Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2016, **85,** 621–623 doi: 10.1111/1365-2656.12443

FORUM

Are generalist parasites being lost from their hosts?

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Key-words: asymmetry of interaction, biodiversity loss, co-extinctions, host range, host specificity, IUCN

In a recent work, Farrell *et al*. (2015) investigated patterns of host–parasite co-extinctions in terrestrial carnivores and ungulates and found that threatened ungulates harbour a higher proportion of single-host parasites than not-threatened ungulates. Although we think that this paper gives an important contribution to the study of host–parasite co-extinctions, we have various concerns about the Authors' main conclusion that the observed patterns result from a loss of generalist parasites from threatened hosts. In particular, we see some potential problems in the underlying assumption that the proportion of single- and multihost parasites should be comparable between different hosts.

In host–parasite networks, the 'asymmetry of interactions' defines a situation where specialized parasites tend to interact with hosts with high parasite richness, whereas hosts with low parasite richness tend to interact mainly with generalist parasites (Vázquez *et al*. 2005). Notably, this pattern, which is common in many other contexts of species interactions such as in plant pollinator networks (see, e.g. Vázquez & Aizen 2004), can be also observed using the data collected in the Global Mammal Parasite Data base (Nunn & Altizer 2005), which is one of the main sources used by Farrell *et al*. (2015). Figure 1 shows the relationship between the maximum specificity of the parasites using a certain host species and the parasite richness on that host species for both carnivores and ungulates. Box plots in the figure correspond to different classes of hosts identified on the basis of the maximum specificity of their parasites. For example, the first box plot in Fig. 1(a) provides information on parasite species richness of all carnivores whose most specific parasite uses just one host. It is apparent that specific parasites tend to use hosts harbouring many parasites, while species-poor parasitofaunas are often composed by generalist parasites. The number of parasite species found on a host and the minimum host range of its parasites show strong negative correlations for both ungulates (Spearman rank correlation coefficient, $r_s = -0{\cdot}59$, $n = 95$) and carnivores ($r_s = -0{\cdot}62$, $n = 117$; $P < 0{\cdot}00001$ in both cases). This means that the smaller is the set of parasites using a given species, the lower the probability for some of them to be highly host specific. Since parasite richness on hosts could result from host persistence and geographical range (Guégan & Kennedy 1993; Kamiya *et al*. 2014; Strona & Fattorini 2014), the composition of the classes of hosts corresponding to the different box plots is likely not independent from host vulnerability (with hosts harbouring many parasites being likely less vulnerable than hosts harbouring few parasites). This pattern contrasts with Farrell *et al*.'s (2015) claim that there is a reduction in the proportion of multihost parasites on threatened hosts. Conversely, it suggests that specific parasites tend to use hosts with low vulnerability and, more importantly, it indicates that the distribution of parasite specificity among hosts is not homogeneous.

Therefore, the expectation of a comparable proportion of specialist and generalist parasites in different hosts would suggest the existence of assembling and/or disassembling processes (such as co-extinction events, as suggested by Farrell *et al*. 2015) as determinants of asymmetric patterns of interactions. Yet, stochasticity in species encounters provides a more parsimonious explanation to the observed structure of host–parasite networks, that is hosts harbouring many parasites will have more chances to harbour specialists as a simple result of passive sampling.

Other concerns about results and interpretations by Farrell *et al*. (2015) derive from the choice of categorizing parasites into multi- and single host. According to the Authors' criterion, for example, many parasites using a couple of phylogenetically closely related hosts would be considered as much generalists as parasites capable of infecting several species belonging to very different

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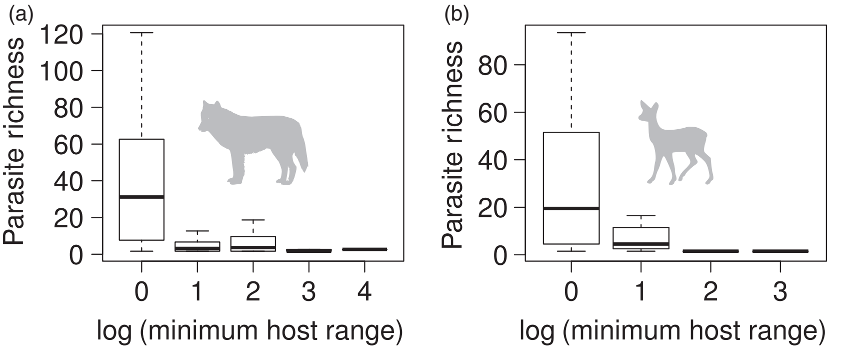

Fig. 1. Relationships between the maximum specificity of the parasites using a certain host species and the parasite richness on that host species in carnivores (a) and ungulates (b). Box plot panels report first and third quartiles (boxes), range values (whiskers) and median values (horizontal lines) of parasite species richness of different host classes identified on the basis of the minimum host range of their parasites.

lineages, which is in contrast with the evolutionary meaning and the ecological implications of host specificity (Poulin, Krasnov & Mouillot 2011).

However, the phylogenetic conservatism of host parasite specificity (Mouillot *et al.* 2006) offers a simple benchmark to test the soundness of Farrell *et al.*'s (2015) approach. An analysis conducted again using the Global Mammal Parasite Data base reveals that, in both ungulates and carnivores, parasites using two hosts are taxonomically more closely related to (i.e. share more genera with) single-host parasites than to multihost parasites. In particular, more than 60% of the genera of parasites that use two hosts (64% in the ungulates and 63% in carnivores, respectively) are found in the corresponding set of single-host parasites, but two-host parasites share only 36% of their genera (in both ungulate and carnivore datasets) with more generalist parasites. This may suggest biases in Farrell *et al.*'s (2015) host-specificity classification.

A last major point that requires attention is the importance of the approach used to quantify species extinction risk. Host–parasite networks have been assembled over evolutionary time by mechanisms that could be completely unrelated to the ongoing disassembling processes driven by human activities. A vulnerability measure accounting for both co-evolutionary and current ecological processes is hard to define. Strona, Galli & Fattorini (2013) used a measure based on life-history traits (Cheung, Pitcher & Pauly 2005) to investigate the outcomes of host–parasite co-evolution. Their choice was motivated by the fact that life-history traits could reflect species 'intrinsic' vulnerability (i.e. species fitness in an evolutionary perspective) more than a value of current extinction risk derived by species abundance and distribution range (cf. Pullin 2002; Dickman, Pimm & Cardillo 2007; Pearson *et al.* 2014). Conversely, with the only exception of female body mass, the measures used by Farrell *et al.* (2015), that is IUCN categories, geographical range and population density, are mainly the result of human influence (Davies *et al.* 2006) and climate change (Thomas *et al.* 2004), and thus representative of species extinction risk in the present context. These two approaches (life-history traits vs current extinction risk) to assess species vulnerability may lead to contrasting results (see Strona 2014), and choosing one over another needs to be clearly justified. Moreover, the lack of consistency between intrinsic and current species vulnerability may highlight conceptual drawbacks in trying to integrate co-evolutionary information (such as host specificity) with current trends of extinction.

In conclusion, even if we cannot exclude that co-extinction processes have accelerated in recent time, there is no convincing evidence to the idea that the relative abundance of specialist parasites on currently threatened hosts is a result of the extinction of generalist parasites on those hosts. Although the absence of evidence is not evidence of absence, we feel more cautious in availing the conservative explanation that present patterns could have resulted from the co-evolutionary mechanisms discussed above and reflected in the commonness of asymmetrical patterns of interactions. The potential methodological issues we highlighted in the previous paragraphs, and the inconsistency observed by Farrell *et al.* (2015) between ungulates and carnivores (for which 'no significant effect of host threat status on the proportion of single-host parasites, the richness of single-host or the richness of multi-host parasites' was found), urge caution in drawing conclusions.

In our opinion, co-extinctions should be regarded as fundamental co-evolutionary events promoting species turnover, prior than a consequence of human-induced biodiversity loss. We do recognize that focusing on current scenarios is key to biodiversity conservation, but we also think that predicting future trends could be harder (and perhaps less fruitful) than trying to get a better grasp on the past (Wood *et al.* 2013). Farrell *et al.* (2015) have had the great merit of emphasizing that generalist parasites could be currently at a higher risk than expected from the solely consideration of their host specificity. In particular, as they pointed out, fragmentation could severely threaten generalist parasites due to a reduction in the size of host populations and in cross-species contacts. A better understanding of this aspect would be extremely important for future conservation studies, but, again, it would require a more in depth comprehension of the co-evolutionary mechanisms regulating the trade-offs between the probability of a parasite to encounter a suitable host, and the efficiency in using it.

More in general, we feel that searching for universal patterns and processes by trying to integrate parasite specificity and current, human-induced ecosystem threads could be misleading. The black rhino is critically endangered (IUCN 2014), and so it is its stomach botfly *Gyrostigma rhinocerontis* Hope, 1840 (Stringer & Linklater 2014). But, how would it make sense to relate rhino poaching (Brown & Layton 2001) with the evolution of specialization in the botfly?

Data accessibility

Data have not been archived because this article does not contain data.

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Received 29 June 2015; accepted 20 August 2015
Handling Editor: Andy Fenton