

Simplified model assumptions artificially constrain the parameter range in which selection at the holobiont level can occur

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van Vliet and Doebeli (1) present a multilevel selection framework simulating host–microbiome evolutionary dynamics. The model explores the conditions under which the association between hosts and their “helper” microbiome—microbes that developed a trait that provides a benefit to the host at a cost to themselves—is strong enough to allow for selection at the holobiont level. The model is an important contribution to the holobiont debate, making the notion quantifiable and highlighting the involved parameters.

van Vliet and Doebeli conclude that the parameter space in which selection occurs at the holobiont level is extremely restricted (Fig. 1). We show that this result stems from specific model assumptions. Although these assumptions are reasonable as a modeling starting point, slight biologically reasonable modifications lead to qualitatively different outcomes.

One model assumption that can readily be altered is the relation between microbiome composition and host fitness. In van Vliet and Doebeli’s model, the probability to reproduce increases linearly with the quantity of the helper microbes. Many alternatives are reasonable, reflecting different intergenerational selection dynamics of the host.

One plausible scenario is that the fitness acts as a step function. This may occur, for example, if the helper microbiome supplies a vital nutrient, otherwise inaccessible to the host, required in small amounts (2). To test this, we ran van Vliet and Doebeli’s model with host fitness determined by a discrete step function, at a threshold of 1% helper microbes. Host individuals that had a microbiome in which the helper microbes’ frequency was above the threshold received fitness 0.95, and others, 0.05. This simple alteration of van Vliet and Doebeli’s model assumptions leads to a broad parameter space in which a stable population of helper microbes is maintained despite their costly behavior, suggesting selection at the holobiont level (Fig. 2). Such a nonlinear dependency of fitness on an underlying factor that can be influenced by the microbiome is not uncommon in the real world, stemming from physiological, ecological, or behavioral factors (2–5). van Vliet and Doebeli’s model may thus suggest the opposite conclusion from the one they reach, depending on the choice of fitness function.

Other assumptions of van Vliet and Doebeli’s model may be altered to reflect realistic dynamics. The ability of the host to select among microbial partners, even partially (e.g., ref. 6), is expected to dramatically alter the parameter range in which holobiont-level selection can act. Another aspect implicitly assumed in van Vliet and Doebeli’s model is its unusual combination of hard and soft selection; modeling selection as primarily soft—a common situation in reality—is also expected to alter the model’s results in favor of holobiont-level selection.

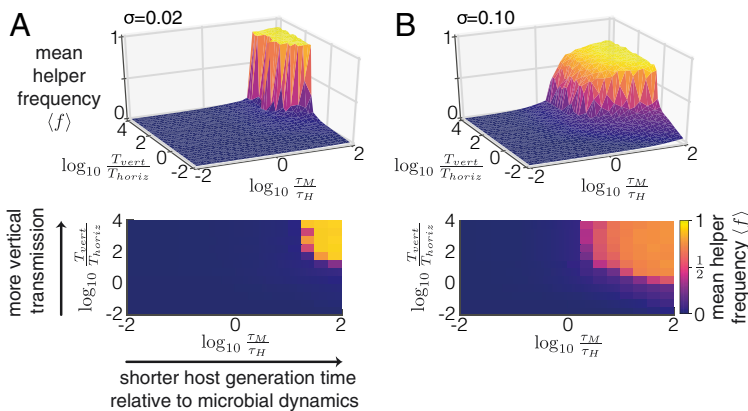


Fig. 1. van Vliet and Doebeli’s original results (1). Selection can only act at the holobiont level under stringent conditions. The mean helper frequency is shown as a function of the timescale of the evolutionary dynamics at the microbe level relative to the host generation time and the ratio of vertical to horizontal transmission. Two different levels of sampling variance are shown: The SD of the sampling distribution is 0.02 in A and 0.1 in B; A (Top) and B (Top) show the results of single simulations, and A (Bottom) and B (Bottom) show the same data, averaged within discrete bins.

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Author contributions: I.D. and O.K. designed research; I.D. performed research; I.D. analyzed data; and I.D. and O.K. wrote the paper.

The authors declare no competing interest.

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First published May 28, 2020.

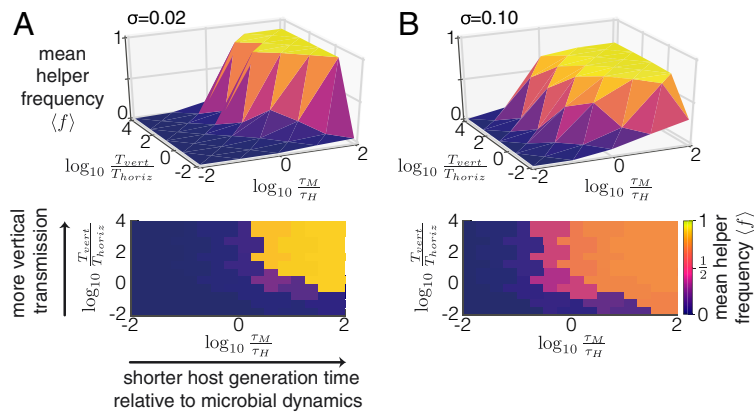


Fig. 2. When replacing the assumed fitness function by a simple, biologically reasonable, step function, van Vliet and Doebeli’s model (1) predicts that selection would act at the level of the holobiont across a much broader range of parameter values than in van Vliet and Doebeli’s original findings (compare each panel to its counterpart in Fig. 1; panel descriptions are analogous to those of Fig. 1).

The framework van Vliet and Doebeli propose provides a useful demonstration of the way to constructively tackle questions of host–microbiome evolutionary dynamics with a simplified model that captures essential components of the system. In our view, the assumptions that were chosen in their implementation are an appropriate choice for an initial exploration. However, they are far too limiting and simplistic to derive general

conclusions about the likelihood of selection at the holobiont level, warranting cautious interpretation and calling for further exploration.

Acknowledgments

This work was partially funded by the Gordon and Betty Moore Foundation (Grant GBMF9341, DOI: 10.37807/GBMF9341).

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