[Re] Insect natural enemies as regulating factors

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> **A reference implementation of**
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> → Hassell, M. P. Insect Natural Enemies as Regulating Factors. Journal of Animal Ecology, vol. 54, no. 1, 1985, pp. 323–334.

Introduction

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 systems are very different. Thompson [8] 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 [6] proposed other models for which the rate of increase of the parasites is limited by their capacity to find hosts. These were the basis for many other models where parasites act as regulating factors (Hassell [5]; Rockwood [7]).

In 1983, Dempster [3] 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 [4] analyzed an 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 host-parasitoid 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 [9]).

We used information from Hassell [4] to replicate the model. We were able to replicate the results central to the article. In addition, we made new analyses for the stochastic models that bring additional support to Hassell [4] arguments. To our best knowledge, the original implementation was not available. The code for the simulations and the figures were written in *Julia* v0.6.2.

Methods

The mathematical formulation used in this paper to show the difficulties of detecting natural enemies as regulating factors are the same that were used in the original paper by Hassell [4] . First of all, the host population dynamics are given as

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

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

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

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.

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

where a is the per capita searching efficiency of the parasitoids, m is the extent of clumping of the parasitoids attacks and T_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. Generalist parasite dynamics follows the equation

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

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

To determine if the natural enemies can be declared as density-dependent factors, the host population mortality due to parasitism ($k - value$) is plotted against population density for each simulated generation. The correlation coefficient r of the resulting scatter plot indicates the strength of the density-dependence of natural enemies. The higher r is, the strongest the relation between hosts and parasites is. The host mortality is given by

$$k_{\text{value}} = \log_{10} \frac{N_t}{S} \tag{5}$$

where S is the number of hosts that survived parasitism. This number is given by the host population density multiplied by the probability of escaping mortality from natural enemies (eq. 6).

$$S = N_t \times f(N_t, P_t) \tag{6}$$

The objective in this paper is to reproduce the main results of the original publication. Therefore, we did not reproduce figures 1, 2 and 7. Figure 1 was a schematic representation of an insect life cycle. Figure 2 and Figure 7 represent relationship between parameters and population size/proportion of parasited host. 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 used the exact same values that were used in the original paper for the different parameters.

The software used to code and 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

Deterministic model

The reproduced population dynamics for the host population and for the specialist parasitoids (fig. 1 (a) and (b)) 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 stabilize, 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 (c) and (d), where we standardized the axes of the graphs. At first sight, in Hassell's paper, the $k - values$ in fig. 1 (c) seem almost as high as in fig. 1 (d). However, when using the same scale for the two graphs, we can see that the $k - values$ in the case of high level of clumping show a lot less variation than with a lower level of clumping.

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 (fig. 2). This shows 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 fig. 1 (a) and (c).

Stochastic model

When the models include stochasticity, the resulting population dynamics between hosts and parasites are very different compared to the deterministic models. Overall, the results obtained in the replications are very similar to the original paper. Whether we look at the model for the specialist parasitoids or the one for the generalist parasitoids, both show irregular oscillations in the host-parasitoid population dynamics (fig. 3 and fig. 4, (a), (b) and (c)). The addition of stochastic parameters prevents the stabilization of host populations and makes it more difficult to identify parasitoids as a density-dependent control factor, except in fig. 4 (a). The relationships between the $k - values$ and the host density are similar in Hassell's publication and in ours. However, the regression for these relationships in our replication tend to have a determination coefficient (R^2) higher than the one found by Hassell, but they are generally really close. Discrepancies in the coefficient of determination can be explained by different routines for pseudo random number generation.

Moreover, the oscillations we obtained in fig. 4 (b) are not the same range compared to the original paper. More precisely, the oscillations we obtained with h stochastic are smaller compared to the original paper (fig. 4 (b)).

Because the inclusion of stochastic parameters in the population dynamics causes variability in the outputs, the results from two successive simulations can be very different. In order to account for this variability and to show how it can affect the population dynamics of the hosts and parasites, we added fig. 5 and fig. 6. These figures show the extent of the variation of the correlation coefficient (r) obtained in 5000 different simulations (as opposed to a single simulation in the original article). A dotted line was added to represent the value of the correlation coefficient (r) that came out of the deterministic models. The values of r vary greatly for every stochastic parameter. In every case, the mean value of r is lower in the stochastic models than in the deterministic models. This is in agreement with Hassell's results, and shows that stochasticity makes it harder to see the density dependence effect of the parasites, whether they are generalist or specialist.

Discussion

Overall, we were able to replicate most results from Hassell [4]. We found the exact same results for the deterministic model. We standardized the limits for the axes, which was not the case in the original paper. This allows a more convenient comparison of the different results.

As expected, we did not find the exact same dynamic for the stochastic model. The figures we added (fig. 5 and fig. 6) showed how adding stochasticity into the model can cause great variability in the output. For example, in the specialist parasitoid model with a stochastic density-dependent host survival (D), the correlation we found (fig. 5 (a)) was sometimes very weak ($r \approx 0.2$) and some other times almost as strong as the deterministic model ($r \approx 0.7$). Also, the correlation between the mortality from parasitism (k-value) and host density (N) found in the stochastic model was almost always weaker than in the deterministic model (fig. 5 and fig. 6). Therefore, the results we added strongly support the main argument from the original paper: adding stochasticity almost always obscures the density-dependent effect of natural enemies.

The discrepancies we noted in the dynamics of the stochastic model with the generalist parasite and a stochastic saturation number of parasitoid (h; in fig. 4 (b)) are difficult to explain. It seems unlikely that it is cause to the model implementation itself or computational errors since we successfully replicated results from all the other numerical experiments. Without the original implementation, we can only speculate on the difference between the original implementation and ours. This model is the only one with a stochastic parameter normally distributed with a mean not equal to its associated standard deviation. We tried with an h normally distributed with a mean and a standard deviation of 5 (fig. 7), and the results were a lot more similar to the one from Hassell [4] than what we originally had (fig. 4 (b)). Again, this is only an hypothesis on the kind of error that could explain the differences between the original paper and ours.

The mathematical model from the original paper was well detailed, which allowed us to create our own implementation. The equation for the number of survivors from parasitism (S) was the only one we needed to deduce from our own interpretation. This variable is used in the computation of the mortality (k_{value}) which is a well documented index. Therefore, this has not limited us in the replication of the article, and the fact that the deterministic simulations match these of the original paper suggests that we used the same formulation for S.

Conclusion

We were able to replicate the original results. Even if we did not find the exact same dynamics for the stochastic models, we draw the same conclusions : the density-dependent effect from natural enemies is obscured by time delays and/or stochasticity. This makes it very difficult to detect natural enemies as regulating factors from life table data. In addition, we added density plots for the correlation coefficient from 5000 iterations of each stochastic model. This allowed us to determine that the differences between our results and Hassell's were explained by the stochasticity of the models. Also, these new results add a strong support to the arguments of the original paper. To conclude, the reproduction of the reference article Hassell [4] was successful and we hope it adds to the legacy left by this significant paper in the history of population dynamics.
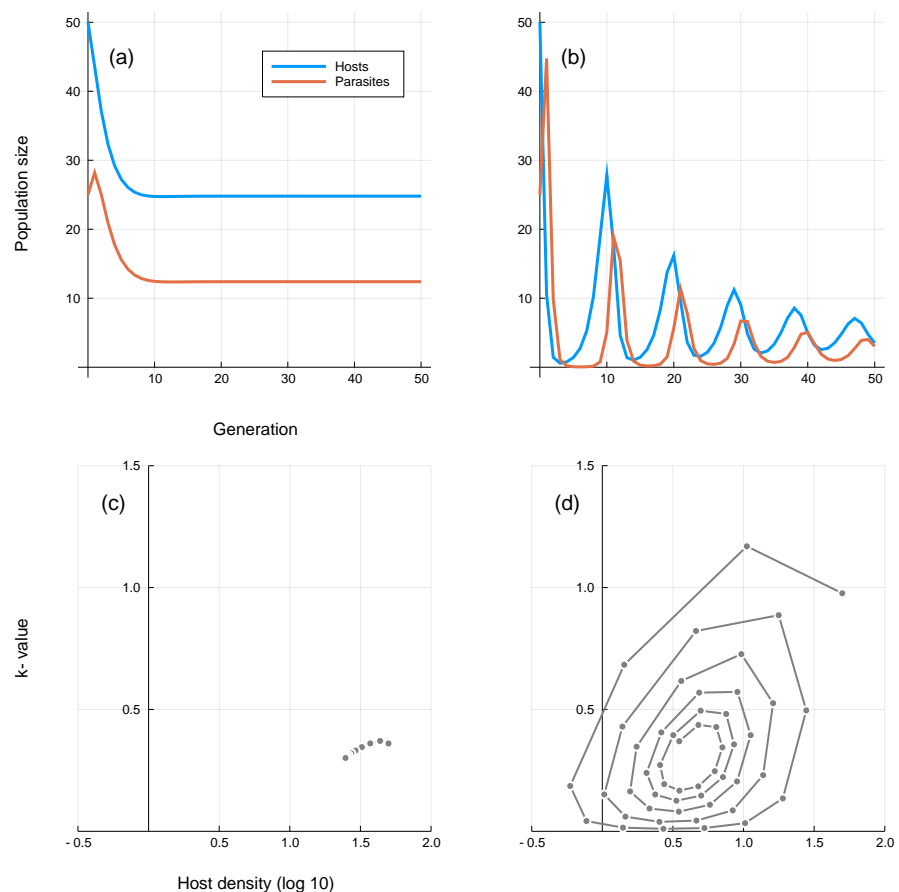
Figure 1: (a) and (b) Deterministic simulations of the host and specialist parasite population dynamics (Eq.1, Eq.2, Eq.3) using two different level of clumping in the parasitoid attacks: (a) $m = 0.2$; (b) $m = 0.8$. The other parameters used are the same in both (a) and (b): $F = 4$, $D = 0.5$, $c = 1$, $a = 0.5$ 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.
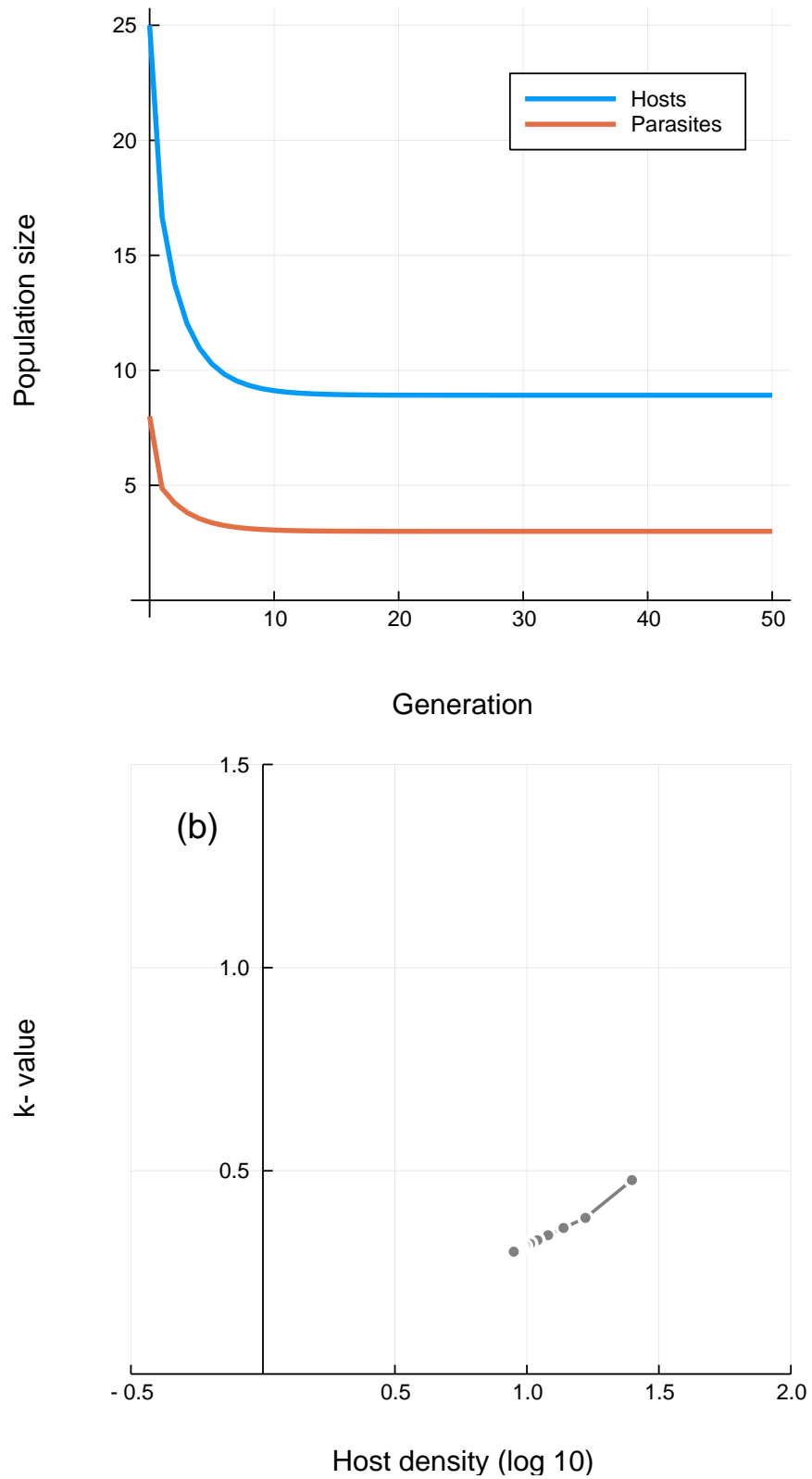
Figure 2: (a) Deterministic simulations of the host and generalist parasite population dynamics (Eq.1, Eq.3, Eq.4) with the following parameters: F = 4, D = 0.5, h = 10, b = 25, a = 0.5 and Th = 0 and m = 0.5. (b) The relationship between the mortality caused each generation by parasitism (k-values) and the log10 host density for the fifty first generations of the population dynamics in (a).
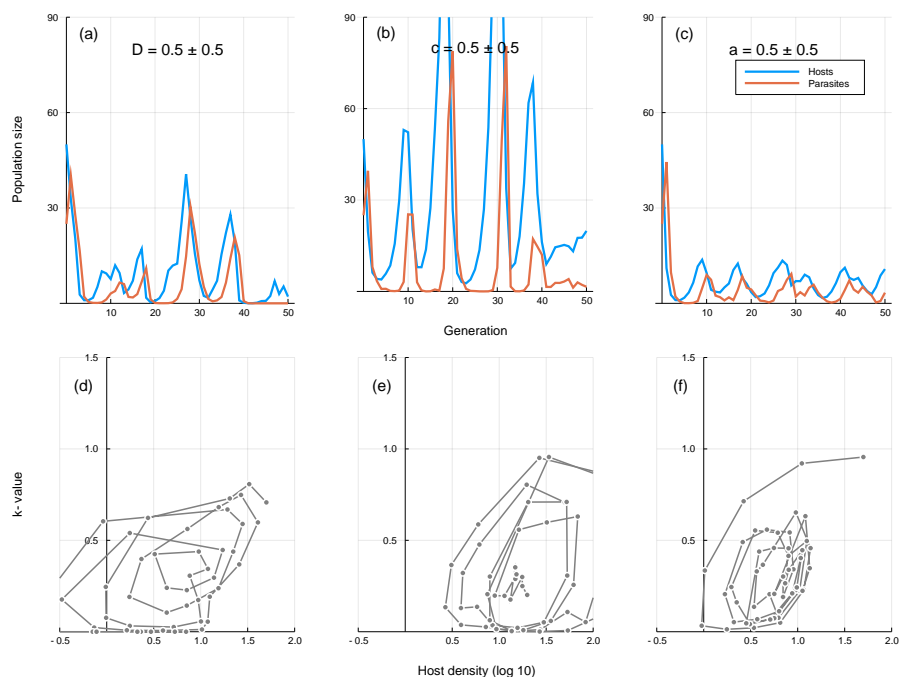
Figure 3: (a) - (c) Deterministic simulations of the host and specialist parasite population dynamics (same as in Figure 3a) except for one parameter that is treated as a normally distributed stochastic variable: (a) D = 0.5 ± 0.5, (b) c = 0.5 ± 0.5 and (c) a = 0.5 ± 0.5. The other parameters are the 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) $y = 0.145 + 0.203x$; $r^2 = 0.312$. (e) $y = 0.044 + 0.204x$; $r^2 = 0.106$. (f) $y = 0.069 + 0.331x$; $r^2 = 0.223$.
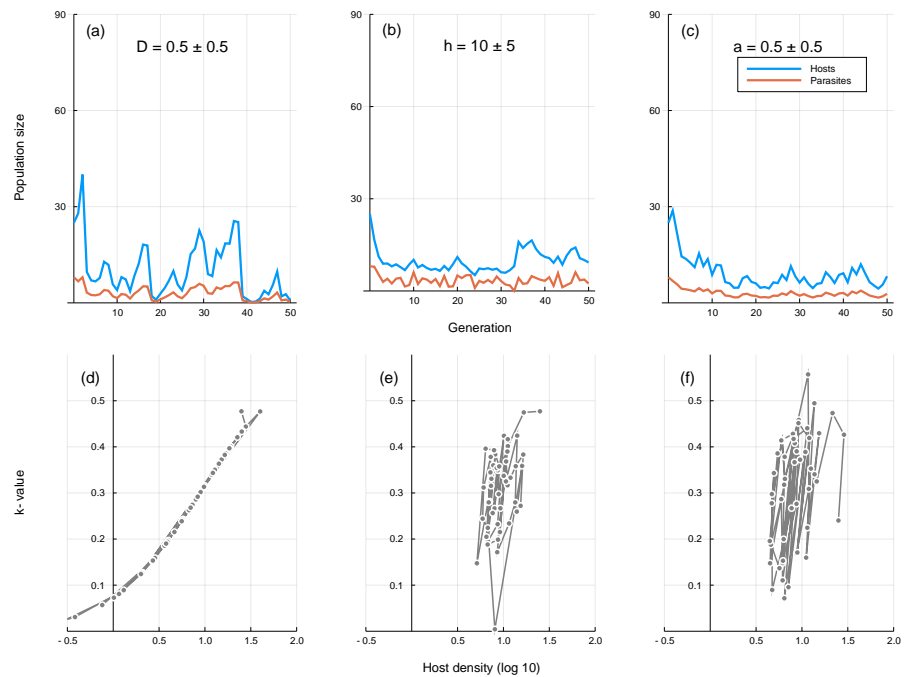
Figure 4: (a) - (c) Deterministic simulations of the host and generalist parasite population dynamics (same as in Figure 4a) except for one parameter that is treated as a normally distributed stochastic variable: (a) D = 0.5 ± 0.5, (b) h = 10 ± 5 and (c) a = 0.5 ± 0.5. The other parameters are the same 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) $y = 0.070 + 0.249 \times x$; $r^2 = 0.967$. (e) $y = 0.018 + 0.302x$; $r^2 = 0.223$. (f) $y = 0.062 + 0.272x$; $r^2 = 0.178$.
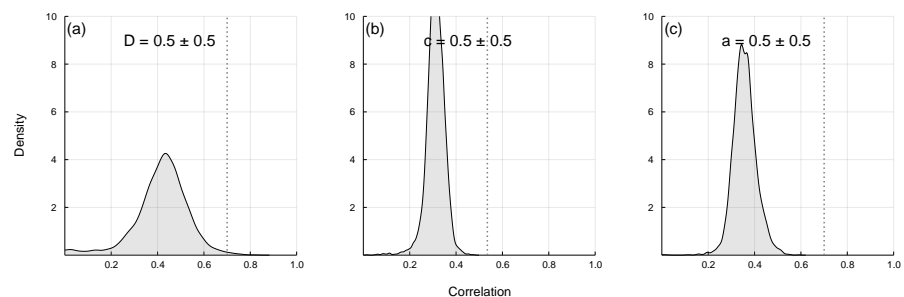

Figure 5: (a) - (c) Distribution of the values of correlation coefficient (r) obtained for the 5000 simulations done in Figure 5(d) to Figure 5(f) respectively. The dotted line represents the value of r obtained in the deterministic model.
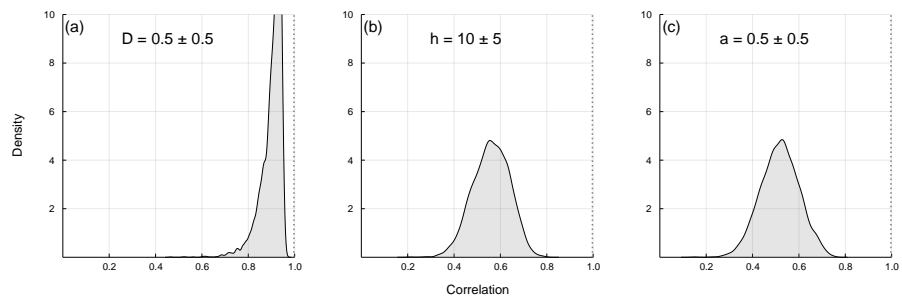
Figure 6: (a) - (c) Distribution of the values of correlation coefficient (r) obtained for the 5000 simulations done in Figure 6(d) to Figure 6(f), respectively. The dotted line represents the value of r obtained in the deterministic model.

References

[1] Roy M Anderson and Robert M May. "Regulation and stability of host-parasite population interactions: I. Regulatory processes". In: *The Journal of Animal Ecology* (1978), pp. 219–247.

[2] Jeff Bezanson et al. "Julia: A Fresh Approach to Numerical Computing". In: *SIAM Review* 59.1 (2017), pp. 65–98. DOI: 10.1137/141000671. eprint: https://doi.org/10.1137/141000671. URL: https://doi.org/10.1137/141000671.

[3] JP Dempster. "The natural control of populations of butterflies and moths". In: *Biological Reviews* 58.3 (1983), pp. 461–481.

[4] M. P. Hassell. "Insect Natural Enemies as Regulating Factors". In: *Journal of Animal Ecology* 54.1 (1985), pp. 323–334. ISSN: 00218790, 13652656. URL: http://www.jstor.org/stable/4641.

[5] Michael Patrick Hassell. *The dynamics of arthropod predator-prey systems*. Princeton University Press, 1978.

[6] Alexander J Nicholson and Victor A Bailey. "The Balance of Animal Populations.—Part I." In: *Journal of Zoology* 105.3 (1935), pp. 551–598.

[7] Larry L Rockwood. *Introduction to population ecology*. John Wiley & Sons, 2015.

[8] WR Thompson. "La theorie mathematique de l'action des parasites entomophages et le facteur du hasard." In: *Annu Fac Sci Mars* 2 (1924), pp. 69–89.

[9] Peter Turchin. "Rarity of density dependence or population regulation with lags?" In: *Nature* 344.6267 (1990), p. 660.
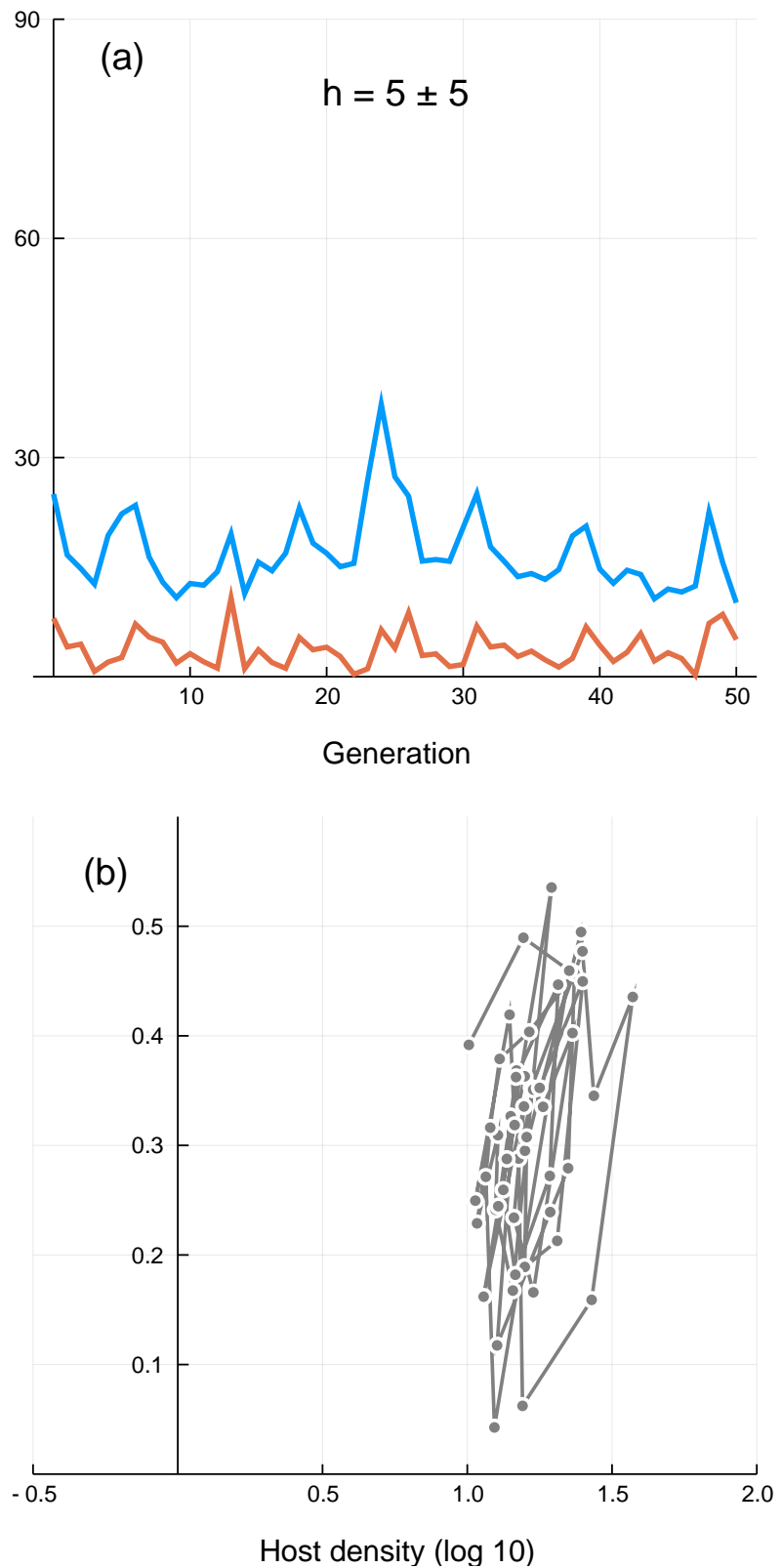
Figure 7: (a) Deterministic simulations of the host and generalist parasite population dynamics (same as in Figure 6b) except that we used $h = 5 \pm 5$. (b) The relationship between the mortality caused each generation by parasitism (k-values) and the log10 host density for the fifty first generations, linked to (a). The regression statistics go as follows: $y = \text{-}0.169 + 0.395x$; $r^2 = 0.181$.