

FORUM

Response to Strona & Fattorini: are generalist parasites being lost from their hosts?

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Key-words: asymmetry of interactions, coextinction, conservation, host range, host specificity, infectious disease, macroecology, parasite richness

Introduction

Strona & Fattorini (2015) raise concerns about the conclusions of a recent analysis by Farrell *et al.* (2015) on patterns of host–parasite associations among free-living carnivores and terrestrial ungulates. Contrary to expectations from coextinction theory, our study found ungulate species threatened with extinction are associated with a higher proportion of single-host parasites compared to non-threatened species. The increased proportion of single-host parasites in threatened ungulates appears to result from decreased richness of multi-host parasites as we do not observe significant differences in the richness of single-host parasites between threatened and non-threatened ungulates. We suggest one explanation may be that multi-host parasites are being lost from declining ungulate populations due to decreased cross-species contact as species' ranges contract. We offer the hypothesis that strong Allee effects and selective pressures to maintain minimum group sizes in these species facilitate the transmission of single-host parasites within host groups, even while the species as a whole is in decline.

We appreciate the thoughtful commentary by Strona & Fattorini and are pleased that our recent work is sparking debate regarding the ecological mechanisms behind our unexpected results. However, Strona & Fattorini raise three main concerns about our analysis:

- 1 Our results may be explained by non-random distributions of specialist and generalist parasites (Vazquez *et al.* 2005) leading to hosts that harbour greater numbers of parasite species being more likely to harbour specialist parasites.
- 2 Analysing parasite host specificity as a binary variable (single-host vs. multi-host) may bias our interpretations as this classification may not reflect the evolutionary and ecological implications of host specificity.

- 3 The inclusion of both host life-history traits and measures of current extinction risk as predictors in our analyses was not properly justified and could lead to contrasting results if we were attempting to explain the evolution of parasite specialization.

We believe these criticisms arise from a few simple misunderstandings; we address each point in detail below.

Non-random distributions of specialist and generalist parasites

In various species interaction networks, non-random distributions of specialist and generalist affiliates have been observed in which specialists interact more often with highly connected species in the network (Bascompte & Jordano 2003; Ings *et al.* 2009). This pattern, reflecting an 'asymmetry of interactions', has been shown for macro-parasites of Canadian freshwater fish and of small mammals in Siberia (Vazquez *et al.* 2005).

Strona & Fattorini suggest that hosts harbouring many parasites should also be associated with a greater proportion of specialist parasites. Under their assumptions, threatened hosts are associated with fewer parasite species and, due to a process of passive sampling, will be associated with fewer specialist parasites. Our results do not match these predictions. We find threatened ungulates are associated with a higher proportion of specialist parasites. The bias described by Strona & Fattorini is thus in the opposite direction of our findings, and their proposed mechanism is unable to explain our results. This may suggest that our finding is even more striking than we initially presented, or that their assumption of an asymmetry of interactions is not supported by the data.

We agree that threatened hosts should be associated with fewer parasite species, and this has been found in previous comparative studies (Altizer, Nunn & Lindenfors 2007) and again in our study. However, Nunn & Altizer (2005) did not show any pattern of asymmetry of interac-

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tions in their original description of the data, and we additionally find no evidence of this pattern or the suggested mechanism of assembly.

Strona & Fattorini purport to show a pattern of asymmetric interactions in our data by depicting the relationship between minimum host range of parasites that infect a given host and parasite richness on that host. Host range refers to the number of host species a parasite infects, and the minimum host range is defined as the smallest observed value of host range for all parasites associated with a particular host species. Minimum host range is a property of the suite of parasites that are associated with a particular host species and as such, each data point in Strona & Fattorini's original figures represents the parasite assemblage of a single-host species. We take issue with their analysis for two reasons.

First, Strona & Fattorini disguise important variation in the data by rounding the logged values of minimum host range and then using boxplots to visualize the relationship with parasite richness. We re-plotted this relationship using a scatterplot (Fig. 1a). We find considerable variability in the data and show that single-host parasites are not only relegated to parasite-rich hosts, and parasite-poor hosts do not interact mainly with generalist parasites.

Secondly, we are concerned that Strona & Fattorini are drawing conclusions about the central tendency of a distribution by investigating the behaviour of its minimum value (i.e. using minimum host range). If we visualize the same relationship between host range and parasite richness, but use maximum rather than minimum host range, we can see that hosts with greater numbers of parasite species also harbour additional generalist parasites (Fig. 1b). However, assessing whether networks are characterized by an asymmetry of interactions typically involves examining average host range across parasite assemblages (e.g. [Vazquez et al. 2005](#); [Poulin 2007](#)), which takes into account the host range of all parasites in the assemblage. When visualizing the relationship using mean

host range of all parasites associated with a particular host, we find no trend for hosts with high parasite richness to harbour a greater proportion of specialist parasites (Fig. 1c). This indicates that drawing conclusions on the distribution of host ranges in a parasite assemblage using only the minimum observed value, as Strona & Fattorini have done, can be misleading. Unfortunately, this biased description of host–parasite networks is further propagated in Strona (2015).

While we agree that an asymmetry of interactions in host–parasite networks could be an exciting pattern to explore, and may hint at consistent properties similar to those of mutualistic networks, it is important to re-iterate that networks with asymmetric interactions are not found across all ecosystems ([Poulin 2007](#); [Campaio et al. 2015](#)). The application of network analysis to host–parasite associations is in its early stages ([Poulin 2010](#)), and additional work is needed to determine the extent to which properties of host–parasite networks generalize, and the causal mechanisms responsible ([Vazquez et al. 2005](#)).

Defining parasite host specificity

We appreciate that there are many ways of quantifying host specificity depending on the question of interest and information at hand ([Poulin, Krasnov & Mouillot 2011](#)), and we previously explained in [Farrell et al. \(2015\)](#) our rationale for using the single-host/multi-host distinction. Pragmatically, it is much easier to make inference about extinction dynamics using this framework compared to continuous measures of host specificity. For example, the extinction of a host will result in the extinction of all host-specific parasites, but when parasites are found on two or more hosts (which may differ in threat status), it is much harder to make predictions on the extinction risk of the parasite. In this context, we suggest that using the single-host/multi-host distinction allows us to make more explicit predictions, and we can see no reason why this should bias our results.

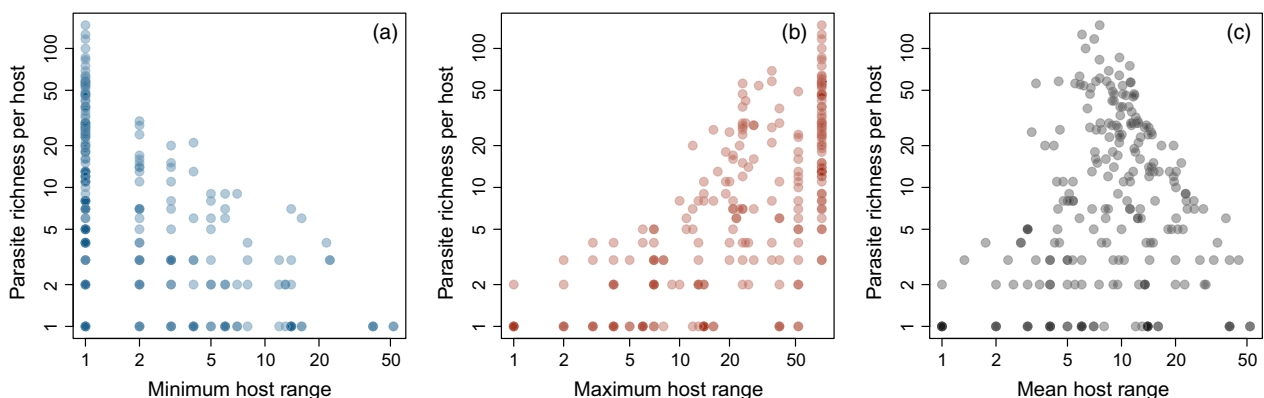


Fig. 1. Relationships between the minimum (a), maximum (b) and mean (c) host range of parasites associated with a particular host species, and the parasite richness of that host species (data from [Farrell et al. 2015](#)). Transparency of points is set to $\alpha = 0.3$ to allow visualization of overlapping data.

Life-history traits vs. extinction risk

In our study, we investigated how extinction processes resulting from human influence change host–parasite associations. It is possible that Strona & Fattorini misunderstood the goals of our analysis as it was not our intention to explain the evolutionary drivers of parasite specificity. We recognize that there are many host life-history traits that influence parasite richness and the potential to harbour both specialist and generalist parasites (Ezenwa *et al.* 2006; Lindenfors *et al.* 2007; Kamiya *et al.* 2014). In our analysis, we purposely included key host traits in an attempt to control for these intrinsic characters and quantify the independent effect of external threat processes captured by the IUCN categories. While our original intention was not to comment on the effect of these life-history characters (but rather to statistically control for them), it is encouraging that all significant predictors were in the expected positive direction of increasing parasite richness (body mass, range size, population density).

Conclusion

We are thankful for the detailed commentary and discussion by Strona & Fattorini, and hope our reply helps resolve any misunderstandings that may have been highlighted in their response. Our analysis found results that were counterintuitive to our initial hypotheses, and from these, we generated new hypotheses based on the comparative biologies of the host groups studied. By nature of being non-experimental, macroecology is founded on the inductive generation of hypotheses followed by the testing of these hypotheses with alternative data (Brown & Maurer 1989; Brown 1995). We hope that hypotheses about the interaction of sociality and extinction processes generated by our study will prompt discussion and further investigation in the fields of coextinction, conservation and infectious disease management.

The impact of human-induced host extinction on parasites undoubtedly has ramifications for parasite coextinction. A need for a better understanding of coextinction is highlighted by the example of the rhinoceros stomach botfly *Gyrostigma rhinoceronitis* (for synonyms and attribution see Evenhuis 2012), also discussed by Strona & Fattorini. The botfly is assumed to be at risk of extinction because one of its hosts, the black rhinoceros (*Diceros bicornis*), is critically endangered (Colwell, Dunn & Harris 2012). However, this botfly is known to use another host species, the white rhinoceros (*Ceratotherium simum*) (Knapp, Horak & Kreecek 1997; Colwell, Dunn & Harris 2012), which is currently assessed as being near threatened (International Union for the Conservation of Nature 2014). If the black rhinoceros were to go extinct, the stomach botfly could still persist as it has an alternative host, but we would then consider it to be host specific. The loss of the black rhinoceros would undoubtedly change our perception of host speci-

ficity and risk of coextinction for the rhinoceros stomach botfly, and it is the potential for changes in the specificity and structure of host–parasite systems resulting from host decline that we hope to highlight with our work. Perhaps the perceived shift in host specificity of parasites as their alternative hosts decline to extinction may also be a possible explanation for our results, and potentially a promising area for future research.

Data accessibility

Data available from the Global Mammal Parasite Database <http://www.mammalparasites.org/> (Huang *et al.* 2015).

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Received 15 September 2015; accepted 30 October 2015

Handling Editor: Andy Fenton