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RESPONSE

Investigating community disease dynamics can lead to more effective conservation efforts

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Wildlife disease ecology focuses on understanding the effects of disease on a species or community, and aiding the development of feasible, appropriate and effective management techniques for threatened species. In the *Bd*-amphibian disease system, much of the research effort has focused on understanding disease dynamics in susceptible, declining species, and less on understanding the role of disease in sympatric reservoir hosts. Reservoir hosts can have a major impact on disease dynamics in multispecies communities, and need to be considered as part of conservation management aimed at reducing mortality in declining species. Our study was a collaboration of

government and university researchers, and investigated the competence of the common eastern froglet, *Crinia signifera*, as a reservoir host. The role of *C. signifera* in contributing to declines in threatened sympatric species has long been suspected, but remained unquantified.

We thank all commenters for contributing to the discussion of our paper, Brannelly *et al*. (2017), and addressing the importance of studying reservoir hosts, for both understanding disease dynamics, and assessing their relevance to conservation management. All three commentaries mentioned that disease dynamics are context specific and that reservoir hosts may vary in importance. Bower (2018) drew attention to the fact that our high elevation study system has low amphibian richness where one species like *C. signifera* could be key in maintaining and driving disease within the system. However, other amphibian communities may have more complex inter- and intra-specific species interactions, and any single reservoir host species might have less effect on *Bd* dynamics (Bower, 2018). Similarly, both Pasmans *et al*. (2018) and Bower (2018) mentioned that reservoir hosts might not be as important in the *Batrachochytrium salamandrivorans*, *Bsal*, system because the pathogen is more stable in the environment. This highlights the broader fact that disease dynamics are system-dependent, and that understanding dynamics in individual species, and the community as a whole, will help inform management decisions.

Pasmans *et al*. (2018) drew attention to the potential for underestimated fitness costs associated with *Bd* infection in reservoir hosts that we did not directly test in our study. We focused on mortality and body condition changes as a result of *Bd* infection, and not a full range of fitness costs that could be associated with infection. Indeed it is likely that *Bd* infection has some sublethal effects of disease that do not result in direct mortality, and has been shown to decrease jumping ability, cause weight loss and change reproductive effort (Chatfield et al., 2013; Cheatsazan et al., 2013). Such sublethal effects could have population level impacts as Pasmans *et al*. (2018) suggest, and collecting such data is important for estimating the true impact of *Bd* infections on less susceptible hosts. However, sublethal effects of infection are likely more subtle than changes in body

condition or increased mortality in *C. signifera*, and its competency as a reservoir host of *Bd* infection remains strongly supported by our findings.

We agree with Garner's (2018) call for caution in the interpretation of our population age structure results, as we lack a contrast to the age structure of naïve populations. However, despite this limitation, our results support our conclusion that the presence of individuals between two and six years old indicates that even in populations with high *Bd* infection rates, many individuals survive for multiple years. This finding is in direct contrast to the declining *Litoria verreauxii alpina*, a sympatric species where *Bd*-infection caused extreme age structure truncation, with most adults dying after their first breeding season, but aligns with the complex age structure of adults in *Bd*-naïve populations (Scheele *et al*., 2016). Therefore, our results suggest that even with rampant infection *C. signifera* are surviving across years.

In our study we did not quantify the inter- and intra-specific host transmission coefficients, which are important for modeling disease dynamics, as highlighted by Garner (2018). While we agree that close geographic proximity or shared habitat do not always predict high interspecific pathogen transmission, we note that in our study system, *C. signifera* directly shares habitat with at least four declining species, and are often in close physical proximity. For example, *C. signifera* are regularly found sharing terrestrial refuges, in aquatic breeding habitat, and observed in attempted amplexus with other susceptible species. While mechanisms of transmission of this pathogen are poorly understood (as Pasmans *et al*. 2018 points out), physical contact is one mode of transmission and infection levels often increase during the breeding season when rates of physical contact increase (Kinney *et al*., 2011; Brannelly *et al*., 2015). Additionally, previous research in our study systems has demonstrated that infection prevalence of *Bd* is reduced dramatically in the critically endangered *Pseudophryne pengilleyi* when *C. signifera* is absent (Scheele *et al*., 2017).

Our study was born through a series of observations where reservoir host competence was hypothesized, but not explicitly and empirically tested. Our results stress the

importance of investigating the role of reservoir hosts in the context of conserving species experiencing ongoing declines associated with chytridiomycosis. This is particularly important when considering potential candidate sites for reintroductions, and the information presented in our paper is already being considered in conservation planning for threatened anurans in southeastern Australia. Experimental management to control the effects of reservoir hosts is one way to collect the additional data and understanding that Garner (2018) and Pasmans *et al*. (2018) advocate. This is an efficient approach that enables urgent action based on current evidence, while updating our understanding. Additionally, funding for studies of *Bd* hosts of least conservation concern is difficult to obtain. Brannelly *et al*. (2017) was not specifically funded but rather incorporated into our other work on sympatric declining species. But more broadly, our research demonstrates the value of using a holistic approach, of both veterinary and biological techniques (Pasmans, Canessa, & Martel, 2018), when investigating the role of reservoir hosts in community disease dynamics. In agreement with the commentaries, our research highlights the sometimes underappreciated value of understanding disease dynamics in wildlife disease ecology, and demonstrates the importance of investigating the disease impacts of non-declining hosts in other chytridiomycosis threatened landscapes.

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