change and the emergence of infectious diseases in wildlife. *Acta trop.*, **78**, 103-116.
20. Drózdź J., Demiaszkiewicz A.W. & Lachowicz J. (1998). – *Ashworthius sidemi* (Nematoda: Trichostrongylidae) a new parasite of European bison *Bison bonasus* (L.) and the question of independence of *A. gagarini*. *Acta Parasitol.*, **43**, 75-80.
21. Dunn A.M. (2009). – Parasites and biological invasions. *Adv. Parasitol.*, **68**, 161-184.
22. Eckert J., Conraths F.J. & Tackmann K. (2000). – Echinococcosis: an emerging or re-emerging zoonosis? *Int. J. Parasitol.*, **30**, 1283-1294.
23. Ederli N.C., Bonadiman S.F., de Mores Neto A.H.A., DaMatta R.A. & Santos C.P. (2008). – Mixed infection by *Libyostrongylus douglassii* and *L. dentatus* (Nematoda: Trichostrongylidae) in *Struthio camelus* (Ratites: Struthioniformes) from Brazil with further morphological characterization of adults. *Vet. Parasitol.*, **151**, 227-232.
24. Elton C.S. (1958). – The ecology of invasions by animals and plants. Methuen & Co. Ltd, London.
25. Ferté H., Clévas D., Depaquit J., Gobert S. & Léger N. (2000). – Status and origin of *Haemonchinae* (Nematoda: Trichostrongylidae) in deer: a survey conducted in France from 1985 to 1998. *Parasitol. Res.*, **86**, 582-587.
26. Ficetola G.F., Bonin A. & Miaud C. (2008). – Population genetics reveals origin and number of founders in a biological invasion. *Molec. Ecol.*, **17**, 773-782.
27. Giudici C.J., Cabaret J. & Durette-Desset M.C. (1999). – Description of *Haemonchus placei* (Place, 1893) (Nematoda: Trichostrongylidae; Haemonchinae), identification and intraspecific morphological variability. *Parasite*, **6**, 333-342.
28. Harvell C.D., Mitchell C.E., Ward J.R., Altizer S., Dobson A.P., Ostfeld R.S. & Samuel M.D. (2002). – Climate warming and disease risks for terrestrial and marine biota. *Science*, **296**, 2158-2162.
29. Hellmann J.J., Byers J.E., Bierwagen B.G. & Dukes J.S. (2008). – Five potential consequences of climate change for invasive species. *Conserv. Biol.*, **22**, 534-543.
30. Henttonen H., Fuglei E., Gower C.N., Haukisalmi V., Ims R.A., Niemimaa J. & Yoccoz N.G. (2001). – *Echinococcus multilocularis* on Svalbard: introduction of an intermediate host has enabled the local lifecycle. *Parasitology*, **123**, 547-552.
31. Hewitt G.M. (1996). – Some genetic consequences of ice ages, and their role in divergence and speciation. *Biol. J. Linnean Soc.*, **58**, 247-276.
32. Hoberg E.P. (1997). – Parasite biodiversity and emerging pathogens: a role for systematics in limiting impacts on genetic resources. In *Global genetic resources: access, ownership and intellectual property rights* (K.E. Hoagland & A.Y. Rossman, eds). Association of Systematics Collections, Washington, DC, 71-83.
33. Hoberg E.P. (1997). – Phylogeny and historical reconstruction: host-parasite systems as keystones in biogeography and ecology. In *Biodiversity II: understanding and protecting our biological resources* (M. Reaka-Kudla, D.E. Wilson & E.O. Wilson, eds). Joseph Henry Press, Washington, DC, 243-261.
34. Hoberg E.P. (2002). – Foundations for an integrative parasitology: collections, archives and biodiversity informatics. *Comp. Parasitol.*, **69**, 124-131.
35. Hoberg E.P. (2005). – Coevolution and biogeography among Nematodirinae (Nematoda: Trichostrongylina) Lagomorpha and Artiodactyla (Mammalia): exploring determinants of history and structure for the northern fauna across the Holarctic. *J. Parasitol.*, **91**, 358-369.
36. Hoberg E.P. (2006). – Phylogeny of *Taenia*: species definitions and origins of human parasites. *Parasitol. int.*, **55**, S23-S30.
37. Hoberg E.P., Abrams A., Carreno R.A. & Lichtenfels J.R. (2002). – *Ashworthius patriciapillitae* n. sp. (Trichostrongyloidea: Haemonchinae), an abomasal nematode in *Odocoileus virginianus* from Costa Rica, and a new record for species of the genus in the Western Hemisphere. *J. Parasitol.*, **88**, 1187-1199.
38. Hoberg E.P., Abrams A. & Ezenwa V.O. (2008). – An exploration of diversity among the Ostertagiinae (Nematoda: Trichostrongyloidea) in ungulates from sub-Saharan Africa with a proposal for a new genus. *J. Parasitol.*, **94**, 230-251.
39. Hoberg E.P., Alkire N.L., de Queiroz A. & Jones A. (2001). – Out of Africa: origins of the *Taenia* tapeworms in humans. *Proc. roy. Soc. Lond., B, biol. Sci.*, **268**, 781-787.

40. Hoberg E.P. & Brooks D.R. (2008). – A macroevolutionary mosaic: episodic host-switching, geographical colonization and diversification in complex host-parasite systems. *J. Biogeogr.*, **35**, 1533-1550.
41. Hoberg E.P. & Brooks D.R. (2010). – Beyond vicariance: integrating taxon pulses, ecological fitting and oscillation in evolution and historical biogeography. In *The geography of host-parasite interactions* (S. Morand & B. Krasnov, eds). Oxford University Press, 7-20.
42. Hoberg E.P., Kocan A.A. & Rickard L.G. (2001). – Gastrointestinal strongyles in wild ruminants. In *Parasitic diseases of wild mammals* (W.M. Samuel, M. Pybus & A.A. Kocan, eds). Iowa State University Press, Ames, 193-227.
43. Hoberg E.P., Kutz S.J., Galbreath K.E. & Cook J. (2003). – Arctic biodiversity: from discovery to faunal baselines – revealing the history of a dynamic ecosystem. *J. Parasitol.*, **89**, S84-S95.
44. Hoberg E.P., Kutz S.J., Nagy J., Jenkins E., Elkin B., Branigan M. & Cooley D. (2002). – *Protostrongylus stilesi* (Nematoda: Protostrongylidae): ecological isolation and putative host-switching between Dall's sheep and muskoxen in a contact zone. *Comp. Parasitol.*, **69**, 1-9.
45. Hoberg E.P., Lichtenfels J.R. & Gibbons L.M. (2004). – Phylogeny for species of the genus *Haemonchus* (Nematoda: Trichostrongyloidea): considerations of their evolutionary history and global biogeography among Camelidae and Pecora (Artiodactyla). *J. Parasitol.*, **90**, 1085-1102.
46. Hoberg E.P., Lloyd S. & Omar H. (1995). – *Libyostrongylus dentatus* n. sp. (Nematoda: Trichostrongylidae) from ostriches in North America, with comments on the genera *Libyostrongylus* and *Paralibyostrongylus*. *J. Parasitol.*, **81**, 85-93.
47. Hoberg E.P., Monsen J., Kutz S.J. & Blouin M.S. (1999). – Structure, biodiversity and historical biogeography of nematode faunas in Holarctic ruminants: morphological and molecular diagnoses for *Teladorsagia boreoarcticus* n. sp. (Nematoda: Ostertagiinae), a dimorphic cryptic species in muskoxen (*Ovibos moschatus*). *J. Parasitol.*, **85**, 910-934.
48. Hoberg E.P., Pilitt P.A. & Galbreath K.E. (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.
49. Hoberg E.P., Polley L., Jenkins E.J. & Kutz S.J. (2008). – Pathogens of domestic and free-ranging ungulates: global climate change in temperate to boreal latitudes across North America. In *Climate change: impact on the epidemiology and control of animal diseases* (S. de La Roque, G. Hendrickx & S. Morand, eds). *Rev. sci. tech. Off. int. Epiz.*, **27** (2), 511-528.
50. Hoberg E.P., Polley L., Jenkins E.J., Kutz S.J., Veitch A.M. & Elkin B.T. (2008). – Integrated approaches and empirical models for investigation of parasitic diseases in northern wildlife. *Emerg. infect. Dis.*, **14**, 10-17.
51. Hoberg E.P., Zimmerman G.L. & Lichtenfels J.R. (1986). – First report of *Nematodirus battus* (Nematoda: Trichostrongyloidea) in North America: redescription and comparison to other species. *Proc. Helm. Soc. Wash.*, **53**, 80-88.
52. Höglund J., Morrison D.A., Mattson J.G. & Engström A. (2006). – Population genetics of the bovine/cattle lungworm (*Dictyocaulus viviparus*) based on mtDNA and AFLP marker techniques. *Parasitology*, **133**, 89-99.
53. Janicki Z., Konjević D. & Severin K. (2005). – Monitoring and treatment of *Fascioloides magna* in semi-farm red deer husbandry in Croatia. *Vet. Res. Commun.*, **29**, 83-88.
54. Jenkins E.J., Appleyard G.D., Hoberg E.P., Rosenthal B.M., Kutz S.J., Veitch A., Schwantje H., Elkin B. & Polley L. (2005). – Geographic distribution of the muscle-dwelling nematode *Parelaphostrongylus odocoilei* in North America, using molecular identification of first stage larvae. *J. Parasitol.*, **91**, 574-584.
55. Jetz W., Wilcove D.S. & Dobson A.P. (2007). – Projected impacts of climate and land use on the global diversity of birds. *PLoS Biol.*, **5**, 1211-1219.
56. Jones K.E., Patel N.K., Levy M.A., Storeygard A., Balk D., Gittleman J.L. & Daszak P. (2008). – Global trends in emerging infectious diseases. *Nature*, **451**, 990-994.
57. Karieva P., Watts S., McDonald R. & Boucher T. (2007). – Domesticated nature: shaping landscapes and ecosystems for human welfare. *Science*, **316**, 1866-1869.
58. Kutz S.J., Asmundsson I.M., Hoberg E.P., Appleyard G.D., Jenkins E.J., Beckman K., Branigan M., Butler L., Chilton N.B., Cooley D., Elkin B., Huby-Chilton F., Johnson D., Kuchboev A., Nagy J., Oakley M., Polley L., Popko R., Scheer A., Simard M. & Veitch A. (2007). – Serendipitous discovery of a novel protostrongylid (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.
59. Kutz S.J., Hoberg E.P., Nagy J., Polley L. & Elkin B. (2004). – Emerging parasitic infections in Arctic ungulates. *Integr. comp. Biol.*, **44**, 109-118.
60. Kutz S.J., Hoberg E.P. & Polley L. (2001). – A new lungworm in muskoxen: an exploration in Arctic parasitology. *Trends Parasitol.*, **17**, 276-280.
61. Kutz S.J., Hoberg E.P., Polley L. & Jenkins E.J. (2005). – Global warming is changing the dynamics of Arctic host-parasite systems. *Proc. roy. Soc. Lond., B, biol. Sci.*, **272**, 2571-2576.
62. Kutz S.J., Jenkins E.J., Veitch A.M., Ducrocq J., Polley L., Elkin B. & Lair S. (2009). – The arctic as a model for anticipating, preventing, and mitigating climate change impacts on host-parasite interactions. *Vet. Parasitol.*, **163**, 217-228.

63. Laaksonen S., Kuusela J., Nikander S., Nylund M. & Oksanen A. (2007). – Outbreak of parasitic peritonitis in reindeer in Finland. *Vet. Rec.*, **160**, 835-841.
64. Lafferty K.D. (2009). – The ecology of climate change and infectious diseases. *Ecology*, **90**, 888-900.
65. Lafferty K.D., Allesina S., Arim M., Briggs C.J., De Leo G., Dobson A.P., Dunne J.A., Johnson P.T., Kuris A.M., Marcogliese D.J., Martinez N.D., Memmot J., Marquet P.A., McLaughlin J.P., Mordecai E.A., Poulin R. & Thielges D.W. (2008). – Parasites in food webs: the ultimate missing links. *Ecol. Letters*, **11**, 533-546.
66. Lankester M.W. & Fong D. (1989). – Distribution of elaphostrongyline nematodes (Metastrongyloidea: Protostrongylidae) in cervidae and possible effects of moving *Rangifer* spp. into and within North America. *Alces*, **25**, 133-145.
67. Larson G., Dobney K., Albarella U., Fang M., Matisoo-Smith E., Robins J., Lowdon S., Finlayson H., Brand T., Willerslev E., Rowley-Conway P., Anderson L. & Cooper A. (2005). – Worldwide phylogeography of wild boar reveals multiple centers of pig domestication. *Science*, **307**, 1618-1621.
68. Lebarbenchon C., Brown S.P., Poulin R., Gauthier-Clerc M. & Thomas F. (2007). – Evolution of pathogens in a man-made world. *Molec. Ecol.*, **17**, 475-484.
69. Lichtenfels J.R., Hoberg E.P. & Zarlenga D.S. (1997). – Systematics of gastrointestinal nematodes of domestic ruminants: advances between 1992 and 1995 and proposals for future research. *Vet. Parasitol.*, **72**, 225-245.
70. Lichtenfels J.R. & Pilitt P.A. (2000). – Synopse patterns of Haemonchinae of ruminants (Nematoda: Trichostrongyloidea). *J. Parasitol.*, **86**, 1093-1098.
71. Lv S., Zhang Y., Liu H.X., Yang K., Steinmann P., Chen Z., Wang L.Y., Utzinger J. & Xhou X.N. (2009). – Invasive snails and an emerging infectious disease: results from the first national survey on *Angiostrongylus cantonensis* in China. *PLoS negl. trop. Dis.*, **3**, 368.
72. Merilä J. (2009). – Genetic constraints on adaptation? *Science*, **325**, 1212-1213.
73. Miura O., Torchin M.E., Kuris A.M., Hechinger R.F. & Chiba S. (2006). – Introduced cryptic species of parasites exhibit different invasion pathways. *Proc. natl Acad. Sci. USA*, **103**, 19818-19823.
74. Morgan E.R., Miller-Gulland E.J., Torgerson P.R. & Medley G.F. (2004). – Ruminating on complexity: macroparasites of wildlife and livestock. *Trends Ecol. Evol.*, **19**, 181-188.
75. Morrison D.A. & Höglund J. (2005). – Testing the hypothesis of recent population expansions in nematode parasites of human-associated hosts. *Heredity*, **94**, 426-434.
76. Nadler S.A., Hoberg E.P., Hudspeth D.S.S. & Rickard L.G. (2000). – Relationships of *Nematodirus* species and *Nematodirus battus* isolates (Nematoda: Trichostrongyloidea) based on nuclear ribosomal DNA sequences. *J. Parasitol.*, **86**, 588-601.
77. Nakao M., Okamoto M., Sako Y., Yamasaki H., Nakaya K. & Ito A. (2002). – A phylogenetic hypothesis for the distribution of two genotypes of the pig tapeworm worldwide. *Parasitology*, **124**, 657-662.
78. Palumbi S. (2001). – Humans as the world's greatest evolutionary force. *Science*, **293**, 1786-1790.
79. Parmesan C. & Yohe G. (2003). – A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **412**, 37-42.
80. Patz J.A., Graczyk T.K., Geller N. & Vittor A.Y. (2000). – Effects of environmental change on emerging parasitic diseases. *Int. J. Parasitol.*, **30**, 1395-1405.
81. Pérez-Ponce de León G. & Nadler S.A. (2010). – What we don't recognize can hurt us: a plea for awareness about cryptic species. *J. Parasitol.*, **96**, 453-464.
82. Pimentel D., Zuniga R. & Morrison D. (2005). – Update on environmental and economic costs associated with alien invasive species in the United States. *Ecol. Econ.*, **52**, 273-288.
83. Polley L. (2005). – Navigating parasite webs and parasite flow: emerging and re-emerging parasitic zoonoses of wildlife origin. *Int. J. Parasitol.*, **35**, 1279-1294.
84. Polley L. & Thompson R.C.A. (2009). – Parasite zoonoses and climate change: molecular tools for tracking shifting boundaries. *Trends Parasitol.*, **25**, 285-291.
85. Pozio E., Hoberg E.P., La Rosa G. & Zarlenga D.S. (2009). – Molecular taxonomy, phylogeny and biogeography of nematodes belonging to the *Trichinella* genus. *Infect. Genet. Evol.*, **9**, 606-616.
86. Pritchard G.C., Forbes A.B., Williams D.J.L., Salmi-Bejestani M.R. & Daniel R.G. (2005). – Emergence of fascioliasis in cattle in East Anglia. *Vet. Rec.*, **157**, 578-582.
87. Pybus M.J. (2001). – Liver flukes. In *Parasitic diseases of wild mammals* (W.M. Samuel, M. Pybus & A.A. Kocan, eds). Iowa State University Press, Ames, 121-149.
88. Randolph S.E. (2009). – Perspectives on climate change impacts on infectious diseases. *Ecology*, **90**, 927-931.
89. Rausch R.L. (1972). – Tropical problems in the Arctic: infectious and parasitic diseases, a common denominator. *Ind. trop. Hlth*, **7**, 63-70.
90. Ricciardi A. (2007). – Are modern biological invasions an unprecedented form of global change? *Conserv. Biol.*, **21**, 239-336.

91. Rickard L.G., Hoberg E.P., Allen N.M., Zimmerman G.L. & Craig T.M. (1993). – *Spiculoptera spiculoptera* and *S. asymmetrica* (nematode: Trichostrongyloidea) from red deer (*Cervus elaphus*) in Texas. *J. Wildl. Dis.*, **29**, 512-515.
92. Rickard L.G., Hoberg E.P., Bishop J.K. & Zimmerman G.L. (1989). – Epizootiology of *Nematodirus battus*, *N. filicollis*, and *N. spathiger* (Nematoda: Trichostrongyloidea) in western Oregon. *Proc. Helm. Soc. Wash.*, **56**, 104-115.
93. Rosenthal B.M. (2008). – How has agriculture influenced the geography and genetics of animal parasites? *Trends Parasitol.*, **25**, 67-70.
94. Rosenthal B.M., LaRosa G., Zarlenga D., Dunams D., Chunyu Y., Mingyuan L. & Pozio E. (2008). – Human dispersal of *Trichinella spiralis* in domesticated pigs. *Infect. Genet. Evol.*, **8**, 799-805.
95. Salman M. (2003). – Surveillance and monitoring systems for animal health programs and disease surveys. In *Animal disease surveillance and survey systems: methods and applications* (M. Salman ed.). Iowa State University Press, Ames, 3-13.
96. Schweiger A., Amman R.W., Candinas D., Clavier P.-A., Eckert J., Gottstein B., Halkic N., Muellhaupt B., Prinz B.M., Reichen J., Tarr P.E., Torgerson P.R. & Deplazes P. (2007). – Human alveolar echinococcosis after fox population increase, Switzerland. *Emerg. infect. Dis.*, **13**, 878-882.
97. Smith K.F., Behrens M., Schloegel L.M., Marano M., Burgiel S. & Daszak P. (2009). – Reducing the risks of wildlife trade. *Science*, **324**, 594-595.
98. Sorvillo F.J., DeGiorgio C. & Waterman S.H. (2007). – Deaths from cysticercosis, United States. *Emerg. infect. Dis.*, **13**, 230-235.
99. Suarez A.V. & Tsutsui N.D. (2008). – The evolutionary consequences of biological invasions. *Molec. Ecol.*, **17**, 351-360.
100. Suarez V.H., Busetti R., Fort M.C. & Bedotti D.O. (1991). – *Spiculoptera spiculoptera*, *S. asymmetrica*, and *Ostertagia leptospicularis* from *Cervus elaphus* in La Pampa, Argentina. *Vet. Parasitol.*, **40**, 165-168.
101. Taraschewski H. (2006). – Hosts and parasites as aliens. *J. Helminthol.*, **80**, 99-128.
102. Thompson J.N. (2005). – The geographic mosaic of coevolution. University of Chicago Press, Chicago.
103. Torchin M.E., Lafferty K.D., Dobson A.P., McKenzie V.J. & Kuris A.N. (2003). – Introduced species and their missing parasites. *Nature*, **412**, 628-629.
104. Torgerson P. & Claxton J. (1999). – Epidemiology and control. In *Fasciolosis* (J.P. Dalton, ed.). CABI Publishing, Wallingford, United Kingdom, 113-119.
105. Troell K., Engström A., Morrison D.A., Mattsson J.G. & Höglund J. (2006). – Global patterns reveal strong population structure in *Haemonchus contortus*, a nematode parasite of domesticated ruminants. *Int. J. Parasitol.*, **36**, 1035-1036.
106. Troell K., Tingstedt C. & Höglund J. (2006). – Phenotypic characterization of *Haemonchus contortus*: a study of isolates from Sweden and Kenya in experimentally infected sheep. *Parasitology*, **132**, 403-409.
107. Troell K., Waller P. & Höglund J. (2005). – The development and overwintering survival of free-living larvae of *Haemonchus contortus* in Sweden. *J. Helminthol.*, **79**, 373-379.
108. Van Dijk J. & Morgan E.R. (2008). – The influence of temperature on the development, hatching and survival of *Nematodirus battus* larvae. *Parasitology*, **135**, 269-283.
109. Vermeij G. (1991). – When biotas meet: understanding biotic interchange. *Science*, **253**, 1099-1104.
110. Vermeij G.J. (2005). – Invasion as expectation. In *Species invasions: insights into ecology, evolution and biogeography* (D.F. Sax. & J.J. Stachowicz, eds). Sinauer Associates, Sunderland, Massachusetts, 315-339.
111. Vitousek P.M., D'Antonio C.M., Loope L.L., Rejmanek M. & Westerbrooks R. (1996). – Biological invasions as global environmental change. *Am. Scientist*, **84**, 468-478.
112. Waller P.J., Rudby-Martin L., Ljungström B.L. & Rydzik A. (2004). – The epidemiology of abomasal nematodes of sheep in Sweden, with particular reference to overwinter survival strategies. *Vet. Parasitol.*, **122**, 207-220.
113. Waltari E., Hoberg E.P., Lessa E.P. & Cook J. (2007). – Eastward ho: phylogeographic perspectives on colonization of hosts and parasites across the Beringian nexus. *J. Biogeogr.*, **34**, 561-574.
114. Wilson E.O. (1993). – The diversity of life. Harvard University Press, Cambridge, Massachusetts.
115. Wilson J.R., Dormontt E.E., Prentis P.J., Lowe A.J. & Richardson D.M. (2009). – Something in the way you move: dispersal pathways affect invasion success. *Trends Ecol. Evol.*, **24**, 136-144.
116. Wolfe N.D., Panosian Dunavan C. & Diamond J. (2007). – Origins of major human infectious diseases. *Nature*, **447**, 279-283.
117. Zarlenga D.S., Rosenthal B.M., La Rosa G., Pozio E. & Hoberg E.P. (2006). – Post-Miocene expansion, colonization, and host switching drove speciation among extant nematodes of the archaic genus *Trichinella*. *Proc. natl Acad. Sci. USA*, **103**, 7354-7359.