More competitors than resources: Apparent competition and nonequilibrium coexistence

1. APPARENT COMPETITION

Consider a single resource (R), a consumer (N), and a top predator (P) in the model

$$\frac{dR}{dt} = sR\left(1 - \frac{R}{L}\right) - bRN$$

$$\frac{dN}{dt} = cRN - dN - \beta NP$$

$$\frac{dP}{dt} = \gamma NP - \delta P$$

Here, the resource is growing according to the logistic model in absence of the consumer. The consumer has a linear functional response, i.e., the amount of resource eaten is proportional both to the density of the resource and to the density of the consumer. The consumer's reproduction is proportional to the amount of resource consumed, whereas the consumers die at a constant rate. Finally, the top predator eats the consumer with a linear functional response, and the top predator's dynamics is analogous to that of the consumer.

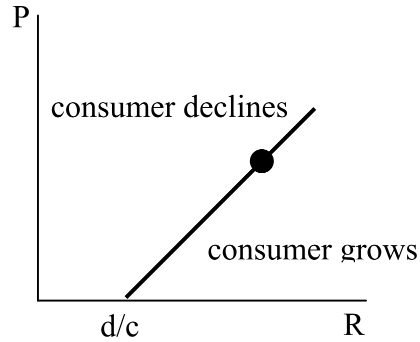
Our focal species is the consumer. The consumer population has zero growth if

$$cRN - dN - \beta NP = 0$$

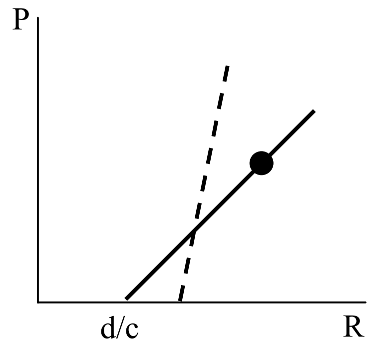
or, after dividing by N (and hence assuming that the population is at the nontrivial equilibrium), if

$$P = \frac{cR - d}{\beta}.$$

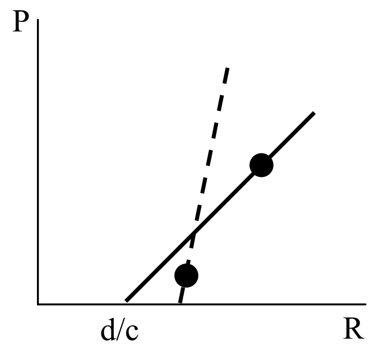
The consumer population will grow if there is more resource and less top predators, as shown below. It is also possible to calculate the joint equilibrium of all three populations (by setting all three equations equal to zero, and solving for R, N, and P). The resulting equilibrium is denoted by the dot in the figure.



You should recognise this figure as pretty similar to the one we drew for two resources and one consumer. Following the same lines of reasoning, you can convince yourself that a second consumer with the dashed zero-growth line can grow when rare:



and if the second consumer species, in absence of the first one, has its equilibrium point as shown below, then the two consumers coexist with one resource and the top predator.



In fact, the top predator behaves essentially analogously to a second resource (except for the obvious difference that less rather than more predator is better for population growth). In this way, it is possible that there are more consumer species coexisting than the number of resources; the predators also count as if they were "resources" when we count the resources in order to determine the maximum number of coexisting species under the principle of competitive exclusion. This has been termed "apparent competition" (the consumers behave as if they were competing for a second resource) and can be visualised as "competition for predator-free space".

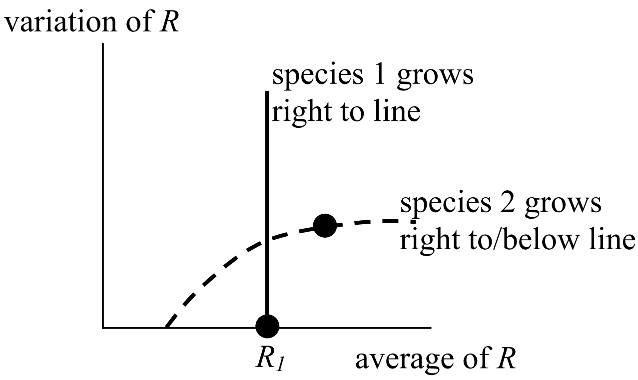
2. NONEQUILIBRIUM COEXISTENCE

It is possible to have more consumer species than resources also if the species coexist not in equilibrium, but e.g. they have a limit cycle. Here, I only sketch the principle; the detailed model analysis is given by Armstrong and McGehee (Am. Nat. 115:151-170, 1980).

Assume that we have one resource and two consumers. One of the consumer species has a linear functional response as in all competition models we have studied so far, but the other consumer eats the resource with a Holling II type functional response. From the predator-prey models we know that the first consumer (with linear functional response) will attain a stable equilibrium if the second consumer is not present; the second consumer alone (with Holling II functional response), however, can have limit cycles.

I demonstrate coexistence by showing that the second consumer can grow if introduced at a low density at the equilibrium of the first consumer, and that also the first consumer can invade the stable limit cycle of the second consumer (with appropriate model parameters). The first part is easy: We can choose the parameters of the second consumer such that it can grow at the stable resource level R_1 set by the first consumer. The second part contains the novel point. If the second consumer is the common one, the resulting limit cycles harm the second consumer itself: The consumer suffers when resource density is low in the cycle, and cannot make full use of the resource when resource density is high, since this consumer cannot eat more than a certain amount of resource per unit of time (cf. Holling II functional response). The lows of resource density are thus not compensated by the highs. The broader the limit cycles are, the higher *average* resource density is necessary for the second consumer to counter the harmful effect of the cycles. With linear functional response, however, the lows of resource density are exactly compensated by the highs, and so the first consumer is not sensitive to cycles, only the average resource density matters for this species. If the average resource density is above R_1 (which is perfectly possible if the cycles of the second species are broad), then the first consumer can invade when the second consumer is common, and the two species will coexist while still exhibiting cycles (coexistence would not be possible at equilibrium).

To summarise graphically, the growth of the first consumer depends only on the average resource density $\overline{R}$, but the growth of the second consumer also depends on the variation of R:



Again, this figure is similar in logic to the case of two resources: Here, the variation of R behaves essentially analogously to a second "resource". Similar effects may be present when fluctuation is due to stochastic environmental effects. In fact, the average density, the variance of density, and all the higher moments of the density distribution might act as independent "resources" (better say independent dimensions). The maximum number of coexisting species in nonequilibrium populations is a pretty difficult, and largely unsolved question.