



Expanding host specificity and pathogen sharing beyond viruses

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Most emerging pathogens of humans can infect multiple host species (Woolhouse & Gowtage-Sequeria, 2005). This simple fact has motivated multiple large-scale, comparative analyses of the drivers of pathogen sharing and zoonotic pathogen richness among hosts as well as the factors determining the zoonotic potential of pathogens themselves. However, most of this work focuses on viruses, limiting a broader understanding of how host range varies within and between pathogen groups. In this issue of *Molecular Ecology*, Shaw et al. (2020) compile a comprehensive data set of host–pathogen associations across viruses and bacteria and test whether previous patterns observed in the former occur in the latter. They find most viruses and bacteria are specialists, and viruses are more likely to be generalists; however, generalist bacteria encompass multiple host orders, whereas viral sharing occurs more within host orders. Lastly, the authors demonstrate that many factors previously identified as predictors of zoonotic richness for viruses occur for bacteria and that host phylogenetic similarity is a primary determinant of cross-species transmission. However, pathogen sharing with humans was more common and more weakly related to phylogenetic distance to *Homo sapiens* for bacteria compared to viruses, suggesting the former could pose greater spillover risks across host orders. This work represents a key advance in our understanding of host specificity and pathogen sharing beyond viruses.

KEYWORDS

cross-species transmission, disease ecology, host range, infectious disease, phylogeography, zoonosis

Many pathogens exact substantial public health and agricultural burdens, including avian influenza viruses, henipaviruses, coronaviruses, flaviviruses and lyssaviruses. This fact has warranted various analyses into the factors that shape the zoonotic potential of viruses and their patterns of cross-species transmission. For example, RNA viruses and those transmitted by arthropod vectors are more likely to infect humans (Olival et al., 2017), and host taxa such as rodents and bats generally harbour more zoonotic viruses by nature of being more speciose than other orders of mammals or birds (Mollentze & Streicker, 2020). Cross-species transmission of viruses is further

structured by seemingly general phylogeographic rules, such that more phylogenetically similar host species and those with greater geographic overlap are more likely to share viruses (Albery, Eskew, Ross, & Olival, 2020).

However, despite the enduring focus on virus ecology, more zoonoses are caused by bacteria than any other pathogen group (Han, Kramer, & Drake, 2016). To develop a more comprehensive understanding of zoonotic risk in bacteria, greater attention should be paid to whether the general patterns in zoonotic potential, pathogen richness and pathogen sharing observed for viruses persist for bacterial

pathogens (Becker et al., 2020). In particular, theory suggests that high levels of phenotypic plasticity, low evolutionary rates and recombination ability typical of bacteria should reduce their propensity to specialize, which may generate distinct pathogen sharing patterns from viruses (Bonneaud, Weinert, & Kuijper, 2019).

To undertake such a comparison, Shaw et al. (2020) combined an exhaustive literature search, with cross-validation from other large-scale data sets, to compile 12,212 interactions between 2,656 vertebrate hosts and 2,595 viral and bacterial pathogens. Although multi-host pathogens have generally been considered common and widespread (Cleaveland, Laurenson, & Taylor, 2001), this new analysis instead demonstrates that half of all viruses and bacteria are specialized on their hosts (Figure 1). Bacterial pathogens as a whole were more likely to be specialists than viruses, which is surprising given theoretical models that predict novel bacterial infections may be more prone to result in transient spillovers or increased host ranges than host shifts (Bonneaud et al., 2019).

Although bacteria were more likely to specialize on a single host species, generalist viruses tended to infect multiple host species in the same family or order (Figure 1). When measuring host range, past work has often used broad taxonomic groupings; however, the field is increasingly using quantitative measures of host

phylogenetic distance (Albery et al., 2020; Olival et al., 2017). Here, the authors extend previous approaches using the mitochondrial gene cytochrome *b* to build a comprehensive phylogeny using nine mitochondrial genes, providing a more precise estimate of genetic similarity between host species. Using this revised measure of host breadth, the authors further show that generalist viruses have a more restricted host range than generalist bacteria, which suggests the latter may be able to infect a broader diversity of hosts. Given these results, one especially important question for future research is whether host cell receptors for bacterial pathogens are more phylogenetically conserved than those for viruses.

Trait-based analyses also revealed interesting comparisons between viral and bacterial zoonoses. Although viruses were more likely to be transmitted by arthropod vectors, vector-borne transmission was associated with greater generalism and zoonotic potential for both viruses and bacteria. Such results support prior findings for viruses (Kreuder Johnson et al., 2015; Olival et al., 2017) but extend these claims for bacteria, suggesting consistent effects across pathogens. Phylogenetic host breadth also had positive effects on the propensity for both viruses and bacteria to be zoonotic, and well-studied pathogens were broadly more likely to be zoonotic. For bacteria in particular, motile and aerobic species were more likely to be generalists, which suggests traits that facilitate survival both inside and outside of hosts can expand host breadth.

From the host perspective, Shaw et al. (2020) show that viral and bacterial pathogen richness were positively correlated, suggesting animals that harbour more zoonotic viruses are also more likely to harbour more zoonotic bacteria. As with the pathogen trait analyses, study effort was also a consistent predictor of zoonotic richness for both viruses and bacteria. Yet although species geographic range size and sympatry with other mammals were strong predictors for both pathogens, they had opposing effects on the richness of viruses and bacteria. Larger geographic ranges and greater sympatry were associated with greater viral richness but lower bacterial richness. Further, pathogen sharing with humans was more common and weakly related to phylogenetic distance to *Homo sapiens* for bacteria than viruses, suggesting the former could pose greater spillover risks across host orders. Although these analyses confirm that host phylogeny is a key driver of cross-species transmission risk (Olival et al., 2017), they also suggest intriguing differences in pathogen sharing between viruses and bacteria. This data set could accordingly open doors to assess how host phylogeny and geographic range overlap interact to affect cross-species transmission of bacterial pathogens (Albery et al., 2020) and how other aspects of host ecological similarity broadly affect bacterial sharing (McKee et al., 2019).

Both viral and bacterial pathogens are responsible for substantial infectious disease burdens in humans, domestic animals and wildlife (Han et al., 2016). Here, Shaw et al. (2020) illuminate key similarities in the host range and zoonotic potential of these two pathogens, with particular attention to the importance of robustly characterizing phylogenetic host breadth and how host phylogenetic distance

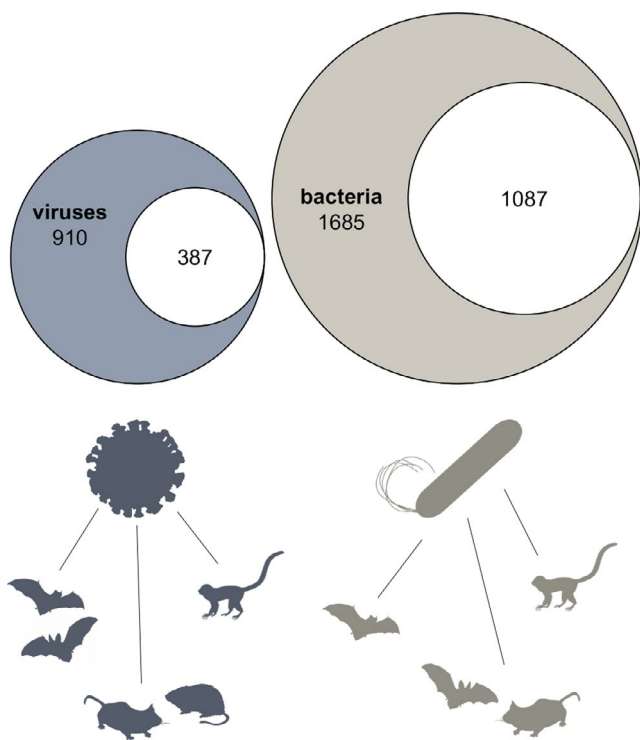


FIGURE 1 Approximately half of all pathogens are specialists (white), and bacterial pathogens are more likely to specialize and infect a single host species (64.5%) compared to viruses (42.5%). However, generalist viruses are more likely to infect multiple species in the same order, while generalist bacteria have greater phylogenetic host breadth. Silhouettes show illustrative hosts within mammal orders (Chiroptera, Rodentia, Primates) using images provided by PhyloPic

is a key determinant of cross-species transmission across pathogens. More broadly, the authors provide a valuable resource for future comparative research, which will be critical to understand the differences between viral and bacterial zoonoses and their disease risk.

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How to cite this article: Becker DJ, Albery GF. Expanding host specificity and pathogen sharing beyond viruses. *Mol Ecol*. 2020;29:3170–3172. <https://doi.org/10.1111/mec.15573>