

## Interactive versus isolationist helminth communities reconsidered

The community ecology of gastrointestinal helminths of vertebrates has recently received considerable attention<sup>1,2</sup>. Sousa's *TREE* review<sup>2</sup> concentrated largely on the 'interactive-isolationist' hypothesis originally formulated by Holmes and Price<sup>3</sup>. Sousa<sup>2</sup> showed that the helminth communities in vertebrate definitive hosts often do not fit the prediction of the hypothesis. Without additional data and improved methods, however, it is premature to assess reliably the role of negative interactions in helminths of vertebrates.

Specifically, my concern is that: (1) the identification of parasite communities either as interactive or isolationist is often based on tests that do not address the critical problem (i.e. the presence of negative interspecific interactions); and (2) tests used for detecting interspecific interactions often do not consider the possibility of positive interactions.

Helminth communities listed by Sousa<sup>2</sup> were classified as 'interactive' if one or more pairs of species showed negative interspecific relationships in co-occurrence, abundance, intestinal position or intestinal overlap. The classification of communities as 'isolationist' was, however, often based on different criteria. The predominance of independent or positive co-occurrence patterns and species numbers per host fitting the Poisson were used as evidence of non-interactive structure, even if the presence of negative interactions was not tested for. However, most of the significant co-occurrence patterns observed in natural populations are because of processes other than direct interspecific interactions, for example, similarities and differences in transmission pathways and various sampling heterogeneities. Furthermore, even strong interactions may remain unnoticed, because the dependence between various pairs of species obscures these associations and produces other, artificial associations<sup>4,5</sup>. Although covariance data are unfit for critical assessment of interspecific interactions (larval trematodes in snails are a noticeable exception<sup>2</sup>), these data are needed because they provide a means of explaining and predicting occurrence of interactions<sup>6-8</sup>. Lotz and Font<sup>9</sup> have convincingly shown that the Poisson approximation of species numbers per host does not indicate absence of interspecific interactions.

In eight of 11 cases indicative of interactive communities, the evidence of negative interactions was based on information about intestinal overlap between pairs of helminth species<sup>2</sup>. Negative interspecific interactions were indicated if the realized overlap was smaller than the fundamental overlap (the summed overlap of helminth populations in all host individuals), or if the overlap between species did not increase with increasing infrapopulation density and expanding intestinal ranges. Both of these approaches have the drawback of testing the presence of negative interactions only, that is, the possibility of overlap being higher than expected is not considered. However, positive interactions between helminth species do exist,

and they may be more common than negative interactions<sup>10</sup> (for the role of positive interactions in communities, see Bertness and Callaway<sup>11</sup>). If the possibility of positive overlap is ignored, the role of negative interactions is overemphasized, especially in species-rich communities. In addition, diverse communities may have more interactive pairs than species-poor communities partly because of the high number of pairs tested and high probability of artificial interactions.

The role of interspecific interactions in structuring helminth communities remains largely ambiguous. Negative interactions have been tested rigorously in relatively few helminth assemblages, most of them from birds and surprisingly few from fish (only one study listed in Sousa<sup>2</sup>). The apparent differences between mammals, waterfowl and other birds largely reflect the variation in methods used to evaluate the nature of helminth communities. In addition, the comparative data are still biased: most of the avian and mammalian data are from waterfowl and bats, respectively<sup>2</sup>.

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### Reply from W. Sousa

Haukisalmi asserts that the data presently available are insufficient, in quantity and quality, to support general conclusions regarding the relative importance of processes that structure assemblages of helminth parasites. I fully concur with this view, and I refrained from making such conclusions in my review<sup>1</sup>. In fact, I spent nearly

a page (pp. 53-54) discussing the circumstantial and non-experimental nature of the evidence that has been employed in tests of competing hypotheses in this area, and the evidence was clearly labelled as circumstantial in Box 1. I also mentioned a number of confounding sampling biases, and the problems associated with formulating appropriate null models. Furthermore, I was careful to indicate in Table 3 that the classification of a particular assemblage as interactive versus isolationist was the author's, not my own.

Haukisalmi's comment that in most cases different criteria have been used to define a parasite assemblage as interactive versus isolationist is well taken. Interactive assemblages have usually been identified from detailed information on species abundances and distributions within individual hosts, whereas studies that report isolationist assemblages have tended to rely on less-direct lines of evidence (e.g. randomization procedures that evaluate the patterns of interspecific association among hosts, or tests of the fit of the observed distribution of the number of species per host to statistical distributions that are presumed, sometimes incorrectly<sup>2</sup>, to represent null non-interactive assemblages). Clearly, it would be preferable to apply a more standardized set of criteria when evaluating the degree of interspecific interaction in helminth infracommunities.

On the other hand, a single piece of solid counterevidence can falsify a general hypothesis, and I stand by the main conclusion of my original review that the patterns revealed in several rigorous studies of host-parasite associations are in direct conflict with recent theories<sup>3,4</sup> concerning the processes that structure assemblages of helminth parasites. As I discuss at some length in my review, these theories fail to explain a good deal of the observed variation in helminth community structure. This conclusion is only further reinforced by the results of Haukisalmi and Henttonen's study of gastrointestinal helminths in the bank vole (*Clethrionomys glareolus*)<sup>5,6</sup>, published after my review had gone to press.

The second point raised by Haukisalmi is that positive interspecific interactions have been overlooked in studies of the processes that structure parasite infracommunities. While this is not entirely true, the role of negative interspecific interactions has indeed received far greater conceptual and empirical attention than that of positive interactions. This bias is understandable given the historical precedence of the one-tailed hypothesis that interspecific competition is responsible for the observed site specificity of helminth infections<sup>7</sup>. However, it is inaccurate to say that existing studies have not considered the possibility that the spatial distributions of co-occurring species overlap more than expected by chance. Several of the studies considered in my review<sup>8-10</sup> found evidence of negative interspecific interaction by comparing observed overlaps in within-host spatial distributions to those expected if the species were distributed at random. As applied, this test was two-tailed and capable of detecting pairs of species that overlap more, as well as less, than expected. In fact, each of the above studies reported instances of greater overlap than expected between particular species. As Haukisalmi notes, Lotz and Font<sup>8</sup> found that the number of species pairs whose

intestinal distributions were positively correlated exceeded the number whose distributions overlapped less than expected; however, positive associations were relatively uncommon in the other studies. It should be remembered that these are not, in fact, *bona fide* cases of positive interaction between species; they simply represent situations in which different species are distributed similarly within a host. Moreover, Haukisalmi cites no supporting evidence for his statement that 'positive interactions between helminth species do exist'. Unambiguous examples of direct mutualism or indirect positive effects of one helminth species on another are rare. Whether they occur within or among individual hosts, positive interspecific associations are not necessarily the product of positive interspecific interactions. For example, there are larval trematodes that appear to obligately occur in mixed-species infections within the same organ of their snail intermediate host, yet have a negative impact on each others' development<sup>11</sup>.

In summary, Haukisalmi raises some valid criticisms of the evidence I have used to evaluate recent theories of helminth community structure. Nonetheless, I believe the quantity and quality of the available data adequately support the specific conclusions that I reached.

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## Palaeoecology and ecology

Willis' recent *TREE* article<sup>1</sup> does a valuable job in emphasizing that 'paleoecology and ecology are not ... two distinct disciplines but rather [are] one entity'. She does this mainly by summarizing studies in Harvard Forest in Massachusetts, which show that this woodland has changed continuously, at a variety of different spatial scales, over the past 10 000 years or so. In particular, she emphasizes that much of Harvard Forest was farmland before US agriculture moved west after the Civil War, so that – as for most of

the woodland on the East Coast of the USA – what one sees today is a poor reflection of the presettlement forest. Willis also summarizes other studies, at various sites in the British Isles, showing that what are often thought of as 'undisturbed ancient woodlands' are in fact communities that bear the clear stamp of disturbances over the past 200–1000 years. She concludes by quoting Foster<sup>2</sup>: 'the ramifications of this history in terms of contemporary ecological processes are too great to be dismissed by modern-day ecologists'.

I think this conclusion is a bit misleading, in that no ecologists of my acquaintance hold the view imputed to them by Foster and Willis. To the contrary, the past 20–30 years have seen a fairly well-developed body of theory dealing with the dynamics of successional processes in tree communities (following disturbances which may be either at a specific point in time or occurring continuously). One clear message from such models of 'Markovian forest succession' by Horn, Shugart and others is that the characteristic time for a community to recover from a major disturbance such as clearance, is at least many centuries, and more likely millennia<sup>3–9</sup>. And this is providing nothing else changes, which is recognized as unlikely. These theoretical studies of community dynamics are backed by data from the history and ecology of yet other well-studied woodlands in the northeast USA, such as the Institute Woods in Princeton<sup>3,4</sup>. More generally, Botkin's<sup>9</sup> book emphasizes that change is a dominant ecological theme, and that, for woodlands in particular, we cannot properly understand the present if we do not understand the past.

In short, Willis' review is important in reminding us that ecologists need to be aware of advances in paleoecological research, and conversely that paleoecologists need to keep abreast of ecological advances. But, as written, her review deals more explicitly with the first half of this couplet than with the second. I do, however, agree strongly with Willis' underlying message: many of the most important problems in conservation and ecological management demand that we deal with larger spatial scales and longer sweeps of time than is currently the norm in ecological research<sup>10</sup>.

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## Reply from K.J. Willis

I welcome the opportunity to discuss the role of palaeoecology within mainstream ecology. The fact that there is a well-developed body of theory dealing with the dynamics of successional processes in tree communities is important, and these models should not be overlooked. But like all theoretical models, extrapolation is dangerous and data are needed to test them. It is in the testing of these models that I would argue that ecologists ignore the palaeoecological record.

Most successional studies assume that the modern world offers all that is needed in the way of observable processes for full understanding of the long-term record. Some even prefer a space-for-time substitution ('forcing functions for vegetation change over large areas tend to be the same as those causing change over long time periods'<sup>1</sup>) rather than examination of a historical record. Time and again the palaeoecological record proves such assumptions to be incorrect. The importance of the work of Foster<sup>2</sup> and others mentioned in my *TREE* article<sup>3</sup> is that they not only highlight the problems in modelling long-term succession from currently observable processes, but they also offer an alternative method. The palaeoecological record is available to test ideas developed in modern systems, and to help generate new hypotheses that might be tested by experimental or theoretical work. Yet the palaeoecological option is still ignored by the majority of ecologists, at least from evidence available in their publications. As long as published research on successional studies (including May's own edited volumes, e.g. Refs 4 and 7 in his letter) does not cite palaeoecological work, and mainstream ecology journals, such as *TREE*, continue to bring out special issues such as 'Evolutionary Ecology and Conservation in New Zealand'<sup>4</sup> that do not contain a single palaeoecological paper, I shall continue to complain!

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