



Succinctus

Explaining parasite aggregation: more than one parasite species at a time



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ABSTRACT

Studies generally have neglected parasite-centric views in explorations of whether the oft-seen patterns of parasite aggregation are adaptive. Using simulation models, we explored the effects of aggregation on coinfection with hetero- or conspecific parasite species characterised by different mean abundances. Increasing aggregation increased the probability of conspecific co-occurrence for parasites with low mean abundances, and increased median numbers of conspecifics for all species. In comparison, increasing aggregation generally decreased the probability, intensity and diversity of heterospecific co-occurrence, irrespective of mean abundance. Researchers should weigh the respective costs and benefits of increasing co-occurrence with conspecifics and decreasing coinfection with heterospecifics in explaining aggregation.

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Aggregation of macroparasites within host populations is a general law of parasite ecology: the majority of hosts are infected with few or no parasites of a given species, whereas a small proportion of hosts are infected with many parasites (Crofton, 1971; Shaw and Dobson, 1995; Poulin, 2007a). Most proposed mechanisms generating this near-universal pattern fall into two broad categories: environmental heterogeneity and heterogeneity in host susceptibility. That is, aggregation arises principally from variation in the distribution of hosts or infective parasite stages across space or time, or is due to variation in the potential of hosts to attract, defend against, and/or provide resources to parasites (Wilson et al., 2002; Poulin, 2007b). Additional factors suggested to influence the degree of macroparasite aggregation include direct reproduction in or on hosts, and parasite accumulation with host age or with trophic level (Poulin, 2007b; Lester and McVinish, 2016).

Among those studies exploring the causes of macroparasite aggregation, few consider adaptive benefits of aggregation. However, parasite aggregation lends stability to systems wherein a host species is attacked by multiple parasite species (Dobson, 1985; Dobson and Roberts, 1994; Morand et al., 1999; Krasnov et al., 2006) and might therefore be adaptive by reducing fitness costs to parasites. Additionally, aggregation of single-species infective stages in the environment, a cause of parasite aggregation among hosts, might be a means of overwhelming host defenses upon host encounter (Morrill and Forbes, 2016). Whether these adaptive

explanations of parasite aggregation are generalizable, remains unknown. However, cases of infective stage clumping to overcome host defenses might be evident for only some parasite-host associations or, while beneficial, might not explain entirely the degree of aggregation observed. Thus, efforts should focus on adaptive explanations for parasite aggregation that consider the potential for interactions and selection from both conspecifics and heterospecifics, and which might be candidates for universal explanations.

Such explanations will require due consideration of how distributions are experienced by parasites. Parasite distributions are typically described from a host-centric perspective using measures such as prevalence, mean intensity and various indices of aggregation, all of which are useful for describing the potential for selection on hosts (and indirectly, potential selection on parasites). However, such measures provide less insight into the infection intensities experienced by average parasites. Whereas a host may have only a low probability of being infected by many parasites when loads are aggregated, parasite individuals in those few high-intensity infections experience a high proportion of the parasite population (Poulin, 2007b).

We used simulation models to address how parasite aggregation among hosts, relative to random distributions, affects the probability and the degree of co-occurrence, or the potential for interactions, with conspecifics and heterospecifics. That is, we explored the significance of parasite aggregation in terms of its potential for heterospecific interactions among parasites within infracommunities, building on earlier perspectives and rationales (Dobson and Roberts, 1994; Krasnov et al., 2006). We did so by

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considering conspecific and heterospecific co-occurrences separately. These questions are important insofar as host individuals are generally infected by multiple parasite taxa (Petney and Andrews, 1998). From the individual parasite species' perspective, we can ask: what are the consequences of aggregation on the probability and the intensity of coinfection with one or more heterospecifics? This question implicitly ignores the direction and magnitude of potential interactions and selection imposed by conspecifics, so it is also important to ask how these heterospecific patterns compare with co-occurrence of conspecifics.

In exploring this series of questions, we could assume first that co-occurring conspecifics show a low net cost from intraspecific competition, or show a net benefit from aggregation. This could occur even if the growth, fecundity and/or survival of parasites is negatively affected at high intensities of infection if aggregation also favours the overcoming of host defenses or favours mate finding and outbreeding, given that some degree of outbreeding is likely optimal even for species capable of self-fertilisation (Vázquez-Prieto et al., 2015). We could assume, secondly, that more heterospecifics per host have a greater negative effect on the fitness of hosts and the focal parasites that are infecting them, than do fewer parasite species and parasite individuals per host. While this is likely true for hosts, it need not always be the case for parasites as some parasite species might well facilitate others in nature (Ewing et al., 1982). However, beyond such intricate interactions, net negative effects attributable to coinfection by heterospecifics are expected due to other direct and negative parasite-parasite interactions (e.g. competition for similar host resources) or due to indirect interactions through debilitation of the host (e.g. eliciting cross-immunity).

Our model simulates four parasite species, each with a different mean abundance ($\mu = 1, 2, 5$ and 10), infecting a single host population. Coinfecting parasites do not interact; the presence of one parasite species does not change the probability or degree of infection by any additional species. Rather, 1000 hosts are randomly assigned parasites from each of these species based on negative binomial distributions, which as a rule fit well to macroparasite distributions (Shaw and Dobson, 1995; Poulin, 2007b). Parasite species distributions are similarly aggregated in each trial: the parameter k , which varies inversely with aggregation, was set across all four simulated distributions at either 0.1 (highly aggregated), 1.0 (moderately aggregated), or 10 (approximately random; convergence with a Poisson distribution occurs at $k > 8$ (Southwood and Henderson, 2000)). As such, we compared the more frequently observed natural patterns of aggregation with the rarer instance of parasite species being randomly distributed among hosts to test the effects of parasite distributions on species co-occurrences and overall measures of parasitism (Shaw and Dobson, 1995). All simulations were performed using R (v. 3.1.2; R Development Core Team, 2014. R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>).

In every trial, conspecific and heterospecific co-occurrence was assessed from the perspective of each of four focal parasite species. For each individual parasite of each species, we recorded the total number of heterospecifics coinfecting the same host, as well as the number of co-occurring conspecifics. For example, if a single host is infected by five *A* parasites, one *B* and one *C* parasite and no *D* parasites, then for the *A* parasite each of five individuals co-occurs with four conspecifics and two heterospecifics, whereas for each *B* and *C* parasite one individual co-occurs with six heterospecifics and no conspecifics. Probabilities and median numbers of co-occurring conspecifics and heterospecifics were tallied for each parasite and averaged over all parasites within species over 1000 runs of the model for each degree of aggregation. We could then assess, from the perspective of the parasite, whether a given level

of aggregation resulted in higher or lower numbers of co-infecting conspecifics and heterospecifics than others.

The results of our simulations demonstrated that effects of aggregation on coinfecting heterospecifics were much more consistent than its effects on coinfecting conspecifics. We started first with the effects of aggregation on conspecifics. Aggregation did not have a pronounced effect on the mean probability of coinfection with conspecifics for parasite species with a high mean abundance

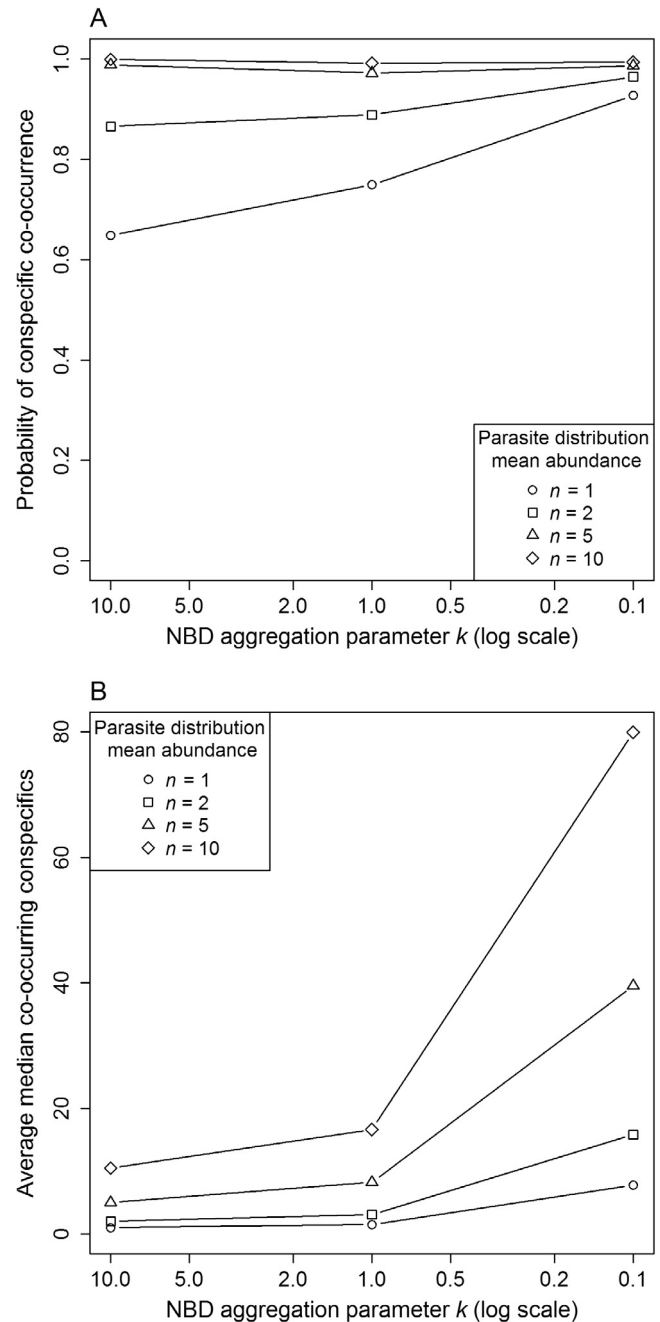


Fig. 1. Parasite perspective of the effect of macroparasite aggregation on conspecific co-occurrence for four species of macroparasites of varying mean abundances. Macroparasite distributions are simulated from negative binomial distributions (NBDs), with mean abundances ranging from $n = 1$ – 10 and aggregation parameters (k ; inversely related to degree of aggregation) ranging from 0.1 to 10. (A) Probability of focal parasite co-occurrence with conspecifics. (B) Average median number of co-occurring conspecifics. Results are averaged over 1000 trials. Bootstrap 95% confidence intervals were small enough to fit within the plotted symbols; vertical non-overlap of points therefore indicates significant differences at $\alpha = 0.05$.

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