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How will global climate change affect parasite–host assemblages?

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Parasites are integral components of the biosphere. Host switching correlated with events of episodic climate change is ubiquitous in evolutionary and ecological time. Global climate change produces ecological perturbations, which cause geographical and phenological shifts, and alteration in the dynamics of parasite transmission, increasing the potential for host switching. The intersection of climate change with evolutionary conservative aspects of host specificity and transmission dynamics, called ecological fitting, permits emergence of parasites and diseases without evolutionary changes in their capacity for host utilization.

Interconnectedness of climate change, biodiversity and infectious disease

The human population grows daily, deepening its technological footprint on this planet. Introducing ourselves and other species into novel regions of the biosphere accelerates landscape alteration and ecological perturbation, which leads to potentially irrevocable changes in biotic structure. Accelerated perturbation in global ecosystems can initiate events that link climate change, loss of biodiversity and emerging infectious diseases (EID) [1–9]. Whether we adapt successfully to these changes depends on how we develop and apply knowledge about the responses of parasite systems during episodes of climate change.

Responses of parasite–host systems to climate change

The effects of global warming on assemblages of hosts, parasites and pathogens can be numerical, functional or microevolutionary, and can involve cascading changes in ecosystems [2,10–14]. Numerical responses include amplification and emergence of parasite populations associated with changing rates for parasite development and survival, and alteration in seasonal dynamics of transmission, constrained by environmental and ontogenetic lag times [15]. Such EID drivers have been implicated for marine, terrestrial and aquatic assemblages of micro- and macroparasites [16], and have been demonstrated empirically in a few systems: nematode–gastropod–ungulate systems in the Arctic [15,17–19], nematode–avian systems in Scotland [20] and digenean–amphipod systems in intertidal environments [14]. Despite the paucity of empirical data

for assessing numerical- and density-dependent impacts on hosts and parasites during global warming, such responses are expected to be widespread [14,17,20].

Functional responses include biotic expansion by hosts and parasites with potential for host and geographic colonization, shifting patterns of geographic range, changing phenology for habitat use, modification of ecotones and contact zones [8,21], and even local extinction [9,11]. Such responses have had major influences on biotic structure and the distribution of parasite–host assemblages throughout earth history [21]; recent responses might result from anthropogenic effects beyond those caused by climate warming [13,15,22–24].

Microevolutionary responses include mosaic-like, ephemeral patterns of local adaptation, directional changes in gene frequencies through mutation, and selection for parasites associated with emergence [22,25]. These mechanisms have not yet been linked directly to climate change, but could represent a component of expected ecological isolation [22].

Numerical, functional and evolutionary drivers for EID can be synergistic or cumulative, which affect the structure of entire parasite–host communities during climate change episodes. Such changes might begin with host colonization and outbreaks of disease on local spatial and fine temporal scales, which lead to ‘mosaics of emergence’ [21,25] that arise from established associations. New associations might proliferate and emerge through geographic or host colonization, potentially associated with disease in a changing array of ‘reservoir’ hosts [22,23].

Strategic approaches for dealing with EID are predicated on particular evolutionary and ecological models of parasite–host relationships, themselves implying particular relationships between climate change, biodiversity and EID. We believe the EID crisis is ‘new’ only in the sense that this is the first such event that scientists have witnessed directly. Previous episodes of global climate change and ecological perturbation, broadly defined, throughout earth history have been associated with environmental disruptions that could have led to EID [6,21]. The evolutionary basis for such episodes has been elucidated [26,27], but not internalized within parasitology.

Two traditions of parasite–host interactions

Two traditions in ecology and evolutionary biology concern parasite–host associations: (i) the parasite-centred view

with roots in Darwinism; and (ii) the host-centred view with roots in orthogenetic concepts of evolution [27,28]. Both agree that parasites are ecological specialists with respect to their microhabitat requirements (e.g. their preferred site of infection) and their mode of transmission from host to host through the environment (their life cycle patterns) [27,29]. They differ in the nature and significance of host specificity, particularly the ease or difficulty with which parasites can switch hosts (parasite-centred terminology) or with which hosts can capture parasites (host-centred terminology). This distinction is fundamental for EID studies, because EID often occur when parasite species begin infecting and causing disease in hosts with which they have no previous history of association. If the nature of host specificity is such that host switches are likely to be rare, 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.

The host-centred tradition assumes that the focus of coevolution is the host species. The host-centred view implies that progressive specialization on particular host species mitigates against capture by other hosts, so coevolution provides a safeguard against EID. This seems reasonable, what host species would want to 'capture' more parasites? Thus, EID can be considered rare events.

The parasite-centred view, by contrast, assumes that the resources for parasites are particular attributes of the host species, not the host species themselves. It does not question the assumption that parasites are ecological specialists, but questions the premise that host switches are rare events. This is not as paradoxical as it might seem. Phylogenetic conservatism in host attributes upon which a parasite is specialized might produce a range of susceptible hosts, whereas restricted geographic distribution of the parasite at any given time would mean that many susceptible hosts are not infected. Parasites inhabit all susceptible hosts with which they come into contact; at any given place and time that might be one host. Changes in geographical distribution or local ecology associated with parasite transmission should produce immediate changes in host range. This is called 'ecological fitting' [5,26,30–33]. If the host trait (or trait complex) is a persistent ancestral attribute, the susceptible hosts might not form a clade, so host switching could involve species that are not 'close relatives' [6].

Empirical studies indicate that few parasite groups conform to the phylogenetic patterns of parasite–host associations expected by the host-centred view. Clades, primarily ectoparasitic arthropods, which exhibit limited host switching [34–36], 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 [27,37,38]).

A macroevolutionary dynamic: taxon pulses, ecological fitting and climate

What drives host switching by way of ecological fitting? The taxon pulse hypothesis [39,40] 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 [5,38,41–45] 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 [38,42,46,47]. 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*) and pinworms (*Enterobius*) in hominoids, and nematodes (*Trichinella*) in carnivores [5,38,44,45,48]. 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 disseminated the risk for EID on a global scale.

Dimensions of EID risk space

From an epidemiological standpoint, episodes of global climate change should be associated with the origins of new parasite–host 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 [6,22,28]. Paleontological studies suggest that species with large geographic ranges and with the high ability to disperse are most successful at surviving large scale environmental perturbation and mass extinctions [49]. 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.

The host-centred view suggests that parasites with complex life cycles should be less successful at dispersing geographically than those with direct life cycles, assuming that multiple coadapted host species are required to transplant a parasite with a complex life cycle [50]. Brooks *et al.* [32] recently reported the lung fluke *Haematoloechus floeidae*, normally a parasite of bullfrogs that live in the south-eastern US, inhabits other ranid frog species in northwestern Costa Rica. The parasite was apparently introduced to Costa Rica with imported bullfrogs, and established itself in local hosts. Bullfrogs do not occur in the collection area, which shows that the parasite is capable of surviving despite the extinction of the host in

which it was originally introduced. The parasite-centred view suggests that conserved trophic connections, rather than particular species, are required for such dispersals. For *H. floedae*, successful establishment required only an ecosystem that has aquatic pulmonate snails, dragonflies, and frogs that eat dragonfly naiads. Nor does *H. floedae* appear to be an unusual case. Phylogenetic conservatism in life cycle patterns on the part of most parasite species, coupled with phylogenetic conservatism in diet and habitat preference on the part of anurans explains pronounced ecological similarities in communities of plathyelminth parasites of frogs in temperate deciduous forests, temperate grasslands and two different sets of tropical dry forest and tropical wet forests, despite little cospeciation [33]. These examples indicate ecological isolation and ecological fitting have a greater influence on the structure of complex parasite–host assemblages than do coevolutionary processes.

Synoptic data inform appropriate action

If current climate changes will have a prolonged duration and global scope, we should expect an increase in EID. We are concerned about our preparedness to handle such events in a timely and cost effective manner. The potential risk space is geographically and biologically extensive, and climate change will make more of the risk space accessible to more parasites. As a result, the planet is an evolutionary and ecological minefield of EID through which millions of people wander daily.

Public health, veterinary and wildlife parasitologists regularly base tactical responses on systematic, ecological and evolutionary information. Taxonomic names provide access to knowledge of evolutionarily conservative traits and history that form the basis for predictive and thus proactive measures. When linked to archival collections that represent historical baselines for assessing patterns of perturbation in host and geographic associations [12,47], such information allows us to understand change in complex biological systems over broad spatial scales that link evolutionary and ecological time.

Managing EID requires facilitating communication, integrative strategic planning by public, veterinary and wildlife health specialists who are on the front lines of the EID crisis, and monitoring shifts in host associations that are mediated by ecological fitting and climate change, so we can assess the rate of change in the potential risk space assessed against archival collections and established baselines. This requires support for systematics infrastructure including people, inventories, collections and information. In the absence of taxonomic names there is no information, and with the wrong names there is incorrect information. Both situations emphasize the consequences for how we identify and understand dynamic change for parasite–host assemblages under a regime of climate warming.

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