[Re] On the coexistence of specialists and generalists

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> **A reference implementation of**
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> → 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. Wilson and Yoshimura [4] 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* [1], and show that it is able to reproduce most figures from the original manuscript.

Methods

The Wilson and Yoshimura [4] 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:

$$\mathbf{K} = \begin{bmatrix} K_1 & aK_1 \\ aK_2 & K_2 \\ bK_1 & b_K2 \end{bmatrix} . \tag{1}$$

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 $1 > b > a > 0$. The initial value of K_1 is chosed randomly, using

$$K_1 = K_{1,\min} + \mathrm{rnd}_1(K_{1,\max} - K_{1,\min}) .$$

If the variation of the two environments is linked, then

$$K_2 = K_{2,\min} + (1 - \mathrm{rnd}_1)(K_{2,\max} - K_{2,\min}) .$$

If the variation is independent, then

$$K_2 = K_{2,\min} + \mathrm{rnd}_2(K_{2,\max} - K_{2,\min}) .$$

Both rnd_1 and rnd_2 are random numbers uniformly distributed in $[0, 1]$.

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:

$$D_{l1} = \frac{\sum_{i \in l,m,n} p_i N_i}{K_{l1}} \tag{2}$$

and

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

The value of p_l for which $D_{l1} = D_{l2}$ (checked using Maxima [2]) is

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

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:

$$\mathbf{N} = \begin{bmatrix} N_1(\frac{g}{2} + (1-g)p_1) & N_1(\frac{g}{2} + (1-g)(1-p_1)) \\ N_2(\frac{g}{2} + (1-g)p_2) & N_2(\frac{g}{2} + (1-g)(1-p_2)) \\ N_3(\frac{g}{2} + (1-g)p_3) & N_3(\frac{g}{2} + (1-g)(1-p_3)) \end{bmatrix} . \tag{5}$$

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

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

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

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

where $\odot$ is the element-wise multiplication.

Table 1: Default parameters. Unless otherwise specified, these parameters have been used for all figures.

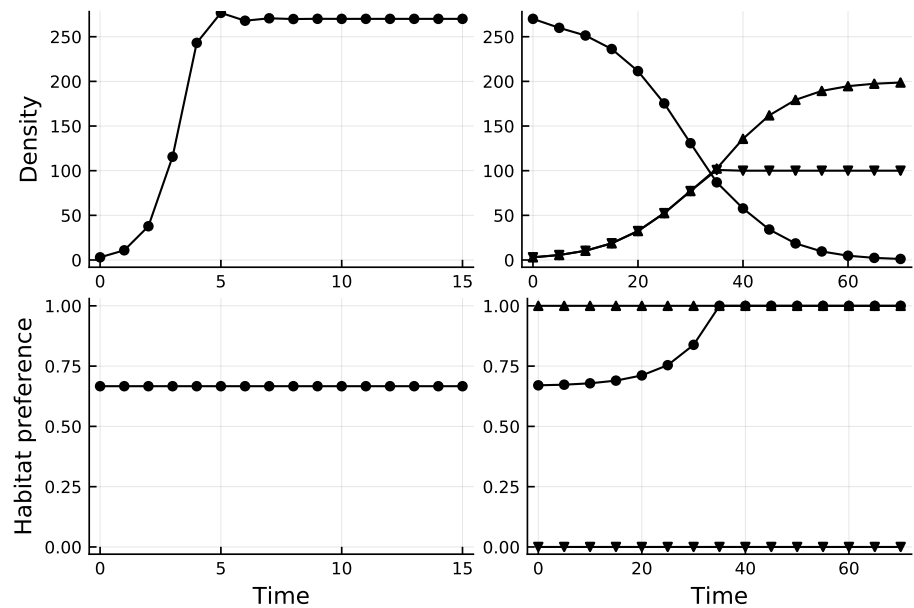| Parameter	Meaning	Default value
r	*per capita* growth rate	1.3
a	fitness cost of specialism	0.1
b	fitness cost of generalism	0.9
K_1	range of habitat quality (1)	$[200, 200]$
K_2	range of habitat quality (1)	$[100, 100]$
g	proportion picking a random habitat	0.0

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

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. All default parameter values are given in 1. In all figures, circles represent the generalist, upper and lower triangles represent the specialists of habitats 1 and 2 (respectively), and a diamond is used when both specialists have the same behaviour.

Figure 2A and 2B in the original manuscript provide a good diagnostic value, as they are based on non-stochastic situations. These are reproduced in 1. As in the original simulations, the generalist alone overshoots its carrying capacity at $t = 5$, and the stabilizes at a value of $N_3^\star = 270$. Note also that $p_3 = 2/3$, which represents the ratio of habitat qualities. When adding specialists at initial densities of $N_1 = N_2 = 1$, we observe (i) that the preference of the generalist shifts towards habitat 1 to avoid competition in the smallest habitat, and (ii) the density of the specialist of habitat 2 stabilizes as soon as the generalist abandons habitat 2 (at $t \approx 35$).

In 2, this implementation gives the same qualitative results as the original article. There are small quantitative differences in output, which are in my opinion explained by the initial population densities (which are not given in the original article). Absent variation in habitat quality, generalists cannot persist, and the specialists both reach $N^\star = \bar{K}$. There is a value of variation for which the densities of specialists and generalists are equal (about 110 for tied variations, and 130 for independent variations).

In 3, the same qualitative result (generalists increase in abundance when one habitat becomes larger). The quantitative differences can, again, be explained by changes in the initial population densities. Finally, the results in 4 and 5 can also be replicated.
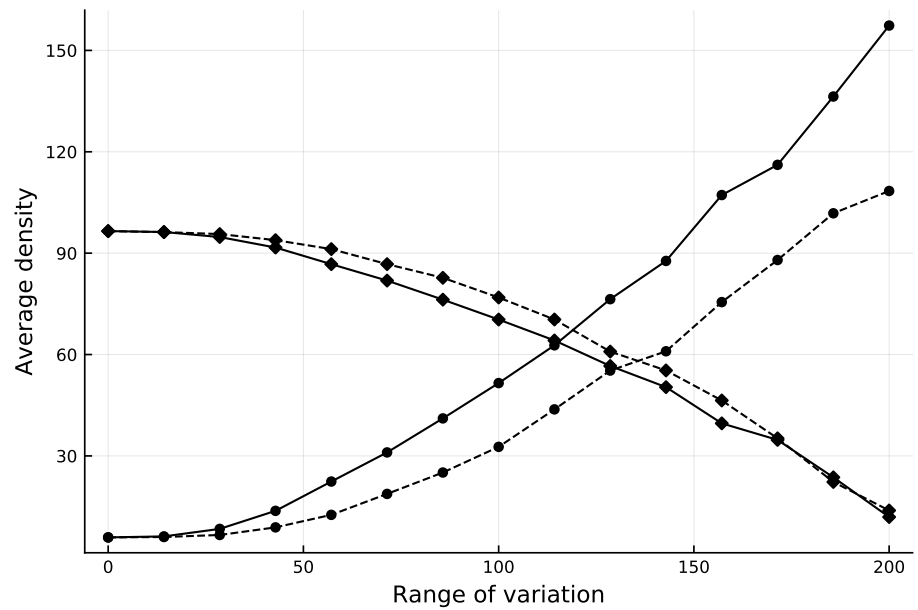
Figure 2: Consequences of increasing the range of variation of both K_1 and K_2. Dashed lines represent independent variation, and solid lines tied variations, as in the original article.
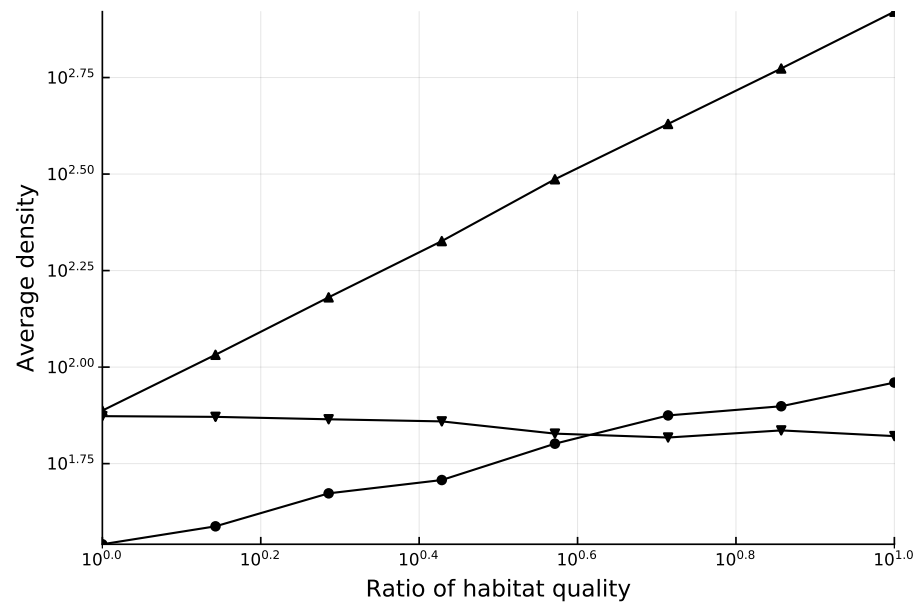

Figure 3: Consequences of changing the relative quality of habitats 1 and 2 on coexistence.
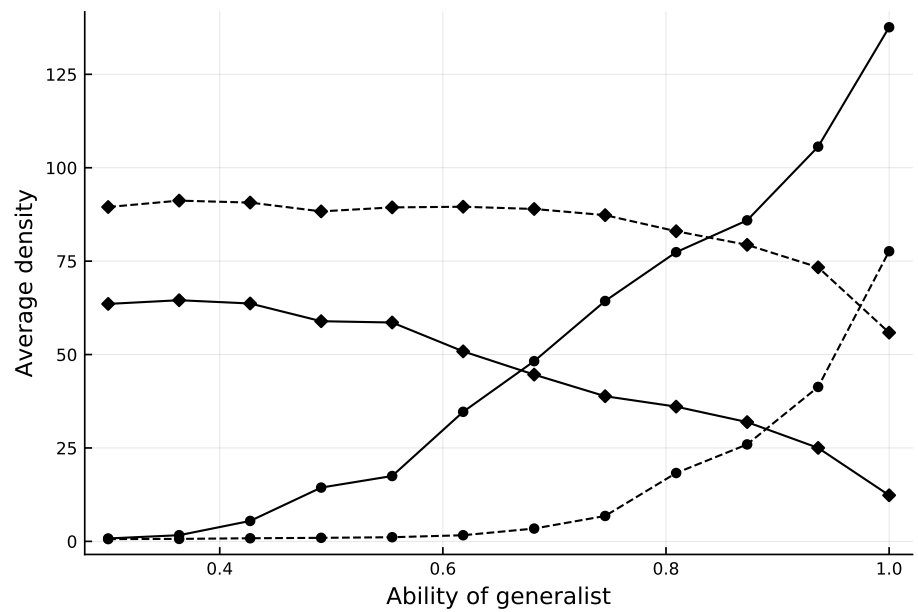
Figure 4: Consequences of changing g, the ability of the generalist, on coexistence. Dashed lines represent independent variation, and solid lines tied variations, as in the original article. Note that the direction of the axis is *reversed* with regard to the original figure.
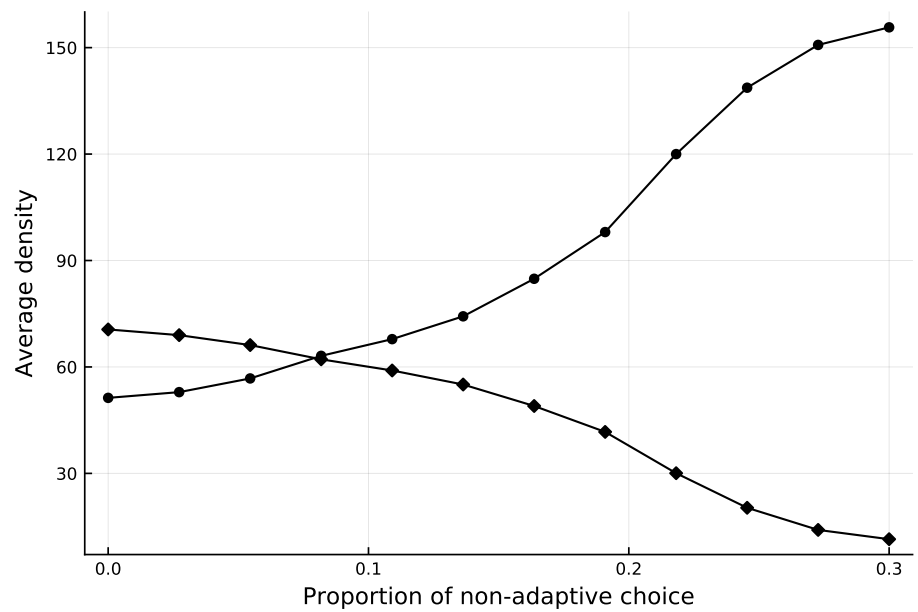

Figure 5: Consequences of changing the proportion of individuals picking their habitat at random.
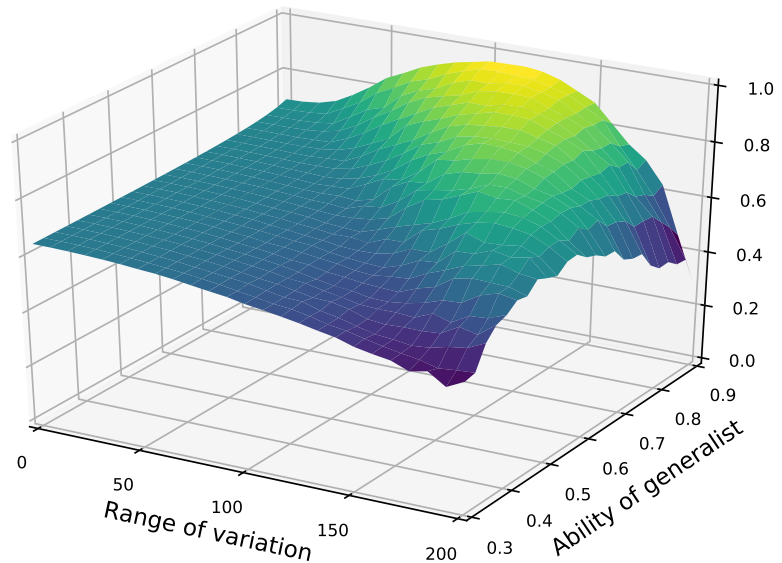
Figure 6: Response of the model to changing the ability of the generalist *and* the range of variation. While the response to environmental change is hump-shaped when generalists are competitive (b close to unity), it becomes monotonously decreasing for generalists with lower competitive ability (b close to a).

Conclusion

I believe that this implementation faithfully reproduces the results of Wilson and Yoshimura [4]. A single run of the model (using 100 generations as in the original article) completes in $\approx 5 \times 10^{-3}$s. This makes this implementation usable for teaching, as it is not time consuming to generate results. As an example, I merged the output of 2 and 4, to generate the response of Pielou's evenness [3],

$$J' = - \left(\sum_{i=1}^{3} \frac{N_i}{N} \ln \frac{N_i}{N} \right) \frac{1}{\ln 3} \,,$$

which measures the extent to which all species have the same density. It appears that J', a measure of coexistence, changes in response to both the rate of variation *and* generalist ability. The results are presented in 6.

References

[1] J. Bezanson et al. "Julia: A Fresh Approach to Numerical Computing". In: *SIAM Review* 59.1 (Jan. 2017), pp. 65–98. DOI: 10.1137/141000671. (Visited on 03/21/2017).

[2] Maxima. *Maxima, a Computer Algebra System. Version 5.34.1.* 2014.

[3] E. C. Pielou. "Shannon's Formula as a Measure of Specific Diversity: Its Use and Misuse". In: *The American Naturalist* 100.914 (Sept. 1966), pp. 463–465. DOI: 10.1086/282439. (Visited on 10/18/2017).

[4] David Sloan Wilson and Jin Yoshimura. "On the Coexistence of Specialists and Generalists". In: *The American Naturalist* 144.4 (Oct. 1994), pp. 692–707. DOI: 10.1086/285702. (Visited on 10/10/2017).