A Candide response to Panglossian accusations by Randolph and Dobson: biodiversity buffers disease

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SUMMARY

Randolph and Dobson (2012) criticize the dilution effect, which describes the negative relationship between biodiversity and infectious disease risk. Unfortunately, their commentary includes distortions, errors of omission, and errors of commission, which are rebutted herein. Contrary to their claims, the dilution effect is not a 'mantra' that asserts that reduced disease risk is a 'universal' outcome of high diversity. Although universality of the dilution effect has not been claimed, and conditions under which diversity can amplify disease risk have been described, the growing literature indicates that the dilution effect is indeed a widespread phenomenon.

Key words: Biodiversity, dilution effect, disease ecology, Lyme disease, tick-borne disease.

In a commentary published as a 'Review Article', Randolph and Dobson (2012, hereafter 'RD') describe the dilution effect – a negative relationship between biodiversity and disease risk – as Panglossian. They agree that the dilution effect occurs in nature, but they object to specific pieces of evidence and to what they perceive as over-generalizations about its broad applicability. To justify their allegation of Panglossian thinking, RD present a caricature of dilution effect studies, suggesting that these studies are unaware of contrasting effects of biodiversity on disease and inappropriately applied to policy and management. The generality of the dilution effect, factors that strengthen, weaken, or reverse it, and the underlying causal mechanisms, are rich topics currently being addressed. Unfortunately, however, the RD commentary is replete with distortions and errors of commission and omission that undermine its merit. Below I list the most serious of these shortcomings in order to advance the dialogue on the importance and generality of the dilution effect.

DISTORTIONS

1. RD repeatedly call the dilution effect a 'mantra' (pp. 847, 848, 853 and 857), although their descriptions of the mantra differ at each mention. Each is placed in quotations but only one is attributed to a source, and this quotation is not present in the source cited (Keesing *et al*. 2010). Their religious analogies extend to the unreferenced accusation that proponents of the dilution effect 'preach that high biodiversity always protects against disease' (p. 860). Neither such mantras nor preachings exist in the published literature. **2.** RD repeatedly state that proponents have argued that the dilution effect is 'universal' (pp. 850, 853, 854), but this too is incorrect. To the contrary, it is obvious in RD's own descriptions of the dilution effect that universality is never claimed; indeed, RD borrow from some of the earliest descriptions of the dilution effect that delineate circumstances under which it is expected not to occur (e.g. Table 1, a restating of Ostfeld and Keesing, 2000*a*). The dilution effect literature has been careful to describe conditions under which biodiversity is expected to amplify disease risk (Ostfeld and Keesing, 2000*a*,*b*; Schmidt and Ostfeld, 2001; Ostfeld and LoGiudice, 2003; Keesing *et al*. 2006, 2010; Pongsiri *et al*. 2009; Johnson and Thieltges, 2010). Examples of such an amplification effect, and neutral effects, exist (Keesing *et al*. 2006; Ostfeld and Keesing, 2012), but reduced disease risk appears to be a far more common consequence of high host diversity (Cardinale *et al*. 2012).

ERRORS OF OMISSION

1. One important error of omission is the removal of data points from scatterplots (Figs 1 and 2) in order to reanalyse relationships within subsets of data. Data removal was not justified by statistical norms, e.g. status as significant outliers. Indeed, the data point removed from Fig. 2 (redrawn from Ostfeld *et al*. 2006), which shows a positive relationship between acorn production and subsequent Lyme disease risk, represents a masting year, which, although infrequent, illustrates highly influential ecological events that should not be obscured. **2.** RD thoroughly

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discuss the roles of vertebrate hosts in both abundance and infection prevalence of ticks, arguing that while increasing total host density (across all species) might reduce infection prevalence, it must increase tick density. Unfortunately, there is no evidence to support this assertion, and this discussion omits the evidence (Keesing *et al*. 2009) that some hosts kill far more ticks (via grooming) than they feed, potentially reducing tick density. **3.** RD repeatedly argue that host community composition rather than species richness is more informative in understanding the dilution effect, failing to recognize how thoroughly this idea has been explored. From the very inception of the dilution effect (Van Buskirk and Ostfeld, 1995; Norman *et al*. 1999; Ostfeld and Keesing, 2000*a*,*b*; Schmidt and Ostfeld, 2001; LoGiudice *et al*. 2003; Ostfeld and LoGiudice, 2003), the composition of the host community has been identified as the most relevant metric of host diversity, as it provides more information than species richness alone. In dismissing species richness, RD fail to indicate that, whenever the pattern of community assembly or disassembly is nonrandom, species richness and community composition will be correlated. When patterns are highly nested, this correlation will be quite strong (Johnson *et al*. 2013).

ERRORS OF COMMISSION

1. In critiquing an influential model of Lyme disease in eastern North America (LoGiudice *et al*. 2003), RD state that the structure of the model guarantees that high diversity of hosts will reduce tick infection prevalence, but this is incorrect. Ostfeld and LoGiudice (2003) showed that the same model is capable of producing a positive correlation between diversity and infection prevalence, but this occurs only when an unrealistic assumption (each host species has an equal probability of entering as communities are assembled) is made. RD also claim that this study assumed constant tick burdens on each given host, when in fact the study empirically determined tick burdens on each host. **2.** RD claim that a subsequent model (Keesing *et al*. 2009) 'assumed that constant total numbers of ticks are fed, with all ticks that are not picked up by one host type being re-distributed to others' (p. 3). This too is incorrect. In the model of Keesing *et al*. (2009), the percentage of ticks redistributed onto other hosts was systematically varied from 0 to 100%. **3.** RD criticize the study by Ostfeld *et al*. (2006), which compared the impact of varying deer density with that of rodent density in affecting tick density. They erroneously state that 'direct estimates of deer abundance were attributes of the entire study site but were treated as characteristics of individual plots' (p. 5). In fact, two estimates of deer density were used, one of which was specific to each individual plot, while the other was treated as a characteristic of all plots. Neither was positively correlated with subsequent tick abundance. **4.** Moreover, RD's misunderstanding of this study's design leads them to falsely accuse it of inflating degrees of freedom and pseudo-replicating. In fact, the maximum-likelihood statistics used to compare models with and without deer accommodated the hierarchical design, and because specific hypotheses were not tested using a frequentist approach, degrees of freedom were not relevant. **5.** Referring to several recent reviews of diversity–disease relationships, RD state: 'Results consistently show that the effect of increasing biodiversity in all its various forms … is not uniform; amplification or neutral effects have been observed as much as reduced infection prevalence' (p. 859). In fact, equal frequencies of amplification, neutrality and dilution are not shown in any of the reviews cited. Indeed, a recent review (Cardinale *et al*. 2012) found dilution (a statistically significant, negative relationship between diversity and disease) in 91 of 107 (85%) statistical tests of plant diseases and in 30 of 45 (67%) statistical tests of animal diseases, for a total of 80% of all 152 tests reviewed.

CONCLUSIONS

As research on the dilution effect in a variety of disease systems has grown and its applications to policy and management are discussed, it is important to critique both the theory itself and the degree to which it is supported by evidence. Development of dilution effect theory has proceeded cautiously, with careful attention paid to alternative and complex effects of biodiversity. I am confident that continued research will reveal the degree to which it is general and useful. RD invoke Voltaire's infamous character Pangloss to imply that dilution effect theory is naïvely optimistic. They fail to recognize that, in fact, dilution effect theory has much more in common with the views of Voltaire's central character, Candide, who rejects Panglossian hyper-optimism to develop a pragmatic philosophy based on empirical observations. I hope that discussions of the generality and applicability of the dilution effect will continue more dispassionately.

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REFERENCES

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S. and Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature* **486**, 59–67.

Johnson, P. T. J. and Thieltges, D. W. (2010). Diversity, decoys and the dilution effect: how ecological communities affect disease risk. *Journal of Experimental Biology* **213**, 961–970.

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Johnson, P. T., Preston, D. L., Hoverman, J. T. and Richgels, K. L. (2013). Biodiversity decreases disease through predictable changes in host community competence. *Nature* **494**, 230–233.

Keesing, F., Holt, R. D. and Ostfeld, R. S. (2006). Effects of species diversity on disease risk. *Ecology Letters* **9**, 485–498.

Keesing, F., Brunner, J., Duerr, S., Killilea, M., LoGiudice, K., Schmidt, K., Vuong, H. and Ostfeld, R. S. (2009). Hosts as ecological traps for the vector of Lyme disease. *Proceedings of the Royal Society B* **276**, 3911–3919.

Keesing, F., Belden, L. K., Daszak, P., Dobson, A., Harvell, C. D., Holt, R. D., Hudson, P., Jolles, A., Jones, K. E., Mitchell, C. E., Myers, S. S., Bogich, T. and Ostfeld, R. S. (2010). Impacts of biodiversity on the emergence and transmission of infectious diseases. *Nature* **468**, 647–652.

LoGiudice, K., Ostfeld, R. S., Schmidt, K. A. and Keesing, F. (2003). The ecology of infectious disease: Effects of host diversity and community composition on Lyme disease risk. *Proceedings of the National Academy of Sciences USA* **100**, 567–571.

Norman, R., Bowers, R. G., Begon, M. and Hudson, P. J. (1999). Persistence of tick-borne virus in the presence of multiple host species: tick reservoirs and parasite mediated competition. *Journal of Theoretical Biology* **200**, 111–118.

Ostfeld, R. and Keesing, F. (2000*a*). The function of biodiversity in the ecology of vector-borne zoonotic diseases. *Canadian Journal of Zoology–Revue Canadienne De Zoologie* **78**, 2061–2078.

Ostfeld, R. S. and Keesing, F. (2000*b*). Biodiversity and disease risk: the case of Lyme disease. *Conservation Biology* **14**, 722–728.

Ostfeld, R. S. and Keesing, F. (2012). Effects of host diversity on infectious disease. *Annual Review of Ecology, Evolution and Systematics* **43**, 157–182.

Ostfeld, R. S. and LoGiudice, K. (2003). Community disassembly, biodiversity loss, and the erosion of an ecosystem service. *Ecology* **84**, 1421–1427.

Ostfeld, R. S., Canham, C. D., Oggenfuss, K., Winchcombe, R. J. and Keesing, F. (2006). Climate, deer, rodents, and acorns as determinants of variation in Lyme-disease risk. *PLoS Biology* **4**, 1058–1068.

Pongsiri, M. J., Roman, J., Ezenwa, V. O., Goldberg, T. L., Koren, H. S., Newbold, S. C., Ostfeld, R. S., Pattanayak, S. K. and Salkeld, D. J. (2009). Biodiversity loss affects global disease ecology. *Bioscience* **59**, 945–954.

Randolph, S. E. and Dobson, A. D. M. (2012). Pangloss revisited: a critique of the dilution effect and the biodiversity-buffers-disease paradigm. *Parasitology* **139**, 847–863.

Schmidt, K. A. and Ostfeld, R. S. (2001). Biodiversity and the dilution effect in disease ecology. *Ecology* **82**, 609–619.

Van Buskirk, J. and Ostfeld, R. S. (1995). Controlling Lyme disease by modifying the density and species composition of tick hosts. *Ecological Applications* **5**, 1133–1140.