

What abiotic and biotic factors predict the shapes of plant diversity-productivity relationships?

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Abstract:

Anthropogenic influence over biodiversity has altered ecosystem functions. One important ecosystem function related to diversity is productivity. Plant richness has long been considered for determining productivity. Despite the importance of the relationships between diversity and productivity, their shapes are debated and what determines variation in shapes is not well understood. We examined diversity-productivity relationships from local to landscape scales in a mountain ecosystem. We first asked: what is the shape of the richness and productivity relationship at the landscape? We compared fits of linear and Michaelis-Menten models to richness predictions of productivity. Also, we evaluated whether the humped-back model of productivity and diversity applies in the system. Second, we asked: what abiotic and biotic factors predict the shapes of richness-productivity relationships within sites? We collected plant community composition data including richness and plant cover of each species as a proxy for productivity in 67 sites across 6 peak-valley combinations spanning elevation gradients. Also, abiotic and biotic factors were recorded in all sites. The Michaelis-Menten model was a better predictive fit than the linear model for predicting cover with richness. We found a positive relationship between richness and productivity at landscape scale. But, the saturation curve of the Michaelis-Menten model predicts better the increase of productivity with richness. We found evidence for the humped-back model of productivity and richness across the landscape. Finally, abiotic factors were identified predicting derived parameters β , $V_{\max}$, and K . Importantly, our results suggest that fewer species can make high biomass production with high nitrogen and potassium.

Introduction:

Anthropogenic influence over biodiversity has greatly altered ecosystem functions and services. Diversity can be lost via a myriad of processes, including lack of adaptation to the rapidly changing conditions, phenological changes altering species interactions, shifts in species abundance and geographic ranges, and habitat loss (Rinawati et al. 2013). For example, climate change caused biodiversity loss has the potential to negatively affect ecosystem functions such as productivity, trophic interactions, biogeochemical cycling, and other processes by eliminating key species that disable functions (Craven et al. 2016). Humans benefit from ecosystem services like pollination, air and water purification, decomposition, nutrient cycling, and many others are affected by diversity loss (Liang et al. 2016). The roles of biodiversity in ecosystem functioning are very important and humans should focus on species conservation to sustain ecosystems.

One of the most important ecosystem functions related to diversity is productivity. Net primary production provides chemical energy for consumers promoting higher level trophic interactions and food chains (Young et al. 2013) and maintains ecosystem functioning and stability (Cleland 2011). Previous studies have found that productivity generally increased with plant diversity (Van Ruijven and Berendse 2005, Craven et al. 2016) and that diversity loss caused productivity loss (Lambers et al. 2004, Craven et al. 2016). Moreover, decreased tree diversity resulted in decreased forest productivity worldwide (Liang et al. 2016). Productivity is controlled by abiotic factors, including light, soil moisture and pH, temperature, organic matter, nutrient availability (e.g. N, P, K), CO₂, and O₂, and biotic factors such as herbivory (e.g. grazing) (Haferkamp 1988, De Lafontaine and Houle 2007, Craven et al. 2016).

Biodiversity is similarly controlled by abiotic factors (Loreau et al. 2001). Results indicate that it has a unimodal relationship with altitude at local and regional scales (Bhattarai et al. 2014). Abiotic factors that determine species richness are light, temperature, precipitation, soil moisture, abiotic stress, and productivity itself (De Lafontaine and Houle 2007). Past work has found that plant richness increases with soil pH and biotic factors such as grazing and pocket gophers' mounds (Baker et al. 2003, Bhattarai et al. 2014). Van Ruijven and Berendse (2005) found that aboveground nitrogen increased with species richness. This result suggests that nutrients like nitrogen play an important role

in determining species diversity. Resources affecting diversity and productivity along abiotic gradients could help us understand what drives and predicts the shapes of diversity-productivity relationships, what can be done to maintain ecosystem functions, and inform the conservation of biodiversity and ecosystems.

Plant richness has long been considered an important component determining ecosystem productivity. Also, for years ecologists have focused on predicting plant richness with productivity. Both, richness-productivity and productivity-richness relationships, show variation in shape because they depend on spatial scales (Waide et al. 1999, Mittelbach et al. 2001). Waide et al. (1999) & Mittelbach et al. (2001) classified relations results of published studies into five types which are positive, negative, hump-shaped, u-shaped, or no relationship. The humped-back model suggests that plant diversity peaks at intermediate productivity, is low at high productivity where a few species dominate available resources, and is low at low productivity where the environment is so stressful that a few species have evolved the capacity to survive in it (Grime 1973). Fraser et al. (2015) provided evidence in support of the humped-back model pattern at regional and global scales. In contrast, Adler et al. (2011) found no clear relationship between productivity and richness within sites, regions, or across the globe.

The shape of the diversity-productivity relationship is important because it tells how much productivity there is in an ecosystem given a number of species. Also, it can predict how ecosystem functions like productivity will shift with plant diversity loss. Liang et al. (2016) found a concave-down tree richness-tree productivity relationship across forests at global scale. The results of other studies showed a positive log linear model between plant richness and productivity at large scale (Van Ruijven and Berendse 2005, Marquard et al. 2009). The positive relationship between richness and productivity was found to be driven by increased density of more productive species in mixtures (Marquard et al. 2009). Lambers et al. (2004) found that competition for limiting resources, diversity-promoting interactions, niche differentiation, and facilitation by nitrogen-fixing legumes stimulating productivity of other species were the main mechanisms that contributed to the positive relation at Cedar Creek experimental diversity gradient. Also, complementarity in resource use was also a driver of increased productivity at higher levels of species richness (Van Ruijven and Berendse 2005).

Despite the importance of the relationships between plant diversity and productivity, their shapes are hotly debated and what determines variation in shapes is not well understood. Here, we examined plant diversity-plant productivity relationships from local to landscape scales in a mountain ecosystem. We first asked: what is the shape of the plant richness and productivity relationship across sites in the landscape? Specifically, we compared fits of linear and Michaelis-Menten models to plant species richness predictions of productivity. Additionally, we evaluated whether the humped-back model of productivity and diversity applies in the system. Second, we constructed models of plant richness-productivity relationships for local communities and derive their parameter estimates to ask: what abiotic and biotic factors predict the shapes of plant richness-productivity relationships within sites? We hypothesized that the plant richness-productivity relationship across the landscape will show a positive linear model. Also, we predicted that larger slopes of the linear models (fewer species required to reach high productivity) would have higher resources (e.g. soil N, P, K) and less climatic stress (e.g. higher temperature and precipitation). For the Michaelis-Menten function, we predicted that maximum productivity (the asymptote, $V_{\max}$) would relate to well established abiotic limitations on productivity (e.g. resources, climatic stress), while the richness required to meet half the possible productivity (half saturation point, K) for a site will increase with fossorial mammal and livestock disturbance. This research tries to clarify the shapes of the relationships and identify factors that cause variation and can predict the relations.

Materials and Methods:

We collected plant community composition data including species richness and plant cover of each species as a proxy for productivity in 67 sites across 6 peak-valley combinations spanning elevation gradients ranging from 2700-4000m a.s.l. The peaks sampled included Avery, Cinnamon, Hunters Hill, Teocalli, Treasury, and Ruby located in the Gunnison Basin, Colorado, USA. Also, abiotic and biotic factors were recorded in all sites within gradients. Abiotic factors data included soil nutrients (N, P, K), soil moisture and pH, slope aspect, and climate data generated from interpolations of regional weather

station data. Additionally, we sampled pocket gopher disturbance and livestock presence at each site to serve as biotic predictors.

For the vegetation surveys, we established 1 vertical transect with the prevailing slope and 3 horizontal transects at the 0, 10, and 20m points on the vertical transect. Each transect was 20m long. Plant composition was identified within a 20x20cm quadrant. Vegetation was sampled every 2.5m along each transect, excluding areas of intersection, resulting in a total of 33 quadrants sampled per site. Plants sampled included species from the following families: *Asteraceae*, *Apiaceae*, *Brassicaceae*, *Caryophyllaceae*, *Chenopodiaceae*, *Cyperaceae*, *Campanulaceae*, *Caryophyllaceae*, *Fabaceae*, *Juncaceae*, *Linaceae*, *Polemoniaceae*, *Poaceae*, *Polygonaceae*, *Primulaceae*, *Rosaceae*, *Rubiaceae*, *Scrophulariaceae*, *Salicaceae*, *Valerianiaceae*, and *Violaceae*.

Statistical methods included ordinary least squares regressions to analyze fit of linear, Michaelis-Menten, and humped-back (quadratic) models. We use Bayesian model fitting procedures to derive linear slopes and Michaelis-Menten V_{max} and K for each site. We use ordinary least squares to analyze relationships between abiotic and biotic data and the derived parameters. Then, we utilized partial residual plots to predict parameters with abiotic and biotic factors given that we included all factors as independent variables in the model and we have to consider their effect. Also, we use AICc metric to compare all model fits with the same dependent variables and obtain the probability that a model is better. The Michaelis-Menten function is given by:

$$P = \frac{V_{max} * S}{K + S}$$

Where P is the total productivity (cover) for a given site or quadrant, and is predicted by richness, S , with parameters K and V_{max} , which are the half-saturation and asymptote, respectively.

Results:

The Michaelis-Menten model was a better predictive fit than the linear model for predicting plant cover (log-transformed) with species richness across the landscape (AICc = 25.2 vs. 262.7 respectively; Table 1). Even so, we found a statistically significant positive linear relationship between plant richness and productivity across sites in the landscape, with plant cover (log) increasing with richness ($p < 0.05$; Table 2; Fig. 2A). But, the

saturation curve of the Michaelis-Menten model predicts better the increase of log productivity with richness (Fig. 2B). Switching the axes, we found evidence for the humped-back model of productivity and richness across the landscape ($p < 0.05$; Table 2; Fig. 2C). The humped-back model was a better fit than the linear model for predicting richness with cover ($AICc = 409.5$ vs. 423.4 respectively; Table 1).

Abiotic factors were identified predicting parameters β , V_{max} , and K within sites. We obtained a significant positive correlation between nitrogen and partial residuals of β describing the local relationships of richness and plant cover ($p < 0.05$; Table 2; Fig. 3). As a result, linear β coefficients increased with plant available nitrogen. The partial residuals of V_{max} were positively related to north facing slopes, although it was not significant ($p > 0.05$; Table 2; Fig. 4). The Michaelis-Menten asymptote (V_{max}) increased with the cosine of aspect. Finally, we obtained a negative relation between potassium and partial residuals of K and a positive relation between the cosine of aspect and partial residuals of K ($p < 0.05$; Table 2; Fig. 5 respectively). The half saturation point in the Michaelis-Menten equation, K , increased with north facing slopes and decreased as potassium increased.

Discussion:

Our result of a positive linear relationship between plant richness and productivity is consistent with our hypothesis and previous studies that have found positive log linear models at large scales (Van Ruijven and Berendse 2005, Marquard et al. 2009). This evidence supports the idea that the relationship is usually positive linear at landscape scale (20-200km). The Michaelis-Menten model is a different and accurate approach to understand the relation between richness and productivity. We can infer that the shape of the plant richness and productivity relationship across sites in the landscape takes the form of a saturation curve. More plant species may have managed to achieve higher productivity in this study by mechanisms as facilitation by nitrogen-fixing legumes (*Fabaceae*) and non-legumes (*Rosaceae*) promoting other species productivity (Lambers et al. 2004). Also, increased density of more productive species, niche differentiation, and complementarity in resource use could influence a higher productivity with high richness (Lambers et al. 2004, Van Ruijven and Berendse 2005, Marquard et al. 2009). The evidence we provide here for the humped-back model of productivity and richness across the landscape supports Grime

(1973) and Fraser et al. (2015). This suggests that the negative quadratic pattern is a good fit for productivity predictions of richness showing that plant richness peaks at intermediate productivity where competition for resources is moderate and there are enough resources for plant richness to increase (Grime 1973).

Sites with more nitrogen had steeper linear relationships between richness and productivity. This result agrees with our predictions of larger slopes of the linear models having higher resources. This indicates that nitrogen is an important abiotic factor predicting the shapes of richness-productivity relationships at local scale. Steeper slopes representing fewer species achieving high productivity can be due to competition with highly competitive species dominating available nitrogen, excluding other species, and inducing less richness but high productivity (Grime 1973). Evidence that nitrogen availability increased productivity has been reported on previous studies (Craven et al. 2016, Leghari et al. 2016). Contrary to our predictions that $V_{\max}$ would relate to abiotic limitations as less resources or nutrients and climatic stress, we found that it is predicted by the cosine of aspect. Two studies also found that productivity of plant and tree species as poplars was higher on northerly aspects (Thelemann et al. 2010, Albaba 2014). The increase on maximum productivity a system can achieve ($V_{\max}$) with north facing slopes in our results can be caused because north aspects have fertile soils with resources like soil moisture and nutrients that enhance productivity (Måren et al. 2015).

K for a site was not found to increase with fossorial mammal and livestock disturbance as we proposed, instead it was predicted by potassium and the cosine of aspect. The increase of K with north aspects and the decrease with potassium means that in north aspects we need more species to meet half productivity and when there is more potassium less species are needed to reach half productivity. North facing slope aspects receive less amounts of solar radiation limiting productivity and needing more species to meet half productivity (Måren et al. 2015). Potassium availability leads to competition decreasing richness but allowing dominant species to increase productivity reaching half of the productivity with less species (Grime 1973, Zelelew et al. 2016). Evidence of productivity increasing with potassium was reported with potato tuber and tomato species (Zelelew et al. 2016, Woldemariam et al. 2018). Future research should consider nitrogen and potassium manipulations to see the direct effect on productivity and species richness. Also,

experiments can be designed to test how abiotic factors gradients in north and south facing slopes affect biomass production and richness. A more complex experiment could include nitrogen and potassium manipulations on north and south aspects to identify and compare the mix effects on productivity and the number of species. Finally, additional work can focus on developing conservation management plans to preserve plant diversity.

Conclusion:

In conclusion, the Michaelis-Menten model was better predicting plant cover with species richness at landscape scale. This highlights the importance of exploring different models with plausible mechanistic underpinnings. This model can be used in the future to understand the richness-productivity relationships at different scales and other relations in studies within ecology. We conclude from our observations that there is high variation in the shapes of richness-productivity relations at local scale including positive linear, negative linear, and no relationship. For the relationship between productivity and richness, we can conclude from our results and previous evidence that the humped-back model applies and best describes it at landscape, regional, and global scales (Fraser et al. 2015). Importantly, our results suggest that fewer species can make high biomass production with high nitrogen and potassium. At last, we infer that few species productivity can be increased adding nitrogen and potassium to counteract the decline in productivity caused by biodiversity loss aiming at ecosystems stability and conservation.

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Appendix:

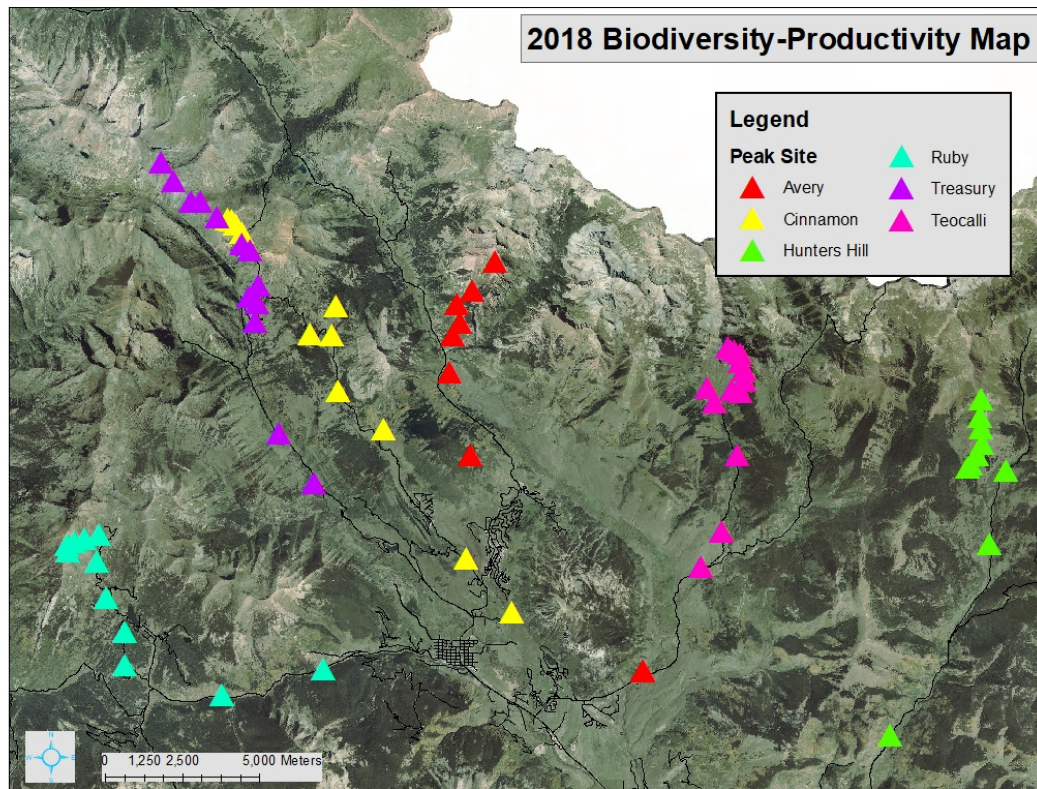


Fig. 1. Peaks-sites sampled located in the Gunnison Basin, Colorado, USA.

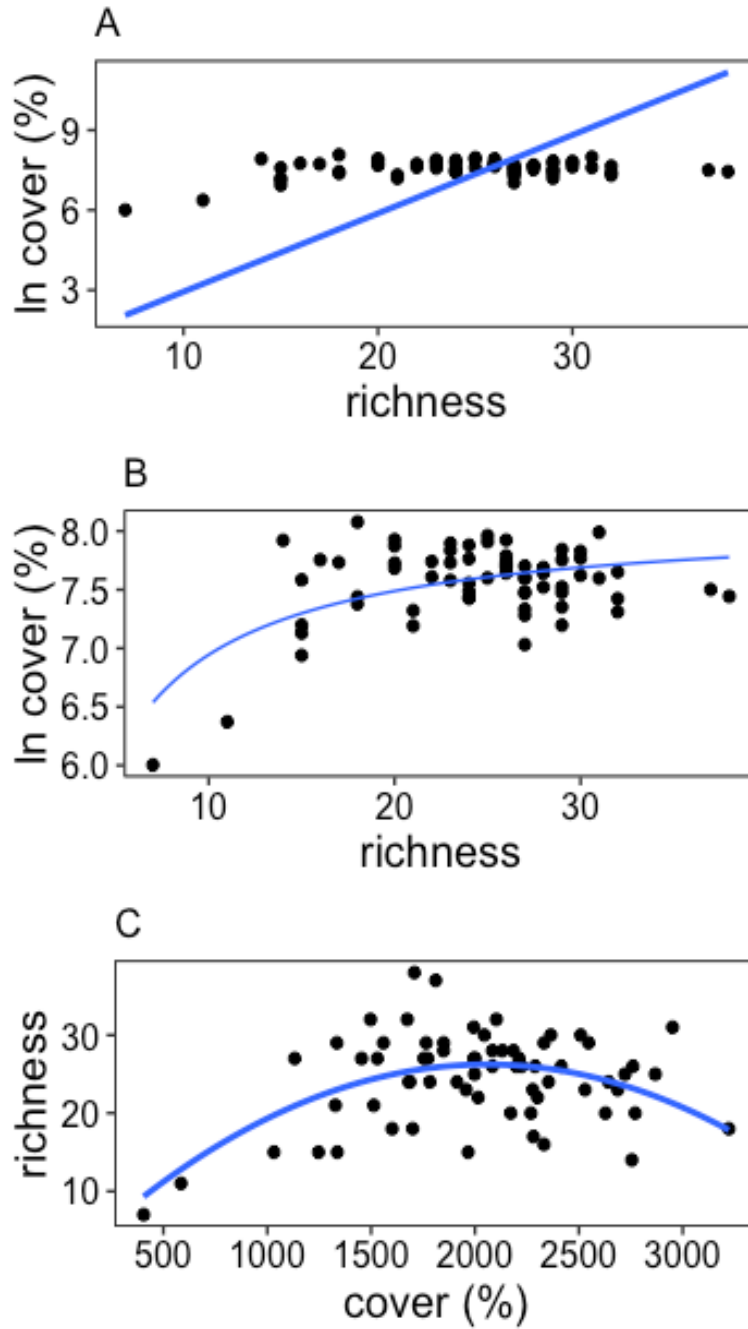


Fig. 2. Positive linear model between plant richness and the logarithm of plant cover at landscape scale (A). Michaelis-Menten model between richness and log cover at landscape scale (B). Humped-back model between cover and richness at landscape scale (C).

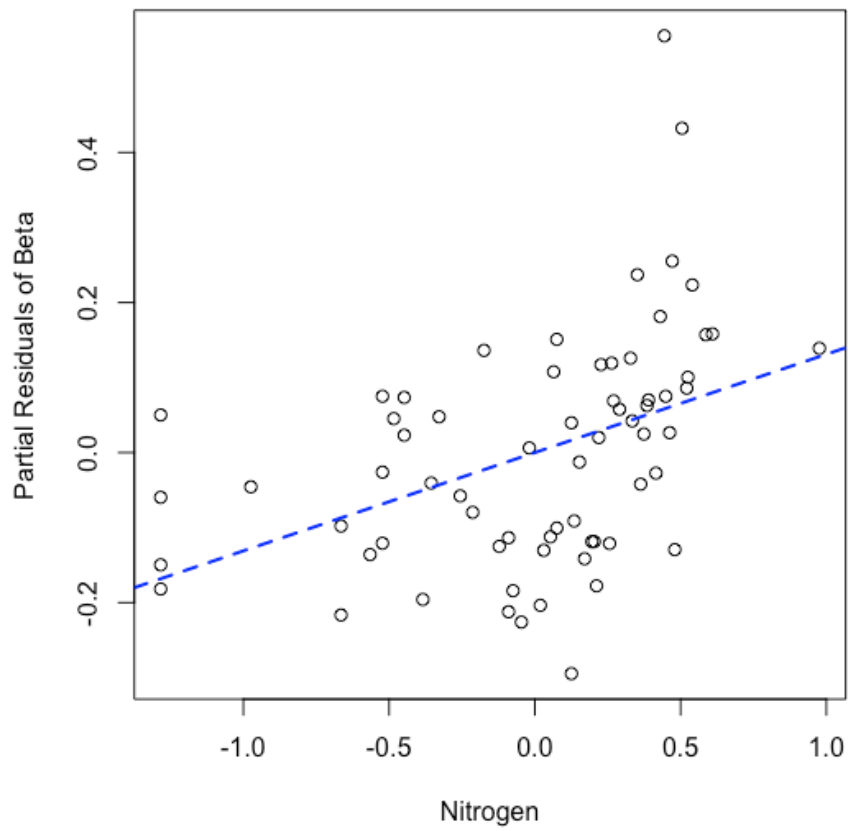


Fig. 3. Positive correlation between nitrogen and partial residuals of beta describing the local relationships of richness and plant cover.

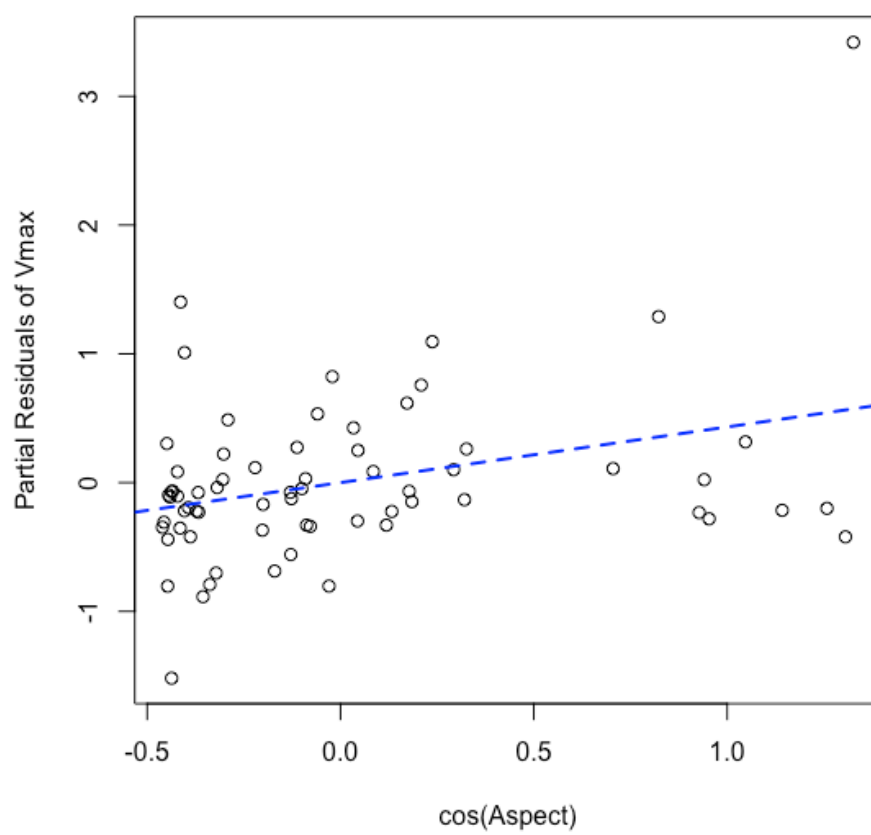


Fig. 4. Positive correlation between the cosine of aspect and partial residuals of $V_{\max}$ at local scale.

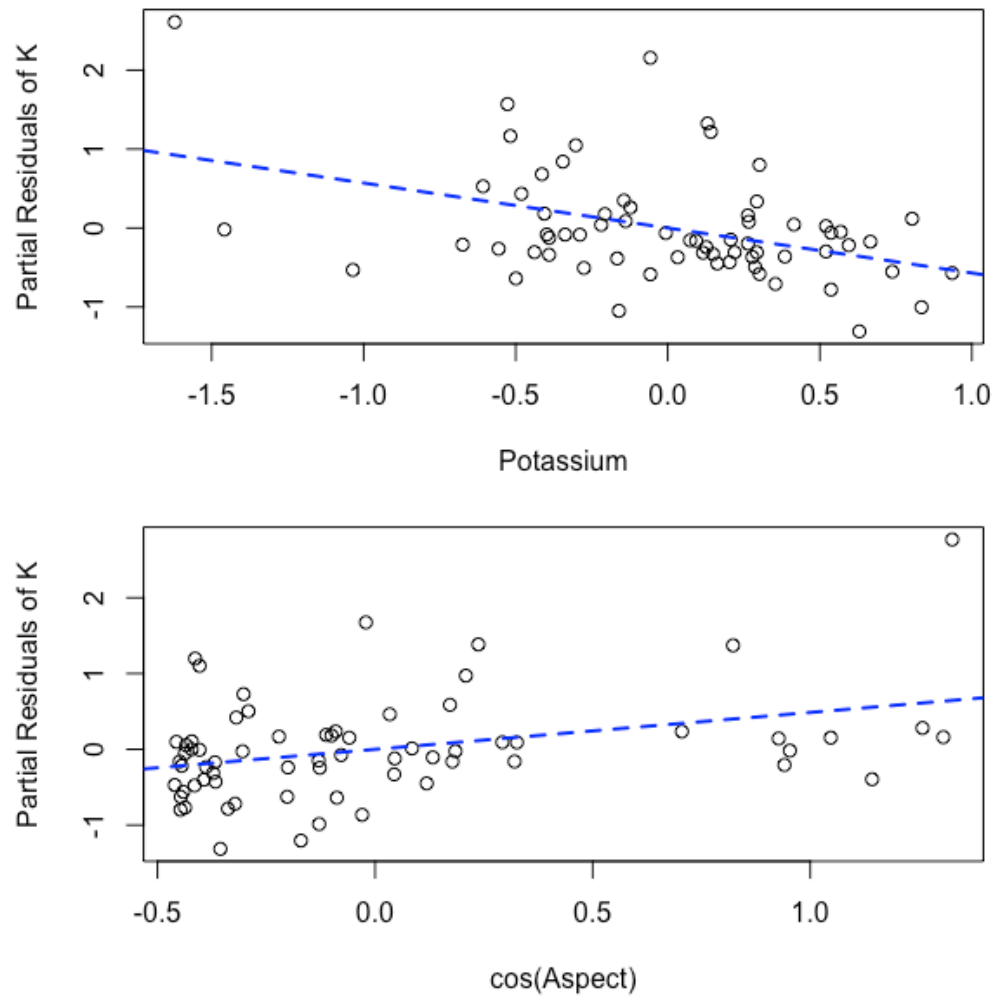


Fig. 5. Negative correlation between potassium and partial residuals of K and positive correlation between the cosine of aspect and partial residuals of K at local scale respectively.

Table I. Models' AICc. AICc is an information criterion that accounts for model complexity while assessing within sample predictive ability, such that lower AICc is better predictive model given the complexity of the models compared. Delta AICc is the difference between model predictive scores; weights are interpreted as probability of a model to be best out of the candidate set.

Model Name	AICc	Delta AICc	Weights	DF
Productivity (log)~Richness				
Michaelis-Menten	25.2	0	1	65
Linear	262.7	237.5	0	66
Richness~Productivity				
Linear (log productivity)	423.4	13.9	0	66
Humped-back	409.5	0	1	65

Table II. Ordinary least squares regressions. The F statistic determines the p-value and both are used to decide if the results are significant. p-value is the probability the results are due to chance (alpha level of 5%). R^2 is a statistical measure of how close the data are to the fitted regression line.

Model Name	p-value	r^2	F Stat.	DF
Linear	2.20E-16	0.9508	1296	66
Humped-back	2.20E-16	0.9607	820.6	65
Beta linear	0.04347	0.1524	1.989	54
Vmax linear	0.4413	0.004273	1.024	54
K linear	0.004445	0.2498	2.831	54