SPECIAL PAPER

A macroevolutionary mosaic: episodic host-switching, geographical colonization and diversification in complex host–parasite systems

Eric P. Hoberg[1]* and Daniel R. Brooks[2]

[1]*US National Parasite Collection, Animal Parasitic Diseases Laboratory, US Department of Agriculture, Agricultural Research Service, Beltsville, MD, USA and* [2]*Department of Zoology, University of Toronto, Toronto, ON, Canada*

ABSTRACT

Aim To integrate ecological fitting, the oscillation hypothesis and the taxon pulse hypothesis into a coherent null model for the evolution of complex host–parasite associations.

Location Global.

Methods This paper reviews and synthesizes literature that focuses on phylogenetic analyses and reciprocal mapping of a model system of hosts and their parasites to determine patterns of host–parasite associations and geographical distributions through time.

Results Host-switching and geographical dispersal of parasites are common phenomena, occurring on many temporal and spatial scales. Diversification involving both co-evolution and colonization explains complex host–parasite associations. Across the expanse of Earth history, the major radiations in host–parasite assemblages have been preceded by ecological disruption, ecological breakdown and host-switching in a context that can be defined by the concept of ecological fitting. This cyclical process sets the stage for co-diversification during periods of relative stability, punctuated by host-switching during episodes of regional to global environmental disruption and climatological change.

Main conclusions Most observed host–parasite associations can be explained by an historical interaction between ecological fitting, oscillation (episodes of increasing host range alternating with isolation on particular hosts) and taxon pulses (cyclical episodes of expansion and isolation in geographical range). Major episodes of environmental change appear to be the main drivers for both the persistence and diversification of host–parasite systems, creating opportunities for host-switching during periods of geographical expansion and allowing for co-evolution and co-speciation during periods of geographical isolation.

Keywords
Ecological fitting, episodic host-switching, geographical colonization, historical biogeography, hosts, oscillation hypothesis, parasite diversification, parasites, taxon pulse hypothesis.

*Correspondence: Eric P. Hoberg, US National Parasite Collection, Animal Parasitic Diseases Laboratory, US Department of Agriculture, Agricultural Research Service, BARC East 1180, 10300 Baltimore Avenue, Beltsville, MD 20705, USA.
E-mail: eric.hoberg@ars.usda.gov

INTRODUCTION

The advent of modern methods of phylogenetic analysis and their elaboration as tools for comparative evolutionary studies brought into sharp relief two different perspectives on the evolution of host–parasite associations. The simplest perspective is one in which parasite lineages persist through time and speciate in parallel to their hosts. Under this view, when hosts go extinct, so do their parasites (Koh *et al.*, 2004). This orthogenetic perspective stems from theories about the evolution of host–parasite systems developed early in the 20th century (e.g. Fahrenholz, 1913; for a review, see Klassen, 1992).

By the late 1930s, this perspective had produced an integrated view of co-evolution called the 'parasitological method' (for a review, see Brooks & McLennan, 1993). One assumption of this view was based on the circularity that

parasites are highly host-specific, so they co-evolve with their hosts, and, because they co-evolve with their hosts, they become highly host-specific. Since host specificity was the *cause* of co-evolution, rather than a function of the ecological interaction between lineages, any conflicting or inconsistent observations were treated as either erroneous or irrelevant because they failed to conform to the orthogenetic view of co-evolution. Vestiges of orthogenetic thinking persist today. This is especially true for the assumption that hosts and parasites 'ought' to have congruent phylogenies, and instances of incongruence (owing to host-switching or extinction) are considered rare enough to be treated as the equivalent of a statistical 'error term' in the systems under examination (reviewed in Paterson & Banks, 2001; Page, 2003).

The modern phylogenetic co-evolutionary protocols descending from the parasitological method of the 1930s have been called the 'maximum co-speciation' approach (reviewed in Brooks & McLennan, 2002; Page, 2003), which has three phylogenetic corollaries: (1) apparent incongruence between host and parasite phylogenies is more likely to be the result of extinction than of host-switching; (2) for parasites exhibiting a host range greater than a single host species, the main focus of co-evolution will always be on the host that shows the greatest degree of co-speciation (as judged by highest level of congruence between host and parasite phylogenies), all other hosts being largely irrelevant; and (3) the most diverse and/or persistent parasites should exist within the most diverse and/or persistent host groups. These corollaries were initially integrated, as Assumptions 1 and 2 (for definitions see van Veller *et al.*, 1999), into methods for assessing host and parasite phylogenies. Later, they were used as the foundations for formalized models about pattern and process and the dominance of co-evolution and co-speciation as determinants of the structure and history of host–parasite systems (e.g. reviewed in Page, 2003).

An alternative view to the maximum co-speciation approach has its foundation in a Darwinian 'ecological adaptation' framework. Kellogg's (1896, 1913) studies of birds and their biting lice suggested that, although some host–parasite systems might show strong phylogenetic associations, there were substantial cases of what he termed 'straggling' or 'host-switching'. This perspective was adopted primarily by researchers interested in studying the interactions between plants and phytophagous insects (e.g. Verschaffelt, 1910; Brues, 1920, 1924). Plant–insect associations often show little phylogenetic congruence, despite high host-specificity, an observation that led researchers in this tradition to focus on discovering the ecological ties between organisms, particularly the cues that insects use to locate their host plants. This perspective was extended by researchers, including Ehrlich & Raven (1964), Clay (1964), Hennig (1966), Manter (1966), Ross (1972) and Jermy (1976, 1984, 1988).

With the advent of modern phylogenetic methods for studying the evolution of host–parasite systems (Brooks, 1979, 1981), concerns that Hennig (1966) had expressed about the parasitological method were addressed (for a discussion, see

Klassen, 1992). Brooks underscored Hennig's concerns when he proposed that the extent to which host and parasite phylogenies were congruent (which he termed co-speciation) was decoupled from host specificity (which he termed co-accommodation; later co-adaptation). This delineation formed the basis for a perspective that considered co-speciation as a weak null hypothesis (in contrast to its status as a strong null hypothesis under the maximum co-speciation perspective) for empirically exploring a world in which diversification was assumed to involve a mosaic of co-speciation, host colonization and extinction. It also led to the development of methods for comparing host and parasite phylogenies that were sensitive to host-switching and did not assume co-speciation a priori (Brooks, 1981, 1990; Wojcicki & Brooks, 2004). Here we recognize that co-evolution (association by descent) has dual components represented by: co-speciation, a macroevolutionary process linking diversification in associated lineages of hosts and parasites; and co-adaptation, a microevolutionary process perhaps best exemplified by arms-race phenomena and reciprocal adaptation (Brooks, 1979; Brooks & McLennan, 2002; Hoberg, 2005a; Thompson, 2005).

Over the past 25 years, the maximum co-speciation null hypothesis has dominated phylogenetic thinking in co-evolution. And yet, maximum co-speciation has been claimed empirically for only a narrow spectrum of host–parasite systems – specifically, a subset of associations involving ectoparasitic arthropods (e.g. Hafner & Nadler, 1988; Paterson *et al.*, 1993, 2003; Dabert & Mironov, 1999; Paterson & Poulin, 1999; Demastes *et al.*, 2003; Johnson *et al.*, 2003). In many of these studies, which involve phthirapteran chewing lice, the null hypothesis was rejected in favour of an alternative involving complex patterns, including post-speciation colonization of new hosts (Paterson *et al.*, 2000; Taylor & Purvis, 2003; Clayton *et al.*, 2004; Weckstein, 2004).

The empirical data suggest that macroparasites (internal and external) and their vertebrate hosts frequently have not maintained a phylogenetic signal of co-speciation (e.g. Barker *et al.*, 1992; Brooks & McLennan, 1993; Brant & Gardner, 2000; Verneau *et al.*, 2002; Hoberg *et al.*, 2001a; reviewed in Hoberg & Klassen, 2002; Clayton *et al.*, 2004; Hoberg *et al.*, 2004; Weckstein, 2004; Brooks & Ferrao, 2005; Cook *et al.*, 2005; Hoberg, 2005c; Huyse & Volckaert, 2005; Bentz *et al.*, 2006; Zarlenga *et al.*, 2006). These findings suggest that maximum co-speciation is not the norm, and must be replaced by a more complex empirical framework or general model that recognizes an important role for host-switching in the history of parasite diversification. Addressing complex systems in this manner emphasizes the ontological differences between the two views of the evolution of host–parasite associations, and parallels the treatment for the roles of vicariance vs. dispersal in historical biogeography (van Veller & Brooks, 2001; Dowling *et al.*, 2003). Until recently, the prominence of the maximum co-speciation view led to the assumption that empirical patterns suggesting widespread host-switching were an artefact of incomplete data (Dowling *et al.*, 2003; Taylor & Purvis, 2003; Brooks *et al.*, 2004).

Nonetheless, the challenge of accommodating such evidence of widespread host-switching has led the maximum co-speciation school to methodological convergence with alternatives represented by 'a posteriori' approaches (e.g. van Veller et al., 2000; Huelsenbeck et al., 2003; Johnson & Clayton, 2003; Brooks et al., 2004; Wojcicki & Brooks, 2004). Recent perspectives by proponents of maximum co-speciation (Clayton et al., 2004; Huyse & Volckaert, 2005; Nieberding & Olivieri, 2007) may presage conceptual convergence as well, based on the (re)discovery that parasites can exhibit evolutionary trajectories independent of their hosts, at least to some degree (see Brooks & McLennan, 1993).

AN EMPIRICAL AND CONCEPTUAL FRAMEWORK

An exploration of relationships among complex host–parasite assemblages indicates that, from archaic to near-contemporary systems, the dominant drivers for diversification have spanned a continuum from co-evolution to colonization (Manter, 1966; Brooks & McLennan, 1993; Brooks & Hoberg, 2000; Hoberg & Klassen, 2002). Our ability to recover this history is temporally scale-dependent. When dealing with deep or evolutionary time, we articulate hypotheses with respect to *what we can infer*, most often in a comparative context for host and parasite phylogenies.

In contrast, dealing with systems in relatively shallow or ecological time affords an opportunity to explore strong empirical data (for example, ongoing processes at contact zones for complex assemblages), and in such circumstances, for these associations, we can deal with *what we 'know' or can*

directly observe. From a macroevolutionary perspective, a further distinction is evident. Events in deep time address the origins of clades and radiation, diversification and extinction or persistence of higher taxa relative to physical and biotic processes that may be global in scale (e.g. plate tectonics) and span longer timeframes. By contrast, events in shallow time encompass shorter timeframes, often resulting in reticulate rather than dichotomous branching relationships between populations and taxa. The resulting patterns are primarily ecological and geographical associations among populations and species of hosts and parasites as they emerge from a deeper historical background (Thompson, 1994, 2005; Avise, 2000). As such, rather than being inextricably tied to the evolutionary history of their hosts, parasites (like free-living organisms) can exhibit independent trajectories in which biogeographical context, palaeoenvironmental parameters, and ecological settings are critical in determining faunal structure and patterns of diversity over time (Hoberg, 1997a, 2005a; Erwin, 1998; Hoberg & Klassen, 2002).

What allows colonization?

Parasites with indirect life cycles, including tapeworms, digenean flatworms and some nematodes, track broadly and predictably across trophic levels because the completion of transmission in a complex system is dependent on the structure of food webs (e.g. Manter, 1966; Hoberg, 1997a; Marcogliese, 2002). Current data indicate that host-switching and diversification of parasites occurs more often within than among guilds of definitive hosts (Hoberg & Adams, 2000; Hoberg et al., 2000, 2001a; Hoberg & Klassen, 2002;

Table 1 Host–parasite systems, environmental bottlenecks and ecological transitions – the effect of habitat shifts by definitive hosts on parasite diversity.

(1) **Anurans and fishes** – Although fishes and anurans share aquatic lifestyles, basal frogs are burrowers. There are very few platyhelminths in frogs showing a relationship to those among 'fish', and faunal continuity during a shift from fully aquatic to terrestrial patterns of life history resulted in substantial loss of an ancestral freshwater parasite fauna. Macroparasite faunas among frogs are depauperate.

(2) **Freshwater and marine stingrays** – Potamotrygonid rays in aquatic habitats of the Neotropics and Amazonia have maintained an extensive helminth fauna derived from marine elasmobranchs through co-speciation, but have acquired few species from freshwater fishes (e.g. no exchange between catfish and stingray cestodes in Amazonia) (Brooks et al., 1981; Brooks & Amato, 1992).

(3) **Marine turtles vs. freshwater turtles** – Bi-directional habitat shifts between marine and aquatic systems have driven host-switching and radiation for pronocephalid digeneans among turtles; marine and freshwater chelonians that are hosts are phylogenetically disparate. Further host-switching in marine environments has resulted in three independent events of colonization from turtles to marine iguanas and three events from turtles to fishes (Pérez Ponce de Leon & Brooks, 1995).

(4) **Marine birds vs. freshwater/terrestrial birds** – The fauna characteristic of seabirds has its origins in marine systems, and there are no major elements typical of continental assemblages (Hoberg, 1996).

(5) **Marine birds vs. aquatic birds** – Sulidae (gannets and boobies) and Anhingidae (anhingas) are sister groups, with the latter secondarily invading freshwater habitats. Phalacrocoracidae (cormorants and shags) and Pelecanidae (pelicans) contain either species or species groups that have undergone a transition from marine to aquatic habitats. An ecological shift from oceanic systems was accompanied by the loss of an ancestral tetrabothriidean fauna (Hoberg, 1996).

(6) **Marine and terrestrial mammals** – Cestode faunas found in cetaceans and pinnipeds are depauperate, representing a legacy of their terrestrial ancestors (artiodactyls and arctoid carnivorans, respectively). Independent ecological transitions to marine systems in the Tertiary resulted in the loss of a land-based assemblage (Hoberg & Adams, 2000).

(7) **Crocodilians** – Macroparasite faunas among crocodilians are depauperate relative to the situation for most tetrapods, and especially when compared with diverse assemblages among avian hosts, their only extant relatives. Entire parasite groups are absent, including tapeworms and acanthocephalans (both dominant in birds), suggesting losses attributable to multiple transition events across terrestrial, aquatic and marine systems (Brooks & O'Grady, 1989; Brooks & McLennan, 1993).

Marcogliese, 2002; Zarlenga *et al.*, 2006; Table 1); in parallel, among parasites with direct life cycles, host-switching is a function of ecological structure, opportunity and proximity. Historically continuous trophic associations within guilds and ecosystems suggest long-term stability of parasite life-history patterns, thus serving as a foundation for predicting the dynamics, or the ecological, temporal, spatial and epidemiological context, of transmission for parasites. In this sense, trophic structure refers to the interactions based on food webs that link an array of hosts and parasites within an assemblage, whereas guilds are exemplified by an array of phylogenetically disparate hosts that exploit a common food or prey resource.

There seems to be widespread agreement that parasites are resource specialists. Fundamental disagreement, however, exists on the question of host-switching. Can a resource specialist still switch hosts readily? Brooks & McLennan (2002) discussed a number of ways in which this could happen. Beginning with the parasite, a species might be a resource specialist but also might share that specialist trait with one or more close relatives. That is, specialization on a particular resource can be a plesiomorphic characteristic of a clade of parasites. As a result, a given host species occurring in more than one area might be inhabited by two different species of parasites that are perhaps related to each other but not necessarily as sister species. Such persistent plesiomorphic traits might be co-opted to perform novel functions or may remain as 'anachronisms' that originated in a co-evolutionary context that no longer exists (Janzen & Martin, 1982; Trouvé *et al.*, 1998; Brooks & Hoberg, 2008).

Alternatively, and from the hosts' perspective, the resources themselves might be very specific and yet still taxonomically and geographically widespread. In such cases, a given parasite might inhabit more than one non-sister species of host as a result of host-switching. Two major categories of parasite specialization are preferred site of infection (Adamson & Caira, 1993; Brooks & McLennan, 1993) and transmission dynamics (Brooks & McLennan, 1993, 2002; Hoberg & Adams, 2000; Hoberg *et al.*, 2000; Brooks *et al.*, 2006). Phylogenetic conservatism in parasite biology, coupled with phylogenetic conservatism in host biology, would create a very large arena for host-switching, even without the evolution of novel capabilities for host-utilization.

If historical conservatism in the specialization, rather than specialization *per se*, determines the ease or difficulty of host-switching, the extent of such historical conservatism should dictate our expectations about the frequency of occurrence of host-switching. Two ubiquitous findings from the historical ecology revolution of the past 20 years are that all aspects of evolution, including ecology and behaviour, are phylogenetically conservative, and that host-switching is a regular feature of co-evolutionary history (Brooks & McLennan, 1991, 1993, 2002; Hoberg & Klassen, 2002).

Factors serving as determinants of host-switching have been explored from a number of perspectives. For example, phenomena controlling the potential for colonization of new hosts, or the continuity of parasite lineages in evolutionary and ecological time, have been defined as 'ecological filters' (Combes, 2001), strongly influenced by ecological structure and context (Clayton *et al.*, 2004). In this view, however, filters are more static than dynamic. Co-evolutionary arms races (Ehrlich & Raven, 1964), resource tracking (Jermy, 1976, 1984, 1988), and maximum co-speciation models of co-evolution assume that host-switching (even if it mirrors host phylogeny: see Brooks & McLennan, 2002) is driven by the evolution of novel capabilities for host utilization.

Janzen (1968, 1973a,b, 1980, 1981, 1983, 1985a,b) argued, however, that the appearance of tight co-evolutionary associations at any single locality could be misleading. No matter where a given species evolved in the first place, its inherited functional abilities may allow it to survive in a variety of places under a variety of conditions through arbitrary amounts of time. In other words, species and their phylogenetically conservative traits may disperse through time and space. 'Ecological fitting' defines this fundamental interaction between the history of species and their present-day associations (Janzen, 1985b). This has led evolutionary biologists to predict that, although generalists may be at an evolutionary disadvantage relative to specialists with respect to particular host species in the short term, they are at an advantage in the long term, because their ability to utilize multiple hosts increases the chances of survival during episodes of major environmental perturbation and climate change, with associated cascading effects in species composition and trophic structure in affected ecosystems.

The role of ecological fitting

Brooks & McLennan (2002) suggested that ecological fitting, in the form of phylogenetically conservative capabilities for host utilization, produces a more complex situation. In addition to true generalists, actively using different host species representing different resources, and true specialists, capable of surviving in association with only a single species of host, there are what Brooks & McLennan (2002) termed 'faux generalists' and 'faux specialists'. Faux generalists are resource specialists whose resource is widespread among host species (synapomorphic, symplesiomorphic, or homoplasious). At any given place and time, only a restricted subset (often only one species) of all potential host species is available to the specialist, but over a large geographical range, the specialist may be associated with many hosts. By having a large class of potential hosts, this class of specialists may have the same long-term evolutionary advantages as true generalists without giving up their short-term advantages as resource specialists. Faux specialists, by contrast, are resource generalists who, at any given place and time, are excluded from some suitable hosts by specialists on those hosts. By participating in associations with a small number of hosts, such generalists may have many of the same short-term benefits as true specialists, without losing the long-term advantages of being a resource generalist. Interestingly, this view is compatible with a microevolutionary perspective for co-speciation in which optimal but ephemeral associations

for hosts and parasites are distributed in space and time (e.g. Thompson, 1994, 2005).

Phylogenesis in taxa exhibiting close and evident ecological associations with host taxa should be characterized by cyclical processes where episodes of increasing host range alternate with episodes of isolation on particular hosts. Janz *et al.* (2006) recently proposed such a model, which they call the 'oscillation hypothesis' (OH), and provided empirical evidence supporting it, based on studies of various lepidopteran taxa and their host plants (Janz & Nylin, 2007). Ecological fitting suggests that true generalists, faux generalists and faux specialists can all host-switch rapidly when changes in the geographic and ecological context in which a parasite is embedded allow the parasite to exploit previously unavailable resources without having to evolve novel capabilities for host utilization. Therefore, host-switching could be a common phenomenon.

Consequently, ecological fitting defines the arena of opportunity and potential for events of host colonization, whereas oscillation and the OH describe or predict the outcomes of such events in the continuum of evolutionary to ecological time. Ecological fitting and oscillation are interactive, in that colonization events that initially result in a broader host range may be followed by a narrowing of associations with isolation on or in a particular subset of hosts within the original assemblage.

Patterns of host-switching

Evidence for host-switching is pervasive and not limited to particular host–parasite assemblages or systems. Colonization occurs along two routes: (1) switching between or among ecologically equivalent resources (hosts as resources and ecological fitting); or (2) resulting from a radical change in the capacity of a parasite to utilize an array of potential hosts – essentially through derivation of novel attributes relative to transmission and infectivity.

Assumptions derived from a model of maximum co-speciation predict that parasites as extreme resource specialists should not diversify by means of colonization; parasites may radiate through co-speciation and sympatric speciation, or may become extinct (Page, 2003; Clayton *et al.*, 2004). As we have explored, the paradox is how resource specialists have the capacity for host-switching, a process that, based on empirical evidence, appears to be common in evolutionary time (Hoberg & Klassen, 2002). The process of colonization is mechanistically complex, and switching becomes a function of phylogenetic conservatism, changes in ecological structure among hosts, the 'apparency' for host specificity (defined as the realized versus potential range of suitable hosts), and opportunity (Hoberg *et al.*, 1999a, 2001a; Clayton *et al.*, 2003).

Host-switching events further comprise two broad categories, each with a particular geographical or ecological context. Stochastic events (passive; accidents of history; background) may pertain to a particular parasite species or clade. These events in evolutionary time are limited by the historically conservative dynamics of predictable guild associations, and

occur within particular geographical areas (Hoberg & Adams, 2000). They are often characterized by increased host range without parasite speciation, although such shifts may set the stage for parasite speciation. For example, taeniid tapeworms (Hoberg *et al.*, 2001a) and *Trichinella* nematodes (Zarlenga *et al.*, 2006) exhibit host-switching and diversification within specific parasite clades through shifts among phylogenetically unrelated definitive hosts that historically exploited a common prey resource across a specific biogeographical region. In the evolution of parasitic groups with complex life cycles, the acquisition of novel definitive hosts may occur more often than shifts among alternative intermediate hosts representing constituents of ecologically disparate guilds (Hoberg & Adams, 2000; Hoberg *et al.*, 2000). However, even ectoparasitic chewing lice and species of *Gyrodactylus* Nordmann, 1832 (monogenean flatworms), which, unlike other neodermatans, have direct patterns of transmission, also frequently demonstrate patterns consistent with host shifts in ecological proximity (Clay, 1964; Weckstein, 2004; Huyse & Volckaert, 2005).

The second category of host-switching events is episodic (active; causal) and occurs when regional or global environmental perturbations lead to a break down in allopatry and trophic structure (see also Clayton *et al.*, 2004). These events affect multiple groups of hosts and parasites over multiple geographical areas. Processes are characterized by a loss of ecological constraints on host range, and, when coupled with geographical colonization, may serve as drivers for diversification (Hoberg *et al.*, 2004). Perturbations such as those that characterized the Quaternary drove substantial changes in many ecological associations and geographical distributions of parasites (e.g. Lister, 2004; Cook *et al.*, 2005; Waltari *et al.*, 2007), leading to the acquisition of a new or broader spectrum of hosts. Among some taxa, such shifts subsequently served as the basis for a new round of allopatric speciation (Hoberg, 1986, 1992, 1995; Hoberg *et al.*, 1999c; Huyse & Volckaert, 2005; Zarlenga *et al.*, 2006).

Historical biogeography of the host–parasite associations

Host–parasite associations can be explored in the context of the 'taxon pulse hypothesis' (TPH), which addresses both general and unique patterns in diversification and biogeography (Erwin, 1981; Halas *et al.*, 2005). General patterns are (1) wholesale isolation of a biota by the formation of a barrier (a vicariance event), leading to two adjacent sister biotas (pairs of sister species can be found in many clades), and (2) wholesale expansion of a biota following the breakdown of the original barrier. Thus, the TPH specifies that episodes of vicariance, which produce stable and isolated/endemic ecological associations, alternate with episodes of biotic expansion, during which members of ecological associations living in adjacent geographical areas may come into contact with each other. The first-order consequences for such expansion and contact between evolutionarily divergent biotas are interactive and may be manifested as establishment, competition, accommodation or

extinction for associated lineages of hosts and parasites (e.g. Hoberg, 2005c).

Under the TPH, parasite lineages ought to show alternating geographical patterns of expansion and isolation, just like free-living species. For parasites, geographical expansion may lead to a variety of host associations (Table 2), since the OH dynamic will be operating in an historically correlated but causally independent manner. The TPH and OH represent interacting and to some extent hierarchical components of a larger process. The taxon pulse establishes the 'opportunity' or defines the arena for associations over time (the alternating patterns of vicariance and subsequent expansion). The expansion phase of the taxon pulse and ecological fitting define the potential for processes of colonization that may result in a broader host range. Subsequently, oscillation comes into play, with the downstream narrowing of host range or associations over time following the initial events of expansion and host colonization.

Under the simultaneous interaction of TPH and OH, four outcomes are possible: (1) co-evolutionary affinities retained – hosts and parasites exhibit the same expansion – there is no host-switching, and any trophic change on the part of the parasites is mirrored by trophic change in all hosts in the life cycle; (2) parasite colonization – parasites disperse and switch hosts; (3) host colonization – hosts disperse and acquire new parasites; and (4) host and parasite colonization – hosts and parasites disperse and host-switching occurs in both directions. Furthermore, clade-specific biotic expansion may produce clade-specific cases of host-switching, and cyclical or temporally recurrent biotic expansion may be a driver for episodic host-switching.

Ecological fitting and the persistence of parasite lineages during ecological and geographical change

Host–parasite systems are components of complex biotas (parasites nested within hosts). Whole biotas are influenced by episodes of isolation and expansion under the TPH, and within these biotas we expect host–parasite systems to respond in particular ways. Among host–parasite systems, correlated geographical colonization events are principal factors in distributional history; for example, phylogenies may reveal that cladogenetic nodes are linked to dispersal, followed by isolation and divergence. Such histories are documented in the Beringian region (e.g. Hoberg & Adams, 2000; Cook et al., 2005; Zarlenga et al., 2006; Waltari et al., 2007) and between Eurasia, Africa and the Nearctic (e.g. Hoberg et al., 2004; Bentz et al., 2006; Zarlenga et al., 2006). Alternating periods of biotic subdivision and biotic expansion have been identified in many systems and at various temporal scales (e.g. Beringian and Amazonian; Hoberg & Klassen, 2002). Examination of the relative frequencies and outcomes of host-switching during the two distinct phases of the taxon pulse (biotic expansion and biotic isolation) allows us to explore the interaction of these processes as determinants of faunal structure and diversification.

Biotic expansion resulting in contact under static ecological conditions may result in (1) maintenance of discrete faunal

structure (no overlap, no exchange), or (2) mosaics of faunal mixing with various degrees of ecological interactions (competition; exclusion; niche-breadth reduction; extinction) (Hoberg et al., 1999c, 2002; Hoberg, 2005c). Where parasite transmission dynamics are conservative, it is more likely that a change in the host taxon will result in loss of the parasite from the biota rather than in adaptive modification of the parasite and its persistence through co-evolution with concomitant changes in transmission.

During the vicariance or isolation phase, stochastic host-switching would not lead to diversification but to a broadened array of hosts through colonization in geographical proximity. Only those switches that are driven by a change in capacity to infect a novel host may be relevant in the context of diversification (essentially idiosyncratic switching). In the isolation phase, co-speciation is a by-product of vicariance (fragmentation, etc.), with hosts and parasites in geographical stasis and extinction rates being maintained at background levels.

Biotic expansion with changing ecological conditions may be a driver for episodic switching. Co-speciation results from hosts and parasites dispersing together, but with less co-speciation expected during biotic expansion than with vicariance because dispersal leads to widespread species (geographically) and reticulated area relationships. Where host-switching exceeds co-speciation (ecological conservatism), what may be termed the 'apparency arena' (potential versus realized host range across the distribution of an assemblage) is altered without the parasite changing. For example, specificity or narrow distribution may be more apparent than real, and may be controlled by relative degrees of ecological isolation or accessibility with the acquisition of new hosts resulting from expansion and breakdown of those mechanisms that historically maintained segregated faunas (e.g. Hoberg et al., 2002). In addition, some parasites expand by staying with the original hosts or by acquiring new hosts. Extinctions will increase and exceed a background level, whereas instances of pseudo-extinction (missing the boat) will be common, with parasites being lost during the geographical expansion of hosts or host populations.

Ecological structure may be persistent but the players may change (ecological fitting), or ecological structure may change (sources of extinction/ real extinction rates increase). In these scenarios, extinctions are predicted when trophic structure changes because parasites are ecologically conservative. However, this also drives the potential for host-switching (owing to changes in the arena for apparency, changing the players, or changing the rules), and overall rates of host-switching will be elevated during biotic expansion.

Ecological fitting and the persistence of parasite lineages during extinction events

If large-scale geographical and climatological events have catalyzed host-switching and the geographical spread of parasites, then global-level extinction events may also have a detectable impact on host–parasite associations (Hoberg et al.,

Table 2 A context-based model and scenarios for host–parasite systems – exploring geography, colonization, and extinction, with downstream predictions for diversity.

Geographical: Dispersal among regions

A. Dispersal into a region (new hosts/parasites, immigration)

a. Old host extinct

  i. Old parasite goes extinct: net loss

  ii. Old parasite switches to new host: no net change

b. Old host not extinct

  i. Old parasite goes extinct: net loss

  ii. Old parasite does not go extinct, does not switch to new host: no net change

  iii. Old parasite does not go extinct, adds new host: no net change in number, but increase in host range

c. Old parasite extinct

  i. Old host does not acquire new parasite: no net change

  ii. Old host acquires new parasite: increase in host range

d. Old parasite not extinct

  i. Old host keeps parasite: no net change

  ii. Old host loses parasite: net loss

  iii. New host acquires parasite: net increase in number of parasites in that host

  iv. New host does not acquire parasite: no net change

B. Dispersal out of a region (emmigration)

a. Rapid definitive host range expansion outruns parasites

  i. Parasites eventually catch up: no net change

  ii. Parasites never catch up – host impoverished in new areas; if host speciates in new areas, new host species are parasite-poor

  iii. Host acquires local parasites – dynamics of host specificity: increase in number of parasite species associated with the host species

b. Host range expands, but parasites expand with it

  i. Widespread parasite species

  ii. Parasite speciation by peripheral isolates allopatric speciation; host may or may not speciate at the same rate, leading to many possible scenarios, including co-speciation that is due to dispersal, not vicariance: hosts may accumulate closely related parasite species, each occurring, initially, in a different part of the host geographical range

Ecological: Extinction Processes

A. Hosts go extinct

a. Not replaced, changing ecological association – parasites dependent on that association go extinct: net loss of parasites, but no change in relative parasite faunal richness

b. Other hosts expand their niches – parasites accumulate in these hosts: parasite faunas become unusually species-rich

c. Replaced by ecological equivalents – parasites persist in new host: no net change

B. Hosts do not go extinct, but change their niches

a. Parasites change with them – parasite clade remains associated with host clade, showing a shift in ecology of transmission dynamics at that point in phylogeny – no net change in number of parasite clade members/host species

b. Parasites transmission dynamics are more conservative – host species loses the parasite clade; impoverished parasite fauna

C. Hosts persist without changing their niches

a. Parasites persist; no net change

Corollaries: At some place and some time, there must be temporal, ecological, and spatial overlap in order for parasites to switch hosts. Dispersal among locales or regions may offset extinction within a region to the extent that ecologies are phylogenetically conservative and dispersal is from adjacent areas where close relatives of the hosts are expected to be found.

Dynamics for Environmental Change, Host-switching and Diversity

A. Host and parasite not affected by environmental change –

non-relictual associations

B. Host goes extinct, parasite goes extinct –

on a larger scale leads to numerical relicts

C. Host switches ecology, parasites lost from those that changed –

on a larger scale this produces a type of phylogenetic relict (of parasites) not previously distinguished (previous discussions limited phylogenetic relicts of parasites to parasite clades restricted to definitive hosts that were themselves phylogenetic relicts). There is a second class of parasite phylogenetic relicts, i.e. where conservative transmission dynamics constrained them from persisting in members of the host group whose ecologies changed in such a way that they left the ecological association in which the parasite transmission was possible.

D. Host goes extinct, parasite persists –

a. *Haematoloechus* as an exemplar: *H. parviplexus* occurs primarily in *Rana clamitans* except in Nebraska, where *R. clamitans* does not exist. Is this an indication that *R. clamitans* was there recently and has gone extinct, since it occurs in Missouri, Iowa, Kansas, and Minnesota? Native parasite persists in native area after native host has gone extinct

b. on a larger scale, host-switching to new host group(s) within the ancestral guild association leads to ecological relicts
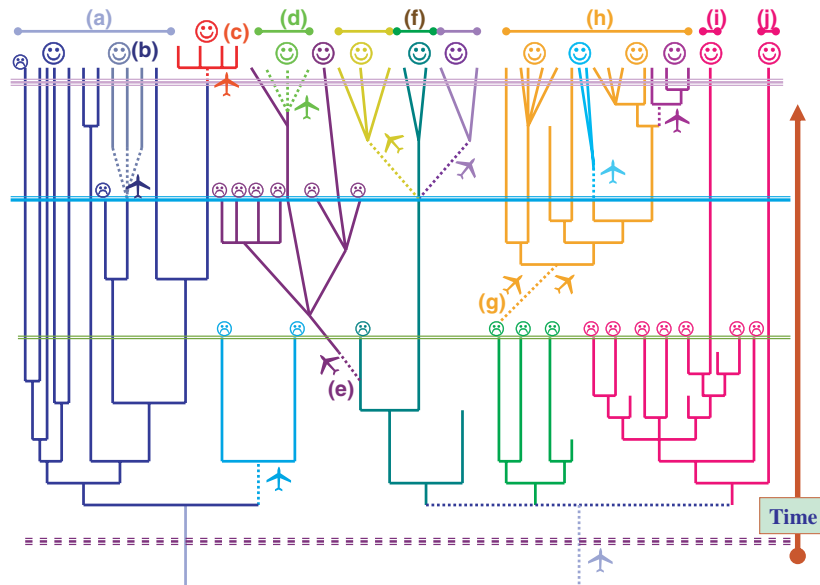

Figure 1 A general model for lineage persistence and diversification in deep time, showing the interaction between co-evolution, extinction, colonization and radiation. Ecological perturbations associated with extinction events of global extent are postulated to act as significant downstream determinants of diversity. Differential extinction across complex host–parasite systems determines heterogeneity relative to taxa that serve as either definitive or intermediate hosts and defines the potential for lineage persistence relative to a specific event horizon. Mechanisms for persistence and radiation are diverse: (a) co-speciation; (b) colonization and extinction; (c) colonization and diversification in new host group; if the host group is basal or ancestral such events are termed *retro-colonization* (young parasites in old hosts); (d) persistence of ancestral association and acquisition of new hosts; (e) colonization prior to event horizon with subsequent radiation; (f) retention of ancestral association and acquisition of new hosts through *ecological release*; (g) loss of ancestral association, and colonization at event horizon with secondary radiation in new hosts; note that colonization serves as the foundation for secondary radiation by co-speciation resulting in *ecological relicts*, where an archaic parasite lineage occurs in a relatively young host lineage; (h) maintenance of plesiomorphic or persistent ecological associations and sequential events of colonization within parasite lineage; (i) persistence as *numerical relicts*; (j) persistence as *phylogenetic relicts*. Characters and symbols are as follows: distinct, hypothetical parasite clades showing host associations are denoted by coloured clades and branches; ☺, lineage persistence; ☹, lineage extinction; ✈ ▬ ▬ ▬ ▬, colonization event. Extinction event horizons are indicated by horizontal lines.

1999a; b). Lineage persistence and ecological continuity are functions of interactive effects such as the differential extinction of intermediate hosts and definitive hosts, or of parasites through the dynamics of host-density effects or stage-specific mortality. Colonization may contribute to the persistence of a parasite taxon through host-switches before, during or after an event horizon (Hoberg *et al.*, 1999b) (Fig. 1). Environmental disruption is predicted to be a driver for the relaxation of ecological isolating mechanisms (ecological release) that enhance the potential for host-switching (e.g. Hoberg *et al.*, 2002; Brooks *et al.*, 2006). Alternatively, habitat shifts by potential hosts may lead to the loss of an assemblage of dependent parasites (e.g. Table 1). Episodic refugial effects and bottlenecks may further lead to punctuated cycles of diversification among host–parasite assemblages (Hoberg, 1995; Hoberg *et al.*, 1999a; Huyse & Volckaert, 2005). Bush & Kennedy (1994) suggested that the extinction of a parasite species structured as a metapopulation would be unlikely if populations of the host species were undergoing local rather than globally pervasive extinction.

Mass extinction events after the Palaeozoic, including the end of the Permian (P/T, at 250 Ma), the Late Triassic (200 Ma), and the end of the Cretaceous (K/T, at 65 Ma), are expected to have had substantial consequences for the patterns of diversity observed in contemporary faunas. Global extinction events undoubtedly caused extensive fragmentation across the ranges of widespread host–parasite assemblages. In marine and terrestrial environments, extinction horizons can be characterized by ecological perturbation or collapse of varying extent and duration. Variation is evident in taxonomic scope, regional effects, and the degree to which such environmental crises resulted in major ecological re-organizations and elimination or turnover for many taxa (Raup & Sepkoski, 1982; Jablonski, 1991; Briggs, 1995; Hallam & Wignall, 1997; Erwin, 1998; Miller, 1998; Jin *et al.*, 2000; Kriwet & Benton, 2004; Ward *et al.*, 2005; Wilf *et al.*, 2006).

Mass extinctions set the stage for diversification during the intervals of relative stability that punctuate periods of maximum ecological perturbation (Miller, 1998; Wilf *et al.*, 2006). 'Protracted' events occurring over long temporal durations result in gradual, slow and often differential rates for extinction, such as those observed at the Permian–Triassic (P/T) boundary (Ward *et al.*, 2005): perturbation was substantial, with the loss of an estimated 90–96% of marine species (Bowring *et al.*, 1998; Jin *et al.*, 2000). Species-loss in protracted time contrasts with the rapid rates of extinction

occurring during 'instantaneous' or short-term catastrophic events, such as those associated with bolide impact at the Cretaceous-Tertiary (K/T) boundary, when more than 70% of all species were eliminated (Crowley & North, 1988; Jablonski, 1991; Briggs, 1995). Parasite lineages that made the transition through large-scale extinction events include those that co-speciated with host lineages that also survived those events, and assemblages that persisted through processes of colonization (Hoberg et al., 1999a,b).

Parasite taxa may persist as: (1) *phylogenetic relicts* of archaic groups that have persisted with minimal change; (2) *numerical relicts* of once-dominant groups through ancestor–descendant relationships (Bandoni & Brooks, 1987a,b; Brooks & Bandoni, 1988); or (3) *ecological relicts*, namely archaic parasites of ancestral but now extinct host taxa that have survived into shallow time through colonization and secondary (co-evolutionary) radiation in a novel, but ecologically equivalent, host group (Hoberg et al., 1999a,b; Hoberg, 2005a; Grimaldi & Engel, 2006; Fig. 1).

Extinction events define the potential and set the conditions for pervasive host-switching through the disruption of conservative trophic pathways, changing ecological associations, ecological release and breakdown in mechanisms for isolation, or substantial transformation in abiotic environmental parameters. These are the same factors that influence the structure of free-living systems during mass extinctions (Wilf et al., 2006). For parasites, the conservative nature of transmission dynamics – *or fidelity to guild dynamics, rather than to a host or host clade* – may serve as a primary mechanism providing for the persistence of a taxon or clade following ecological disruption.

Within a Darwinian framework, which suggests that when the environment changes drastically most species will go extinct, all parasites dependent on particular hosts that go extinct, or on particular ecological associations that are modified as a result of major environmental disruption, would be expected to go extinct (Koh et al., 2004). Definitive host groups experiencing a severe ecological bottleneck (restricted ranges for ecological associations) during diversification may be unusual in lacking particular groups of parasites that are common in their sister groups; for example, crocodilians lack cestodes and acanthocephalans altogether (Brooks & McLennan, 1993). So, we believe that, during these episodic events, substantial parasite diversity disappears, but more survives than might be expected by maximum co-speciation (Fig. 1; Table 1). An interesting comparison may be made among neoselachians (sharks and rays) and patterns of diversity at the K/T boundary, at which ecologically equivalent families originated and replaced their archaic counterparts (Kriwet & Benton, 2004). Differential extinction resulted in the elimination of nearly all batoids (rays and skates), whereas losses among sharks were not as severe. Under an ecological bottleneck model of an episodic event, we would predict that parasite faunas originating in batoids would appear to be reduced, with lower taxon diversity, relative to those originating in sharks.

SELECTED EMPIRICAL EXAMPLES

Exploring age and temporal duration for marine and terrestrial parasite faunas

Phylogenetic studies among neodermatan flatworms – including Digenea, Monogenea, Gyrocotylidea, Amphilinidea and the Eucestoda – indicate a great age for the origins of parasitic groups and their characteristic associations (Gardner & Campbell, 1992; Brooks & McLennan, 1993; Kearn, 1994; Boeger & Kritsky, 1997; Hoberg et al., 1999a,b; Littlewood et al., 1999; Hoberg & Klassen, 2002; Verneau et al., 2002). For example, the initial diversification of tapeworms occurred among actinopterygian and neopterygian fishes 350–400 Myr BP; the phylogenetically older chondrichthyans were apparently colonized secondarily (Hoberg et al., 1999a, 2001b), and many groups appear to be relictual (Hoberg et al., 1999a,b). Patterns of host association among tapeworms suggest episodes of sequential colonization followed by rapid radiations among neoselachians, basal teleosts and tetrapods, including those lineages leading to contemporary mammals and birds.

Tetrabothriideans, archosaurs and marine birds

Among the true tapeworms, the Tetrabothriidea is a crown clade, with contemporary genera and species distributed among seabirds, cetaceans (whales, dolphins) and pinnipeds (seals) (Hoberg, 1989; Hoberg et al., 1997, 2001b; Olson et al., 2001). These tapeworms are an archaic lineage that is older than the modern orders of marine birds (Hoberg, 1989; Hoberg & Adams, 1992, 2000). Ecologically, tetrabothriideans were already distributed in marine environments when the first marine birds arrived in the Cretaceous (Cracraft, 1982, 2001; Hedges & Sibley, 1994; Cooper & Penny, 1997; You et al., 2006). We can infer an age for the initial radiation of the tetrabothriideans by using calibration points within their sister-group, the Cyclophyllideans, that are compatible with an early Mesozoic origin in excess of 200 Ma (Spasskii, 1993; Hoberg et al., 1997, 1999a,b; Hoberg & Adams, 2000). Radiations by seabirds in the late Mesozoic (Cooper & Penny, 1997), and episodes of invasion of the marine environment by cetaceans and pinnipeds in the Tertiary, were determinants of persistence and diversification of the contemporary tetrabothriidean fauna, as all other marine tetrapods (presumably former definitive hosts) were extinct by the termination of the Cretaceous (Berta & Sumich, 1999; Feduccia, 1999).

We can strongly infer that the first tetrabothriids were parasites in early marine archosaurs, and that marine birds acquired these tapeworms and supplanted pterosaurs and others in their marine ecological associations as apex carnivores (Hoberg et al., 1999a). Saurians (icthyosaurs, plesiosaurs, mosasaurs), non-avian archosaurs (pterosaurs and crocodilians) and marine birds were represented in oceanic habitats of Mesozoic age, and through the late Jurassic and Cretaceous represented sympatric assemblages in marine ecosystems (Cracraft, 1982; Hedges & Sibley, 1994; Callaway

& Nicholls, 1997; Cooper & Penny, 1997; Unwin, 2006). Marine birds must have acquired tetrabothriids before other archosaurs went extinct; thus, tetrabothriideans among sea-birds and marine mammals are ecological relicts or archaic parasites in ecologically equivalent young hosts (Hoberg, 2005a,b).

Palaeoguilds involving marine saurians and non-avian archosaurs + aves foraging on cephalopods or piscine species during the Mesozoic represent the plesiomorphic resource for circulation and radiation of the tetrabothriideans (Hoberg, 1996, 2005b; Hoberg & Adams, 2000). Following the K/T boundary event, species of *Tetrabothrius* Rudolphi, 1819, a basal genus, would have represented contextual specialists occurring in a narrow spectrum of avian hosts. Thus, the appearance of host-specificity or specialization in avian hosts is one of apparency and is a function of inaccessibility to an array of ecologically equivalent non-avian archosaurs that were eliminated via extinction. It has been suggested that species within *Tetrabothrius* were less specialized than they now appear. Avian hosts account for lineage persistence of the tetrabothriids through ecological fitting and as ecological relicts across the K/T boundary (Hoberg *et al.*, 1999a,b). Subsequent diversification involved sequential colonization events initially from birds to toothed and baleen whales (odontocetes and mysticetes), and secondarily from odontocetes to pinnipeds (Hoberg & Adams, 1992, 2000). Both mammalian host groups for tetrabothriideans have origins in the Palaeogene and subsequent radiations after the Oligocene (Berta & Sumich, 1999). As persistent ecological relicts (Fig. 1), *Tetrabothrius* serve as a model system in which the signature for deep extinction, sequential host-shifts, secondary radiation, and late episodic expansion in diversification can be explored.

Tetrabothriideans have had differential drivers for persistence and diversification at deep vs. shallow temporal scales (Hoberg, 1989, 1995; Hoberg & Adams, 2000). In a shallow temporal framework, the exploration of episodic events, such as those involved with multiple invasions of the North Pacific by phocine pinnipeds and their tetrabothriid parasites in the genus *Anophryocephalus* Baylis, 1922, allows us to develop a finer-scale understanding of the importance ascribed to different modes and tempos of geographical expansion and colonization and of the links that are emergent from deeper historical patterns and processes (Hoberg, 1995; Hoberg & Adams, 2000).

Anophryocephalus: *geographical colonization and diversification*

Species of *Anophryocephalus* are obligate parasites in pinnipeds and specifically among crown phocids (true or earless seals), as well as the basal otariid (eared seals), *Eumetopias jubatus* (Schreber), with a geographical range encompassing the Holarctic region (Hoberg, 1992, 1995; Hoberg & Adams, 1992, 2000). Their history of diversification is limited to the Pliocene and Quaternary, and has been intimately associated with cyclical and episodic climate change as a driver for host-switching and geographical colonization from the North Atlantic to the North Pacific through the Arctic Basin and Bering Strait. *Anophryocephalus* originated through colonization of phocids by parasites of odontocetes less than 5.0 Ma, and subsequent radiation was limited to hosts among 'Phocinae' and 'Otariinae' (Hoberg & Adams, 2000). Basal species are historically linked to the North Atlantic, and two independent invasions or events of geographical colonization into the North Pacific within the last 2–3 Myr are postulated. Expansions coincided with sequential marine transgressions across Beringia during interstadials and the opening of the Bering Strait, whereas isolation during stadials is attributed to intervening barriers caused by marine regression and the formation of the Bering Landbridge. Cyclical climatological processes at Beringia resulted in alternating periods of biotic expansion, geographical colonization, host-switching, intense isolation, and rapid speciation for assemblages of helminth parasites in pinnipeds (among phocids, and from phocids to otariids) and among seabirds (Hoberg, 1992, 1995, 2005a). A general model for the northern marine parasite fauna (cestodes, nematodes and digeneans) in seabirds and pinnipeds is one of sequential geographical and host colonization, followed by episodes of isolation and divergence, during the periodic extremes of climate variation and ecological perturbation that have characterized the past 2.5–3.0 Myr (Hoberg & Adams, 2000).

Exploring the Beringian nexus, beyond marine faunas

At a general level, Beringian parasite assemblages, both marine and terrestrial, represent an elegant model for exploring the intricacies of geographical colonization in shallow evolutionary time (Rausch, 1994; Hewitt, 1996, 2000, 2004; Hoberg *et al.*, 2003; Wickström *et al.*, 2003; Lister, 2004; Cook *et al.*, 2005; Jenkins, 2005; Haukisalmi *et al.*, 2006; Zarlenga *et al.*, 2006; Waltari *et al.*, 2007). Characterized by Sher (1999) as the crossroads for the northern continents, the Beringian nexus has heavily influenced patterns of distribution and speciation for the northern biota, alternately serving as a barrier or pathway for expansion of marine and terrestrial faunas and as a centre for diversification over the past 4–5 Myr. Furthermore, the episodic nature of stadial–interstadial cycles and patterns of intra- and inter-continental isolation across the Holarctic have had pervasive effects on the history (speciation, extinction) and distribution of complex host–parasite systems (Rausch, 1994; Hoberg *et al.*, 2003; Cook *et al.*, 2005; Hoberg, 2005c; Zarlenga *et al.*, 2006). In Beringia, we can begin to appreciate that faunal expansion and geographical colonization have occurred at different modes and tempos over the late Tertiary and Quaternary.

Such ecologically and phylogenetically disparate terrestrial faunas as the nematodes inhabiting lagomorphs (rabbits, hares and pikas) and artiodactyls (even-toed hoofed mammals) (Hoberg, 2005c; Jenkins, 2005), those inhabiting carnivores (Zarlenga *et al.*, 2006), and the cestodes inhabiting arvicoline rodents (voles) and Ochotonidae (pikas) (Haukisalmi *et al.*,

2001, 2006; Hoberg *et al.*, 2003; Wickström *et al.*, 2003; Cook *et al.*, 2005) all exhibit patterns of episodic biotic expansion between the Palaearctic and Nearctic at specific times during the late Tertiary and Quaternary. Adjacent Beringian marine biotas exhibit complementary patterns for the same time periods (Hoberg *et al.*, 2003; Hoberg, 2005c). Beringia represents an important empirical system in which outcomes for natural events can serve as a model for understanding factors that either limit or facilitate the introduction of potentially invasive species under anthropogenic control, and the responses of biotic systems to ongoing environmental perturbation (Cook *et al.*, 2005; Hoberg, 2005c; Brooks & Hoberg, 2006; Hoberg *et al.*, 2008).

Out-of-Africa and Eurasian connections

Processes for episodic biotic expansion and host-switching have represented dominant drivers for diversification in other regional settings, particularly across the connection linking Africa and Asia through the Tertiary, further indicating the generality of these mechanisms. For example, a recent analysis using PACT (phylogenetic analysis for comparing trees) explored the associations of two nematode groups inhabiting Old World primates (Brooks & Ferrao, 2005) and suggested that about 30% of the observed host associations were the result of host-switching. Only one represented a switch to a non-primate host (rodents), a good exemplar for the evolution of novel host-utilization capabilities. The remainder, all of which involve primate-to-primate switches, are presumably cases of ecological fitting, and included parasites that were more or less the same age as (three cases), that were younger than (one case), and that were older than (three cases) the hosts. Furthermore, nearly 70% of the host switches were correlated with episodes of host biotic expansion driven by episodes of global climate change since the Miocene (for a discussion of host biogeography, see Folinsbee & Brooks, 2007).

The distribution of *Trichinella* Railliet, 1895 nematodes represents evidence of pervasive host-switching and a minimum of three independent episodes of expansion from Eurasia into Africa since the Miocene (Zarlenga *et al.*, 2006). Expansion of the Eurasian carnivore fauna into Africa during the Miocene, Pliocene and Pleistocene was facilitated by the development of land connections; subsequent isolation resulted in speciation. The importance of guild associations in promoting host-switching among hyaenids, felids, viverrids and other carnivores is evident. *Trichinella* is significant in representing an archaic group, with origins dating to nearly 300 Ma, in which diversification of a contemporary fauna occurred in the late Tertiary to Quaternary (Zarlenga *et al.*, 2006).

Taenia tapeworms provide a contrast to *Trichinella* in that an ecological shift linked to guild structure was the initial driver for host-switching by parasites from hyaenids and felids to early humans in Africa after 2.5 Ma (Hoberg *et al.*, 2001a; Hoberg, 2006). A dietary shift from herbivory towards carnivory by hominids on the sub-Saharan savanna pre-dated the expansion of a newly established host–parasite assemblage

out of Africa into Eurasia during the Pleistocene. Thus, host-switching initially resulted in two independent events of parasite speciation: biotic expansion and subsequent geographical isolation led to further diversification of the *Taenia* fauna. These examples serve to relate the significance of guild structure, mechanisms for ecological isolation, and the relationship between biotic expansion and ecological fitting in faunal diversification.

COLONIZING SYSTEMS AND EPISODIC CHANGE

Associated host and parasite lineages of different ages are manifested by incongruence of host and parasite phylogenies. Some hosts will maintain faunas of great diversity, whereas others (most) will have relatively few parasites. Each episode of general environmental change will be associated with phenomena that reduce the number of parasites generally, as well as with phenomena that increase the number of parasites in specific hosts (Fig. 1). Given these observations, the parasite faunas of hosts that have an unusual number of parasites should be historical mosaics, including (co)evolutionary anachronisms (i.e. old parasites acquired by host-switching from hosts that are no longer extant; Table 2; Fig. 1). Within these diverse and historically complex faunas, episodic bursts of host-switching are associated with events of environmental transformation across all time scales. Various signatures in terrestrial, aquatic or marine systems, are predicted: (1) extinction-mediated diversification resulting in phylogenetic gaps; (2) episodic and cyclical forcing, such as that associated with alternating patterns of range expansion and retraction or vicariance within single parasite clades, or faunas resulting in hierarchical phylogenetic patterns; and (3) pervasive host-switching resulting in complex phylogenetic linkages among hosts and parasites in a specific regional setting (Hoberg, 1995, 2005a; Hoberg *et al.*, 2003; Weckstein, 2004; Huyse & Volckaert, 2005) (Fig. 1).

Mechanistically, lessons learned from the study of historical diversity and diversification in deep time serve as analogues for defining determinants in shallow time or in contemporary systems, an issue particularly significant in effectively predicting and responding to emergent or invasive parasites and pathogens (Brooks & Ferrao, 2005; Brooks & Hoberg, 2006; Brooks *et al.*, 2006). Generalities are apparent in considering the controls and drivers for establishment following processes of passive or natural dispersal, or in situations involving anthropogenic translocation, which often involve invasive species (e.g. Torchin *et al.*, 2003; Hoberg, 2005c). It is phylogenetic conservatism, the changing arena for apparency of specificity, ecological fitting, and the potential for host colonization that are critical in limiting or facilitating introduction, establishment and emergence. Parasites in introduced species may rapidly colonize resident hosts, even if the parasite appears to be highly host-specific in its native range, and introduced hosts may acquire resident parasites. Furthermore, parasites, either introduced or native, may persist in a colonized host after the original host goes extinct.

There is no distinction among mechanisms involved in the expansion, geographical colonization, establishment and emergence of invasive species that have operated historically in contrast to those that now serve as determinants in ecological or near time (Hoberg, 2005c; Brooks & Hoberg, 2007). Conceptually, we can establish a general evolutionary/ecological model that can be applied to the current crisis for invasive species and emerging infectious diseases on global, regional and local scales (Brooks & Ferrao, 2005; Brooks & Hoberg, 2006). Modes of host-range expansion/dispersal will play a role in determining the outcomes of interactions among endemic and introduced faunas under current regimes of global climate change and anthropogenic forcing (Hoberg & McGee, 1982; Hoberg, 1997b, 2005c; Hoberg et al., 2008). Even more evident is a corollary: the only way to eliminate the unpleasant surprises of emergent diseases is to engage in detailed taxonomic and natural history inventories (Brooks & Hoberg, 2000, 2006; Brooks & Ferrao, 2005; Woolhouse & Gowtage-Sequeria, 2005; Wolfe et al., 2007). We emphasize the need to integrate history and historical processes as underlying factors, or the backbone, serving to influence the fundamental mechanisms, determinants and emergent patterns of ecological structure in complex systems (e.g. Hudson et al., 2006; Pedersen & Fenton, 2006; Lebarbenchon et al., 2008).

TESTING PREDICTIONS – BIG PICTURE CRITERIA

The exploration of structure and diversity within host–parasite systems that incorporate a full range of signals of responses to deep evolutionary as well as to shallower ecological processes is based on the fulfillment of multiple criteria: (1) evidence that host–parasite systems have been assembled on scales extending on a temporal continuum into deep time – for example, the origin and radiation of lineages within time frames consistent for the Palaeozoic or Mesozoic (e.g. Brooks & McLennan, 1993; Dabert & Mironov, 1999; Littlewood et al., 1999; Hoberg & Klassen, 2002; Verneau et al., 2002; Grimaldi & Engel, 2006; Zarlenga et al., 2006) to the late Tertiary and pre-Pleistocene of the Cenozoic (e.g. Hoberg & Adams, 2000; Hoberg et al., 2004; Hoberg, 2005c; Zarlenga et al., 2006); (2) inclusive phylogenetic resolution from higher-level relationships to species groups, species, and populations for specific parasite and host clades (e.g. Hoberg, 1989, 1995; Hoberg & Adams, 1992, 2000; Brooks & McLennan, 1993; Nieberding et al., 2004, 2006; Huyse et al., 2005; Bentz et al., 2006; Nieberding & Olivieri, 2007; Whiteman et al., 2007); (3) knowledge of physical processes in Earth history (Brooks & McLennan, 1993); and (4) resolution of historical biogeography and phylogeography linking faunas at local, regional and global scales and in near and deep time (Brooks & McLennan, 1993, 2002; Hoberg, 1997a; Hoberg & Klassen, 2002; Nieberding & Olivieri, 2007). Emphasized here is the potential for a powerful integration of data for historical biogeography and population genetics to explore coalescent processes as a basis for understanding regional history, the direction and duration of colonizing events, and temporal persistence for assemblages of hosts and parasites (Lessa et al., 2003; Richards et al., 2007; Waltari et al., 2007). These criteria set a framework for exploring the interaction of co-evolution and colonization in persistence and diversification of complex biotas that emerges from elucidation of the phylogenetic context of traits that confer specificity and an understanding of what environmental contexts favour host-switching, and an increase in the likelihood of colonization.

Extensive testing of hypotheses requires parasite clades for which data specifying phylogenetic relationships, definitive host range, transmission dynamics, and aspects of spatial and temporal scale are known. We lack robust information for all of these categories, but our greatest ignorance is in the area of complex life cycles. Complete life history data among eucestodes is rare; only among the taeniid tapeworms in terrestrial carnivores have more than 80% of the cycles been elucidated (Hoberg, 2006). In contrast, 44% of cycles are known for tapeworms in the family Aploparaksidae, which represents the best known group among avian hosts (Bondarenko & Kontrimavichus, 2006). Life-cycle information for zooparasitic nematodes remains incomplete across this mega-diverse group (Anderson, 2000). In the absence of comprehensive information, the relative contribution to diversification by intermediate hosts can be examined only at a general level. Temporal scale and calibrations for estimates of divergence times also remain problematic, whether derived biogeographically (e.g. Hoberg, 1995; Bentz et al., 2006) or through estimates of rates for molecular evolution (e.g. Verneau et al., 2002; Zarlenga et al., 2006). Refined temporal data could lead to the correlation of divergence times for particular taxa with specific periods of ecological disruption in Earth history (e.g. Verneau et al., 2002; Donoghue & Moore, 2003).

CONCLUSIONS

The appropriate empirical framework or general model for the evolution of parasite biotas emerges from the combination of ecological fitting and the oscillation hypothesis (Janz et al., 2006) to explain the evolution of host range and host-switching and the taxon pulse hypothesis (Erwin, 1981; Halas et al., 2005) to establish the context for geographical distributions. This leads to complex and historically contingent patterns of distribution among hosts and over geography that are relevant in a continuum for evolutionary to ecological time. The explanatory power of this synthesis is apparent for describing and predicting the outcomes of contemporary introductions and the emergence of pathogens under a regime of ecological perturbation (Brooks & Hoberg, 2006, 2007; Hoberg et al., 2008).

In explanations of the structure and history of complex biotas, the integration of co-speciation and historical biogeography was recognized as a necessity (Hoberg & Klassen, 2002). A 'simple' world might be described by processes of vicariance, sympatric speciation and extinction (or in a co-evolutionary sense by co-speciation, sympatric speciation and extinction). Complexity is introduced by mechanisms of

dispersal in which host-switching may occur with speciation (peripheral isolates = dispersal + speciation), or in which host-switching may be linked to broadened host associations (range expansion by post-speciation dispersal). These six phenomena [co-speciation, sympatric speciation, extinction (real extinction/ pseudo-extinction), host-switching with speciation, host-switching without speciation] define potential interactions and outcomes for diversification and host-switching during biotic expansion. Complexity is derived from co-speciation + colonization, with each on its own not being sufficient as a determinant of history and structure.

A concept for macroevolutionary mosaics linking episodic colonization, co-speciation and faunal diversification can be defined. Drivers for persistence and diversification emerge from episodic events (parallel to taxon pulses) of geographical colonization, faunal turnover, and host-switching, alternating with periods of regional stability and co-speciation. Diversification proceeds on multiple pathways that involve: (1) co-evolution, representing the deep historical backbone or background for complex associations during periods of relative stasis; or (2) colonization, as the basis for radiation and speciation (co-evolutionary processes come into play secondarily). Across the expanse of Earth history the major radiations in host–parasite assemblages have precursors in maximal ecological disruption, ecological breakdown, and host-switching in a context that may be defined by ecological fitting. This sets the stage for co-diversification during periods of relative stability. These periods of stability may coincide with co-speciation that diversifies or is microevolutionary, leading to maximized local adaptation (reciprocal co-adaptation) of an ephemeral and reticulate or reversible nature (e.g. Thompson, 1994, 2005).

The persistence of lineages and faunas across ecological crises will involve components of both co-evolution and colonization. Current evidence is consistent with a process in which maintenance of an ecological association, and one that parallels or maximizes trophic linkages, is more important that co-speciation. It raises the question of what is happening if there are host switches historically, but host ranges are restricted at any given time. This emphasizes and reflects the interplay of macroevolutionary determinants and the micro-evolutionary aspects of co-adaptation and host specificity (e.g. Thompson, 1994, 2005). This macroevolutionary mosaic has structured the biosphere and complex host–parasite systems on a continuum from deep history to relatively shallow ecological time, with different determinants being in play on varying temporal and spatial scales for populations, species, single clades and more broadly for intricate faunas.

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BIOSKETCHES

Eric P. Hoberg is curator of the US National Parasite Collection, a centre for systematics and collection-based biodiversity studies on terrestrial, aquatic and marine parasite faunas maintained by the Agricultural Research Service, USDA. His research interests include historical biogeography and co-evolution, currently emphasizing the structure of complex parasite faunas among free-ranging and domestic ungulates and processes at the interface of natural and managed ecosystems.

Daniel R. Brooks is Professor of Zoology at the University of Toronto, and Fellow of the Royal Society of Canada, specializing in the systematics and evolution of parasitic helminths. He is currently coordinating the inventory of eukaryotic parasites of vertebrates, Area de Conservacion Guanacaste, Costa Rica. He is co-author of *Phylogeny, ecology and behavior: a research program in comparative biology* (1991), *Parascript: parasites and the language of evolution (1993)* and *The nature of diversity: an evolutionary voyage of discovery* (2002).

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