COMMENTARY

Commentary on 'A Candide response to Panglossian accusations by Randolph and Dobson: biodiversity buffers disease' by Dr R. Ostfeld (*Parasitology* 2013, in press)

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We are disappointed with Ostfeld's parochial commentary (Ostfeld, 2013) because we hoped we had addressed the dilution theory debate from a wider perspective, taking into account studies beyond those originating in New York State (Randolph & Dobson, 2012). We emphasized the inherent variability in the effects of biodiversity on the risk of zoonotic disease, noting explicitly that Ostfeld's own work allowed for positive, neutral and negative outcomes depending on the precise circumstances and biological interactions. The wider the range of studies, the greater the evidence for neutral and positive outcomes (i.e. biodiversity may have no effect or exacerbate infection risk) as the literature bias is gradually overcome. Publication bias, however, may still persist and be identified by appropriate meta-analyses (Salkeld *et al*., 2013).

Disagreement and differences in interpretation are the very stuff of science, not to be mistaken for 'accusations' (Ostfeld, 2013); we made no accusations, but merely called for a more balanced synopsis of the available evidence. Ostfeld has clearly – and regrettably – taken our review very personally, even though we made every effort to include recent studies from other authors. We wish to make no judgements beyond the purely objective and scientific.

Ostfeld takes issue with our complaint that dilution effect proponents claim too much generality. We deliberately chose un-nuanced language (e.g. our exhortation against preaching 'that high biodiversity always protects against disease') in order to voice an exasperation with what we felt was an unwarranted stream of studies that either misinterpreted results in favour of the dilution effect, or sought out those idiosyncratic ecological conditions under which it might actually occur. Our thesis is that the balance of the literature does not reflect the balance of evidence; words such as 'mantra' and 'preach' were designed to be evocative rather than literal, to characterize broadly what we deemed a degree of promotion of the dilution phenomenon that strayed too far towards the optimistic. We suggest that the context (i.e. the rest of the paper) makes it abundantly obvious that we are well aware of the full range of views, studies and results, and we have little doubt that the vast majority of readers will have read the paper in the correct spirit.

We admit, however, to the punctuational error in assigning quotation marks to the words 'diversity protects against infection risk' – it was not our intention to attribute the words to any particular source. This particular criticism, whilst undeniably accurate, seems a trifle disingenuous, however; the source in question (Keesing *et al*. 2010) does contain the statement, 'current evidence indicates that preserving intact ecosystems and their endemic biodiversity should generally reduce the prevalence of infectious diseases', which is functionally little different. Again, our deliberate exaggeration was borne of exasperation, and we have little doubt that it will typically have been understood in this way, too. In general, we find this line of argument to be more akin to pedantry than serious criticism; quibbling over our precise definitions of a figurative mantra, for example, seems a fairly pointless exercise. Our review makes clear to the reader the full scope of the available literature, and to label our treatment a 'caricature of dilution effect studies' is to read it selectively and defensively, at best.

To say that there was an 'error of omission' in 'the removal of data from scatterplots' is to be misleading to the point of unwitting irony. In contrast to the original paper (Ostfeld *et al*. 2006), we showed the result of both including and excluding the points, in order to illustrate the effect that each had on the statistical relationship. In short, we were addressing an omission in the original. We, and many others, have always recognized the importance of exploring the impact of isolated outlying data points on overall regressions. We never remove them, but always present the comparison between results with

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and without them, which is far more transparent, and offers greater biological insight, than invariably including them. This turns the blunt instrument of statistics into a more precise exploratory tool. Of the other statistical issues, we remind readers that this has already been dealt with in correspondence in *PLoS Biology* (2006) (http://www.plosbiology.org/annotation/listThread.action?root=16133 and http://www.plosbiology.org/annotation/listThread.action?root=1167) in response to the original paper. Ostfeld will know, as do we, that the referees on this correspondence were not convinced by his defence.

We also maintain our concern regarding the LoGiudice *et al*. (2003) model parameterization. We do not, and did not, imply that tick burden was incorrectly held constant across all hosts. The burdens are species-specific, and empirically derived, yes. We clearly acknowledged this by reiterating 'the density of ticks is always the sum of all N*i*B*i*, where N*i* and B*i* are the abundance and tick burden, respectively, of the *i*th host'. The problem is that, for host species *i*, tick burden remains constant across *all densities of individuals* of that species (and the others, including the ticks). This assumes that, for any given species, total tick burden increases linearly with the number of individual hosts. This is a potentially problematic and certainly unrealistic assumption. The point regarding the redistribution of ticks in the Keesing *et al*. (2009) model is, however, valid. We apologize for the mistake.

In response to our warning that increases in host density can lead to increases in tick density ('can', not 'must', as Ostfeld avers), Ostfeld claims that there is no evidence that increasing vertebrate host density increases tick density. We would be pleased to direct him towards a range of papers, including host removal experiments and other empirical studies (such as the lizard results we discuss), as well as the results of theoretical modelling work, which should disabuse him of this idea. Grooming by rodents might well remove a large number of ticks, but we know of no evidence that deer grooming is effective. Further research on this issue might be interesting.

We find Ostfeld's summary of Cardinale *et al*. (2012) (which, along with Ostfeld and Keesing 2012, was published after our paper and therefore not available to us) to be rather selective. In their wide-ranging review, which touches on biodiversity/infection only as a very small part, Cardinale *et al*. (2012) specifically warn against making sweeping statements that biodiversity always brings benefits to society because more diverse pathogen populations are likely to create higher risks of infectious disease. Results from audits of the literature, such as those in Cardinale *et al*. (2012), cannot be distinguished from publication bias. The meta-analysis by Salkeld *et al*. (2013) provides a robust quantitative measure of the publication bias (in favour of negative relationships between biodiversity and disease risk). The confidence limits of levels of significance indicate that the null hypothesis cannot be rejected. The proportion of statistically significant studies (using only those based on direct biodiversity indices rather than assumed proxies) varies between disease systems: 3/8 for hantaviruses, 0/4 for tick-borne infections (*Anaplasma phagocytophilum* and *Borrelia burgdorferi* combined), and 1/3 for West Nile Virus.

Regarding the issue of species richness *vs* community composition, we do not claim primacy in highlighting the distinction, and we have indeed referred to such ideas expressed in some of Ostfeld *et al*.'s papers. We do not 'dismiss species richness', but we do question whether increased richness will usually involve a greater proportion of transmission non-competent host species. Finally, we too welcome dispassionate discussion, and must also acknowledge a fine pun when we see one; touché, Candide.

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