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Variance in measured traits leads to more resolute findings using the Jensen Inequality

When measuring phenotypes, or traits, for ecological research many studies involve the mean phenotypic measurement, instead of a metric of the population, which could lead to a reduction in the models ability to show the actual behavior of the system. This can overshadow the dynamics occurring in the population, and generally results in figures only as linear models while the bulk of variance is ignored due to the nature of the model (Wetzel 2016 & Coley 1988). This type of variance is pervasive through the literature, and in a paper by Karban (et al 1997) we see that the methodology at that times was to use mean plant values and then to just measure the response of the herbivore. The ignoring of the importance of variance in trait models, and environmental variance, in classical papers was the results of earlier investigators not realizing the importance of variation in the context of their models. However, over the last few decades there has been an acknowledgement of the importance of environmental variation in ecological models, and variation has been implemented into these models at an increasing rate (Ruel and Ayres, 1999). In order to explicitly include the variance into the analysis using a methodology termed Jensen’s inequality is used in order to include the variance of the measurements using secant line transformations. The Jensen’s inequality allows for the graph to take on a convex (or concave) shape which allows for better analysis of the rates of the system. The application can be beneficial for understanding a complex interactions, such as those in Wetzel (2016), where the transformation using Jensen’s inequality show that the relationship between nutrient concentration in a plant species and its growth/survival is not a linear model but a concave one. This indicates that there is not an initial rate of decay in the system, but a gradual tapering off until a certain nutrient concentration level is achieved which then causes the graph to take a sharp decline.

The use of variance when modeling ecological interactions by way of the Jensen’s inequality allows for previously linear models to be reinterpreted into a multivariate model relies on the phenomena where a secant line lies above the parabola and intersects at two points -- which are the weighted means of the convex function. This allows the model to agree with the variation seen in the data, but also shows the actual behavior of the data set in a manner more in line with the entire data set instead of just the means. It also allows for inverse convex secant line graphs, and also is capable of transforming the function on the Cartesian plane (see Wetzel 2016). These transformations of the graphs allow for more complex shapes such as an inverse ‘J’ shape showing a gradual decline with various changes in the rate. These, along with other transformations, allow researchers to model otherwise simple linear models into ones which vary in rate and intensity. The Jensen’s correction allows for more resolute and accurate representation of measured data than its counterpart, a linear model. This inclusion allows us to determine non-linear relationships between two variables allowing for the dissemination of complex interactions which would have not been elucidated without it.

The Jensen inequality is a useful tool when looking at population wide data of a species in response to an environmental pressure such as nutrient concentration or nectar concentration. The power lies in its ability to be sensitive to changes in the variance, and to respond in an appropriate way which allows for graphs with varying rates such as those in Wetzel et al. 2016 (Fig. 2c) where there are three separate lines indicating the possible outcomes of using the inequality. Using the inequality is not only useful when it comes to population data, but it inherently can help show the phenotypic variance within a population through transformation of the previous function derived from the linear data to one which accounts for the variance in the traits measured resulting in a more detailed graph. It can show the heterogeneity of the population through the variance in the measured attributes of the population giving more power to the Jensen’s inequality graph. An interesting application of this modeling techniques is used by Garibaldi et al (2011) where they used the Jensen’s inequality to show that pollen deposition and yield of agricultural produce follows a negative Jensen’s pattern (see Wetzel et al. 2016 Fig1c for an example). This application is further explored when they parse apart the plants which require greater levels of pollen deposition and have different levels of nonspecific pollen present resulting in data which reflects the species themselves instead of the community. The application of Jensen’s inequality in this circumstance is quite useful because it gives a better picture of what levels of pollinator dependence and levels of pollen needed for agricultural crops. The use of the Jensen’s inequality is not just limited to use in plant pollinator interactions, but it also has many different applications outside of this ecological interaction and is a general mathematical relationship applied to biology.

Another use of this model is to apply it in a similar fashion to herbivores and levels of secondary metabolite levels in plants. Previous studies, such as Carmona et al (2006), used a meta analysis on multiple data sets to measure different plant traits with herbivore resistance. Within this analysis, they found no correlation between herbivore susceptibility and secondary metabolite levels using a linear regression, but also did not implement the Jensen’s inequality into their system. If they were to implement the Jensen’s inequality to their data they may have found a correlation between secondary metabolite levels and its effects on herbivory. In another meta analysis by Wetzel et al (2016) they look at the relationship between secondary metabolite levels and nutrient levels using the Jensen’s inequality. The paper itself does not deal directly with agricultural pests, but instead is a large scale analysis using various studies in order to see if there is an overall average Jensen’s effect with secondary metabolites, herbivore performance, and growth. What they found is that for when the herbivore species *Heliothis virescens* is exposed to defense chemicals there is a mixture of results where we see positive/negative Jensen effects alongside null Jensen effects. While there is a lot of variation in the Jensen effects, the typical response is similar to a negative linear regression. When the herbivore species *Helicoverpa zea* is analyzed with respect to nutrient levels there is a negative Jensen effect across the spectrum indicating that there is an optimal nutrient level for the growth of the herbivore while each side of that optimum is a sharp decline in growth for the herbivore (see Fig. 2b). In the study by Carmona et al (2006), they looked at the effect of secondary metabolite concentrations and herbivore resistance and found no relationship. However, when Wetzel et al (2016) investigated defense compounds on survival they found different Jensen’s effects depending on which secondary metabolite was analyze which ended up causing the overall Jensen’s effect to have a mean around one (Fig 3b). This could be informative of differential effects on the herbivore depending on which secondary metabolite is analyzed. Between these two papers there is an obvious bias towards the Wetzel et al (2016) paper which used the Jensen inequality in their meta analysis yielding more informative results which are indicative of varying Jensen’s effects if secondary metabolite are analyzed individually with respect to herbivore response.

The application of the Jensen equality has not only been applied to herbivore system, but also to systems which include predator prey dynamics and resource acquisition in the case of photosynthesis in plants. In a review by Ruel and Ayres (1999) they investigate the use of the Jensen inequality through a predator prey dynamic by creating a graph which includes the prey mass versus the energy potential for the predator. We see that the application of the Jensen inequality can yield positive/negative concavity alongside an instance where there is no concavity where the Jensen inequality is not applicable. It indicates that not only does the mass of the prey item has have a positive Jensen’s affect on the predator, but also that there is variability even within the prey masses themselves where the energy gained is either lessen or increased depending on what predator is considered. These graphs themselves would also be very useful when looking at population dynamics of predator prey relationships using Lokta-Voltera models where we see similar concavity and fluctuations in population size. A further implementation is its use in photosynthesis carbon assimilation where we see that the general curve of the assimilation follows a positive Jensen dynamic. This is in contrast to a paper which (Brix 1962) where the photosynthetic rates were recorded, but no Jensen dynamic was seen in the data since they just plotted the data points as a regression. If they were to have instead used the Jensen equation, to model the lines in a corrected manner taking into account variation, they may have seen results which were similar to those seen in Ruel and Ayres (1999) where there are obvious changes in both of the trait values has an impact on the population outcome.

The application of the Jensen inequality to ecological systems is an important improvement in ecological studies due to its ability to take into account variation in the traits measured measured. Through the inequality, investigators can model and explain how dynamic certain systems are; and provide us with novel findings showing a more resolute picture when we are comparing between species and also the environment. Due to the simple nature of the inequality we can also return to previous studies in the field and extract even more information from these dynamic systems – such as the meta analysis done by Wetzel et al (2016). One such system which would be interesting to explore would be seeing the actual dynamics of pollinator frequency and inflorescences size which could be easily be used in previous research I conducted on plant floral traits and floral visitation (Peck et al in prep). It would be informative to look at the effect that larger inflorescences have on the number of visits by insects to see if it is not just a linear relationship, but instead a more dynamic relationship where larger inflorescences sizes end up resulting in a reduction in floral visitation. Another potential project would be to explore the idea of infection rate of a plant disease and secondary metabolite levels. It would be interesting to see if higher levels of secondary metabolites confer additional resistance to different concentrations of pathogens in *Arabidopsis thaliana.* If a Jensen’s inequality was applied to either project we may see positive or negative Jensen’s respectfully instead of a standard linear regression.

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