Ecological Applications of Multilevel Analysis of Variance

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Abstract

A Bayesian representation of the analysis of variance by Gelman (2005) is introduced with ecological examples. These examples demonstrate typical situations we encounter in ecological studies. Compared to the conventional methods, the multilevel approach is more flexible in model formulation, easier to setup, and easier to present. Because the emphasis is on estimation, multilevel model results are more informative than the results from a significance test. The improved capacity is largely due to the changed computation methods. In our examples, we show that (1) the multilevel model is able to discern a treatment effect that is too weak for the conventional approach, (2) the graphical presentation associated with the multilevel method is more informative, and (3) the multilevel model can incorporate all sources of uncertainty to accurately describe the true relationship between the outcome and potential predictors.

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1 Introduction

Analysis of variance (ANOVA) is widely used in scientific research for testing complicated multiple hypotheses. As presented originally in Fisher's seminal work (Fisher, 1925), ANOVA can be seen as the collection of the calculus of sum of squares and the associated models and significance tests. These tests and models have had a profound impact on ecological studies. ANOVA provides the computational framework for the design and analysis of ecological experiments (Underwood, 1997). As a data analysis tool, ANOVA is used in ecology for both confirmative and explorative studies. When used in a confirmative study, the randomized experimental design ensures that the resulting difference between treatments can be unambiguously attributed to the cause we are interested in testing. When used in explorative studies, the ANOVA framework reflects a basic scientific belief that correlation implies a causal relationship (Shipley, 2000). The simple steps of ANOVA computation, along with the associated significance test (the F-test), allow quick implementation and seemingly straightforward interpretation of the results.

Interpretation of ANOVA results can be problematic. Difficulties arise when the normality and independence of the response data are not met, when the experimental design is nested, when using an unbalanced design, or when missing cells are present. More importantly, ANOVA results are difficult to explain in ecological terms because significance test results are usually not scientifically very informative (Anderson et al., 2000). On one hand, when an experiment is proposed, we almost always have reasons to believe that a treatment effect exists. Therefore, we want to know the strength of the effect a treatment has on the outcome rather than whether the treatment has an effect on the outcome. By using a significance test basing the inference on the assumption of no treatment effect, we emphasize the type I error rate (erroneously reject the null hypothesis of no treatment effect) often at the expense of statistical power, especially when multiple comparison is used. On the other hand, a nonexistent treatment effect can be shown to be statistically significant if one tries often enough (hence the article by Ioannidis, 2005).

From this practical perspective, we find the concept of variance components (Searle et al., 1992) especially useful. The relative sizes of the two variances indicate the effects of the factors of interest. When graphically presented, this partitioning of total variance into compartments is actually more informative than the results of a significance test. The ambiguity and difficulty of ANOVA can be alleviated by using a multilevel (or hierarchical) modeling approach for ANOVA proposed by Gelman (2005). His method can be summarized as the estimation of the variance components and treatment effects using a hierarchical regression. The results are often presented graphically. This approach is intuitively appealing and its implementation is straightforward even when the experimental design is nested and the response variable is not normally distributed. The multilevel ANOVA is Bayesian and inference about treatment effects are made using Bayesian posterior distributions of the parameters of interest. Gelman and Tuerlinckx (2000) suggested that the hierarchical Bayesian approach for ANOVA includes the classical ANOVA as a special case. We introduce Gelman's multilevel ANOVA using three examples. Statistical background are presented in Gelman (2005), Gelman and Hill (2007), and Gelman and Tuerlinckx (2000), and are briefly discussed in the supplementary materials.

2 Methods

We illustrate the multilevel ANOVA approach using a one-way ANOVA setting. For a one-way ANOVA problem, we have a treatment with several levels, and the statistical model is:

$$y_{ij} = \beta_0 + \beta_i + \epsilon_{ij}. \tag{1}$$

where β_0 is the overall mean, β_i is the treatment effect for level i and $\sum \beta_i = 0$, and j represents individual observations in treatment i. This is a multilevel problem because we are interested in parameters at two levels: the data level and the treatment level. At the data level, individual response variable values are governed by the group level parameters, and the group level parameters are further governed by a distribution with hyper-parameters. The term "multilevel" is used to describe the data structure (data points are clustered in multiple treatment levels) and the hierarchical model structure. We avoid the usually used terms "fixed" or "random" effects to avoid confusion as described in Gelman and Hill (2007, sections 1.1 and 11.4) and Gelman (2005, section 6). The term "multilevel" encompasses both fixed and random effects. The total variance in y_{ij} is partitioned into between group variance ($var(\beta_i)$) and within group variance ($var(\epsilon_{ij})$). Instead of using the sum-of-squares calculation, we use a hierarchical formulation and model the coefficients β_i as a sample from a normal distribution with mean 0 and variance σ^2_β:

$$\beta_i \sim N(0, \sigma^2_\beta) \tag{2}$$

The model error term ϵ_{ij} is also modeled as from a normal distribution:

$$\epsilon_{ij} \sim N(0, \sigma^2)$$

Or, equivalently,

$$y_{ij} \sim N(\beta_0 + \beta_i, \sigma^2) \tag{3}$$

The variance component for the treatment can be naturally estimated by σ_β, or the standard deviation of $\hat{\beta}_i$ (s_β, the finite population standard deviation). The computation expressed here is standard for random effect coefficients under classical random effect model (Clayton, 1996). We can view fixed effects as special cases of random effects ($\sigma_\beta = \infty$) in a Bayesian context. Therefore, this computation framework is not unique for Bayesian.

Model coefficients (β's and σ_β, or s_β can be estimated using the maximum likelihood estimator, and the likelihood function of this setting is a product of two normal distribution density functions defined by equations 1 and 2. Analytical solutions are often available, but it is easy to implement the computation using Markov chain Monte Carlo simulation (MCMC, Gilks et al., 1997; Qian et al., 2003).

When there is more than one factor affecting the outcome, we can easily extend the approach by using the same hierarchical representation of the additional factors. Furthermore, as suggested by equation 3, this approach is not limited by the normality assumption. That is, the normal distribution in equation 3 can be replaced with any distribution from the exponential family, similar to the generalization from linear models to the generalized linear models (GLM, McCullagh and Nelder, 1989).

2.1 Data Sets and Models

We illustrate the multilevel ANOVA using three data sets. The intertidal seaweed grazers example, a textbook example of ANOVA, is intended to make a direct comparison between the multilevel ANOVA and the classical ANOVA. The Liverpool moths example is used to illustrate the application of multilevel model under a logistic regression setting, where the response variable follows a binomial distribution. The seedling recruitment data set illustrates the use of this approach for count data (Poisson regression) that may be spatially correlated. Results from applying the classical ANOVA or linear modeling are presented in the Supplementary Materials.

2.1.1 Intertidal Seaweed Grazers

This example was used in the text by Ramsey and Schafer (2002) (Case Study 13.1, p. 375), describing a randomized experiment designed to study the influence of three ocean grazers, small fish (`f`), large fish (`F`), and limpets (`L`), on regeneration rate of seaweed in the intertidal zone of the Oregon coast. The experiments were carried out in eight locations to cover a wide range of tidal conditions and six treatments were used to determine the effect of different grazers (`C`: control, no grazer allowed; `L`: only limpets are allowed; `f`: only small fish allowed; `Lf`: large fish excluded; `fF`: limpets excluded; and `LfF`: all allowed). The response variable is the seaweed recovery of the experimental plot, measured as percent of the plot covered by regenerated seaweed. The standard approach illustrated in Ramsey and Schafer (2002) is a two-way ANOVA (plus the interaction effect) on the logit transformed percent regeneration rates. The logit of percent regeneration rate is the logarithm of regeneration ratio (% regenerated over % not regenerated).

Using the multilevel notation, this two-way ANOVA model can be expressed as:

$$Y_{ijk} = \beta_0 + \beta_{1i} + \beta_{2j} + \beta_{3ij} + \epsilon_{ijk} \quad (4)$$

where Y is the logit of regeneration rate, β_{1i} is the treatment effect ($i = 1, \cdots, 6$ and $\sum \beta_{1i} = 0$), β_{2j} is the block effect ($j = 1, \cdots, 8$ and $\sum \beta_{2j} = 0$), and β_{3ij} is the interaction effect ($\sum \beta_{3ij} = 0$). The residual term ϵ_{ijk} is assumed to have a normal distribution with mean 0 and a constant variance, where $k = 1, 2$ is the index of individual observations within each Block – Treatment cell. The total variance in Y is partitioned into four components: treatment, block, interaction effects, and residual.

2.1.2 Liverpool Moths

Bishop (1972) reported a randomized experimental study on natural selection. The experiment was designed to answer the question that whether blackened tree trunks by air pollution near Liverpool, England were the cause of the increase of a dark morph of a local moth. The moths in question are nocturnal, resting during the day on tree trunks. In Liverpool, a high percentage of the moths are of a dark morph, whereas a higher percentage of the typical (pepper-and-salt) morph are observed in the Welsh countryside, where tree trunks are lighter. Bishop selected seven locations progressively farther away from Liverpool. At each location, Bishop chose eight trees at random. Equal numbers of dead light and dark moths were glued to the trunks in lifelike positions. After 24 hours, a count was taken of the numbers of each morph that had been removed – presumably by predators. The original study was published before the time of GLM, but the data set has since been used in several regression textbooks as an example of logistic regression (e.g., Ramsey and Schafer, 2002). We choose to model the moth data as from a binomial distribution and use the typical logistic regression model:

$$\begin{aligned} y_{ij} &\sim Bin(p_{ij}, n_{ij}) \\ \text{logit}(p_{ij}) &= \beta_0 + \beta_{1i} + \beta_{2i} \times Dist_j \end{aligned} \tag{5}$$

where y_{ij} is the number of moths removed for morph i ($i = 1$ (dark) or 2 (light)), at the jth distance (distance from Liverpool), n_{ij} is the total number of moths placed on each tree, p_{ij}, the parameter of interest, is the probability a moth being removed, β_{1i} is the morph effect, and β_{2i} is the slope on distance, representing the interaction between morph color and distance. Bishop (1972) and Ramsey and Schafer (2002) used a categorical predictor "site" instead of distance from Liverpool to account for the apparent outlier at distance of 30.2 km (Figure 3 of the supplementary materials). We choose to use distance as a continuous predictor to illustrate the interaction effect between a categorical predictor and a continuous predictor.

2.1.3 Seedling Recruitment

Shen (2002) reported an observational study on factors affecting the species composition and diversity of a mixed evergreen-deciduous forest community in southwest China. The original study has observations at multiple spatial scales. We use the seedling recruitment data collected along a transect of 128 5×5 meter consecutive plots to study factors affecting seedling recruitment. A total of 49 species of seedlings were observed in the field and were classified into 5 types according to their status in community dynamics (Shen et al., 2000): Pioneer, Early dominant, Early companion, Later dominant (including evergreen species), and Tolerant. Within each plot, number of seedlings (height below 1 meter) was recorded, along with several physical and biological variables, including canopy gap measured in % (Gap), position of each plot measured as relative position along a hillside between valley ($Position = 1$) and ridge ($Position = 5$), soil total organic carbon (TOC, in %).

The observed number of seedlings (the response variable) from different plots are likely correlated, and the correlation is likely due to the spatial layout of the transect. A natural strategy for this problem is to introduce a spatial random effects term ϵ using the intrinsic conditional autoregressive model (CAR) (Besag et al., 1991; Qian et al., 2005):

$$\begin{aligned} y_{ijkl} &\sim Pois(\mu_{ij}) \\ \log(\mu_{ijk}) &= \beta_0 + \beta_{1j} + \beta_{2k} + \beta_{3j} \times \text{logit}(Gap_i) + \beta_{4j} \times TOC + \epsilon_i + \varepsilon_i \end{aligned} \quad (6)$$

where i is the index of plot, j is tree type index ($j = 1, \cdots, 5$), and k is the index of position, l is the index of observations within a plot. The spatial random effect term ϵ_i has a CAR prior. It is used to model the spatially structured variation. The error term ε_i is used to account for unstructured over-dispersion. The sum of ϵ_i and ε_i is termed as the convolution prior (Besag et al., 1991). Only two-way interactions between *Type* and the two continuous predictors were considered.

3 Results

Results from using classical approach are presented in the supplementary materials. All multilevel results are presented graphically, showing the estimated posterior mean (the circle), the 50% (thick line) and 95% (thin line) posterior credible intervals. The ANOVA display shows the estimated posterior distributions of variance components (in standard deviation), and the effects plots are based on estimated posterior distributions of effects.

3.1 Seaweed Grazers

The multilevel model results are qualitatively similar to the conventional ANOVA results (Figure 1). In addition, the estimated main effects are similar to results from a conventional ANOVA (Figures 2 and 3). The emphasis on estimation is clearly displayed in these plots. From the main effects plots, we know that the maximum difference between treatment and control is about 3 in logit scale, or the mean regeneration ratio of the control sites is about 20 times (e^3) larger than that of the treatment LfF sites. Traditional ANOVA does not emphasize the interaction effect beyond whether or not it is statistically significant. See supplementary materials for a comparison of the multilevel interaction plot and the commonly used interaction plot in ANOVA.

3.2 Moths

Using the multilevel model, we can use the traditional analysis of covariance (ANCOVA) setup to calculate the variance components of the main morph effect, main distance effect and the interaction (Figures 4-5). For this particular example, we see a strong interaction effect (clearly expressed by the difference in the `distance` slope in Figure 5) and an unambiguous morph main effect (Figure 4 right panel). The morph main effect is obvious because it is evaluated at a distance of 27.2 (the average distance).

3.3 Seedling Recruitment

The largest variance component is the unstructured over-dispersion term, while the structured spatial random effects (CAR) contributes a smaller than expected variance (Figure 6). The inclusion of spatially correlated predictors may have accounted for some spatial autocorrelation in the response variable data. The variable *Type* explains the most variation in recruitment (Figures 6 and 7 left panel), which is expected since tree species were classified to reflect their different ecological strategies and roles in community dynamics. Similar to the GLM results, we found the effect of GAP is uncertain. However, the $Type : GAP$ interaction effect, as shown in terms of type-specific GAP slope (Figure 8, right panel), indicates that type 4 (late dominant) trees are likely to respond negatively to increased gap, while the rest likely respond positively. The interaction effect between *Type* and *TOC* (Figure 8, left panel) is unambiguous. Because soil carbon concentration is likely to be similar in neighboring plots, including a spatial autocorrelation term reduces uncertainty on type-specific *TOC* slopes. Type 4 and 5 trees include all evergreen species and the shade-tolerant deciduous species which tend to be restricted to relatively steep and higher hillside positions, corresponding to a lower soil TOC value; while the deciduous dominant and pioneer species normally achieve quick recruitment and fast growth in richer habitat. This pattern has also been reported in similar contexts (Tang and Ohsawa, 2002). Compared to the type-specific *TOC* slopes from the multilevel model (Figure 8, left panel), the GLM fit (supplementary materials) is quite different. Because spatial autocorrelation is accounted for, the multilevel model results are more reliable. The position main effect (Figure 7, right panel) shows a clear pattern indicating an increased recruitment as we move from valley to ridge. The large uncertainty associated with the position main effect can be attributed to the qualitative nature of this variable. That is, topographic relief has multiple scales while the plot size is fixed. Assigning position to a plot can be ambiguous depending on the length of a hillside. Plots with the same position level could be at quite different absolute positions on hillsides of different sizes. As a result, an emphasis on estimation is more informative than the hypothesis testing approach which will almost surely lead to non-significant result.

4 Discussion

Our examples used some typical data sets encountered in ecological studies. Although ANOVA is well suited for analyzing the seaweed grazer data, multilevel ANOVA can be more informative and the graphical display is easier to understand

and interpret. In many ecological studies, data are collected from observations or from experiments applied to limited number of plots with unobserved confounding factors. Large natural variability plus small sample size often lead to non-significant results from ANOVA or t-tests, because the significance test is based on the comparison of the variance due to treatment and the residual variance. This situation is very common because of the high cost of collecting ecological data. When using the multilevel ANOVA, we estimate the treatment effect directly. The estimated treatment effect posterior distribution is not directly associated with the residual variance. As a result, we are more likely to show a significant treatment effect.

The seaweed regeneration example compares the multilevel ANOVA to the conventional ANOVA. The comparison illustrates the multilevel ANOVA's emphasis on estimation. This emphasis yields more informative results presented in terms of the estimated effects and the associated uncertainty. As we discussed in the supplementary materials, conventional hypothesis testing on treatment effects can be performed using the 95% posterior distributions of effects. As a result, our emphasis on estimation does not lead to lose of information in terms of comparisons of treatment effects. More importantly, the hierarchical computational framework allows ANOVA concept be applied to non-normal response variables, as illustrated in the Liverpool moth and seedling recruitment examples.

The philosophical basis of the traditional ANOVA is Popper's falsification theory (Popper, 1959). Although not fully compatible with methods practiced by most scientists, Popper's falsification philosophy had an immense impact on Fisher. Because statistical theories are not strictly falsifiable, Fisher devised his methodology based on a quasi-falsificationist view. Fisher held that a statistical hypothesis should be rejected by any experimental evidence which, on the assumption of that hypothesis, is relatively unlikely, relative that is to other possible outcomes of the experiment. Such tests, known as significance tests, or null hypothesis tests are controversial (see for example, Anderson et al., 2000 and Quinn and Keough, 2002).

Although Fisher's principles of randomized experimental design provide a mechanism for discerning the true causal effect of interest from confounding correlations, in practice ANOVA and associated significance tests are applied in both exploratory and confirmatory studies. In a confirmatory study, significance tests associated with ANOVA are used as the "seal of approval," while in an exploratory study ANOVA is often used to infer potential factors that may affect the outcome. While the null hypothesis of a significance test is of little interest, the variance component concept of ANOVA provides a convenient structure that allows scientists to form a causal model and develop hypotheses. The new computational method of multilevel ANOVA allows the classical ANOVA concept be applied to more complicated situations and can be accepted by both Bayesian and frequentist practitioners.

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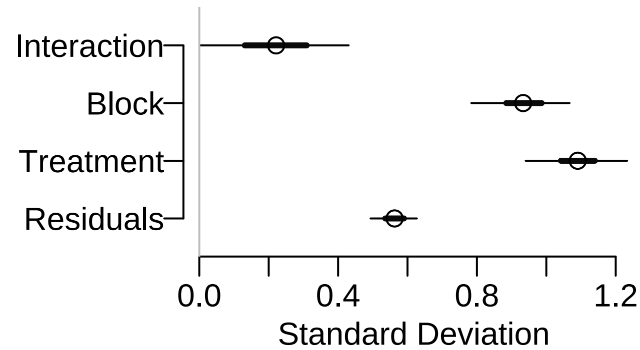

Figure 1: Seaweed Example: ANOVA display of the estimated standard deviation of the estimated variance components shows a similar general pattern as the conventional ANOVA results.

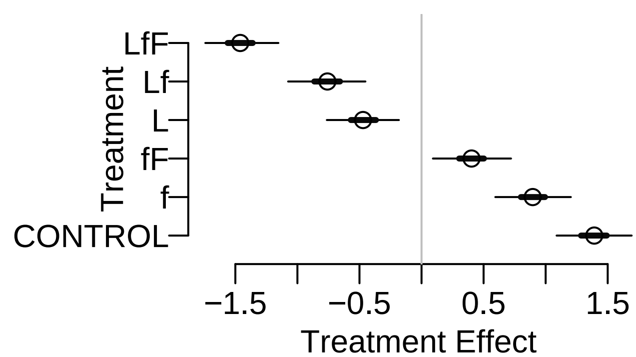

Figure 2: Estimated treatment main effect of the seaweed grazer example show that the regeneration rate decreases as grazing pressure increases. The largest difference between treatments is about 3 (in logit scale) or the regeneration ratio in CONTROL is about 20 times (e^3) larger than the same in treatment LfF.

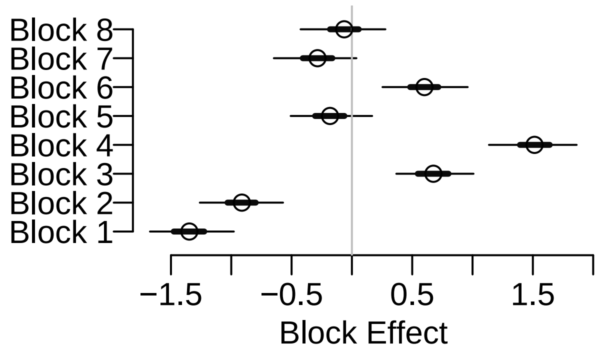

Figure 3: Estimated block main effect of the seaweed grazer example show the block effect has approximately the same magnitude as the treatment effect (3 in logit scale).

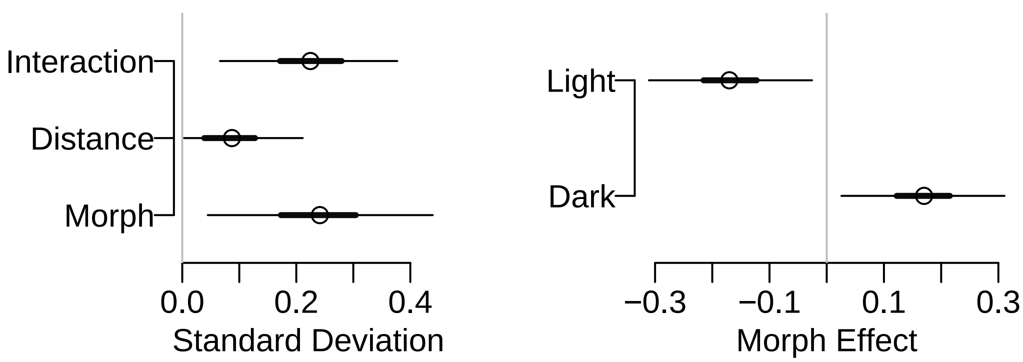

Figure 4: Liverpool moth Example: The left panel shows the ANOVA table indicating strong morph main effect and the morph-distance interaction effect. The right panel shows the estimated morph main effect.

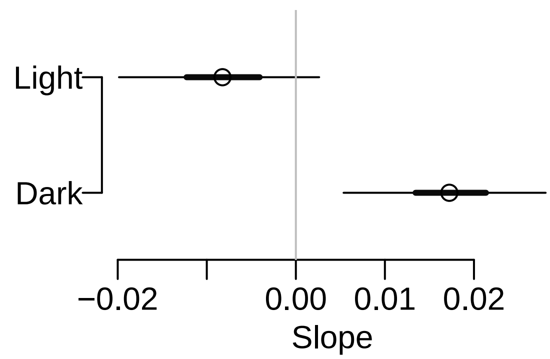

Figure 5: The estimated distance slope is positive for dark moths, indicating increased risk of removal for dark moths away from Liverpool. The distance slope for light moths is most likely negative, indicating increased risk of removal closer to Liverpool.

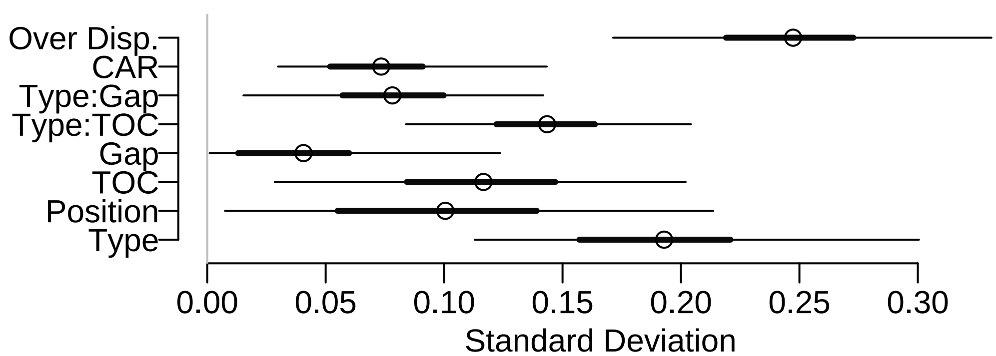

Figure 6: Seedling Example: ANOVA display of the estimated standard deviations of the estimated variance components shows that the unstructured overdispersion is the main contributor of the total variance, followed by tree type, type:TOC interaction, TOC, position, gap, and spatial autocorrelation (CAR).

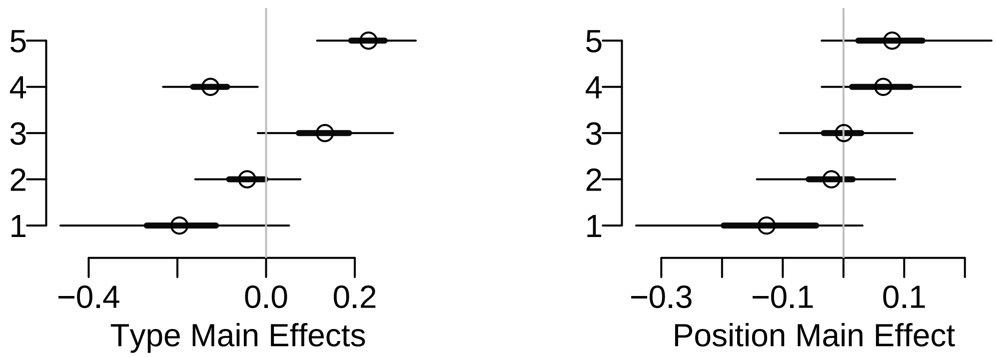

Figure 7: Seedling Example: The tree type main effect (left panel) shows that pioneer type (1) and late dominant (4) tend to have fewer seedlings and tolerant (5) tends to have much higher recruitment, while early dominant (2) and early companion (3) are close to average. The position main effect (right panel) shows that recruitment increases when moving from valley to ridge.

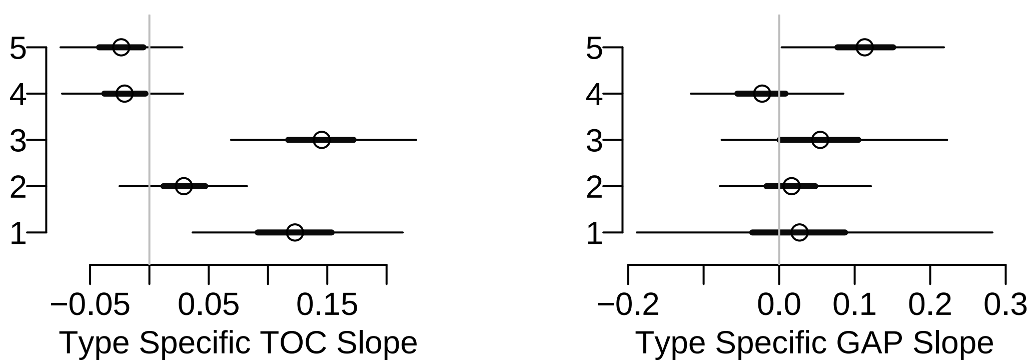

Figure 8: Seedling Example: The type:TOC interaction (left panel) shows positive generally slopes for pioneer (1), early dominant (2), and early companion (3) species and generally negative slopes for late dominant (4) and tolerant (5) species. The type:Gap interaction (right panel) shows only tolerant species respond positively to Gap.