A MODEL SYSTEM FOR ASSESSING COMPETITION FOR SITE OCCUPANCY

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In this paper we describe an experimentation and modelling system for assessing competition in a community where the response measured on each species is categorical. Multinomial responses have previously been modelled using baseline category logit random effects models. Here we extend these models to assess competition over a period of time and over a wide range of initial community compositions. We describe an appropriate experimental design and analysis using data from an experiment comparing three strains of *Rhizobium* competing for the occupation of sites on the roots of legume species.

Rhizobium is a bacterium that can invade the roots of legumes. The *Rhizobium* forms a nodule on an invaded site and can then fix atmospheric nitrogen. On each root there are a limited number of invasion sites and once a site has been invaded by a bacterium it cannot be invaded by another. The experiment tests the competitiveness of three strains of *Mesorhizobium loti*, A, B and C in occupying these sites. Each root in the study was inoculated with a solution (the inoculum) containing a mixture of each of the three strains. Each root gives a trinomial response, the total number of invasion sites occupied by each of the three strains. There are two main questions: (1) which species is the most competitive in occupying sites? (2) is success related to the initial composition of strains?

A simplex design was used in this experiment. There were seven initial mixtures each with a different relative abundance of the three strains. These were repeated at two overall densities in the inoculum. Each mixture by density combination was replicated 5 times, giving 70 'clusters' in total. At time *t* the number of nodules occupied by each strain was counted in each cluster. We modelled the proportion of nodules occupied by each strain at the end of the experiment using a multinomial baseline category model. We included an offset for the initial proportions of each strain present and a random cluster effect. The model is:

$$\log\left(\frac{\pi_{ij}}{\pi_{iC}}\right) = \beta_{j1} p_{iA} + \beta_{j2} p_{iB} + \beta_{j3} p_{iC} + \beta_{j4} D_i + \log\left(\frac{p_{ij}}{p_{iC}}\right) + u_{ij} \qquad \text{for } j = \text{A, B.}$$

where p_{iA}, p_{iB} and p_{iC} are the proportions of strain A, B and C respectively present initially in the innoculum for the i^{th} cluster; D_i is the initial density for the i^{th} cluster; u_{iA} and u_{iB} are random effects assumed normally distributed with mean 0 and variance σ_A^2 and σ_B^2 respectively and the covariance between them is γ_{AB}. A positive (negative) estimate of the parameter β_{A1} indicates that increasing the initial inoculum proportion of strain A causes an increase (decrease) in the relative gain of strain A to strain C over the time period *t*; other fixed effect parameters can be interpreted similarly. A more complex model including interactions may be necessary. Inclusion of the offset allows the model parameters to be interpreted as an explanation of the change in strain proportions from time 0 to time *t* (i.e. assess competition) as opposed to a snapshot of what is happening at time *t*. Including the random effect in the model allows for possible overdispersion due to variation in proportions from replicate to replicate.

Using this novel methodology we identified C as the most competitive strain. Its site occupancy generally exceeded expectation based on initial proportions and it almost always out-competed both strain A and B at both densities.