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INVITED REVIEW

How specialists can be generalists: resolving the "parasite paradox" and implications for emerging infectious disease

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ABSTRACT. The parasite paradox arises from the dual observations that parasites (broadly construed, including phytophagous insects) are resource specialists with restricted host ranges, and yet shifts onto relatively unrelated hosts are common in the phylogenetic diversification of parasite lineages and directly observable in ecological time. We synthesize the emerging solution to this paradox: phenotypic flexibility and phylogenetic conservatism in traits related to resource use, grouped under the term ecological fitting, provide substantial opportunities for rapid host switching in changing environments, in the absence of the evolution of novel host-utilization capabilities. We discuss mechanisms behind ecological fitting, its implications for defining specialists and generalists, and briefly review empirical examples of host shifts in the context of ecological fitting. We conclude that host shifts via ecological fitting provide the fuel for the expansion phase of the recently proposed oscillation hypothesis of host range and speciation, and, more generally, the generation of novel combinations of interacting species within the geographic mosaic theory of coevolution. Finally, we conclude that taxon pulses, driven by climate change and large-scale ecological perturbation are drivers of biotic mixing and resultant ecological fitting, which leads to increased rates of rapid host switching, including the agents of Emerging Infectious Disease.

KEY WORDS. Climate change; coevolution; ecological fitting; host shift; plant-insect interactions; sloppy fitness.

Parasites, organisms that spend most of their life-time feeding in or on a single individual of another species, may exhibit the most common mode of life on this planet (Price 1980). This includes diverse groups of organisms, from viruses and bacteria to worms, plant-feeding insects and parasitic plants. Parasites have managed to spread across impressively diverse taxonomic host groups, often reaching remarkable species numbers along the way. For example, Angiosperms comprise roughly one fourth of all species on earth, yet most plant species host multiple species of specialized plant-feeding insects.

Given the ubiquity of host-parasite interactions, understanding the factors that generate, maintain, and constrain these associations is of primary interest with implications for a wide range of applied ecological issues, including the dynamics of emerging infectious diseases (Brooks & Ferrao 2005, Brooks *et al*. 2006a, Brooks & Hoberg 2007), biological control, biological introductions and invasions, and biotic responses to climate change (Brooks & McLennan 2002). One of the most obvious and intriguing features of parasitism is pronounced conservatism in the range of hosts used (high host-specificity), both on ecological (Thompson 1994, 2005) and evolutionary time-scales (Ehrlich & Raven 1964, Brooks & McLennan 1991, 1993, 2002, Thompson 1994, 2005, Futuyma & Mitter 1996, Janz & Nylin 1998, Winkler & Mitter 2008). Not surprisingly, many think this host specificity holds the key to understanding the evolution of host-parasite associations – selection for increased specialization of parasites to their hosts constrains host use and promotes speciation. However, while this view provides a mechanism for the evolution of existing interactions (i.e., species become increasingly well-adapted to one another once the interaction originates), it provides no basis for understanding the origins of novel interactions. Coevolution can be diversifying, so that local selection in different parts of a geographic range can lead to a set of daughter populations that are locally adapted to different resources (Thompson 1994, 2005, Benkman 1999, Godsoe *et al*. 2008). But how the diversified interaction (host range) of the mother species came into existence in the first place must still be explained. Although coevolution can give rise to "new" species interactions in cases where the host and parasite speciate in tandem, there is little evidence for cospeciation as a major factor in host-parasite evolution (Hoberg & Brooks 2008, 2010). Indeed, 'cospeciation' was first proposed

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as a descriptive term for cases in which hosts and parasites experienced concomitant speciation events, such as being affected by the same vicariance event, not as an evolutionary mechanism (Brooks 1979). Thus the issue of how novel interactions arise remains unresolved. Our aims are to (1) synthesize the resolution to this problem and (2) address the implications for emerging infectious disease in humans.

The paradox – host shifts should be difficult to achieve

Most parasites appear to be resource specialists. The overwhelming majority of plant-feeding insects, for example, use only a tiny fraction of the available plant species in the habitat (Thompson 1994, Novotny *et al.* 2005, Dyer *et al.* 2007, Janzen & Hallwachs 2009). Not surprisingly, this pattern has given rise to the long-standing idea that specialization is a one-way street, an evolutionary dead-end where parasites become increasingly well-adapted to their hosts at the expense of the ability to perform on alternative hosts. The idea of specialization as a dead-end dates back to the 19th century (Thompson 1994) and some recent studies have reported support for the 'dead-end' hypothesis (Moran 1988, Wiegmann *et al.* 1993, Kelley & Farrell 1998). Other studies, however, conclude that generalized lineages are often derived from specialists (Scheffer & Wiegmann 2000, Janz *et al.* 2001, Termonia *et al.* 2001, Radtke *et al.* 2002, Kergoat *et al.* 2005, Yotoko *et al.* 2005). Many groups exhibit higher transition rates from generalization to specialization than vice versa, but host specialization appears to be a dynamic trait with no inherent necessary directionality (Janz *et al.* 2001, Nosil 2002, Nosil & Mooers 2005). If this is the case, why are broad host ranges so rare? There are obvious advantages of wider niches, such as more abundant and reliable food supplies or oviposition sites, so something must consistently select against them (Futuyma & Moreno 1988). A great deal of attention has been devoted to this question, and it now appears clear that selection should favor increased host specificity over time for a variety of reasons (Futuyma & Moreno 1988, Bernays 1989, 2001, Via 1991, Agrawal 2000, Janz 2002, Janz *et al.* 2005). Paradoxically, the successful solution to the original problem of widespread specialization has in many ways led to the new problem of understanding why there are exceptions at all (Johansson *et al.* 2007, Singer 2008).

These exceptions are important, because without them there would be no host shifts. Every host shift must begin with colonization (a process that leads to the establishment of a new, persistent interaction), during which the parasite should retain the capacity to use both the ancestral and novel host. Multiple host use following such colonization may be brief or it may be prolonged (Janz *et al.* 2006, Nylin & Janz 2009), but host shifts must begin with a host range expansion. Initially, additional hosts should typically be inferior alternatives to the original host, to which the parasite is specifically adapted, and special circumstances should be needed to incorporate such a host into the repertoire. Yet, host shifts and host range expansions do occur, and can happen rapidly (Thompson 1998).

Available data on the rate of host shifts are discordant. Phylogenetic comparative studies of hosts and parasites demonstrate two macroevolutionary patterns: (1) high host specialization and conservatism in host use, as well as (2) abundant evidence of switching onto relatively unrelated hosts that in some cases seems to have been the primary driver of diversification (Agosta 2006, Janz *et al.* 2006, Janz & Nylin 2008, Hoberg & Brooks 2008, Winkler & Mitter 2008, Nyman 2009). As a corollary, objective evidence for cospeciation has been rare even among intimately associated parasites, such as helminths inhabiting vertebrates (Brooks & McLennan 1991, 1993, 2002, Brooks *et al.* 2006b, Brooks & Van Veller 2008, Hoberg & Brooks 2008, 2010). For less intimate associations, such as among plants and many plant-feeding insects, it has long been recognized that cospeciation cannot have been a major source of diversification (Agosta 2006, Nyman 2009). Coupled with abundant ecological evidence of rapid shifts to novel hosts, such as introduced plants (Tabashnik 1983, Singer *et al.* 1993, Carroll *et al.* 1997, Fox *et al.* 1997, van Klinken & Edwards 2002, Agosta 2006, Strauss *et al.* 2006) and animals (Cornell & Hawkins 1993, Kelly *et al.* 2009), these observations suggest that host shifts are common in the interaction between hosts and parasites. Colonization of novel hosts must be an important driving force behind the diversification of the interactions themselves (by generating novel species associations) as well as the taxa involved (by increasing net speciation rates). This is the 'parasite paradox': how do highly specialized parasites otherwise shift to novel hosts?

We present what we consider the broad outlines of an emerging synthesis that resolves the parasite paradox without proposing novel mechanisms. Various parts of this synthesis have been proposed in the decades since Ehrlich & Raven (1964) observed broad taxonomic correspondence between butterflies, their host plants, and plant secondary chemistry. They posited that associations between plants and plant-feeding insects result largely from a coevolutionary arms race that leads to increased specialization and tends to restrict associations phylogenetically. Once that idea became internalized as the overarching mechanism behind host-parasite associations, many researchers began to scrutinize it and conclude that (1) host-parasite associations are generally more labile than expected under models of strict one-on-one coevolution between species, resulting in (2) historically and ecologically complex patterns of associations (e.g., Strong 1979, Holmes & Price 1980, Janzen 1980, 1985, Jermy 1984, Brooks 1985; review in Brooks & McLennan 2002). In addition, the development of modern phylogenetic comparative approaches to studying host-parasite evolution has greatly increased the capacity to understand the history and structure of these associations empirically (Brooks & McLennan 1991, 2002).

We first review what is needed to complete a shift to a novel host if the shift requires newly evolved abilities to utilize the novel resource. In this case, a full host shift will require

more or less simultaneous correlated evolution across a number of traits to enable it to locate the new resource, identify it as a possible host, trigger oviposition and allow appropriate handling during oviposition. In addition, offspring finding themselves on this novel resource will need to be triggered to initiate feeding (and must be physically capable of doing so, e.g. to penetrate the cuticle), and their metabolic system will have to be able to digest the new resource and overcome its chemical defense (or immune system). Each new host may come with a different set of external enemies requiring new methods of defense or evasion and a different micro-habitat requiring novel physiological adaptations. Such correlated changes occurring simultaneously across all these sets of characters ought to be so unlikely that host shifts ought to border on the impossible.

Clearly, host shifts are not impossible. We assume host shifts comprise two different "events": (1) colonization of the novel host (host range expansion) followed by (2) loss of the ancestral host (host specialization). Hence, for a host shift to be completed, there must first be a mechanism for generalization (increased diet breadth) and then a mechanism for specialization (decreased diet breadth). Furthermore, in order for specialization not to be an evolutionary dead-end, these mechanisms must be at least partly independent, so specialists maintain the *potential* to become generalists and generalists maintain the potential to become specialists. This links host shifts to the processes that determine host specificity.

Resolution

Ecological fitting

It is hard to escape the conclusion that the capacity to utilize the novel host must have existed before a successful shift was initiated. While this may seem counterintuitive, mechanisms allowing organisms to colonize and persist in novel environments do exist. For example, novel host plants can be added through oviposition "mistakes" (Larsson & Ekbom 1995) if they can be metabolized as a side-effect of existing machinery – a form of phenotypic plasticity (West-Eberhard 2003, Nylin & Janz 2009).

Phenotypic plasticity, in addition to factors discussed below, provides a mechanistic basis for an ecological concept called 'ecological fitting' (Janzen 1985). Ecological fitting describes the case when an organism interacts with its environment in a way that seems to indicate adaptation or more generally a shared evolutionary history (e.g., between a parasite and its host), when in fact the traits relevant to the interaction evolved elsewhere with different species or under different conditions. Such interactions can appear to be coevolved over extended evolutionary time (Janzen 1980), when in fact they may be the result of a relatively recent ecological "fit", possibly followed by rapid local adaptation. Janzen (1980, 1985) suggested that species often form these ecologically fit associations and that ecological fitting plays a major role in shaping communities.

When organisms encounter novel environmental conditions – a new habitat, a changed climate, a change in resources – they survive and persist (achieve realized fitness) where and if they "fit" by means of characters they already possess. In other words, successful establishment in a novel environment requires species having reaction norms that already include conditions in the novel environment. For the species to persist, colonists facing ecological novelty must achieve realized fitness within a more or less evolutionarily unfamiliar web of species (predators, prey, competitors, symbionts, etc.) using traits they already possess. Thus within any given ecological community, and depending on time and contingency, at least some traits relevant to observed species interactions will have evolved elsewhere under different conditions, but were later co-opted (Maynard Smith & Szathmary 1995) or exapted (Gould & Vrba 1982) to form new, ecologically fit, interactions (Janzen 1980, 1985).

Ecological and macroevolutionary evidence for ecological fitting among hosts and parasites is abundant (Agosta 2006, Hoberg & Brooks 2008, 2010, Kelly *et al.* 2009). This suggests that host shifts are often initiated because the parasite is exapted, or "preadapted" to the novel resource. The novel host might share important characteristics with the current host or might have been used in the past (Futuyma *et al.* 1995, Futuyma & Mitter 1996, Janz *et al.* 2001, Wahlberg 2001, Brooks & McLennan 2002, Radtke *et al.* 2002), or the parasite might fortuitously possess capabilities to use a novel resource (Agosta & Klemens 2008, 2009).

Agosta & Klemens (2008) proposed a general framework for ecological fitting as a mechanism behind the assembly of ecological communities and the formation of novel interactions between species within communities. They posited three factors giving rise to ecological fitting and the ability of organisms (genotypes) to achieve realized fitness under novel conditions (e.g., a novel host). First, phenotypic plasticity can allow organisms to mount a response to novel conditions (West-Eberhard 2003). Second, correlated trait evolution (Lande & Arnold 1983) can produce phenotypes that are "preadapted" to some future novel condition. Third, phylogenetic conservatism in traits related to resource use, including design constraints (e.g., the 'spandrels' of Gould & Lewontin 1979) and retention of traits from past selection pressures (e.g., the 'anachronisms' of Janzen & Martin 1982), provide the latent ability to perform under apparently novel conditions, such as a parasite encountering a new host that is actually the same or sufficiently similar to some ancestral host (Brooks & McLennan 2002). These capacities produce organisms possessing potential fitness outside the range of conditions in which the species evolved. Agosta & Klemens (2008) termed this region of fitness space 'sloppy fitness space,' a by-product of direct selection under some other set of conditions (the ancestral 'operative' environment). The operative environment comprises all components defining a host as a resource and therefore the range of host-related vari-

ables affecting parasite evolution. In figure 1a, a parasite evolves in response to the ancestral host operative environment defined by the black circle, but as a consequence, also has potential fitness (sloppy fitness space) beyond the range of conditions encountered with the ancestral host. Thus, the parasite has some ability to perform and persist on other hosts that represent a novel operative environment (host 2 in Fig. 1e; host 2 and 3 in Fig. 1f), in addition to the ability to add new hosts representing the same or highly similar operative environments (host 1 in Fig. 1 d-f).

Armed with adaptations to their ancestral hosts and the sloppy fitness space that results, parasites can ecologically fit with new hosts in at least two ways (Agosta & Klemens 2008). First, due to phylogenetic conservatism or convergence of host resources, parasites may shift to a new host species because the new host possesses the same (or highly similar) resources as the old host: ecological fitting via resource tracking (host 1 in Fig. 1d-f). The possibility that parasites track plesiomorphic resources both ecologically and evolutionarily was termed 'co-accommodation' by Brooks (1979) and more often than not

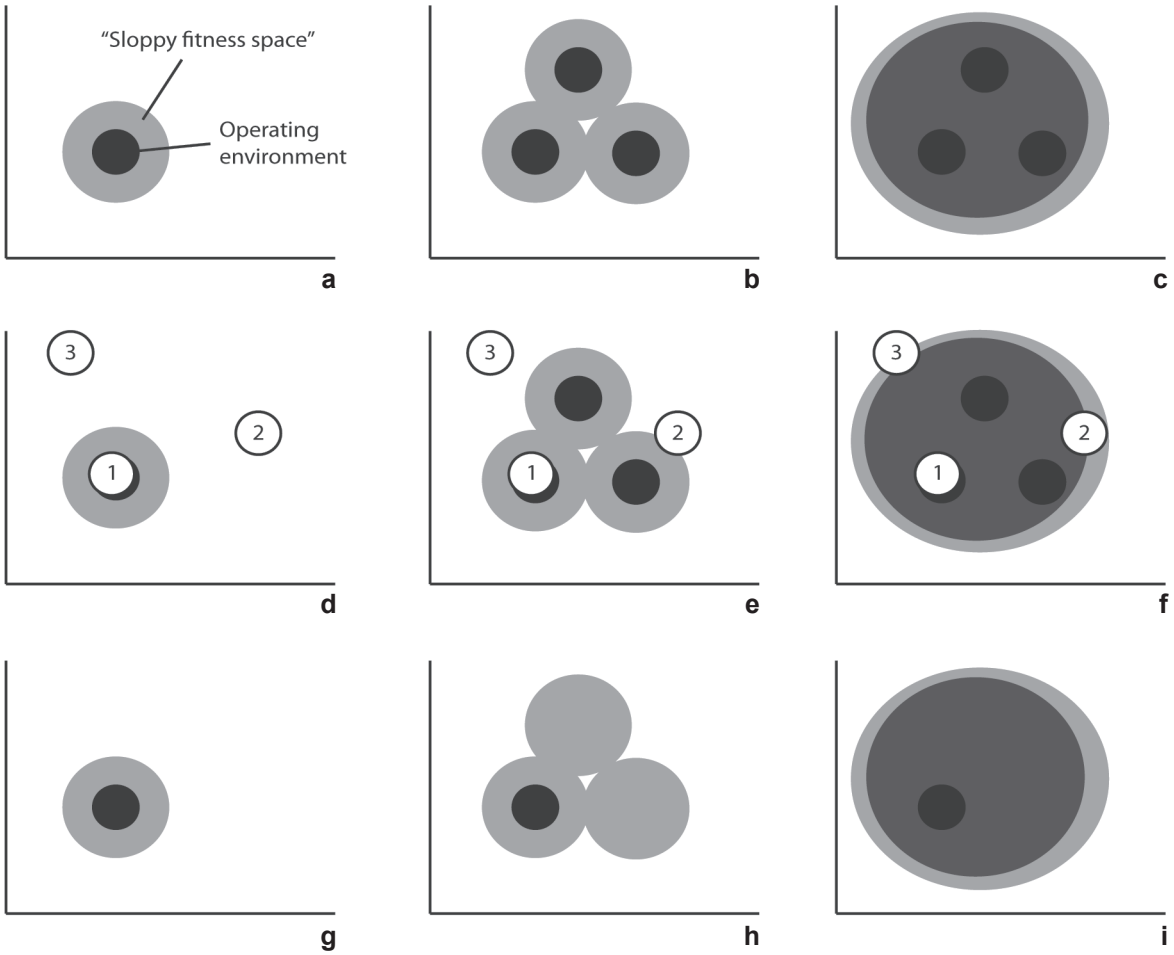

Figure 1. A schematic illustration showing two dimensions of the operative environment associated with fictional host resources (black circles). Sloppy fitness space (see text) can allow realized fitness in an area outside the operative environment to which the parasite is adapted (light grey circles). Panels **a**, **d**, and **g** illustrate a specialist, adapted to a single host resource, panels **b**, **e** and **h** illustrate a polyspecialist that has adapted independently to three different resources, and panels **c**, **f** and **i** illustrate a true generalist with a more general host recognition and tolerance system that allows it to utilize any resource that falls within the dark grey area. The open circles in panels **d-f** represent three novel resources. The specialist in panel **d** can colonize resource 1 (which is more or less identical to the ancestral resource) but not resource 2 and 3. The polyspecialist in panel **e** can colonize resource 1, but also resource 2 that falls within its sloppy fitness space, and the generalist in panel **f** can colonize all three resources. In panels **g-i** only one host is available, and all three parasite species will appear to be specialists, but their ecological and evolutionary potential will be very different.

parasites seem to do so (reviewed in Brooks & McLennan 2002; see also Brooks *et al*. 2006a,b, Hoberg & Brooks 2008, 2010). This is perhaps most evident when host chemistry or ecology takes priority over host phylogeny in explaining host-parasite associations (e.g., Beccera 1997, Wahlberg 2001, Brooks *et al*. 2006b).

Second, parasites may use sloppy fitness space to shift onto new hosts representing a novel resource: ecological fitting via sloppy fitness space (host 2 in Fig. 1e; host 2 and 3 in Fig. 1f). In either case, observed interactions between hosts and parasites will appear to be newly evolved, but are products of ecological fitting. Ecological fitting via resource tracking and via sloppy fitness space are not mutually exclusive and may represent two ends of a continuum (Agosta & Klemens 2008). A typical host shift may involve both tracking plesiomorphic resources and use of sloppy fitness space. In the case of ecological fitting via resource tracking, the new host may be novel only in the sense that it is a different species – from the perspective of the parasite it may not be novel at all. This situation illustrates how parasites can shift to relatively unrelated hosts if the operative environments (e.g., chemicals recognized as oviposition stimulants: Murphy & Feeny 2006) are plesiomorphic or convergent. It also illustrates conceptual problems with our understanding of what constitutes specialists and generalists.

The terms specialist and generalist are vaguely defined, and used variously by researchers. Typically the terms refer to the dimension of niche width that reflects diet. Hosts represent resources, and thus an operational defintion of host-speficity should ideally reflect resource distributions and resource heterogeneity (Nyman 2009). However, host-specificity is most often simply measured as the number of hosts in a parasite's repertoire. As host species are themselves hierarchically related, counting host species may be misleading, and some authors have adopted host use indices that to various extents account for host relatedness (Symons & Beccaloni 1999, Janz *et al*. 2001, 2006). More important is that species with virtually identical present-day host ranges can achieve them in fundamentally different ways, and as a consequence have divergent evolutionary potentials. In figure 1g-i, all three parasites are specialists, each using one host species. However, while the parasite in figure 1g is restricted to one host due to a narrow niche width, the other two are restricted to this host because it is the only host locally available.

Two parasite species in figure 1b and c use the same three host species, but whereas the parasite in figure 1c is a true generalist adapted to a wide niche, the host in figure 1b is best described as a 'polyspecialist', as it has genetically independent adaptive traits for all three niches (West-Eberhard 2003, Nylin & Janz 2009). The true generalist (Fig. 1c) presumably has evolved a more general host recognition and tolerance system that allows it to feed on any host that falls within the grey circle. The polyspecialist (Fig. 1b) uses these three hosts because it has adapted independently to all three.

Brooks & McLennan (2002) suggested that, hidden among the "true" specialists and generalists are 'faux specialists' and 'faux generalists'. Faux specialists are generalists restricted to a few or a single resource by ecological factors, such as competition, local micro-climate or non-concordant distributional ranges (Fig. 1h-i). Faux generalists are specialists specialized on a resource that is phylogenetically widespread. Parasites are not specialized on particular host species; they are specialized on resources that may or may not be shared among several species (Nyman 2009). In some cases, a plesiomorphic resource can be shared among a set of hosts to the extent that, from the parasite's perspective, they are identical and interchangeable. In other cases there will be a quantitative difference between host species in the amount of the resource(s) they possess. For faux generalists and faux specialists, host shifts can be initiated simply by a change in ecological circumstances (e.g., a shift in local host availability or local extinction of a competitor).

Observing ecological fitting

Host shifts are difficult to observe. We often must be content with scattered snapshots from different stages of the process to draw a composite picture of the whole process. Nevertheless, researchers have occasionally observed a host shift from the initial colonization to the final (local) loss of the ancestral host. The butterfly *Euphydryas editha* Boisduval, 1852 occurs in a fragmented population structure across the western USA and Canada. Host use has been studied extensively in several populations over many years (Singer 2003, Singer *et al*. 2008). Singer and colleagues have observed two instances of anthropogenically-induced shifts in host use. In one case, the local flora was altered by the introduction of an exotic plant, and in the other logging removed the original host (Singer *et al*. 2008). In both cases, at least some of the local *E. editha* accepted a novel host for oviposition and survived on it at first encounter (Singer *et al*. 2008). Thus, the initial stage of the colonization occurred through ecological, not evolutionary change.

Transfer to a novel environment may remove the ancestral host and offer alternatives, but more often a parasite population should come into contact with a novel host in sympatry with the ancestral host. Antonovics *et al*. (2002) showed that the recent shift by the anther-smut disease *Microbotryum violaceum* (Pers.) G. Demi & Oberw., 1982 from the ancestral host *Silene alba* Poir. to *S. vulgaris* (Moench) Garcke was contingent on local scale co-occurrence of both species. The pathogen was imperfectly adapted to its new host and susceptibility to the pathogen varied considerably. Similarly, some populations of the prodoxid moth *Greya politella* Walsingham, 1888 in central Idaho have shifted from the ancestral host *Lithophragma parviflorum* (Hook.) Nutt. Ex Torr. & A. Gray to the related *Heuchera grossulariifolia* Rydb. In this case, populations feeding on novel hosts are locally adapted to them, and preference for tetraploid variants seem to have evolved independently in several populations (Segraves *et al*. 1999, Nuismer & Thompson 2001). *Lithophragma*-feeding populations exposed

to the novel host oviposited in it to a low degree, but did not differentiate between plants of different ploidies (Janz & Thompson 2002). Hence, the shift likely was initiated by local contingency, and local preference for tetraploid variants of the novel host have evolved independently after the initial colonization (Thompson *et al.* 2004). These examples suggest host shifts initiated without any evolutionary change, through ecological fitting, followed by rapid evolution of traits associated with host use (Singer *et al.* 2008, Antonovics *et al.* 2002, Thompson *et al.* 2004).

Achieving the fit

As mentioned above, host use involves a number of different processes that must all function in concert. A potential host may possess some but not all of the required resources. For a phytophagous insect, the first step towards a host shift involves a failure to fully discriminate against a plant sympatric with the ancestral host, at least in part of the insect's geographic distribution (Larsson & Ekbom 1995). If offspring have realized fitness on the new plant, natural selection can then begin playing a role in modifying traits involved in host use on this plant, through genetic accommodation and later possibly through character release, allowing utilization of the novel plant to evolve more independently (West-Eberhard 2003, Nylin & Janz 2009).

Host shifts with loss of the ancestral host likely require evolutionary modification of host utilization traits after the initial colonization. The extent to which such modification will happen will depend on both local circumstances and evolutionary history. The butterfly *Pieris napi* Linnaeus, 1758 regularly oviposited on the introduced *Thlaspi arvense* Linnaeus, although the plant was lethal for the larvae (Chew 1977), and apparently this situation has not changed (Carol Boggs, personal communication). Presumably, the introduced plant contains a similar oviposition "resource" as local hosts, but a different larval feeding "resource". Mortality is 100%, leaving no opportunity for evolutionary modification enabling a host shift. Fox *et al.* (1997) reported that initial colonization of *Chloroleucon ebano* (Berland.) L. Rico by the seed beetle *Stator limbatus* Horn, 1873 depended on pre-existing variance in the capacity to accept and utilize this novel host, and populations expanding their host range to include this species had not locally adapted to it. One reason for the lack of local adaptation was a significant non-genetic effect of maternal host plant on offspring survival on the novel host (Fox *et al.* 1997). Hence, successful establishment on *C. ebano* depends on local co-occurrence of one of the other hosts in the repertoire of *S. limbatus*.

These examples show that successful host shifts depend on the history of the association, as well on life history, abundance and distribution of the species involved. Hence, to understand and possibly predict host shifts, both ecological (ecological fitting, local contingency) and evolutionary (evolutionary past, degree of plasticity, genetic variation) processes need to be considered (Brooks & McLennan 2002).

Implications for emerging infectious disease

Our thesis is that otherwise specialized parasites can shift rapidly to novel (naïve) hosts via ecological fitting and that these host shifts play an "important" role in the ecology and evolution of host-parasite associations. "Important" implies that ecological fitting between hosts and parasites occurs with high enough frequency to influence host range dynamics and the diversity of species and interactions among species. Although no quantitative statement of this importance can be made, it is clear from the above discussion that shifts onto relatively unrelated hosts can be inferred routinely in phylogenetic analyses and observed readily in contemporary ecological time. These observations are fundamental for emerging infectious disease (EID) studies: EID arise when parasite species begin infecting and causing disease in host species with which they have no previous history of association. If the nature of host specificity is such that the potential for ecological fitting is small, then host shifts are likely to be rare and attention can be focused on managing each EID as it emerges. Little attention need be paid to its origins, beyond a search for the taxonomic identity of the parasite acting as the pathogen, and its immediate reservoir. However, if the nature of host specificity is such that the potential for ecological fitting is large, then host shifts are likely to be common, and a more predictive, pre-emptive framework for managing EID will be needed, greatly increasing the challenge of an already difficult problem.

As discussed earlier, empirical studies indicate that few parasite groups conform to the phylogenetic patterns of host-parasite associations expected if opportunities for ecological fitting were relatively rare. Clades such as ectoparasitic arthropods which exhibit limited host switching (Hafner & Nadler 1988, Patterson & Poulin 1999, Page 2003), although interesting to evolutionary biologists and ecologists, cannot form the general conceptual framework for dealing with EID because they are rare. The majority of cases indicate substantial host switching throughout history, and extensive diversification through cospeciation appears to be limited (reviewed in Brooks & McLennan 1993, Hoberg & Klassen 2002, Zarlenga *et al.* 2006).

Climate change and ecological perturbation as drivers of EID

As the human population grows daily, its ecological and technogical footprint deepens. Introducing ourselves and other species into novel regions of the biosphere accelerates landscape alteration and ecological perturbation, which in global ecosystems can initiate events that link climate change, loss of biodiversity and EID (Daszak *et al.* 2000, Harvell *et al.* 2002, Woolhouse 2002, Epstein *et al.* 2003, Brooks & Ferrao 2005, Lovejoy & Hannah 2005, Brooks & Hoberg 2006, Parmesan 2006, Pounds *et al.* 2006). Such events include increased biotic mixing of evolutionarily unfamiliar species, and therefore increased opportunities for parasites and pathogens to find and infect

novel hosts. How we adapt to these changes will depend on how well we understand and use knowledge of the responses of host-parasite systems during episodes of large-scale climate and environmental change.

The taxon pulse hypothesis (Erwin *et al.* 1979, Erwin 1981) predicts that historical biogeographic patterns result from alternating episodes of biotic expansion and isolation, which lead to complex geographic distributions. Recent empirical studies in historical biogeography that document marked influence of taxon pulses (Hoberg 1995, Bouchard *et al.* 2004, Brooks & Ferrao 2005, Brooks & Folinsbee 2005, Halas *et al.* 2005, Zarlenga *et al.* 2006, Folinsbee & Brooks 2007) implicate geological phenomena, such as tectonic changes and climatological phenomena, including global or regional climate change, as taxon pulse drivers. During biotic expansion phases, susceptible hosts come into contact with novel (for them) parasites. Host switching occurs rapidly, without the need for any evolutionary innovation. For example, alternating cycles of biotic expansion and isolation across Beringia at the crossroads of the northern continents are clearly associated with cyclical episodes of climate change in the Pleistocene epoch (Hoberg 1995, Zarlenga *et al.* 2006, Waltari *et al.* 2007, Cook *et al.* 2005). Natural selection acts only on what has happened, so there will have been no opportunity for the evolution of resistance to, or tolerance of, the parasite by the new hosts. This suggests that most host switching occurs in conjunction with episodes of global climate change and associated biotic expansion and altered trophic relationships. This has been demonstrated for tapeworms (*Taenia* spp.) in humans, hookworms (*Oesophagostomum* Raillet & Henry, 1913) and pinworms (*Enterobius* Leach, 1853) in hominoids, and nematodes (*Trichinella* Railliet, 1895) in carnivores (Hoberg *et al.* 2001, Brooks & Ferrao 2005, Brooks & Folinsbee 2005, Zarlenga *et al.* 2006, Folinsbee & Brooks 2007). The emerging story of human parasites is one of ancestral, ecological associations with secondary host switches since the Pliocene associated with ecological perturbation.

More recent human activities associated with the evolution of agriculture, domesticated livestock, urbanization, and now global climate change have served to broaden the arena and disseminate the risk for EID on a global scale. If current climate changes have a prolonged duration and global scope, we should expect an increase in EID. Predicted responses to climate change by hosts and parasites include biotic expansion with geographic colonization, shifting patterns of geographic range, changing phenology and habitat use, modification of ecotones and contact zones (Parmesan 2006, Hoberg & Brooks 2008), and local extinction (Pounds *et al.* 2006, Marcogliese 2001). Global and regional climate change events have had major influences on biotic structure and the distribution of host-parasite assemblages throughout earth history (Hoberg & Brooks 2008), but recent cases might result from anthropogenic effects beyond those caused by climate warming (Cleaveland *et al.* 2001, Dobson & Foufopoulus 2001, Haydon *et al.* 2002, Lafferty *et al.* 2004, Kutz *et al.* 2004). Microevolutionary responses including mosaic-like, ephemeral patterns of local adaptation, directional changes in gene frequencies through mutation, and selection for parasites associated with emergence (Dobson & Foufopoulus 2001, Thompson 2005) have not yet been linked directly to climate change. However, such changes could begin with host shifts and outbreaks of disease on local spatial and fine temporal scales, leading to 'mosaics of emergence' (Thompson 2005, Hoberg & Brooks 2008). New associations might proliferate and emerge through ecological fitting, potentially associated with disease in a changing array of 'reservoir' hosts (Dobson & Foufopoulus 2001, Haydon *et al.* 2002).

Conclusions – The big picture

Complete understanding of the complex history of host-parasite associations requires consideration of multiple, non-mutually exclusive evolutionary and ecological mechanisms and phenomena (Brooks & McLennan 2002, Brooks *et al.* 2006b, Hoberg & Brooks 2008, Brooks & Hoberg 2008), but we believe that host shifts via ecological fitting provide a missing link in our general understanding of the evolution and diversification of host-parasite interactions. When ecological fitting provides the necessary first step in the colonization process by initiating a host shift, it also provides essential raw material for coevolutionary interactions. Ecological fitting allows genotypes to be exposed to novel selection regimes.

The geographic mosaic theory of coevolution (Thompson 1994, 2005) emphasizes the interplay between local adaptation and gene flow in geographically structured populations. Species can interact in different ways, and with different species in different parts of its geographic range. This mosaic of interactions can lead to the buildup and breakdown of locally adapted coevolutionary hot spots depending on gene flow and the local presence or absence of other interacting species (Thompson & Fernandez 2006). This perspective provides an appreciation for the observation that polyphagous species are often comprised of geographically-structured populations associated with small sub-sets of the total species in the parasites host range (Fox & Morrow 1981). Raw material for coevolution, however, must be constantly regenerated through colonization of novel resources in parts of a species geographic distribution (Janz & Thompson 2002, Singer *et al.* 2008), which is made possible by ecological fitting via resource tracking and the exploration of sloppy fitness space. Coevolutionary processes can buffer a species against fragmentation, or promote diversification depending on the nature and strength of processes acting on local and regional scales (Thompson 1994, 2005, Benkman 1999, Godsoe *et al.* 2008). Host colonization by ecological fitting promotes diversification only to the extent that the geographic mosaic allows local adaptation to newly formed hosts and sufficient isolation from other populations (Agosta & Klemens 2008).

Host shifts initiated by ecological fitting are not an endpoint, but rather one step in the process that fuels biological expansion and generates novel combinations of interacting species. From these novel interactions, ecological fitting can promote evolutionary stasis (e.g., if there are many ecologically fit populations connected by sufficient gene flow) or facilitate evolutionary diversity, through subsequent divergent local adaptation (Agosta & Klemens 2008). Janz *et al*. (2006), Janz & Nylin (2008), and Nylin & Janz (2009) recently proposed that diversification in these systems is driven by repeated "oscillations" in host range. Coupled with taxon pulses, the oscillation hypothesis predicts phases of host expansion during geographic range expansion followed by phases of host specialization during geographic isolation (or, alternatively, sympatric speciation by host race formation). As with the geographic mosaic concept (Thompson 2005), the oscillation hypothesis relies on constant regeneration of variation in host use; it is the diversification of host use that drives diversification of species whether the actual speciation process relies on allopatric or non-allopatric modes (Janz & Nylin 2008).

In terms of EID, climate and disturbance driven taxon pulses in geographic range and oscillations in host range can be expected to influence their frequency, whereby periods of range shifts and expansions increase biotic mixing and the opportunities for ecological fitting to occur. The current EID crisis is "new" only in the sense that this is the first such event that scientists have witnessed directly. Previous episodes through earth history of global climate change and ecological perturbation, broadly defined, have been associated with environmental disruptions that could have led to EID (Brooks & Hoberg 2006, Hoberg & Brooks 2008). From an epidemiological standpoint, episodes of global climate change should be expected to be associated with the origins of new host-parasite associations and bursts of EID. The combination of taxon pulses and ecological fitting suggests that host and parasite species with the greatest ability to disperse should be the primary source of EID (Brooks & Hoberg 2006, Dobson & Foufopoulus 2001, Fenton & Pedersen 2005). Paleontological studies suggest that species with large geographic ranges and with high ability to disperse are most successful at surviving large scale environmental perturbation and mass extinctions (Stigall & Lieberman 2006). Thus, the species most successful at surviving global climate changes will be the primary sources of EID, so host extinction will not limit the risk of EID. From the standpoint of taxon pulses and ecological fitting, the planet is an evolutionary and ecological minefield of EID through which millions of people wander daily.

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