

[Re] Insect Natural Enemies as Regulating Factors

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The authors have declared that no competing interests exist.

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Introduction

The introduction should introduce the original paper and put it in context (e.g. is it an important paper in the domain ?). You must also specify if there was an implementation available somewhere and provide a link to it if relevant (and in such a case, you have to specify if the proposed replication is based on this original implementation). You should also introduce your implementation by listing language, tools, libraries, etc. and motivate choices if relevant.

Parasitism is a special case of predation. In both interactions, a species (parasitoid or predator) feeds on the other species (host or prey), acting as a regulating factor (Anderson and May [1]). However, the population dynamics of both system are very different. Thompson [6] was the first to propose a model to describe this host-parasitoid system. In his model, parasites are limited by the number of eggs they lay. Depending on the relative increase rate of hosts and parasites, either both population increase indefinitely or decrease to extinction. Later, Nicholson and Bailey [5] proposed other models for which the rate of increase of parasite is limited by their capacity to find hosts. These were the basis for many other models where parasites act as regulating factors (Hassell [4]; Rockwook15).

In 1983, Dempster proposed that natural enemies may not be an important regulating factor in insect dynamics. In fact, he failed to detect density-dependence due to natural enemies in most of the studies on Lepidoptera he reviewed. His proposition really contrasted with what was thought at the time. In response to this article, Hassell [3] analyzed a insect dynamic model in which the only regulating factor was natural enemies. He showed that the difficulties to detect the density-dependent effect of natural enemies was due to time delays and stochasticity. This paper is still considered a classic in fields of insect and parasitoid-host population dynamics. It introduced an important argument on the role of natural enemies on insect populations, a controversial topic that aroused ecologists to debate for almost a decade (Turchin [7]).

We used information from Hassell [3] to replicate the model. We were able to replicate the results central to the article. In addition, we made new analysis to detect the density-dependent effect of natural enemies in the stochastic model. To our best knowledge, the original implementation was not available. The code for the simulations and the figures were written in *Julia*.

Methods

The formulas used in this paper to show the difficulty of detecting natural enemies as regulating factors are the same that were used in the original paper of Hassell [3]. First of all, the equation of the host population dynamics is given as

$$N_{t+1} = F \times N_t \times f(N_t, P_t) \times D \quad (1)$$

where $N(t)$ and $N(t+1)$ represent the host population at generation t and at the next generation, F is the rate of increase of the population and D is the density independent probability of survival of the hosts (mortality). The specialist parasitoids population dynamics are represented by

$$P_{t+1} = c \times N_t \times [1 - f(N_t, P_t)] \quad (2)$$

where P_t and P_{t+1} are the number of parasitoids at generation t and at the next one, while c is the number of female parasitoids emerging from each host parasitized. In both eq. 1 and eq. 2, $f(N_t, P_t)$ represents the probability of escaping mortality from natural enemies (parasitoids) and is given by eq. 3.

$$f(N_t, P_t) = [1 + (a \times P_t) / (m \times (1 + a \times T \times h \times N_t))]^{-m} \quad (3)$$

where a is the per capita searching efficiency of the parasitoids, m is the extent of clumping of the parasitoids attacks and $T \times h$ is the handling time as a proportion of the total time. This paper also explores the relationship between the hosts and a generalist parasitoid population. This population dynamic follows the equation

$$P_t = h \times \left(1 - \exp\left(-\frac{N_t}{b}\right)\right) \quad (4)$$

where h is the saturation number of parasitoids and b is the rate of approaching the saturation number.

In the previous equations, the parameters were assumed to remain constant between successive generations. However, it might not be the case for every one of them because they can be depending on the density of parasitoids and hosts. The searching efficiency of the parasitoids is one of them. To calculate the searching efficiency A at a generation t , the following equation is used :

$$A = \frac{1}{P_t} \times \ln \frac{N_t}{S} \quad (5)$$

where S is the number of hosts that survived parasitism. Finally, to assess the mortality linked to natural enemies (k), eq. 6 will be used.

$$k = \log \frac{N_t}{S} \quad (6)$$

The objective in this paper is to reproduce every result from the original publication. Every figure from the original paper will be reproduced, except for the Figure 2 and Figure 7, which only represent the functions for some equations when a parameter is changed. Therefore, they are not necessary in order to show how difficult it is to detect the regulating effect of natural enemies on a host population. For every figure reproduced, we will use the exact same values that were used in the original paper for the different parameters.

The software used to run the models and to generate the figures is Julia version 0.6.2 (Bezanson et al. [2]) All the code used to replicate the original paper is available alongside the article.

Results

Results should be compared with original results and you have to explain why you think they are the same or why they may differ (qualitative result vs quantitative result). Note that it is not necessary to redo all the original analysis of the results.

Deterministic model

The reproduced population dynamics for the host population and for the specialist parasitoids (Figures 3a and 3b) are very similar to the ones in Hassell's paper. When the level of clumping of parasitoid attacks is high, both populations decrease during the first 10 generations before they stabilise until the end of the simulation, with the host population twice as big as the specialist parasitoid population. When the extent of clumping is lower, both populations show decreasing oscillations during the 50 simulated generations. The difference between this article and the original publication resides in the fig. 1 and Figure 3d, where we standardized the axes of the graphs. At first sight, in Hassell's paper, the k-values in Figure 3c seem almost as high as in Figure 3d. However, when using the same scale for the two graphs, we can see that the k-values in the case of high clumping show much less variation than when the lower clumping is used.

The simulations performed to study the relationship between the population dynamics of the hosts and the generalist parasitoids are also very similar to the ones done by Hassell. This show a density dependant relationship between the two populations, where the natural enemy regulates the host population until they both reach a stable equilibrium. This is also the conclusion when we observe the relation between the two populations in Figures 3a and 3c.

Stochastic model

Discussion

We replicated all the results from Hassell [3]. However (as expected) we did not find the exact same results for the stochastic model. This can be explain by the stochasticity in the model and, maybe, the way Hassell calculated the mortality per generation (k-value). The latter was not explicitly explained in the original paper, so we had to calculate it from our own interpretation. We added two figures (Fig.7 and Fig.8) to take into account the variability in the stochastic models and we had results that matches those from Hassell [3].

In all, we came up with the same conclusion that the original paper : the density-dependent effect from natural enemies is obscured by time delay and/or stochasticity.

Conclusion

Conclusion, at the very minimum, should indicate very clearly if you were able to replicate original results. If it was not possible but you found the reason why (error in the original results), you should explain it.

Table 1: Table caption

Heading 1			Heading 2		
cell1 row1	cell2 row 1	cell3 row 1	cell4 row 1	cell5 row 1	cell6 row 1
cell1 row2	cell2 row 2	cell3 row 2	cell4 row 2	cell5 row 2	cell6 row 2
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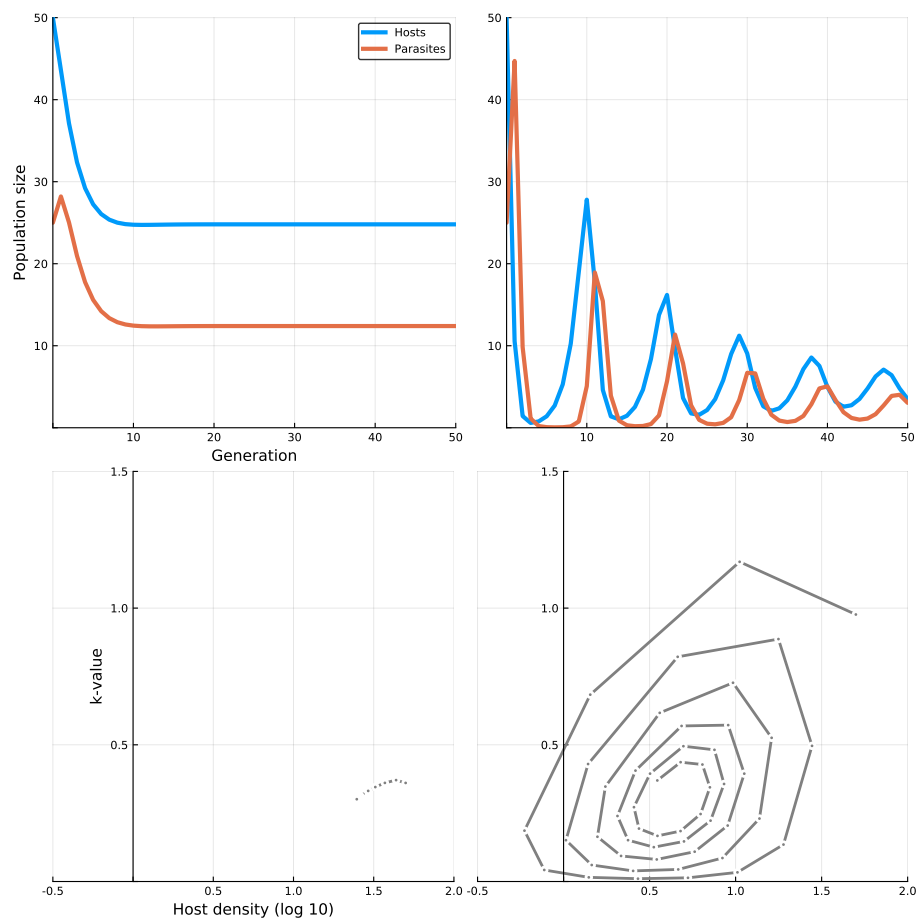
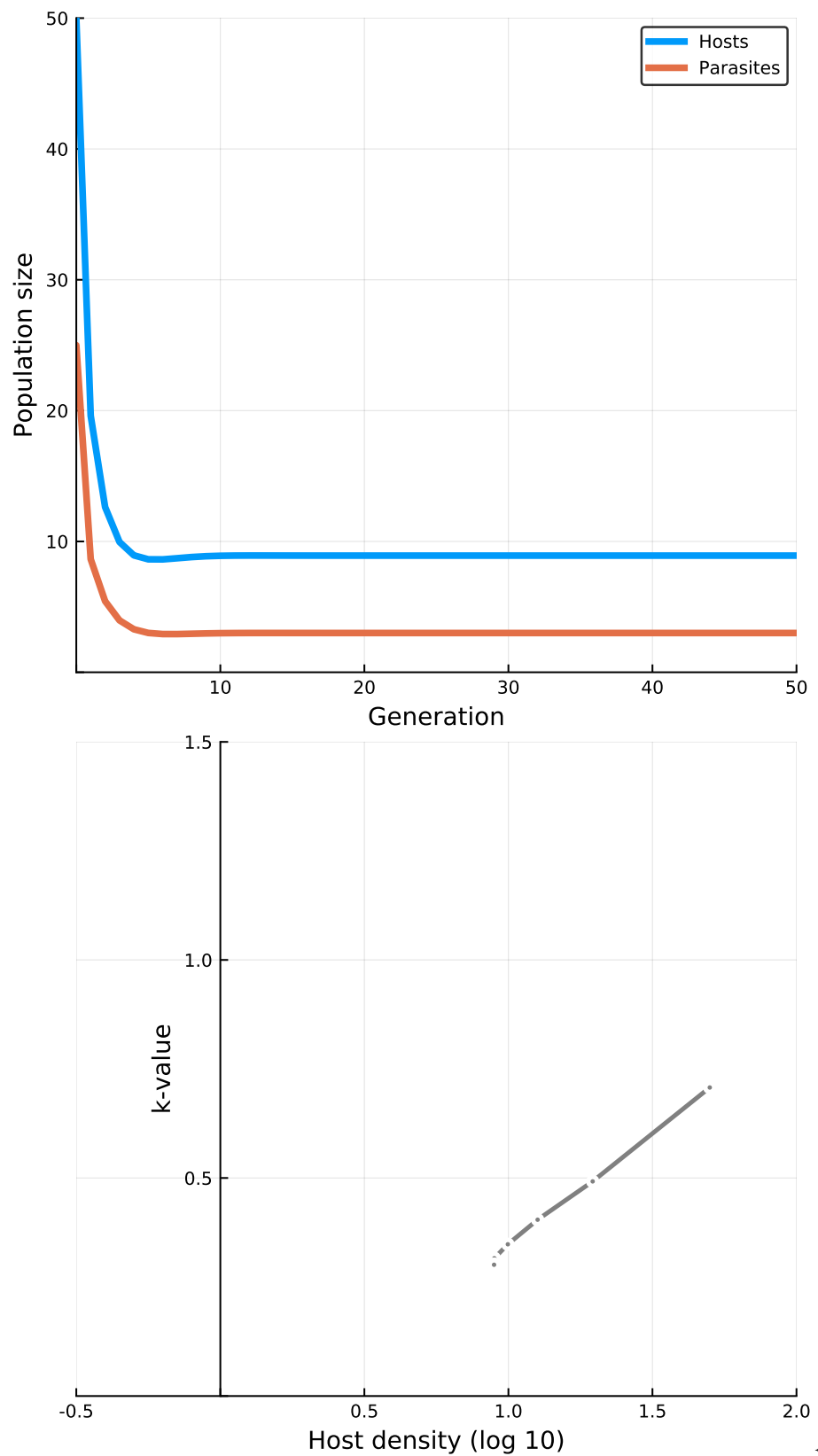


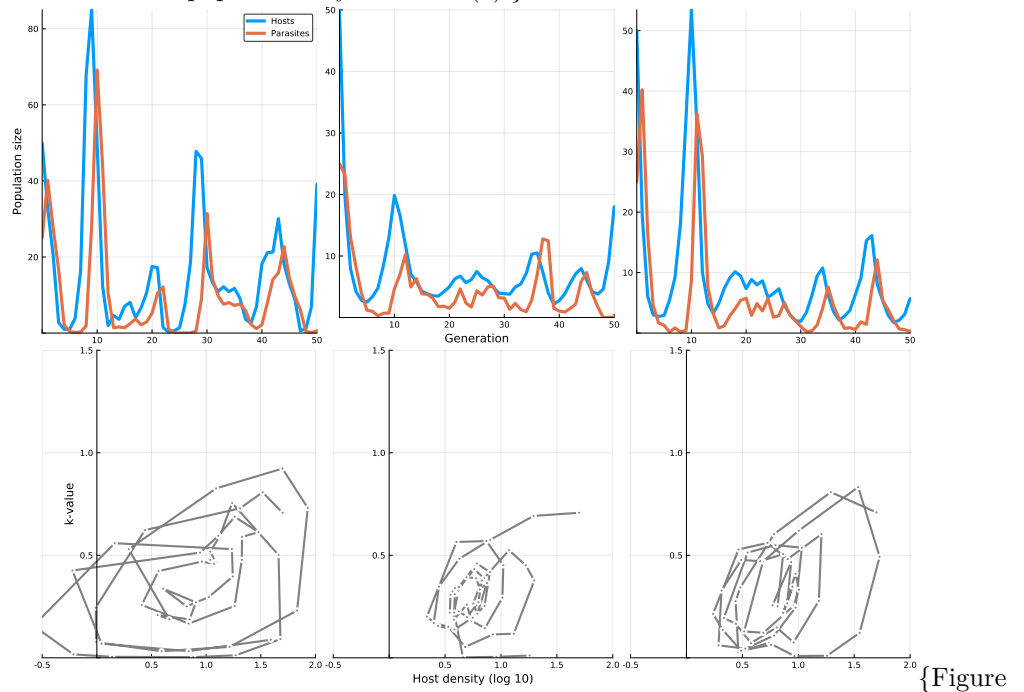
Figure 1: (a) and (b) Deterministic simulations of the host and specialist parasite population dynamics (Eq.1, Eq.2, Eq.3) using two different level of clumping in the parasitoid attacks: (a) $m = 0.2$; (b) $m = 0.8$. The other parameters used are the same in both (a) and (b): $F = 4$, $D = 0.5$, $c = 1$, $a = 0.5$ and $Th = 0$. (c) and (d) The relationship between the mortality caused each generation by parasitism (k-values) and the log10 host density for the fifty first generations, linked to (a) and (b) respectively.

A reference to table [tbl. 1](#). A reference to figure [fig. ??](#). A reference to equation [eq. 1](#). A reference to citation [markdown](#).

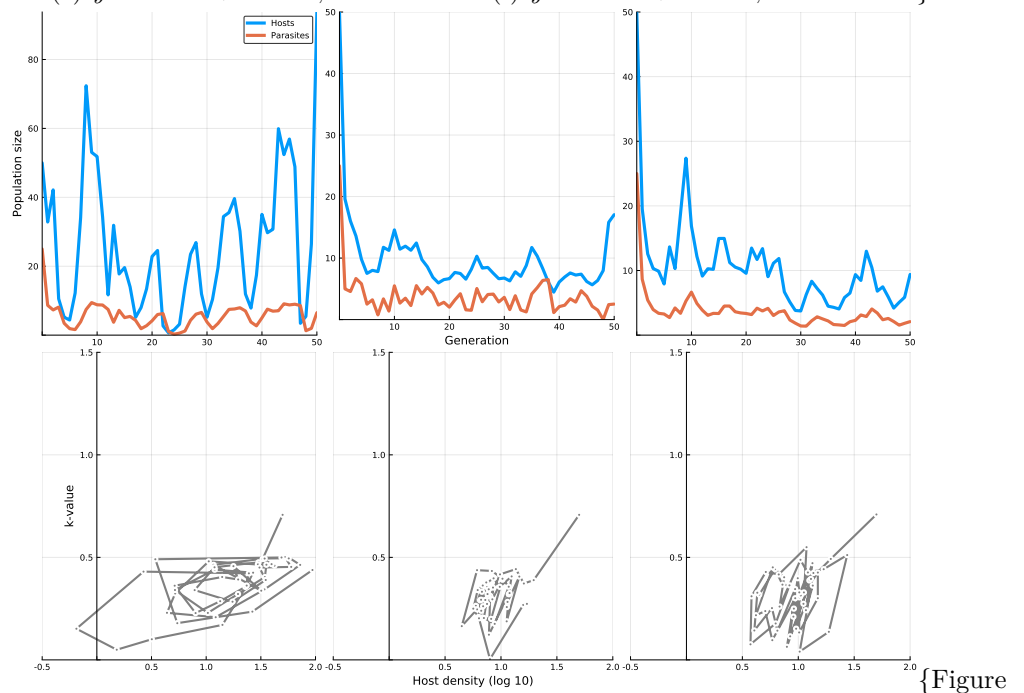


4: (a) Deterministic simulations of the host and generalist parasite population dynamics (Eq.1, Eq.3, Eq.4) with the following parameters: $F = 4$, $D = 0.5$, $h = 10$, $b = 25$, $a = 0.5$ and $Th = 0$ and $m = 0.5$. (b) The relationship between the mortality caused

each generation by parasitism (k-values) and the log10 host density for the fifty first generations of the population dynamics in (a).}

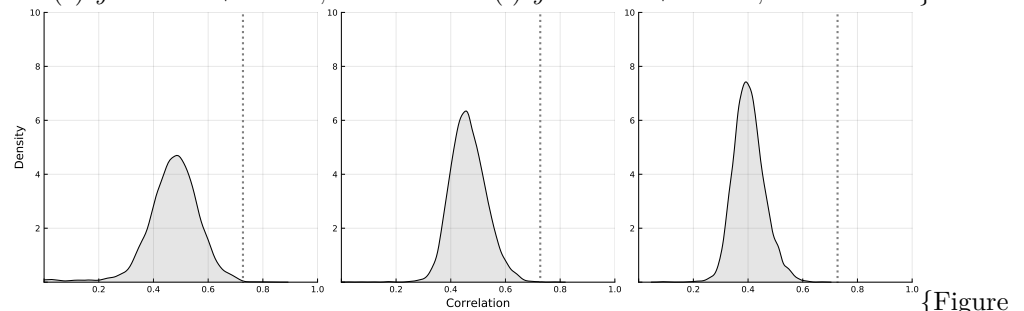


5: (a) - (c) Deterministic simulations of the host and specialist parasite population dynamics (same as in Figure 3a) except for one parameter that is treated as a normally distributed stochastic variable: (a) $D = 0.5 \pm 0.5$, (b) $c = 0.5 \pm 0.5$ and (c) $a = 0.5 \pm 0.5$. The other parameters are the same as in Figure 3a. (d) - (f) The relationship between the mortality caused each generation by parasitism (k-values) and the log10 host density for the fifty first generations, linked to (a), (b) and (c) respectively. The regression statistics for each relationship go as follows: (d) $y = 0.184 + 0.211x$; $r^2 = 0.171$. (e) $y = 0.329 + 0.054x$; $r^2 = 0.254$. (f) $y = 0.190 + 0.158x$; $r^2 = 0.120$ }

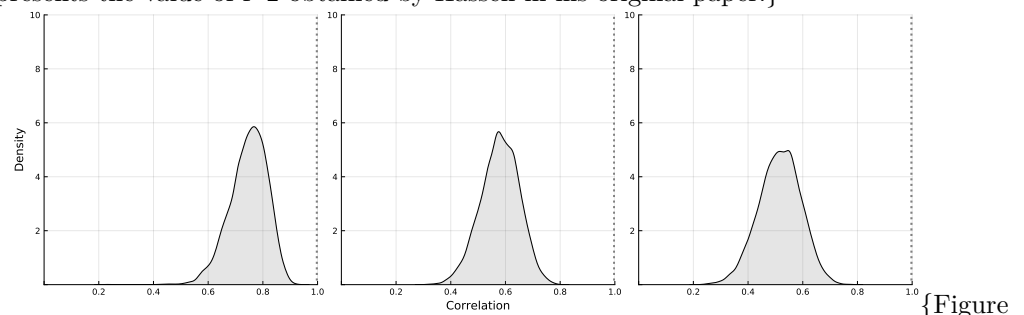


6: (a) - (c) Deterministic simulations of the host and generalist parasite population

dynamics (same as in Figure 4a) except for one parameter that is treated as a normally distributed stochastic variable: (a) $D = 0.5 \pm 0.5$, (b) $h = 10 \pm 5$ and (c) $a = 0.5 \pm 0.5$. The other parameters are the same as in Figure 3a. (d) - (f) The relationship between the mortality caused each generation by parasitism (k-values) and the log10 host density for the fifty first generations, linked to (a), (b) and (c) respectively. The regression statistics for each relationship go as follows: (d) $y = 0.146 + 0.192x$; $r^2 = 0.243$. (e) $y = 0.306 + 0.015x$; $r^2 = 0.214$. (f) $y = 0.149 + 0.160x$; $r^2 = 0.107$ }



7: (a) - (c) Distribution of the values of correlation coefficient (r^2) obtained for the 5000 simulations done in Figure 5(d) to Figure 5(f) respectively. The dotted line represents the value of r^2 obtained by Hassell in his original paper.} {Figure



8: (a) - (c) Distribution of the values of correlation coefficient (r^2) obtained for the 5000 simulations done in Figure 6(d) to Figure 6(f), respectively. The dotted line represents the value of r^2 obtained by Hassell in his original paper.} {Figure

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