

Isopod assemblage in response to management techniques and environmental variables on Nantucket Island

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Introduction:

The sandplain grassland and heathland of the coastal Northeast are part of a rare and protected habitat type. Many species of plants, birds, and insects rely on these remaining sandplain habitats. Managers have focused on using burning and mowing as ways to control invasive species and maintain current plant communities. With any rare landscape, as the area recedes and goes through landscape changes, the species endemic to the area decline (Foster & Motzin 2003). Research on landscape management impacts on biota primarily focuses on the impacts to charismatic creatures such as birds (Zuckerberg & Vickery 2006; Van Dyke et al. 2004); less research is focused on the lower order species such as invertebrates.

Research on the role of soil invertebrates is important in altered grassland ecosystems because of their role in decomposition processes and potential assistance in restoration of degraded lands (Snyder & Hendrix 2008). Terrestrial isopods are arthropods (class: Crustacea) that live in moist humid environments in soil and leaf litter (Heeley 1941). They are important for creating microbiomes and microclimates within ground litter (Souty-Grosset et al. 2005) by eating plant material as well as moving decaying material from the soil surface to deeper moisture microsites in the soil (Hassall et al 1987). In grassland communities, isopods improve soil and maintain litter decomposition (Curry 1994).

Isopods act as bioindicators for habitat quality of grassland (Longcore 2003; Souty-Grosset et al 2005; Snyder Hendrix 2008). Invertebrate responses to burning and mowing management activities in grasslands have been reported in several studies (Anderson et al. 1989; Chambers and Samways 1998; Dunwiddie 1991). These different management techniques can be used to change the microclimates of isopod habitats. Springett (2006) identified changes in litter microclimates in response to fire and reduction of the number of forest isopods. A better understanding of the impacts on isopod communities of Nantucket Island will help drive management decisions on the sandplain grassland and heathland.

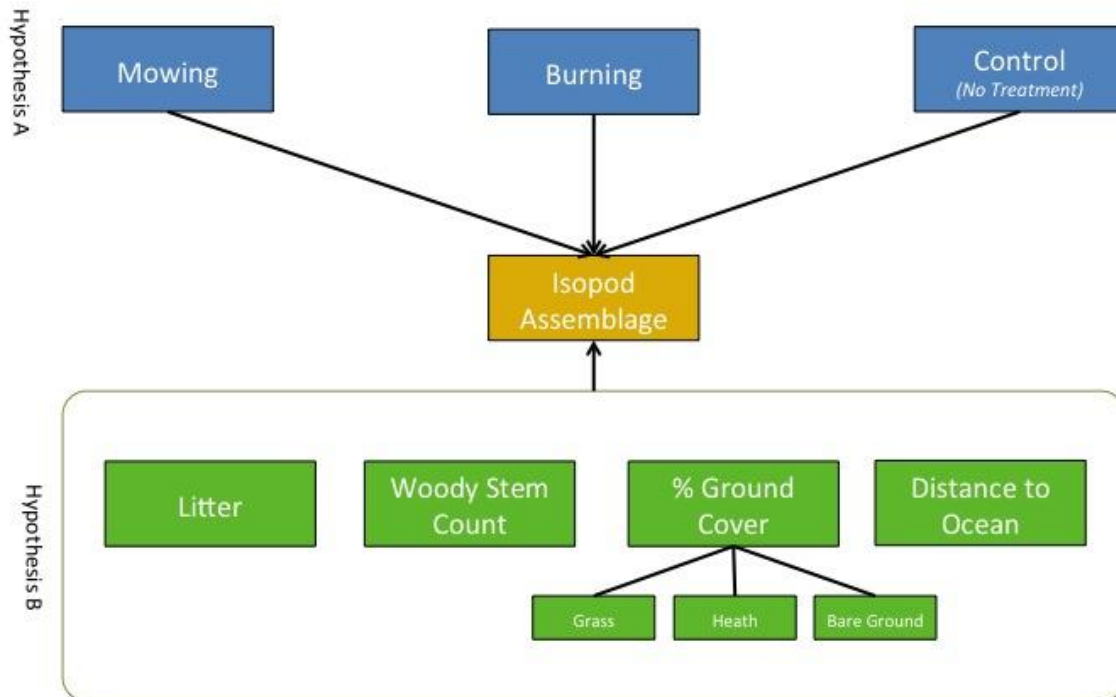


Figure 1: A conceptual model of the study. We hypothesize (Hypothesis A) that mowing, burning, and control type managements affect isopod assemblage with mowing and burning affecting isopod assemblage significantly differently from the control. We further hypothesize (Hypothesis B) that the non-management variables (litter, woody steam count, % ground cover and distance to ocean) affect isopod assemblage with litter being the best predictor.

Using unpublished data from McKenna-Foster (2009) where spider and isopod assemblage in sites representing three management types: burning, mowing, and no treatment were measured, we addressed the question: what is the effect of treatment (fire, mowing, and no treatment) on isopod assemblage? We tested the hypothesis that isopod assemblage in areas managed with burning and mowing would be significantly different from areas with no treatment (Figure 1, Hypothesis A). Then we looked at the impact that plant litter, percent ground cover (grass, heath, and bare ground), distance to ocean, and woody stem count had on isopod assemblage. The second question we addressed was: What is the relative importance of these measured environmental variables on isopod assemblage? The second hypothesis we tested was that litter would have the largest effect on isopod assemblage of the environmental variables (Figure 1, Hypothesis B).

Methods:

Study location

Smooth Hummocks Coastal Preserve (SHCP) located on Nantucket Island is a sandplain grassland and heathland preserve managed by the Nantucket Island Land Bank. Nantucket Island is located 30 miles south of Cape Cod, Massachusetts (Figure 2). Sandplain grassland and heathland are found on Nantucket, Tuckernuck, and Martha's Vineyard islands. The study site SHCP was approximately 345 hectares of sandplain grassland, sandplain heathland, and pitch pine stands.

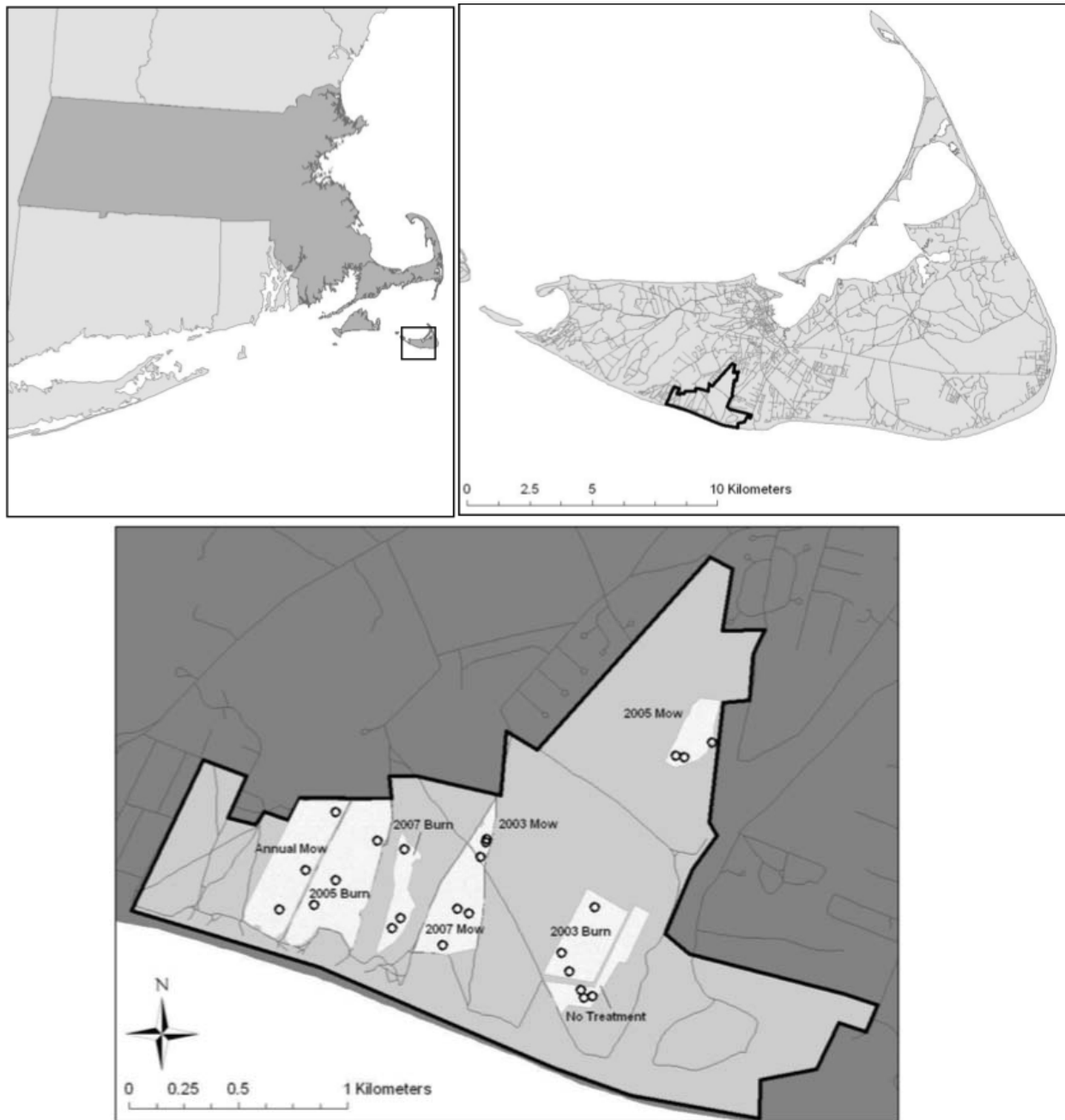


Figure 2: Location of Nantucket Island off the coast of mainland Massachusetts (top left), the location of SHCP on Nantucket Island is outlined (top right), and the location of the eight management sites at SHCP (bottom). Circles indicate plot locations found in each management site. Map by Andrew McKenna-Foster.

Eight management sites (Figure 2) located on SHCP were selected for this study. The sites were selected based on the management they received, they vary in size, and they have unpaved roads with some mowed vegetation breaks. On sites with management regimes of mowing and burning, the management activity had been done at least once between 1998-2008. Data collected for research on arthropods were collected in 2008 from the research plots placed in each management site. Three of the sites had burning as the main management

activity, four of the sites were managed with mowing, one of the mowed sites was mowed every year, and the eighth site had no treatments and acted as the control.

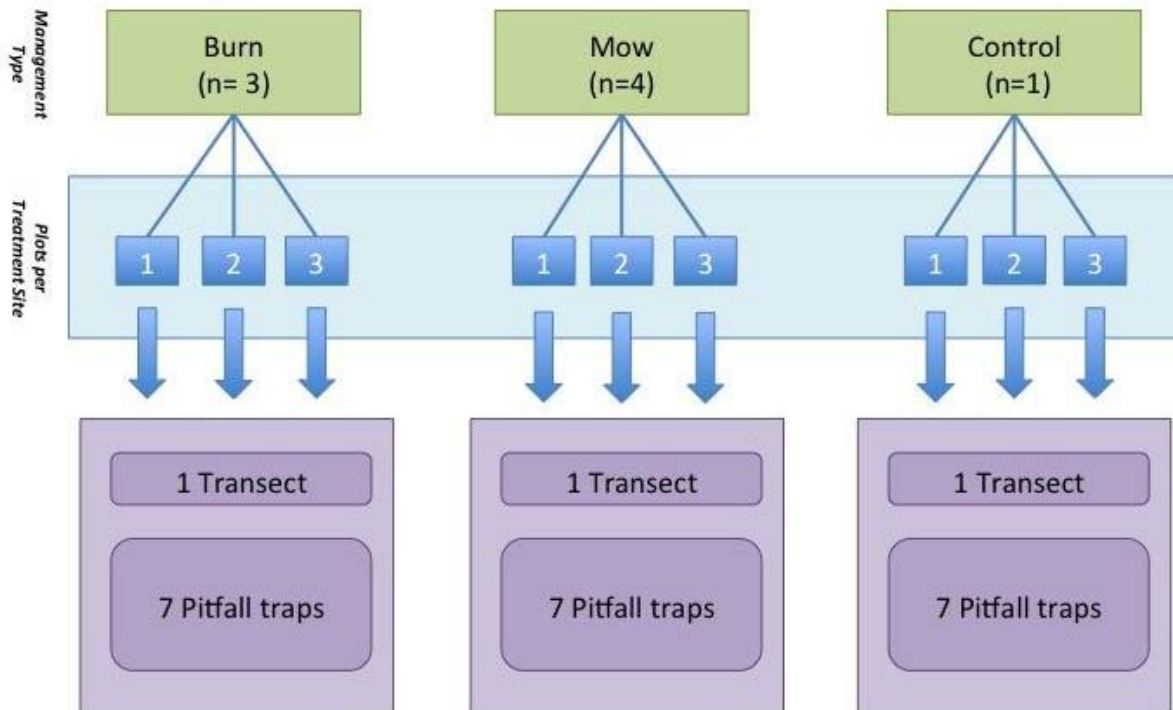


Figure 3. Experimental design. There were three types of treatment site: burn ($n=3$), mow ($n=4$), and control ($n=1$). Each treatment site had three plots. Each plot had one transect and each transect consisted of seven pitfall traps. The total number of pitfall traps per management type varied, burn ($n=63$), mow ($n=84$), and control ($n=21$).

A nested design with management sites, plots, transects, and pitfall traps

Three plots were placed in each of the eight treatment sites (Figures 2 and 3). Plots used for the study were chosen by visiting randomly ordered sites and choosing ones that had specific characteristics: 80% grass cover and 20m from the nearest road. To ensure independence between sites, each plot had to be within its own sandplain grassland patch and separated by shrubby vegetation from the other sites. Each of the plots had one transect ($n=24$) and seven pitfall traps ($n=168$). The seven pitfall traps were set three meters apart in a transect parallel to the southern coastline. The pitfall traps were five cm diameter polypropylene cups filled with 50:50 propylene glycol. Pitfall traps were set and sampled for seven days in both May and August 2008.

Each transect was placed near a randomly selected point in the plot. Even though random, the researchers required that one end of each transect was at least 0.5m or greater from the nearest heath plant. Six environmental variables were measured along each transect: dry leaf litter in grams, grass, heath, and bare ground percent cover, and woody stem count per square meter. Distance to the ocean was calculated using GIS and measured in meters.

Investigating the effects of management treatment on isopod assemblage

To determine whether managing sandplain grassland and heathland by mowing or controlled burning had a significant impact on isopod assemblage, a Kruskal-Wallis rank sum one way analysis of variance test was performed. This test was appropriate due to the non-

parametric nature of the data and because this test could handle our varying sample sizes. To account for the nested experimental design, the mean average of the isopod counts for all pitfall traps within a management site was used as the isopod count for that management site.

Modeling isopod assemblage count based on measured environmental variables

A linear model was generated to predict pooled isopod assemblage across sites based on six predictor variables (dry litter mass, percent cover of grass, heath, bare ground, distance to the ocean, and woody stem count). Prior to model construction, data were split randomly into two subsets. The first subset contained ~75% of the data (131 observations) and the second ~25% (44 observations). Building the model based on 75% of the data (the main dataset) enabled model validation using the remaining 25% (the test dataset).

Diagnostic plots for a full model of the main dataset (including residuals vs. fitted values, standardized residuals vs. theoretical quantiles, standardized residuals vs. fitted values, and standardized residuals vs. leverage) were used to visually determine the need to transform the response variable - isopod assemblage. Based on visual analysis of a correlation matrix from the main dataset (Appendix Figure A), distance to ocean and woody stem count were log transformed to reduce the impact of outliers. A Box-Cox power transformation was used to determine the transformation most likely to result in normally distributed residuals for the response variable (Appendix Figure B). The data were transformed and diagnostic plots for a second full model were checked visually (Appendix Figure C). Having determined the model met necessary assumptions, two methods were employed to determine a minimum adequate model.

An all subsets criterion-based procedure was used followed by a stepwise/criterion-based hybrid procedure to take advantage of the criteria Mallows' CP, adjusted R², the Bayesian Information Criterion (BIC), and the Akaike Information Criterion (AIC). We selected the number of variables and the particular variables for a minimum adequate model based on these four criteria. An ANOVA test was used to determine whether the minimum adequate model was significantly different from the full model. Variance inflation factors (VIF) were calculated to test the minimum adequate model for issues of multicollinearity. The minimum adequate model was scaled using z-scores, and a scaled minimum adequate model was produced. Z-scoring was used to standardize the predictor coefficients. Once standardized, predictor coefficients were compared directly (whereas this was previously impossible due to unit differences) enabling an analysis of the relative predictive power of each predictor variable. Lastly the predictions of the model were tested using the test dataset and assessed by calculating the root mean square deviation.

Results:

The effects of management treatment on isopod assemblage (Figure 1, Hypothesis A)

Isopod assemblage varied widely within treatment groups with standard deviations being greater than the means in all three treatment types (Table 1). Sites treated by mowing appear to have significantly higher levels of isopods than control sites or those treated by burning (Figure 4). Sites managed by burning had a mean isopod assemblage of 78 that was very close to the control mean of 81. Mowed sites had a mean approximately 60% greater with a count of 126 isopods. The standard deviation for sites managed by burning was 176, 162 for mowed sites, and 117 for the control site (Table 1).

Table 1: Descriptive statistics of isopod assemblage (number of individuals) given different management treatments (Burn n=3, Mow n=4, Control n=1).

	Burn	Mow	Control
Minimum	0.0	0.0	5.0
Maximum	902.0	747.0	419.0
Median	14.0	68.0	22.0
Mean	78.4	126.4	80.8
Standard deviation	176.4	162.0	117.1
Variance	31112.9	26255.8	13714.2

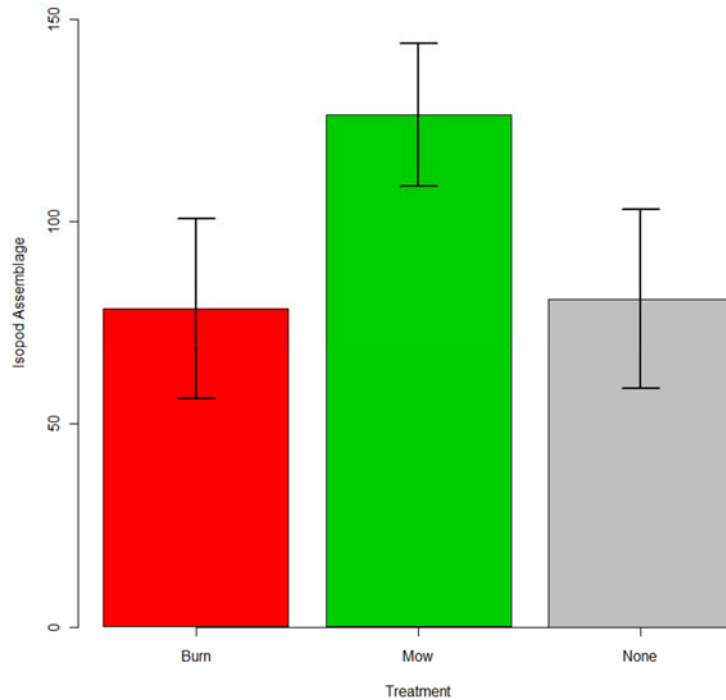


Figure 4: Bar chart of the mean of isopod assemblage (number of individuals) given different management treatments (Burn n=3, mean=78.4, SE=±22.2, Mow n=4, mean=126.4, SE=±17.7 Control n=1, mean=80.8, SE=±22.1).

The non-parametric Kruskal-Wallis test did not indicate a significant relationship between isopod assemblage and any one of the management types ($X^2=1.22$, $df=2$, $p=0.54$). The null hypothesis that there was no relationship between burning and mowing management and isopod could not be rejected based on the data collected.

Modeling isopod assemblage based on measured environmental variables (Figure 1, Hypothesis B)

Histograms, scatterplots, and Spearman coefficients of each variable indicated strong correlations between the four predictors l.stem (the log of woody stem count), heath, grass, litter and the response variable isopod. Potential multicollinearity was seen between grass and heath, grass and l.ocean (the log of the distance to the ocean), grass and l.stem, and heath and l.stem (Figure 5). Visual assessment of Figure 5 shows a potentially strong positive correlation between l.isopod (1+the log of isopod) and litter, and another positive correlation between l.isopod and l.stem.

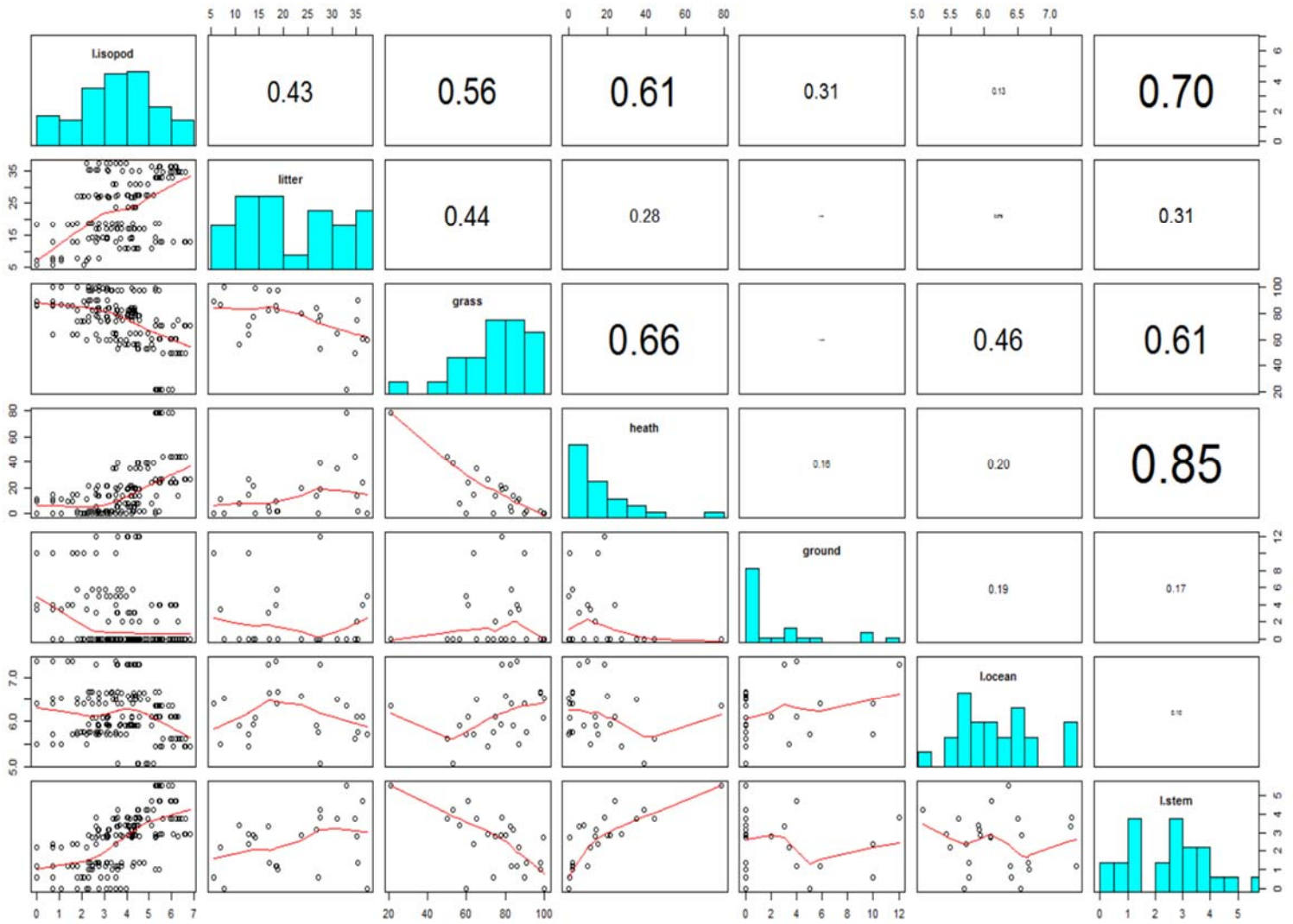


Figure 5: Correlation matrix showing histograms, scatterplots, and Spearman correlations between the response variable isopod assemblage and the six predictor variables.

The full model showing l.isopod as a function of litter, grass, heath, ground, l.ocean, and l.stem yielded:

$$l.isopod = 0.04 \cdot litter - 0.02 \cdot grass - 0.01 \cdot heath - 0.12 \cdot ground + 0.12 \cdot l.ocean + 0.57 \cdot l.stem + 2.18$$

This model indicated that 1+natural log of isopod count would increase as litter, the natural log of the distance to the ocean, and 1+natural log of the woody stem count increased. 1+natural log of isopod count would decrease if the percent cover of grass, heath, or bare ground increased ($R^2=0.4953$, $p=2.2 \times 10^{-16}$, $\alpha=0.05$). The full model passed diagnostics illustrating residuals were normally distributed, without underlying structure, and there were no influential outliers according to the Cook's distance metric (Appendix Figure C).

All subsets criterion-based procedure using the criteria Mallows' CP, adjusted R^2 , and the BIC indicated that a model with three predictors and one y-intercept should be selected (Appendix Figure D). This was determined by the indication that a model with four parameters would have the lowest Mallows' CP, highest adjusted R^2 , and lowest BIC. A stepwise/criterion-

based hybrid method also suggested that a model with three predictors and one y-intercept should be selected and both methods indicated the selection of a minimum adequate model with l.stem, bare ground, and litter as the three predictors.

The minimum adequate model based on an all subsets criterion-based procedure and a stepwise/criterion-based hybrid approach:

$$l.isopod = 0.56 \cdot l.stem - 0.10 \cdot ground + 0.05 \cdot litter + 1.46$$

The minimum adequate model ($R^2 = 0.4989$) was significant overall with a p-value of 2.2×10^{-16} ($\alpha=0.05$). This model indicated that l.isopod will rise with an increase in l.stem and litter and decrease with an increase in ground. The test for multicollinearity between the variables l.stem (VIF=1.1), ground (VIF=1.0), and litter (VIF=1.1) in the minimum adequate model revealed no issues of multicollinearity. Normality of residuals and the absence of high leverage outliers were determined by visual inspection of diagnostic plots (Appendix Figure E). The ANOVA between the full and minimum adequate model ($p=0.7369$) indicated that the null hypothesis of the test (that the two models are not different) could not be rejected thus the simpler minimum adequate model was maintained.

The z-scored minimum adequate model enabled a direct comparison of the relative influence of each predictor:

$$l.isopod = 0.51 \cdot l.stem - 0.23 \cdot ground + 0.28 \cdot litter - 1.34 \times 10^{-16}$$

The z-score transformation of the minimum adequate model has the same R^2 value and significance as the minimum adequate model. This standardization of the model coefficients showed l.stem was the most important of the measured predictors of l.isopod and was approximately as important as the two other predictors combined. Ground and litter were very similar in their predictive power on l.isopod with an increase in ground leading to a decrease in l.isopod while an increase in litter leads to an increase in l.isopod. Our model showed the relative importance ratio of the environmental variables on isopod assemblage to be 0.51 woody stem to 0.23 bare ground percentage to 0.28 dry leaf litter (i.e. a 0.51:0.23:0.28 proportion).

The minimum adequate model predicted the trend seen in both the main data (subset of 131 observations) and the test data (subset of 44 observations not used to construct the model) (Figure 6). The root mean square difference of l.isopod was 1.50 and the untransformed root mean square difference between the minimum adequate model predictions and observed isopod assemblage was 4.48.

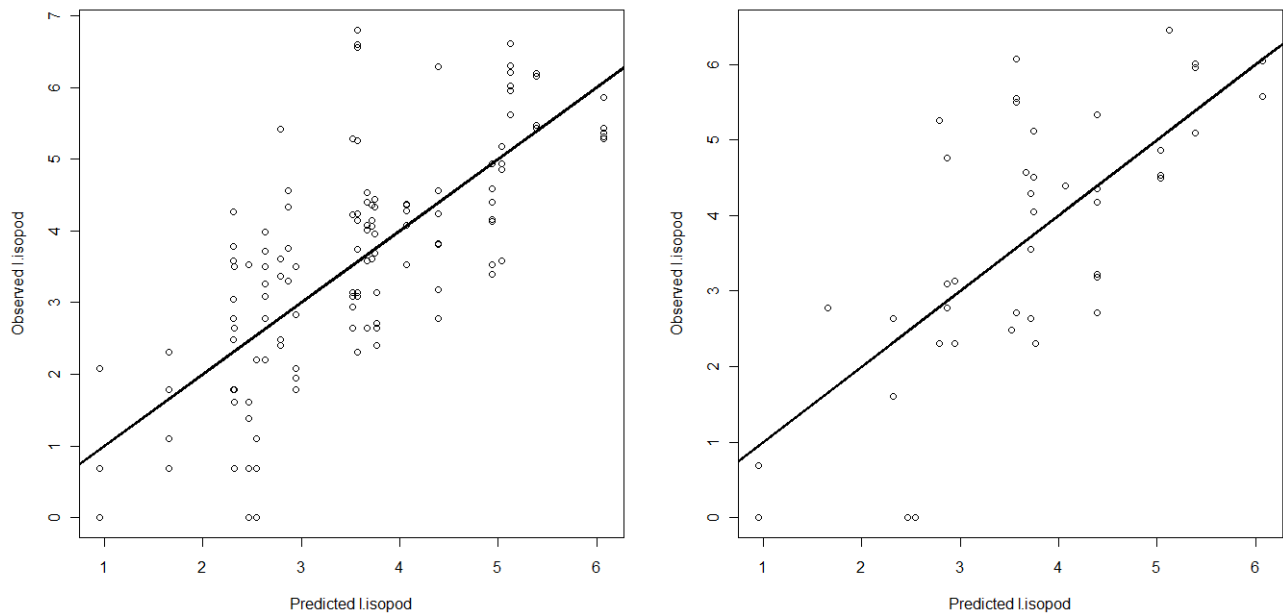


Figure 6: Left: Minimum adequate model prediction with the main data showing the observed versus predicted values of l.isopod. The line shows the predicted l.isopod values based on the minimum adequate model. Right: Minimum adequate model prediction with the test data of 44 points initially subsetted from the observations and not used in the construction of the minimum adequate model. The line shows the predicted l.isopod values based on the minimum adequate model.

Discussion:

Management treatment on isopod assemblage

While management was found to not impact isopod assemblage, this is likely the result of a lack of analytical power due to the small sample size, unequal treatment replication, and the use of a rank based test. The apparent differences in mean between mowed treatment areas and controlled or burned areas (Figure 4) provides further evidence that finding no relationship between isopod assemblage and treatment was due to a lack of statistical power. Other research conducted across arthropod taxa suggests other arthropod populations were either not greatly influenced by mowing and/or burning treatments or there was high variation of responses to treatments across taxa and season (Dunwiddie 1991). Current research shows arthropods, including isopods, generally adapt to management actions (Warren et al. 1987; Dunwiddie 1991). Further, observed managed sites were mowed and burned in different years potentially providing isopod assemblage the opportunity to rebound from treatment making the affects undetectable by the 2008 observation.

The known relationship between management and environmental predictors of isopod assemblage further supports the supposition that a lack of significant effects was due to low power of analysis. Mowing and burning are tools used to maintain the vegetation on sandplain grasslands (Neill 2006). Burning consumes leaf litter and destroys isopod microhabitats (Springett 2006). Mowing should lead to an increase in litter that may also impact isopod habitat availability. Using mowing and burning may indirectly benefit isopod communities by improving the habitat requirements that isopods rely on.

Isopod assemblage in relation to significant environmental variables

While the hypothesis that leaf litter would be the strongest predictor of isopod assemblage was not supported, leaf litter was found to be of second highest importance after woody stem count. Woody stems were mainly represented by living black huckleberry and some bayberry. Understanding the woody stem/isopod assemblage relationship is a key to analyzing isopod populations. Other studies have highlighted the importance of habitat structure, including connective landscape properties and variations in fauna and soil types, on isopod population dynamics (Davis 1984; Souty-Grosset et al. 2005). Isopod species may rely on woody stems for protection from solar radiation and captured rainfall (Volk et al. 2000). Balancing the habitat mosaic of heath and shrubs within grasslands may benefit isopods and the grassland community. Further upkeep of interspersed woody stems within the Nantucket managed ecosystem would likely benefit flora and fauna interactions and isopod populations.

The significant influence of litter and bare ground compared to other measured environmental factors highlight the importance of detritus as a food source for the isopod community. Isopods show very strong preferences for detritus (Hassall et al. 1987; Zimmer 2002), and in this ecosystem ground litter is comprised mostly of decomposing grasses (Burke et al. 1998). The negative relationship between bare ground and isopod assemblage further emphasizes the impact of vegetation and subsequent ground litter on Nantucket isopod assemblage. Maintaining a naturally decomposing ecosystem with high flora richness and scattered vegetation diversity will most benefit isopod assemblage in this ecosystem.

Although more than 90% of isopods counted appeared to be of the same morphological type, the few unique individuals suggests identifying isopods to the species level may identify isopod species indicative of particular important microhabitats. Species level identification could help improve understanding of ecosystem interactions. Rare predatory isopods have been shown to be strong bioindicators of successful restoration efforts in terrestrial shrublands (Longcore 2003), and knowing isopod species could better inform landscape management. Identification of vegetation species may also show isopod preference and contribute to a better understanding of the importance of litter composition.

The role of environmental variables not measured in our study, such as soil moisture, which has been shown to have a significant effect on isopod assemblage (Warburg 1987), may have limited the predictive power of our linear model. A wide range of interacting factors contribute to the creation of microhabitats and microbiomes within shrubs scattered throughout grasslands. Shrubs within grasslands act as areas of intense nutrient flux from root/leaf turnover and excess excrement from surrounding fauna (Vetaas 1992). Terrestrial isopods have undergone evolutionary changes to dwell on land, and despite some species living in arid regions, all species need protection from desiccation (Schmidt & Wägele 2001). Scattered shrubs (woody stems) in grasslands create moist, hospitable microclimates similar to the effect scattered trees can have in a landscape (Manning et al. 2006).

The model validation indicated that the model does a good job of describing related independent data. The root mean square difference of 4.48 for isopod assemblage is assessed based on its comparison with the mean isopod assemblage of 101. A difference of 4.48 is small in comparison to the mean of 101 indicating the applicability of the linear model to independent data.

Study-wide considerations

As strong predictors of isopod assemblage, alterations in management that impact leaf litter and woody stems should affect isopod assemblage. Further study on a greater number of

independent grassland and heathland sites that have been mowed or burned should uncover the relationship between isopod assemblage, management action, and the significant predictor variables from our minimum adequate model. Management affects leaf litter (Andrew et al. 2000), ground cover, and woody stems, and those three predictors indicate isopod assemblage. That the affect of management on isopod assemblage was not found in our study while leaf litter, percent bare ground, and woody stems were found to be significant predictors of isopod assemblage is almost certainly due to our sampling design and provides a clear call to further research.

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Appendix:

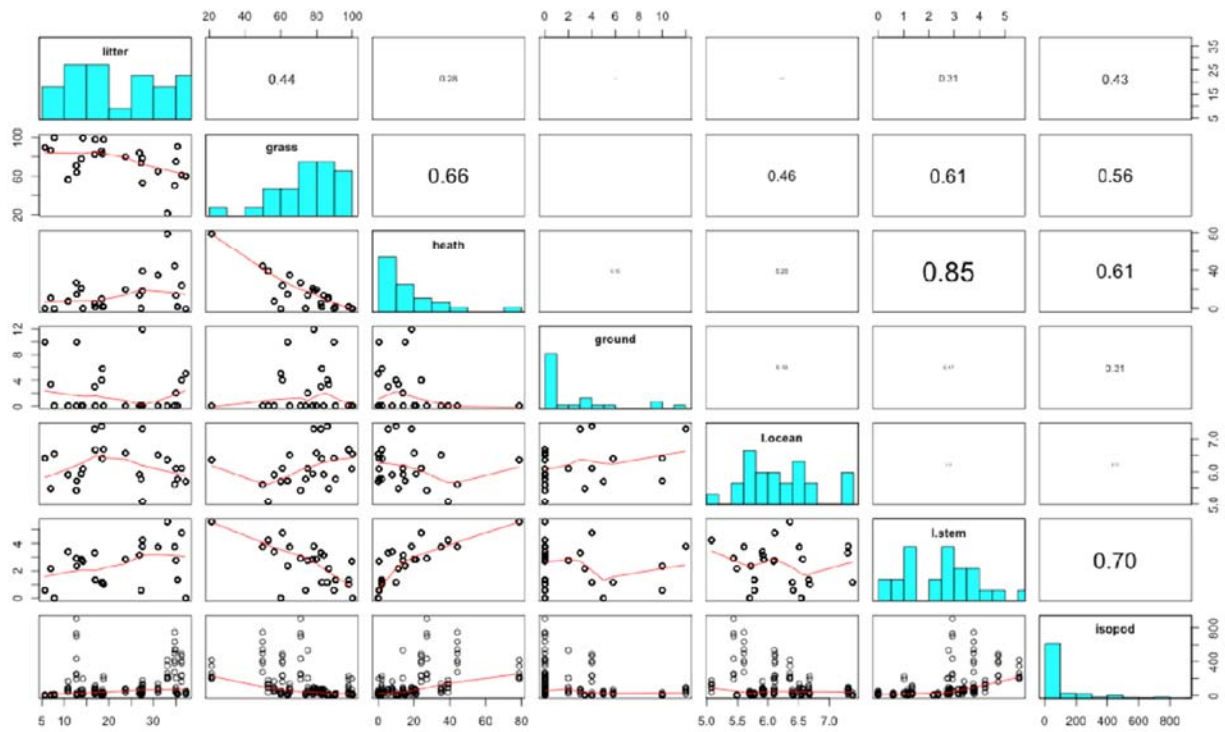


Figure A: Correlation matrix showing histograms, scatterplots, and Spearman correlations between the response variable isopod assemblage and the seven predictor variables.

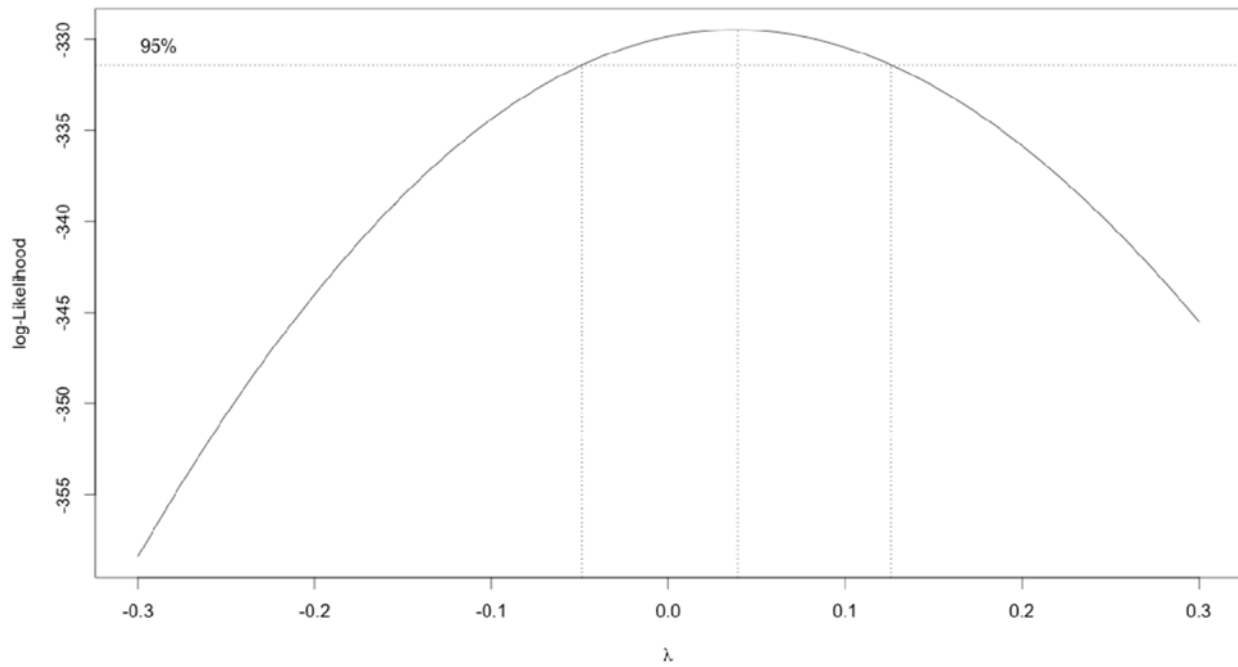


Figure B: Results of Box-Cox power transformation on isopod as a function of litter, grass, heath, ground, l.ocean, and l.stem indicating a log transformation would be appropriate (as seen by the 95% confidence interval lines enveloping 0).

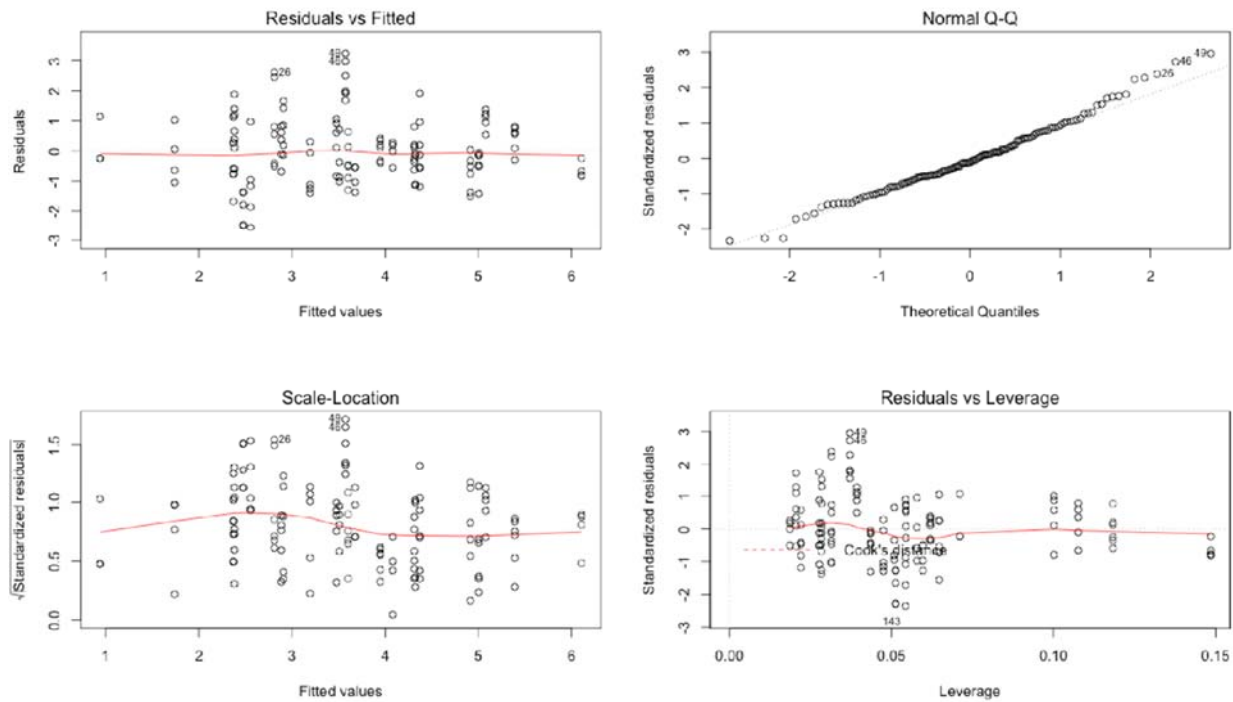


Figure C: Diagnostic statistics of full model. Top left shows that the residuals are normally distributed about a zero line and show no structure, the top right shows the normality of the standardized residuals, the bottom left shows the standardized residuals have no underlying structure, and the bottom right shows that there are no high leverage outliers with Cook's distances of greater than 0.5.

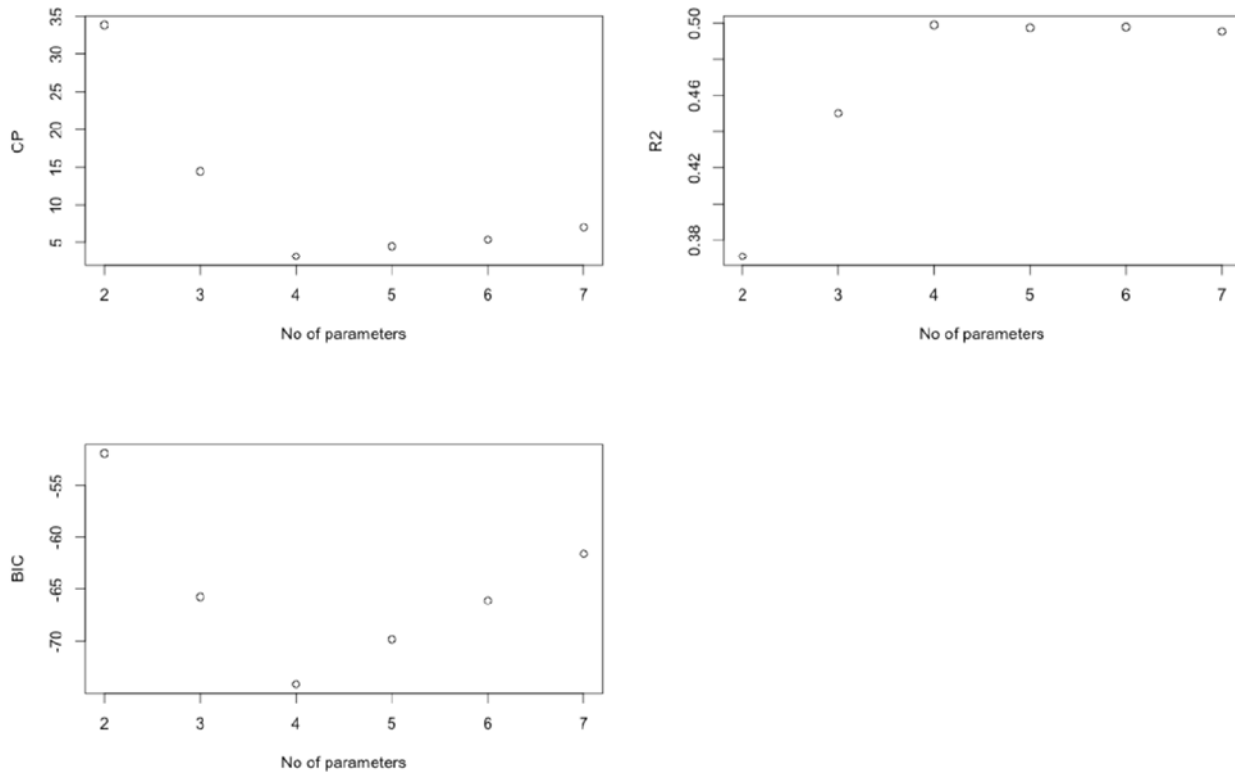


Figure D: Plotting the results of an all subsets criterion-based procedure modeling *I. isopod* as a function of between 1 and 6 variables and 1 y-intercept. Top left shows the lowest Mallows' Cp for models with 1-6 variables + 1 y-intercept. Top right shows the highest R^2 and bottom left the lowest Bayesian Information Criterion for models with 1-6 variables + 1 y-intercept. Each criterion indicates that a model with 3 predictors and 1 y-intercept would be the best.

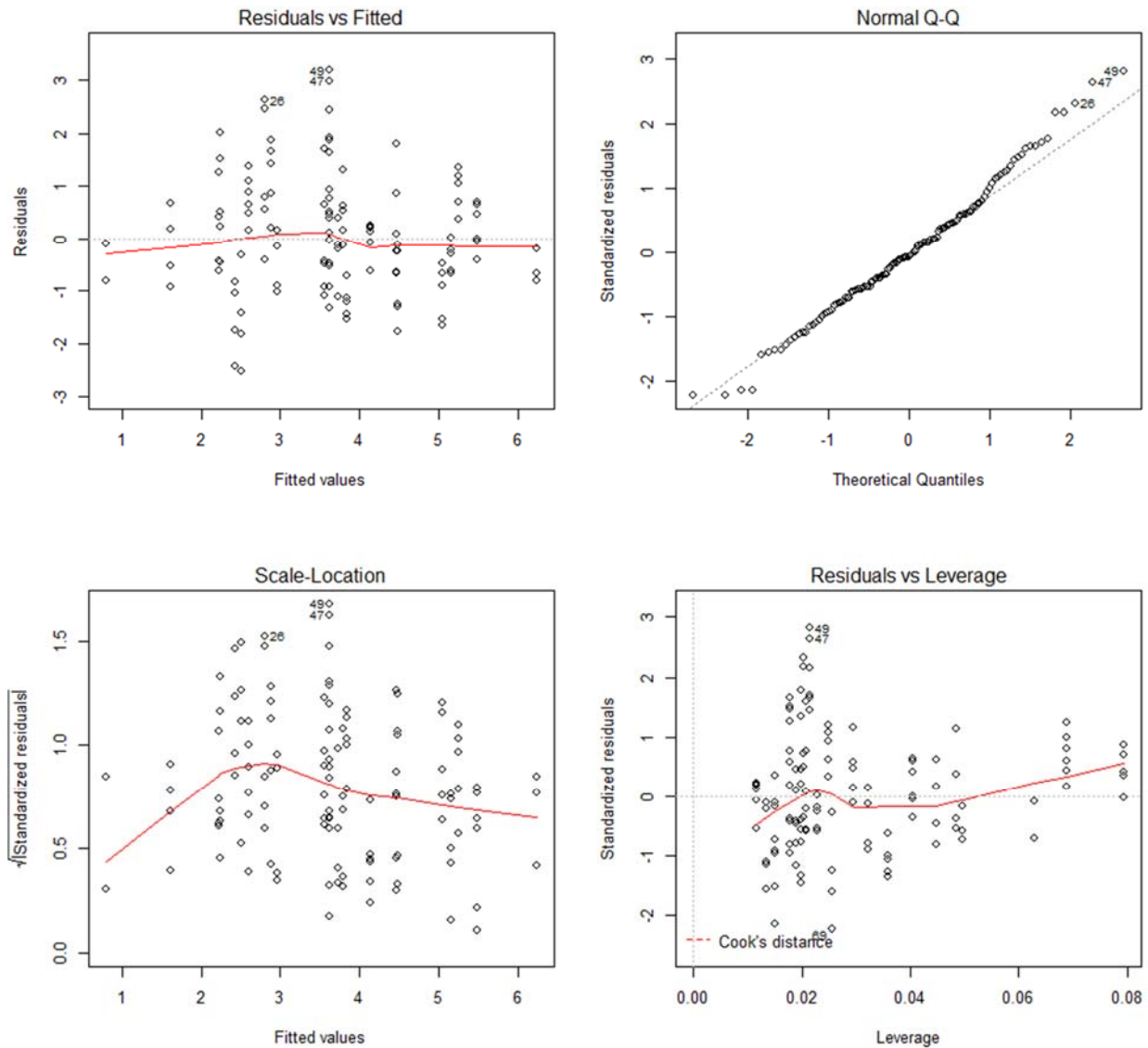


Figure E: Diagnostic plots of the minimum adequate model. Top left shows that the residuals are normally distributed about a zero line and show no structure, the top right shows the normality of the standardized residuals, the bottom left shows the standardized residuals have no underlying structure, and the bottom right shows that there are no high leverage outliers with Cook's distances of greater than 0.5.