Exercises on Interspecific competition

Problem 4.1

Ennik (1960) grew white clover (Trifolium repens) and rye-grass (Lolium perenne) in pots, under conditions of low light and with different initial densities, obtaining the following results. These are formulated as a relationship between the ratio of clover density to rye-grass density at the end of the growing season and the same ratio at the beginning of the season:

<table>
<thead>
<tr>
<th></th>
<th>T/L initial</th>
<th>0.16</th>
<th>0.26</th>
<th>0.40</th>
<th>0.50</th>
<th>0.79</th>
<th>1.16</th>
<th>2.12</th>
<th>2.91</th>
<th>3.33</th>
</tr>
</thead>
<tbody>
<tr>
<td>T/L</td>
<td>final</td>
<td>0.48</td>
<td>0.58</td>
<td>1.00</td>
<td>1.48</td>
<td>1.67</td>
<td>1.98</td>
<td>1.88</td>
<td>2.10</td>
<td>1.49</td>
</tr>
</tbody>
</table>

Assume that at the beginning of the next-year season the ratio $T/L$ between the two densities is equal to the one recorded at the end of the previous-year season. Based on the provided data evaluate the likely time evolution of the ratio $T/L$ and determine whether the two species can coexist or, on the contrary, one species excludes the other.

Problem 4.2

The dynamics of two competing species is described by the Volterra equations

\[
\begin{align*}
\dot{N}_1 &= r_1 N_1 - \beta_{11} N_1^2 - \beta_{12} N_1 N_2 \\
\dot{N}_2 &= r_2 N_2 - \beta_{22} N_2^2 - \beta_{21} N_1 N_2
\end{align*}
\]

where $r_1 = r_2 = 0.5$, $\beta_{11} = 0.1$, $\beta_{22} = 0.2$, $\beta_{12} = 0.05$, $\beta_{21} = 0.2$.

What is the result of competition? Then assume that some predators are introduced that can prey upon the first species only. Their effect is to decrease the intrinsic rate of increase $r_1$ down to $r_1 - d_1$. Of course, the larger the number of introduced predators, the larger $d_1$. Discuss how the result of competition varies for increasing values of $d_1$. 


Problem 4.3
Ayala (1969) cultured two different species of fruitfly, *Drosophila pseudoobscura* and *D. serrata*, in the lab at 23 °C. He obtained the following results at equilibrium:

<table>
<thead>
<tr>
<th></th>
<th>Separate cultures</th>
<th>Mixed culture</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. <em>D. pseudoobscura</em></td>
<td>664</td>
<td>252</td>
</tr>
<tr>
<td>No. <em>D. serrata</em></td>
<td>1251</td>
<td>278</td>
</tr>
</tbody>
</table>

Determine why these experiments cannot be explained by Volterra-like competition models (logistic growth and competition terms proportional to the product of densities, like in problem 4.2).

Problem 4.4
The figure below (Tilman, 1982) shows the reproduction rates of two freshwater algal species (*Asterionella formosa* and *Synedra ulna*) with silicate being the limiting nutrient.

Instantaneous reproduction rate of the two algae species as a function of available nutrient (silicate), after Tilman (1982).

Assume that the two species have the same mortality rate. What is the result of competition for silicate?

Problem 4.5
Silicates are a limiting resource for many freshwater algae, like the diatoms *Asterionella formosa* and *Synedra ulna* of the previous exercise. Tilman *et al.* (1981) studied the competition of the two algae. Indicate with $R^*$ the minimum concentration of silicates that is necessary for the population viability of each species; in other words, if $R > R^*$, the reproduction rate exceeds the mortality rate, if $R < R^*$, it is just the opposite. It turns out that for each algal species $R^*$ is a function of temperature as indicated in the figure below.
The minimal silicate concentration $R^*$ as a function of temperature for the two freshwater diatoms.

Let us suppose that one performs several experiments at different temperatures in which $A. \text{formosa}$ and $S. \text{ulna}$ are competing for the limiting resource silicate. What will the result of competition be at the different temperatures?

**Problem 4.6**

The figure below shows the results of experiments by Tilman *et al.* (1981) with two species of algae: the diatoms *Asterionella formosa* and *Cyclotella meneghiniana*. Graphs of the left panel report the reproduction rates of each alga when phosphates are limiting, while graphs of the right panel report the reproduction rates when silicates are limiting.

Reproduction rates of *Asterionella formosa* (solid line) and *Cyclotella meneghiniana* (dash) as a function of PO$_4$ concentration (left panel) or SiO$_2$ (right panel). The value of constant mortality for both species is shown by horizontal lines.
Assess which of the two species wins the competition under the two different conditions, assuming that mortality rates are constant and equal to 0.25 day\(^{-1}\) for both algal species.

Assume then that the phosphate and silicate concentrations, respectively \(P\) and \(S\), vary with the total number \(N\) of algae according to the relationships

\[
P = \frac{2}{1 + 0.02N} \quad S = \frac{30}{1 + 0.006N}.
\]

Calculate the long-term number of the dominant species under the two conditions.

**Problem 4.7**

Brown and Davidson (1977) studied the ecology of the Arizona deserts. They found out that rodents and ants compete for the same food resources, namely seeds of different size. The two food niches, however, do not overlap too much so that rodents and ants can coexist. To assess the strength of interguild competition, the two ecologists performed the following experiments: in a few enclosures the rodents were completely removed by trapping and the ant colonies were counted after letting the system evolve towards equilibrium, in other enclosures ants were completely removed by insecticide spraying and the rodents were counted after letting the system evolve towards equilibrium. Finally, a few enclosures were not disturbed and were monitored as a control where rodents and ant colonies were counted. Results are reported here below

<table>
<thead>
<tr>
<th>Rodents removed</th>
<th>Ants removed</th>
<th>Control</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ant colonies</td>
<td>543</td>
<td>318</td>
</tr>
<tr>
<td>Rodent numbers</td>
<td>—</td>
<td>144</td>
</tr>
<tr>
<td></td>
<td></td>
<td>122</td>
</tr>
</tbody>
</table>

Assume that results can be considered situations corresponding to stable equilibria of a MacArthur and Levins (1967) model. Estimate the interspecific competition coefficients \(\alpha_{12}\) and \(\alpha_{21}\).

**Problem 4.8**

Roughgarden (1979) reports the distribution of the jaw size for two lizard species, *Anolis aeneus* and *A. richardi*, both hosted by the Caribbean island of Grenada. Assume that the size distribution of the food that is ingested by the individuals of the two species is equal to the jaw size distribution. Then the corresponding utilization functions are given by the following table

<table>
<thead>
<tr>
<th>Food size (mm)</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
<th>15</th>
<th>16</th>
<th>17</th>
<th>18</th>
</tr>
</thead>
<tbody>
<tr>
<td>Utilization of <em>A. aeneus</em> (%)</td>
<td>5</td>
<td>40</td>
<td>45</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Utilization of <em>A. richardi</em> (%)</td>
<td>0</td>
<td>0</td>
<td>8</td>
<td>15</td>
<td>15</td>
<td>15</td>
<td>23</td>
<td>8</td>
<td>8</td>
<td>8</td>
</tr>
</tbody>
</table>

Use MacArthur and Levins (1967) model, assuming that the abundance functions are constant with respect to food size, that the nourishing value of the food is proportional to its size and that the voraciousness is equal in the two species. Find the interspecific competition coefficients \(\alpha_{12}\) and \(\alpha_{21}\). Assume that the two *Anolis* species have the same carrying capacity. What would the result of competition be: coexistence or exclusion?
Problem 4.9
The forest of Stormifrone hosts two very similar species of singing birds, *Pennutus caeruleus* and *Pennutus rubescens*. Both feed on the berries of juniper and firethorn. Observations carried out by the nearby Institute of Ornithology have allowed the scientists to determine that *P. caeruleus* spends 30% of its feeding time on juniper plants and 70% on firethorn plants, while *P. rubescens* spends 80% on juniper and 20% on firethorn.

Also, it turns out that *P. caeruleus* is two times more voracious than *P. rubescens*. Assume that nourishing values, carrying capacities and intrinsic rates of increase are equal in juniper and firethorn. Use MacArthur and Levins (1967) model to calculate the interspecific competition coefficients $\alpha_{12}$ and $\alpha_{21}$.

Problem 4.10
Pyke (1982) studied competition in populations of bumble bees of Colorado mountains. These bees feed on the nectar of various flowers by means of a sort of proboscis. According to the proboscis length, each bee species can visit flowers whose nectar spur is longer or shorter.

The figure below reports the utilization functions of *Bombus appositus* and *B. flavifrons* (the resource dimension is represented by the corolla length of flowers). Use MacArthur and Levins (1967) model, assuming that the two species have equal voraciousness and that abundance functions and nourishing value are constant. Calculate the interspecific competition coefficients $\alpha_{12}$ and $\alpha_{31}$ and the distance between niches. If the two *Bombus* species have the same carrying capacity, what would the result of competition be?

![Utilization functions of two bumble bee populations](image)

Utilization functions of two bumble bee populations: *Bombus appositus* (black) e *B. flavifrons* (grey). Numbers above histogram bars are the utilization percentages of the different resource categories.

Problem 4.11
Heske *et al.* (1994) studied the ecology of the Chihuahua desert in northern Mexico and discovered that five species of small rodents (*Perognathus flavus, Chaetodipus penicillatus, Peromyscus eremicus, Peromyscus maniculatus* and *Reithrodontomys megalotis*) compete for the same food resources with kangaroo rats (genus *Dipodomys*). To assess competition intensity, the researchers completely removed rats from a few enclosures. The experiment lasted several years. The average density of the various species within and outside the enclosures is reported in the table below.
Density [No. per hectare] of the five rodent species (1,2,…5) and the rats in enclosures without kangaroo rats (\(D_A\)) and in areas with kangaroo rats (\(D_P\)).

<table>
<thead>
<tr>
<th>Species ((i))</th>
<th>Density (D_A)</th>
<th>Density (D_P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(P.\ flavus) (1)</td>
<td>3.5</td>
<td>0</td>
</tr>
<tr>
<td>(C.\ penicillatus) (2)</td>
<td>4.8</td>
<td>1.2</td>
</tr>
<tr>
<td>(P.\ eremicus) (3)</td>
<td>7.8</td>
<td>3.6</td>
</tr>
<tr>
<td>(P.\ maniculatus) (4)</td>
<td>1.8</td>
<td>0.2</td>
</tr>
<tr>
<td>(R.\ megalotis) (5)</td>
<td>24.4</td>
<td>8.0</td>
</tr>
<tr>
<td>Rats ((Dipodomys\ spp.)) (6)</td>
<td>0</td>
<td>70</td>
</tr>
</tbody>
</table>

Assume that

a) the five rodent species compete only with the rats, not between themselves;
b) MacArthur and Levins (1967) model can be used;
c) resulting densities can be considered as obtained at long-term equilibrium.

Calculate the five interspecific competition coefficients \(\alpha_{si}\) that correspond to the damage inflicted by kangaroo rats (species 6) onto the rodents (species \(i\), with \(i = 1, 2, \ldots 5\)). Note that the five coefficients \(\alpha_{si}\) cannot be calculated because no experiments of rodent removal has been performed).
Problem 4.12
Suhonen (1993) conducted observations on the behavior of two tits (*Parus montanus* and *P. cristatus*) in central Finland while they foraged on spruce trees. The two bird species utilize the resources located along the tree trunk in different ways. If we conventionally assume the tree crown height to be unity, the proportions of tits foraging at different heights are given by the following table:

<table>
<thead>
<tr>
<th>Relative foraging height</th>
<th>Proportions <em>P. cristatus</em></th>
<th>Proportions <em>P. montanus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>0.00 – 0.25</td>
<td>0.12</td>
<td>0.33</td>
</tr>
<tr>
<td>0.25 – 0.50</td>
<td>0.38</td>
<td>0.42</td>
</tr>
<tr>
<td>0.50 – 0.75</td>
<td>0.30</td>
<td>0.20</td>
</tr>
<tr>
<td>0.75 – 1.00</td>
<td>0.20</td>
<td>0.05</td>
</tr>
</tbody>
</table>

Assume that abundance functions and nourishing values are constant along the tree trunk and that the two species have equal voraciousness. Calculate the position and width of the two food niches as well as the interspecific competition coefficients $\alpha_{12}$ and $\alpha_{21}$ according to MacArthur and Levins (1967) model. Also, determine whether the distance between niches is in accordance with May’s (1973) theory on species packing.

Problem 4.13

In North America, the moose (*Alces alces*) and the white-tailed deer (*Odocoileus virginianus*) compete for the same resource spectrum. Schmitz and Nudds (1994) provide, with reference to two populations of the two species, the following values for the parameters of MacArthur and Levins (1967) interspecific competition model:

- intrinsic rate of demographic growth of deer = 0.2 year$^{-1}$
- carrying capacity of deer = 570 individuals
- intrinsic rate of demographic growth of moose = 0.1 year$^{-1}$
- carrying capacity of moose = 400 individuals
- interspecific competition coefficient $\alpha_{CA}$ (damage of moose onto deer) = 1.6
- interspecific competition coefficient $\alpha_{AC}$ (damage of deer onto moose) = 0.5 .

Prove that these values would lead you to the conclusion that deer should be competitively excluded by moose.

The stable coexistence of moose and deer in many areas of North America is explained by the deer being a vector of parasites (helminthic worms of the species *Parelaphostrongylus tenuis*) which are not lethal to the deer but are lethal to the moose. Analyze how the previously stated result would change under the hypothesis that parasites inflict an additional mortality onto the moose only. Assume that the additional mortality rate is of the kind

$$\text{mortality rate [year}^{-1}] = 0.0125P$$

where $P$ indicates the average parasite number per moose. Determine the outcome for $P = 2$ worms per deer.

Problem 4.14

Gause (1934) made many experiments on interspecific competition. In particular, he performed one experiment with *Paramecium caudatum* and *Paramecium bursaria* (different from the more famous one with *P. caudatum* e *P. aurelia*). Results are reported in the figure below, which shows in (A) e (B) the results of isolated cultures, in (C) that of mixed cultures.
Verify that these results cannot be explained by neither the traditional model of interference competition (logistic growth of the isolated populations and interspecific competition term proportional to the product of densities) nor by MacArthur and Levins (1967) model of competition for a resource spectrum.

Problem 4.15

One of the biggest problem in the fight against pests (such as defoliating insects or bacteria harmful to health) by means of toxic compounds (e.g. insecticides or antibiotics) is the possible selection of resistant genotypes. Describe the phenomenon in the following simplistic way. Assume that a population of asexual noxious organisms grows in a logistic fashion with an intrinsic instantaneous rate of increase $r = 0.1$ year$^{-1}$ and a coefficient of intraspecific competition $\beta = 0.0001$ (No. of organisms $\times$ year$^{-1}$). To control the pest, a toxic compound is sprayed which causes a mortality with rate $m = 0.0999$ year$^{-1}$. However, a tiny fraction of the population (a rare genotype) is practically insensitive to the pesticide ($m = 0.001$ year$^{-1}$) and can transmit this trait to its progeny. All the other traits of this genotype are equal to those of the commoner genotype.

Try to predict what will happen after spraying the pesticide by setting up a model with interspecific competition between the genotype that is sensitive to the toxic compound (indicate the abundance of this genotype with $S$) and the genotype that is insensitive (abundance indicated with $I$). Assume that initially the population number is equal to the carrying capacity of the population without the pesticide and that only a very small fraction of resistant organisms is present in the population. Towards which equilibrium would the population tend after the pesticide is sprayed and how would the numbers of the two genotypes evolve in time?