LETTER

Reply to Chitnis and Smith, Fernandes, Gibbons, and Kane: Communicating theory effectively requires more explanation, not fewer equations

Mathematical theory is an indispensible part of research in ecology and evolutionary biology. Used wisely, equations can capture the essence of fundamental biological processes with greater clarity, precision, rigor, and brevity than purely verbal arguments. In our original article (1), we showed that the citation rate of articles in ecology and evolutionary biology is negatively associated not with the number of equations used—contrary to what Gibbons (2) and Chitnis and Smith (3) claim—but with how densely packed those equations are on each page. This is a crucial difference. It is not equations that are the problem; it is equations without sufficient accompanying text to explain the assumptions and implications for a broad biological audience. We do not recommend the indiscriminate removal of equations from scientific papers.

Explaining the mathematics in sufficient detail for a broad audience can, however, require considerable space. As a pragmatic solution acknowledging the constraints many journals impose on article length, we suggested that authors might move some of their equations to an appendix. Our viewpoint is that essential equations capturing the assumptions and structure of a model should be presented in the main text, whereas less fundamental equations, such as those describing intermediate steps to solutions, should be presented in an appendix. However, we also warned that this approach requires extra care in stating the mathematical assumptions clearly in the main text (1). Chitnis and Smith (3) echo this concern, but go further by concluding that authors presenting equations in an appendix are "less likely to put in the required effort to explain the meaning." We are not convinced this is true; in principle, authors can provide much more detailed and comprehensive explanations when writing an online appendix, for which they are freed from constraints on page space. Furthermore, by moving equations to an appendix, authors would be forced to provide a verbal description in the main text. However, we agree that the mathematical details should be easily accessible to those who want to examine them, so we welcome the suggestion by Kane (4) to build closer links between the main text and online material.

Chitnis and Smith (3) and Fernandes (5) question whether citation rate reflects how well a theory has been understood, which we agree is an important issue. It is easy to find striking counter examples, as Fernandes (5) has done, of astoundingly well-cited articles that have been misunderstood by many readers. However, our concern is with the low-citation end of the scale, where a potentially important theoretical contribution is overlooked because the mathematics are not sufficiently well explained for a broad audience. An article with a high citation rate may have been successful for many different reasons (6, 7), but surely one that is hardly ever cited has little hope of making an impact. Furthermore, citation counts really do matter for the careers of individual scientists, who are increasingly judged by their h-index (8) and similar metrics. It would be a shame if promising scientists failed to reach their potential as a result of how they present their work.

Fernandes (5) asserts that "the mechanism causing impeded communication is from the reader, not the writer." However, both parties have a responsibility to enhance understanding. We emphatically reject the notion that improving the communication of mathematical theory in biology and improving the mathematical education of biologists are somehow mutually exclusive goals. They are clearly complementary, and scientists who fail to recognize the importance of both solutions risk slowing progress in their field and harming their own careers.

The hypothesis put forward by Gibbons (2), that biologists are generally less interested in theoretical than empirical studies, is not supported by the data. As we originally reported (1), we find a significant negative association between equation density and citation rate even after removing papers with zero equations from the analysis. Our study found no evidence for a general aversion to theoretical papers.

Interestingly, the more complex statistical analysis of Gibbons (2) shows that the effect of equation density differs between journals, with a positive effect for articles published in *The American Naturalist*. It is important that future studies extend our analysis to other journals, as well as other years of publication and other fields. Among journals in ecology and evolutionary biology, the three we studied publish a relatively high proportion of theoretical papers (Table 1), and so are likely to be read by mathematically inclined biologists, arguably making our analysis a conservative test of our hypothesis. We expect that the effects would be even stronger for journals with a lower theoretical content.

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1. Fawcett TW, Higginson AD (2012) Heavy use of equations impedes communication among biologists. *Proc Natl Acad Sci USA* 109:11735–11739.
2. Gibbons JM (2012) Do not throw equations out with the theory bathwater. *Proc Natl Acad Sci USA* 109:E3054.
3. Chitnis N, Smith TA (2012) Mathematical illiteracy impedes progress in biology. *Proc Natl Acad Sci USA* 109:E3055.
4. Kane A (2012) A suggestion on improving mathematically heavy papers. *Proc Natl Acad Sci USA* 109:E3056.
5. Fernandes AD (2012) No evidence that equations cause impeded communication among biologists. *Proc Natl Acad Sci USA* 109:E3057.
6. Leimu R, Koricheva J (2005) What determines the citation frequency of ecological papers? *Trends Ecol Evol* 20:28–32.
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8. Hirsch JE (2005) An index to quantify an individual's scientific research output. *Proc Natl Acad Sci USA* 102:16569–16572.

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Table 1. Proportion of articles that reported theoretical work in the top 20 journals in ecology and evolutionary biology in 2011

Journal	5-y Impact factor	No. of papers	Theoretical proportion
Evolution	**5.6**	**304**	**0.188**
Molecular Biology and Evolution	9.9	306	0.176
American Naturalist	**4.7**	**182**	**0.154**
Ecology Letters	15.4	155	0.142
Journal of Evolutionary Biology	3.7	261	0.138
Ecological Applications	5.4	272	0.118
Proceedings of the Royal Society of London B	**5.7**	**495**	**0.109**
Journal of Applied Ecology	5.8	173	0.104
Journal of Animal Ecology	5.0	137	0.095
Heredity	4.5	185	0.081
BMC Evolutionary Biology	4.6	379	0.079
Ecology	6.0	240	0.063
Behavioral Ecology	3.4	201	0.060
Oecologia	3.9	317	0.050
Global Ecology and Biogeography	6.6	81	0.049
Molecular Phylogenetics and Evolution	4.0	257	0.047
Journal of Ecology	6.0	157	0.045
Oikos	3.6	214	0.037
Ecography	5.5	107	0.028
Functional Ecology	4.9	146	0.014

The journals used in ref. 1 are highlighted in bold. Articles were identified as theoretical if the title or abstract contained the search term "model*", excluding some common empirical uses (as described in ref. 1).