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Host specificity in variable environments

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Highlights

- Increasing interests in emerging infectious diseases and parasite spillover coincide with a rise of studies reporting and comparing host specificity for multihost parasite. Intuitively, higher host specificity means less spillover risk but to date, a systematic consensus on such a relationship is lacking.

- Host specificity can vary in space and time due to changing compositions of potential host species and constraints in environmental conditions. Eco-evolutionary dynamics and contemporary conditions synergistically determine ‘realized’ host specificity across regional scales.

- Modelling advances to capture spatiotemporal variation in the distributions and biotic interactions of species provide the basis to quantify variation in realized host specificity and progress towards determining how this relates to spillover risk.

Abstract

Host specificity encompasses the range and diversity of host species that a parasite is capable of infecting and is considered a crucial measure of a parasite's potential to shift hosts and trigger disease emergence. Yet empirical studies rarely consider that regional observations only reflect a parasite's 'realized' host range under particular conditions: the true 'fundamental' range of host specificity is typically not approached. We provide an overview of challenges and directions in modelling host specificity under variable environmental conditions. Combining tractable modelling frameworks with multiple data sources that account for the strong interplay between a parasites' evolutionary history, transmission mode and environmental filters that shape host-parasite interactions will improve efforts to quantify emerging disease risk in times of global change.

Key words: disease spread; pathogen spillover; co-speciation; host shifting; host-parasite interactions; realized host specificity

Host specificity in times of emerging infectious diseases

The diversity of infectious disease affecting humans and animals are strongly determined by parasites capable of infecting multiple host species. Estimates that up to 70% of human parasites are **zoonotic** (i.e. shared by humans and at least one other animal species; see Glossary) showcase that multi-host parasites, as opposed to those that only infect a single host species, are the rule rather than the exception [1, 2]. Frequent identification of **Emerging Infectious Diseases** (EIDs) highlights the global importance of contemporary **host shifting** that can result in infection of novel and often immunologically naïve hosts [3, 4].

Host specificity, representing the number and/or diversity of host species a parasite is capable of infecting, is considered a key indicator of its propensity to shift hosts [5]. Host specificity is a topic of considerable interest in the fields of disease ecology and One Health that is quickly becoming a key feature of research agendas (Figure 1). Much of this work is aimed at delineating possible EID **reservoirs** by attempting to identify parasites that may be capable of shifting between wildlife and human hosts [6-8]. Wildlife parasitology research has uncovered a broad spectrum of host specificity 'strategies' for an impressive diversity of parasites. These range from haemosporidian blood parasites and feather mites that associate with only a small number of closely-related host species [9, 10] to rabies viruses that are seemingly capable of infecting virtually any mammalian species they encounter [11].

Intuitively, one may assume that among multi-host parasites, those that exhibit low host specificity (i.e. high levels of host generalism) are more capable to shift hosts [12]. Indeed, numerous studies have identified so-called ‘generalist’ parasites that seem capable of infecting a broad spectrum of phylogenetically and sometimes ecologically dissimilar host species [5, 13, 14]. Yet whether low host specificity meaningfully reflects a higher risk for EID-related **spillover** remains unresolved [15, 16]. This is largely because there are multiple facets of host specificity, many of which are not captured by common metrics, and there are idiosyncratic ways in which different host species contribute to a parasite’s specificity [17]. Moreover, there is a great deal of uncertainty about whether any retrospective summary of observed host ranges into host specificity measures, which basically reflect the accumulation of historical host-parasite interactions, translate into a parasite’s potential for contemporary host shifting [18].

Here, we summarize the state of current research on host specificity and highlight how such work can play a role in advancing our ability to quantify host shifting capacity. We extend previous reviews of how novel species communities may relate to shifting host ranges and variation in parasite transmission dynamics [4, 17, 19] by discussing challenges in the use of host specificity metrics and outlining frameworks that align common data structures to relevant modelling tools.

The eco-evolutionary backbone of host specificity

Specialization of species in parasitic or mutualistic interactions is assumed to be tightly linked to the levels of adaptation exhibited by interacting partners [20]. Host-parasite interactions often require highly tuned transmission modes and adaptations by the parasite to survive and reproduce in the host environment [21]. It therefore comes as little surprise that much of the emphasis surrounding investigation of host-parasite interactions has been placed on host-parasite co-evolution. Co-speciation, whereby a parasite species evolves into two distinct species in response to host speciation, has long been used to explain apparent congruence in host and parasite phylogenies. The prevailing reasoning is that a parasite’s evolutionary history sets the stage for host specificity by introducing phylogenetic and ecological barriers to host shifting [22, 23]. Host shifting requires parasites to be exposed to new hosts that exhibit certain levels of physiological and/or behavioural overlap with previous hosts (**ecological fitting**), as this allows circumvention of barriers caused by variation in host competence or immunity [22, 24].

An expanded line of thought, primarily derived from studying mutualisms such as animal-plant interactions, suggests that host shifting is probabilistic and relies on opportunity for hosts and parasites to interact under variable environmental conditions [4, 25]. A prominent example involves herbivorous insects introduced as biocontrol agents into different environments, which showcases that regional host ranges are largely determined by local environmental conditions such as plant community composition, relative abundance and phenology in response to climate variation [26, 27].

By analogy, we argue that similar environmental forces will also be important for shaping host-parasite interactions [4, 28-30]. This idea that a parasite's capacity for host shifting can vary in response to environmental conditions (Figure 2) presents a new forefront of research on spillover risk in times of global change [4, 31-34]. Fortunately, a burst in analytical tools designed to explore spatiotemporal variation in species interactions [35-37] make it possible to characterize how host specificity changes across environmental gradients. Consistent frameworks are now needed to disentangle the evolutionary and ecological aspects of host-parasite interactions that should be considered when judging host specificity.

A niche perspective on host specificity

Developing a framework to assess host specificity, and to begin relating specificity to potential spillover risk, relies first on developing a consistent definition for host specificity. This is particularly necessary when considering the staggering diversity of advocated indices and metrics (Table 1). The most common of these focus on the range of hosts a parasite is observed to infect and in which it can persist and/or complete its life cycle. The simplest way to do this is to count the number of host species a parasite infects [10]. But this provides little information about the diversity of host 'habitats' that comprise a parasite's **niche**. Authors have more recently recognized that adapting ecological niche concepts to host specificity can improve understanding of a parasite's host range using concepts from a widely-supported theoretical framework [13, 32]. An important aspect of niche theory distinguishes between **potential resources** (resources that a species could utilise if it encountered them) and surrounding conditions that determine whether resources are available and can be utilized (**environmental filtering**). Recent advances in ecological niche modelling have capitalized on the concept of potential resources to expand our understanding of niche filling by differentiating between a species' **fundamental niche** and its **realized niche**. Here, the fundamental niche refers to resources that can be used in the absence of any restrictive conditions, while the realized niche refers to regional consumer-resource dynamics that are observed under local environmental conditions [38].

Translated to multi-host parasites, the fundamental niche describes a parasite's capacity to explore different host species independently of conditions that may restrict its exposure to these potential hosts. The realized niche, in turn, is based on the regional diversity of host species a parasite is actually observed to infect [39](Figure 2). Biogeographic structuring of host assemblages across regional scales will constrain opportunities for host-parasite interactions. In other words, variation in the diversity of potential hosts occurring in regional species pools can ensure that a parasite's fundamental host specificity is not completely realized [40]. Empirical support for this can be derived from a number of field studies from diverse host-parasite systems. Biogeographic structure in host species distributions likely narrows the realized host specificity of chewing lice infecting toucans, particularly when closely related host species are spatially disconnected [41]. Host range expansions by relatively fast evolving (RNA) rabies viruses depend on local compositions of bat assemblages, as different virus lineages often cannot cross species barriers to infect distantly related host species [11]. Regional climate conditions that influence vector habitats are associated with observed host specificities for widespread avian malaria parasites [34]. Experimental studies that artificially increase the host range accessible to a parasite further support the concept of fundamental vs realized host specificity: the set of hosts that can be infected experimentally can be much larger than the actual range observed under natural conditions, even for parasites that are only observed to infect a single host species [42]. This increasing recognition that local variation changes the suite of hosts to which a parasite is exposed and pre-existing capacity enables host shifting upon newly arising opportunities has been raised by a number of recent studies that collectively contribute to a meta-theory called the **Stockholm Paradigm** [32]).

Inferring host specificity

Ecological dynamics impact the host specificity of parasites across local and regional scales [43, 44]; this has important ramifications for formulating concepts to gather inferences about explanatory mechanisms. Identifying factors that influence opportunities for novel host-parasite interactions, and how these shape realized host specificity, are vital steps to begin uncovering the true fundamental host specificity (see **Box 1**). This requires an understanding of how host communities are shaped and how resources are utilised, both of which have strong parallels in community ecology. A growing consensus states that a suite of factors such as evolutionary contingencies, speciation, adaptive plasticity, dispersal capacity, environmental filters and biotic interactions [45-48] act in concert with stochastic processes [49] to shape communities. Accounting for plasticity in resource utilisation helps to align ecological modelling approaches to reality for understanding shifts in species' habitat use, geographical ranges, or trophic interactions across environmental gradients [20, 50]. Moreover, tractable modelling concepts that can untangle the effects of environmental forcing and species interactions on resource utilisation have recently been developed [51-54].

Note that in most situations, sufficient empirical and experimental evidence is necessary to infer aspects of fundamental host specificity (see Box 2 for some considerations about matching data to study questions and models). We now outline a number of important modelling approaches that are available to begin understanding how host specificity is shaped across scales.

Trait-based approaches to host specificity

Trait-based approaches, which group species of interest according to attributes such as phylogenetic relationships, body size, diet, climate tolerance or distributions, are increasingly adopted to study species ecological preferences and their potential responses to global change [55, 56]. In the context of host specificity, there are at least two trait-based approaches that have received considerable attention recently.

First, indices of functional and phylogenetic diversity are used to delineate host specificity according to the observed (or estimated) variation in traits exhibited by competent host species [5]. Often, such measures are based on pair-wise distances that are calculated among all possible combinations of viable host species [57, 58]. For instance, phylogenetic trees, which depict evolutionary relationships among host species, can be used to generate indices of phylogenetic host specificity [17, 59, 60]. In a similar way, distance-based diversity measures can be generated using host species' ecological traits [14, 61], with supporting computational algorithms readily available in open-source software such as R [62]. The central aim when using these measures is to determine whether the distribution of pairwise distances between infected host species (observed distances) is different to a distribution of distances between potential host species (expected distances). Here, an observed distance distribution that is statistically smaller than expected indicates that infected hosts are more closely related than expected by chance. It is worth noting that such metrics largely depend on sample size (i.e. the number of host species recorded) and thus are potentially subject to sampling bias [63]. Null model permutation approaches [64] and more recently, hierarchical models [40], have been proposed to account for sampling bias while comparing observed and expected distance distributions. Recent studies have put these ideas into practice by demonstrating that host functional traits are as important as phylogenetic relationships for assessing whether primates share the same parasites [15] and by showing that host phylogenetic relationships appear to strongly shape the host ranges of avian malaria lineages [14]. Moreover, a recent multi-taxa study deciphered that phylogenetic specialization among prospective hosts is more pronounced for helminths and viruses than for other parasite groups [65]. Finally, similar trait-based measures were used to show that fleas with certain traits are more likely to infest the same subsets of phylogenetically and functionally related mammalian host species [66], showcasing that evolutionary history and ecological fitting synergistically drive the realized host specificity of these ectoparasites.

Trait-based regression models have also gained popularity for analysing whether the presence-absence of parasites in a suite of host species is linked to host traits [6-8]. Such approaches are of relevance for host specificity measures as model-based estimates of a parasite’s associations with particular host traits can enable projections onto unmeasured host species, enabling prediction of unknown interactions [67]. Generalised linear models (GLMs; readily estimated using Maximum Likelihood or Bayesian frameworks through available R packages; [68-70]) or machine-learning regression trees [71] are the methods of choice as they estimate associations using data from a variety of outcome distributions. Prominent examples have found that higher proportions of zoonotic viruses occur in mammals that are closely related to humans [8], whereas studies of rodents have shown that hosts with faster life histories have higher occurrences of zoonotic viruses [6]. Another study found that the intensity of helminth parasite sharing between humans, domestic animals and wildlife appeared to be predominantly driven by dietary traits of wildlife species [7]. At the species level (i.e. presence-absence of a particular parasite in a suite of host species), however, we stress again that such regressions are only useful if the underpinning data include sufficient numbers of both presence and absence records to allow meaningful inference.

Network approaches to study host-parasite interactions

Ecological networks summarize biotic interactions among groups of species that live in trophic or symbiotic relationships [72]. Amongst the many useful insights gained from such community-scale analysis, they allow users to draw conclusions about the preference (specialization) of species towards a suite of potential partners [73]. Networks can be constructed as bipartite graphs that denote whether species interact or not (e.g., binary 'presence-absence' data of interactions between combinations of host and parasite species) or the frequencies of interactions (e.g., the number/proportion of individuals from a given pool of host species infected with the concerned parasites). A simple measure of a parasite's specialization derived from binary networks can be the proportion of host species infected [74], an index that resembles host specificity without taking link strengths into account. This measure can be linked at the community scale when used in combination with null model analysis [75], allowing users to ask which parasites are more or less specialist. In contrast, many network measures of species-level host specificity, such as the species-specific specialization index *d'* [76], are based on both the link distributions as well link strengths. Such community-scale analysis acknowledges the fact that every single interaction is embedded in a network of species interactions and depicts a parasite's preference/specialization on particular hosts relative to both the overall host availability and the host utilisation by other parasites. Such an approach was recently used to explore network compositions of fish parasites and mammalian fleas across a number of regions [74]. The authors showed that specialist parasites tended to interact with hosts that harboured high richness of parasites, and that hosts with high parasite richness also tended to be more abundant. However, given the fact that network specificity indices are commonly derived from a finite set of community-scale observations, their utility for predicting fundamental host specificity needs to be carefully evaluated. This is because host specificity is a species-specific attribute, and we argue that host specificity is not necessarily shaped by the specificities of other parasites in the community. Moreover, networks assembled under particular regional conditions will only yield measures of realized host specificity and thus do not necessarily provide accurate insights about host specificity under novel (unsampled) environmental conditions. Nevertheless, advances in techniques to model how ecological network properties respond to environmental variation [36, 77] may provide promising opportunities to estimate fundamental host specificity in future research.

Ecological network concepts have also been employed to detect the centrality of key host species and/or the modularity of interaction compositions in observed host-parasite networks [78]. These approaches aggregate host-parasite interactions into adjacency matrices to depict focal species that share similar sets of interactions (i.e. two host species that are infected by similar parasites may be connected within the network; [78, 79]). This of course comes at the cost of losing information about species identity, but can nevertheless be helpful for identifying roles that different host species may play for facilitating parasite spread or for understanding whether host-parasite interactions exhibit a modular or nested structure.

Identifying environmental filters related to realized host specificity

Despite the examples outlined above, few studies have examined how changes in host specificity relate to spatiotemporal changes in environmental conditions [80, 81]. Capturing the complex ways in which environmental filtering can affect realized host specificity is a looming challenge that calls for integrative approaches to consolidate the synergies between species distributions and biotic interactions [46]. For example, if variation in realized host specificity is linked to changes in regional host composition [40], a comprehensive understanding of how environmental filters impact realized host specificity requires disentangling their effects on host species occurrence and on host-parasite interactions (i.e. by influencing epidemiological factors such as host susceptibility, parasite survival and transmission potential). Some first step towards capturing this process have been taken by applying statistical models that estimate how realized host specificity changes in relation to the variation in host community compositions [40, 82] and environmental filters such as climate [34]. These approaches expand on the trait-based methods described above by comparing suites of ecological and/or phylogenetic distances among infected pairs of host species to distances that describe all potential host species within each region that a parasite occupies. Results have provided promising new insights. For example, Wells *et al.* [40] showed that helminth parasites generally exhibited the lowest phylogenetic host specificity in regional ‘hotspots’ that showed high variation in prospective host diversity; despite being globally distributed, some parasites still infected less functionally diverse hosts than expected, indicating limited potential to infect hosts from different ecological niches. Fecchio *et al.* [34] showed that avian malaria parasites are more constrained in their capacity to exploit a diversity of host species in regions with pronounced rainfall seasonality and wetter dry seasons. Other recent developments can account for biotic interactions within multivariate community models, which can be helpful to understand how host-parasite interactions may change across environmental gradients [52]. While we are unaware of these models being used to assess changes in realized host specificity, their ability to detect associations among different parasites opens exciting avenues for uncovering how host specificity is shaped across regional scales.

The need to capture uncertainty: probabilistic tools and an outlook on forecasting host shifting

Because observational data dominates the host specificity literature, the above sections stress that taking advantage of contemporary modelling tools for best-possible inference offers significant improvements over simply drawing conclusions from finite observations at hand. We also urge the use of probabilistic methods when applying such tools, as they can distinguish drivers of host-parasite interactions from underlying observation processes to obtain model-based estimates [83-85]. Probabilistic sampling approaches have a number of benefits that make them suitable to host specificity research, including: (1) Capturing uncertainty and sampling bias in infection and host-parasite association data, and allowing for random data imputation/augmentation (i.e. for poorly sampled host species there might be a certain probability this species is infected, even if records of such associations are missing); (2) Utilising a diversity of data sources such as host-parasite association data, trait variables and spatiotemporal environmental data in consistent model frameworks; (3) Capturing the hierarchical nature of realized host specificity by conceptualizing conditional dependencies such as ‘the probability a host species contributes to realized host specificity, conditional on its presence and compatibility under regional conditions’. The ability to capture uncertainties is particularly imperative for forecasting the possible infection of a novel host species under future or as yet unexplored environmental conditions, which is the basis for mitigating the public and animal health risks posed by EIDs. Given the importance of plasticity in host specificity, quantitative solutions require developing and applying tractable forecasting tools to answer questions such as ’how likely is a parasite to shift from one host species to another under XYZ regional conditions?’. This can be a challenging task for a large range of parasites that affect only a small number of host species and/or for which retrospective data on host shifting events are rare.

Despite these challenges, novel modelling frameworks offer a foundation for prediction about when and in which host species a parasite may occur. Correlative approaches in species distribution and ecological niche modelling, for example, aim to estimate species persistence under a range of surveyed environmental conditions (aiming to describe the pattern but not necessarily the underlying mechanism) and then project species distributions across larger environmental space [86]. The trait-based regression models discussed above fall into this category, and may be useful for prediction as they generally have moderate data needs, including the presence-absence of host-parasite associations and information about host traits and environmental conditions. However, projecting models to estimate a parasite's fundamental host range (and to predict host shifting events) across gradients of substantial spatiotemporal change might significantly violate model assumptions and could be hampered by poor **transferability** [87]. Only for parasites with invariable realized host specificity across environmental gradients would one expect to obtain reasonable accuracy in projected host specificity under unsampled conditions. This raises the need for detailed sampling regimes that cover much (if not all) of the parasite's known distribution. In light of the potential drawbacks of correlative predictions, a key aim for future research could be to use historical data on true host shifting events to see if any patterns of realized host specificity prior to the shift could have been informative for prediction. Using such hindcasting approaches to evaluate our capacity to forecast future EIDs could tell us whether any of our metrics have any real value, or whether other situational aspects (such as rapid changes in contact rates, the emergence of new host-host contacts or the stochastic emergence of new strains) are more important.

In contrast to correlative approaches, processed-based methods explicitly model the important processes underlying patterns [88, 89]. In terms of host-parasite interactions, such models may aim to predict and reproduce host shifting events from a suite of eco-epidemiological factors that jointly drive system dynamics, including variation in contact opportunities among host species and spatiotemporal environmental variation. Perhaps a promising move towards predicting fundamental host specificity and forecasting EIDs could be the establishment of so-called hybrid models. Hybrid models synthesise correlative and process-based models by combining static projections from correlative approaches with simulation of key processes; in species distribution modelling, these processes include aspects such as species abundances, the realistic co-occurrence of interacting species and dispersal events [90]. Hybrid models can improve the transferability of correlation-based approaches by more realistically accounting for key processes while avoiding specification of a large number of parameters [91]. For our purposes, such models could aim to capture the most essential dynamics underlying host shifting, such as possible range shifts of key hosts, expected variation in host community composition in relation to climate change [92] or the emergence of species invasion 'hotspots' [93].

Concluding Remarks

A large body of research on human, animal and plant parasites uses host specificity to gauge the risk of EIDs and spillover events. However, in times of global change and the large-scale spread of parasites across former geographic barriers, drawing conclusions about a parasite's host shifting capacity using simple specificity indices may not be suitable to predict such events under novel conditions. Host specificity cannot be considered a fixed trait, as environmental conditions cause considerable variation in realized host specificity. The task of predicting host shifting events must rely on tractable modelling frameworks that sit at the core of ecological forecasting [94]. Ultimately, accounting for plasticity and uncertainty in a parasite's realized host specificity may be a worthy step to better predict disease emergence and host shifting events (see **Outstanding questions**). But identifying the multifaceted processes involved in multi-host parasite transmission is laborious and will require considerable empirical and quantitative research. Along the way towards understanding such complexities, we should not ignore the fact that disease emergence inevitably means parasites often have a hidden potential to infect novel host species. Initial conclusions based on realized host specificity alone need to be carefully revisited as more data becomes available. This will leverage our growing understanding about which parasites are capable of crossing the species barrier and causing unwanted diseases.

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Outstanding questions

- Are there generalities about the plasticity in host specificity in response to environmental conditional for parasites from different taxonomic groups and/or with different transmission modes?

- Do strong host-parasite co-evolutionary histories constrain the plasticity in host specificity and potential for host shifting across environmental gradients?

- Can integrated model frameworks and validation procedures for inferring fundamental host specificity allow us to better predict future host shifting events?

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Glossary

- **Ecological fitting**: Species association enabled by pre-existing capacity without genetic change. (e.g. a certain suite of potential host traits enables infection by a parasite upon encounter).
- **Emerging infectious disease (EID)**: Infectious disease that recently appeared in a population or is recognized as a ‘novel’ disease with rapid spread.
- **Environmental filtering**: Environmental conditions that constrain resource utilisation by a species (e.g. the use of different host species by a parasite).
- **Fundamental niche (e.g. fundamental host range)**: For parasites, the set of all host species, whether known to be infected or not, that would serve a parasite as hosts under any environmental condition. The overall fundamental host range cannot necessarily be determined empirically, as only the existing (realized) host range across the accessible host species pool can be surveyed.
- **Host shifting**: The event of colonizing of a novel host species by a parasite, involving host range expansion (here defined as colonization of a novel host without losing the ancestral host opposed to considerations that parasites may shift from one host to another without range expansion).
- **Host specificity**: Measures of the number and/or diversity of host species a parasite is capable of infecting.
- **Niche**: Broadly and indistinctly defined environmental space suitable for a species to survive and reproduce. For parasites, the host range broadly refers to the main component of their niche.
- **Potential resources**: The range of resources that a species could utilise if it encountered them. In terms of host species, this is equivalent to fundamental host specificity, representing the full (unknown) range of hosts species a parasite is capable of infecting.
- **Realized niche (e.g. realized host range)**: A set of host species observed to be infected by a parasite in a specific regional and spatiotemporal context.
- **Spillover**: Cross-species transmission of a parasite into a host population not previously infected. In contrast to ‘host shifting’, ‘spillover’ often refers to infection of novel *populations* but not necessarily novel *species* (i.e. no host range expansion). The term appears to be most commonly used to describe cross-species transmission from wildlife to humans.
- **Stockholm Paradigm**: Hypothetical concept arguing that host range expansions by parasites result from the interplay between novel host-parasite opportunities in response to

shifting community assembly and phylogenetic and/or ecological barriers that limit parasite spread to novel hosts.

• **Transferability (models)**: Whether a model (and its parameter estimates) derived from a particular set of spatiotemporal conditions is transferable to other conditions and can be generalized. In terms of resource utilisation, a transferable model would allow accurate predictions of resource use from a model built using data from elsewhere.

• **Transmission**: The transfer of a parasite between different host individuals or other entities (such as relevant vectors). A term typically used in epidemiological studies.

• **Zoonosis (zoonotic)**: An infectious disease of humans caused by parasites acquired from an animal reservoir (host individual/ population/ species infected with a parasite and acting as a source for further infection and parasite spillover).

Box 1: Drivers of contemporary host specificity

Host community composition is influenced by various biotic and environmental filters that can collectively lead to dramatic variation in a parasite's realized host specificity. Here we outline a number of these situations, though it is important to note that this list is by no means exhaustive.

- **Anthropogenic invasion of key hosts:** Changes in host community composition caused by anthropogenic invasions can lead to important changes in parasite realized host specificities. For example, the rapid expansion of chytrid fungus, the parasite responsible for threatening declines of many amphibians globally, largely occurred along wildlife trade routes [95]. In addition, invasive commensal rats have been crucial for the global spread of parasitic helminths that have 'hitch-hiked' their way to encountering novel host species [33], ultimately shaping parasite biogeographic distributions [31].
- **Changing community compositions leading to new transmission dynamics:** The population structure of a parasite depends on the diversities and relative abundances of different host species infected [17]; host abundance is itself a plastic trait that typically varies across environmental gradients, strongly contributing to plasticity in realized host specificity [96, 97]. Following the examples above, introduced species may not only serve as potential vehicles for introduced parasites, but may also directly

alter existing local host-parasite interactions by changing the abundance of endemic host species [19], hence inducing cascading effects on host-parasite interactions.

- **Habitat encroachment and the human-wildlife interface**: As a consequence of habitat conversion and fragmentation, humans and domestic species are in frequent contact with wildlife species. Cat fleas, intestinal helminths, and canine distempter virus are among the increasing number of parasites observed to expand their host ranges to include a diversity of wild mammals following such novel human-wildlife encounters [7, 98, 99].
- **Expanding dietary range of a key host**: Biotic interactions among key host species play a large role in driving plasticity in host specificity. For example, within its exotic range in Australia, the presence of dingos and dingo/dog hybrids that feed on a large range of endemic wildlife has enabled the establishment of stable transmission cycles of the tapeworm *Echinococcus granulosus* through wild dogs and endemic wildlife [100], illustrating how host shifting into novel communities may be facilitated by particular regional conditions.
- **Exposure of parasites to competitors or facilitators**: Parasites themselves can also exhibit important biotic interactions. Antagonistic and synergistic effects in multi-host, multi-parasite systems affect both the co-occurrence of co-infecting parasites within the same host individuals [53, 101] as well as eco-epidemiological transmission dynamics [102].
- **Climate-related changes in the host affinity of vectors:** Climate-driven changes in the feeding patterns of important vectors may facilitate opportunities for vector-borne parasites to contact novel host species. For instance, warming climate influences the human-feeding habits of rickettsiae-vectoring tick species, leading to human spillover events [103]. Climate in combination with habitat changes can also affect the host range of tick-borne *Borrelia* bacteria, the cause of Lyme disease [104, 105].

Box 2: A data primer on host shifting and specificity

Any conclusion on fundamental host specificity depends on a sufficiently large number of individuals and potential host species examined for robust inference. At their most basic level, host specificity analyses rely on binary vectors describing the confirmed presence or absence of infection by a particular parasite from a diversity of sampled host species. Ideally, the scope of the study should be narrow enough that the sampled species will all be suitable potential hosts for the selected parasite (occurring within the parasite's geographical distribution and exhibiting some level of possible exposure). Yet even with good foresight and selection of possible hosts, these presence-absence vectors are surprisingly difficult to acquire. For example, if data from multiple studies are compiled to represent a suite of known host-parasite associations, such data are usually strongly susceptible to bias. This is because such databases typically contain presence-only records. For host specificity inferences beyond simple diversity metrics of the observed host species, the absence records (representing species not found to be host after a reasonable sampling effort) are just as important as presence records and should be included where possible. An option to make presence-only data accessible to analysis could be the utilisation of pseudo presence-absence data, in which infected host species are recorded as 'viable' and uninfected species (i.e. those species present in a pool of potential host species but not recorded to be infected) as 'non-viable' hosts.

Without detailed information on sampling efforts such as the number of host individuals screened for a parasite, there is uncertainty whether parasites are truly absent from a host species that is reported to be uninfected, challenging the estimate of host range [106, 107]. Such absences can represent 'false zeros' (missing observations of interactions) when small sample sizes and a naturally low parasite prevalence result in limited detection probability. A simple proxy of sampling bias could be a measure of research effort, such as the number of scientific publications linked to a particular potential host species (see e.g. [99]). However, conservative interpretation is warranted as indices of research effort are only coarse proxies of the true underlying sampling bias (i.e. the number of publications does not necessarily reflect the true sampling efforts of how many host individuals have been surveyed for a parasite).

Preferably, individual-level data (i.e. detailed data on the number of individuals examined and infected) will be available so that biological patterns and processes can be distinguished from sampling bias arising from unequal and small sample sizes [83, 85, 108]. If detailed information from empirical field surveillances (such as the number of infected and uninfected host individuals captured) are available, the prevalence of parasites in different sympatric host species can be estimated. If combined with further information on host species occurrence and density (which are often available or can be estimated from trap or survey data), such estimates provide valuable information on the relative importance of different host species as parasite reservoirs. These relative importances can be used to weight the contributions of different host species to a parasite's realized host specificity, aligning to the concept that host species may have different reservoir capacities. Incorporating measures on host presence and abundance might be of particular relevance if host abundances are subject to strong fluctuations [13, 109] and/or migration that drives the connectivity of geographically disparate host assemblages [48, 110].

For parasites with complex life cycles, it can also be important to consider details of parasite life histories. For some helminths, for example, different sets of host species are utilised to complete different parts of the life cycle (i.e. predatory carnivorous species that serve as definite host versus herbivorous species that serve as intermediate hosts). In addition, detailed molecular data can provide valuable insight into whether different sympatric host species share the same strains or populations of a parasite [111], eventually narrowing down the pool of host species relevant for analysis.

Table 1. Overview of selected components and methods to define host specificity.

Method	**Methodological approach**	**Example/Reference**
Number of host species infected	Count of the number of infected host species. This basic count ignores host species attributes such as phylogenetic or ecological relationships.	[112]
Diversity indices capturing variation in host community composition (e.g. Shannon-Wiener, phylogenetic diversity, UniFrac)	Diversity measures based on the abundance and/or attributes attributed to the range of observed host species (i.e. phylogenetic diversity).	[5], [113]
Geographic specificity and host range turnover (β-diversity)	Measures of the dissimilarity of a parasite's host ranges in different regions, resembling β-diversity measures.	[114], [17]
Distance-based phylogenetic and/or functional specificity	Measures of the distances between pairs of host species in terms of phylogenetic or functional relationships. Distance measures can be weighted by prevalence to give greater weight to commonly infected host species.	[115], [15]
Network indices of specialization (d')	Calculated from bipartite host-parasite interaction networks, these indices measure of a parasite's interactions with a range of	[76]

	potential host species (i.e. the sampled host species pool), weighted relative to the host interactions displayed by other parasites in the community.	
Degree of matching between host and parasite phylogenies	Measures of the matching between host and parasite phylogenies, used for depicting community-level patterns of possible co-evolution. Specificity inferences are drawn based on how tightly parasite evolution is linked to host evolution.	[116]
Host competence heterogeneity	The spread of parasites through host assemblages can be largely determined by their variation in potential hosts' competence and reservoir potential. Such measures have been rarely used to measure host specificity to date, but could be especially useful to express plasticity in host specificity.	[117], [118]

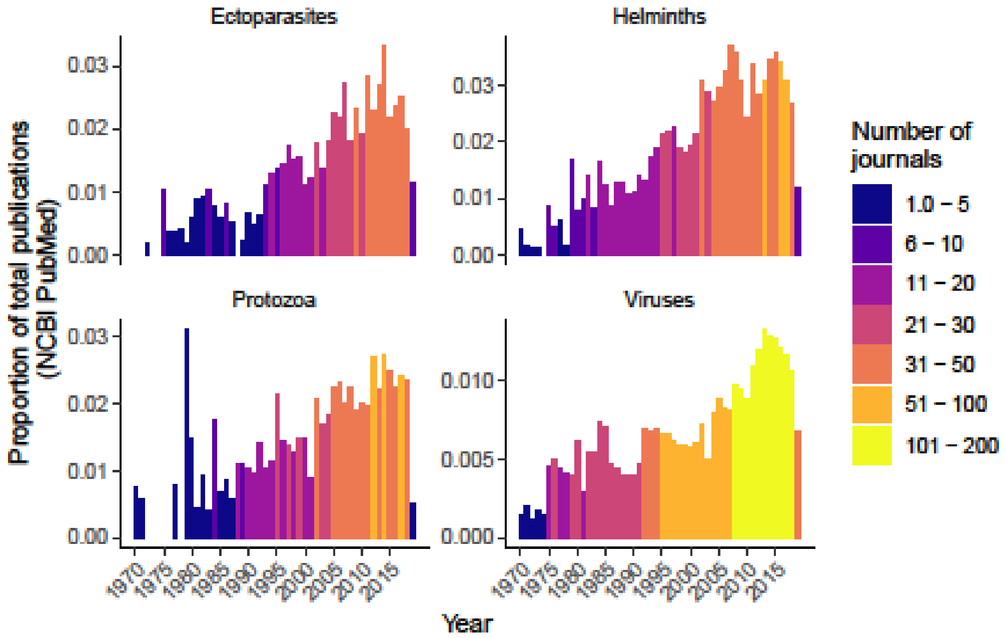

Figure 1. Rise in the proportion of peer-reviewed research articles mentioning ‘host specificity’ for select groups of parasites over time. Colours of bars represent the total number of unique peer-reviewed journals mentioning ‘host specificity’ for each parasite group in each year. Articles were accessed by searching the NCBI PubMed database on 2nd April 2019.

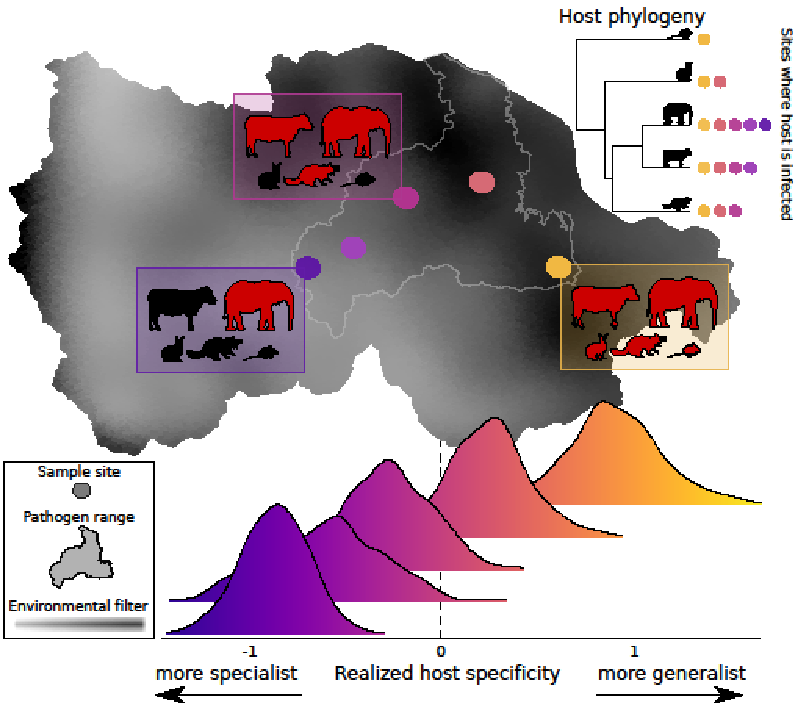

Figure 2. Illustration of how environmental filters across a parasite’s geographical range may impact the parasite’s realized host specificity. Hosts are sampled for the parasite across an environmental gradient that influences opportunity for the parasite to interact with each potential host species. Density plots depict the probabilities that observed host pairwise phylogenetic distances differ from those expected (representing the entire host pool that occurs at a given location) for each site. More negative measures (darker purple tones) indicate a parasite infects hosts that are more closely related than expected, indicating specialism; more positive measures (warmer yellow tones) indicate generalism.