

[Re] On the coexistence of specialists and generalists

Timothée Poisot¹

¹ Département de Sciences Biologiques, Université de Montréal, Montréal, QC, Canada

timothee.poisot@umontreal.ca

Editor

Name Surname

Reviewers

Name Surname

Name Surname

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The authors have declared that no competing interests exist.

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A reference implementation of

→ On the coexistence of specialists and generalists, David Sloan Wilson and Jin Yoshimura, *The American Naturalist* 144:4, 692-707, 1994.

Introduction

The coexistence of specialists and generalist within ecological communities is a long-standing question. **wils94csg** have suggested that this coexistence can be understood when examined in the light of (i) differential fitness loss associated to specialism, (ii) active habitat selection, (iii) negative density dependence due to competition, and (iv) stochastic changes in habitat quality, that allow combinations of species to persist even though coexistence would not be possible in a purely deterministic world. Here I propose an implementation of this model in *Julia* [**beza17jfa**], and show that it is able to reproduce most figures from the original manuscript.

Methods

The **wils94csg** model describes three species across two patches of habitat. Species 1 is a specialist of habitat 1, species 2 is a specialist of habitat 2, and species 3 is a generalist. This results in the maximum density that these species can reach in both habitats:

$$\mathbf{K} = K_1 a K_1 a K_2 b K_1 b K_2. \quad (1)$$

In this matrix, K_1 is the quality of habitat 1, K_2 is the quality of habitat 2, a is the fitness cost of the specialist in its non-optimal environment, and b is the fitness cost of generalism. Note that $1 > b > a > 0$.

Species distribute themselves across habitats in a way that minimizes the negative effect of other species on their fitness. This is modelled by each species having a value p_i , which is the proportion of its species choosing habitat 1. Values of \mathbf{p} are found by measuring the negative density effect of each species in each habitat:

$$D_{l1} = \frac{\sum_{i \in l, m, m} p_i N_i}{K_{l1}} \quad (2)$$

and

$$D_{l2} = \frac{\sum_{i \in l, m, m} (1 - p_i) N_i}{K_{l1}}. \quad (3)$$

The value of p_l for which $D_{l1} = D_{l2}$ is

$$p_l = - \frac{(K_{l1} + K_{l2})(N_m p_m + N_n p_n) - K_{l1}(N_l + N_m + N_n)}{N_l(K_{l1} + K_{l2})}. \quad (4)$$

We fix p_m and p_n , and find the value of p_l , while enforcing the constraint of $0 \leq p_l \leq 1$. Repeating this procedure a few times for the different species yields the optimal values of \mathbf{p} ; we can measure the density of individuals in both habitats. Before we do so, there is a proportion g of individuals that select habitats at random. Given a total population size of N_i , there are $N_i(g/2)$ individuals will go to either habitat, and $N_i(1 - g)p_i$ will pick habitat 1. With this information, we can write the matrix describing habitat selection:

$$\mathbf{N} = N_1 \left(\frac{g}{2} + (1-g)p_1 \right) N_1 \left(\frac{g}{2} + (1-g)(1-p_1) \right) N_2 \left(\frac{g}{2} + (1-g)p_2 \right) N_2 \left(\frac{g}{2} + (1-g)(1-p_2) \right) N_3 \left(\frac{g}{2} + (1-g)p_3 \right) N_3 \left(\frac{g}{2} + (1-g)(1-p_3) \right) \quad (5)$$

Finally, the fitness of every species in each habitat is given by

$$W_{ij} = \exp \left[r \left(1 - \frac{N_{i1} + N_{i2} + N_{i3}}{K_{ij}} \right) \right], \quad (6)$$

where r is the growth rate (assumed equal). The population size at the next timestep is simply given by

$$\mathbf{N}_{t+1} = \mathbf{W} \odot \mathbf{N}_t, \quad (7)$$

where \odot is the element-wise multiplication.

Results

Original sources were not available, and no attempts were made to contact the authors. For some non-stochastic situations, it is possible to calculate expected values by hand. The original manuscript does provide some of these values, and they were used to test this implementation. Figure 2A and 2B in the original manuscript provide a good diagnostic value, as they are based on non-stochastic situations. In **fig:02**,

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.

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 {#tbl:table}

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A reference to table **tbl:table**. A reference to figure **fig:logo**. A reference to equation **eq:1**. A reference to citation **markdown**.

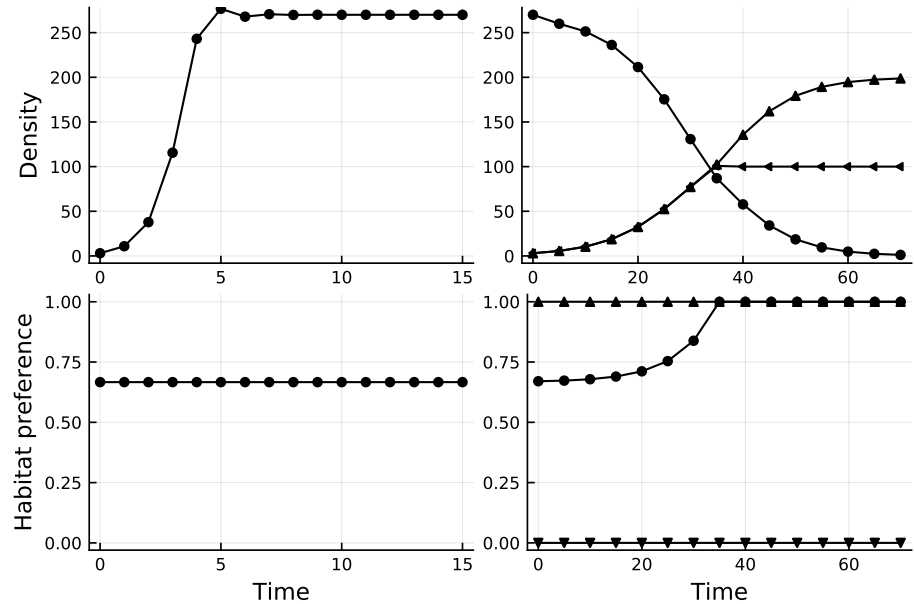


Figure 1: Population dynamics and habitat preference of the generalist alone (left), and following invasion by the two specialists at the generalist equilibrium (right).



Figure 2: Figure caption

{#eq:1}

$$A = \sqrt{\frac{B}{C}}$$