Modeling environmental predictors of *Azteca instabilis* in the coffee agroecosystem

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Abstract: *Azteca instabilis* is an arboreal ant which plays a role in biological pest control in shade-grown coffee agroecosystems. *Azteca* nests display spatial clustering that follows a power law distribution, suggesting self-organization within the ecological community through endogenous factors. One hypothesis is that predators that control the *Azteca* population are density dependent, preventing *Azteca* from colonizing all the trees in a farm by selectively favoring dense nest clusters. Alternatively, nest clusters may reflect exogenous or abiotic controlling factors, such as tree density or slope. To test the second hypotheses, field spatial data from two coffee farms in Chiapas, Mexico were used to create a species distribution model that incorporates environmental (exogenous) variables. The preliminary modeling results show that environmental variables have very weak prediction capability, both when using a logistic generalized linear model (GLM) to model *Azteca* presence/absence, and when using a negative binomial GLM to model *Azteca* abundance. Further work is needed to clarify questions of the appropriate scale and transformation of the predictor data; however, the present results support the hypothesis that *Azteca* distribution is not predominately driven by exogenous variables.

Introduction

The coffee agroecosystem has become part of a global debate within the agricultural management and conservation science fields, on the benefits and trade-offs associated with "land-sparing" and "agroecological matrix" models of conservation. These two theoretical binaries present land managers and farmers with very different directions for what each approach contends to be the most sustainable path to conservation. Land sparing proponents support agricultural intensification in order to reduce the land cover devoted to production and 'spare' it for wilderness conservation (Ewers et al. 2009). Agroecologists contend that diverse and organically-managed farms which provide a wildlife-friendly matrix for migration and persistence of metapopulations are the only truly sustainable way to combine agricultural production and ecological conservation (Perfecto and Vandermeer 2010).

A growing body of literature supports the importance of diversified coffee agricultural practices in fostering biological control mechanisms that are found within their robust systems of ecological relationships (Vandermeer et. al 2010, Hsieh et. al 2012). A well-documented system of relationships is the hemipteran-tending ant *Azteca instabilis* and its ecological associates. *Azteca*, by tending the green coffee scale (*Coccus viridis*), creates large aggregations of scales. When *Azteca* nests are densely clustered, the scale colonies are vulnerable to infestation by the fungus *Lecanicillium lecanii*, which also acts as a hyperparasite of the devastating coffee pest, coffee leaf rust (*Hemileia vastatrix*) (Vandermeer et al. 2009). This density-dependent phenomenon provides biological pest control to the farmer, provided that the natural relationships associated with a robust agroecosystem are allowed to flourish.

The origins of spatial patterns in nature are often described in ecological literature as exogenous, arising from variability in environmental conditions, or endogenous, manifesting as a result of the behavior and ecology of organisms in an effectively homogenous environment (Bolker 2003). The tendency of *Azteca* nests to be clustered in the field is thought to be a spatial signature that is indicative of endogenous processes, such as the density-dependent association between *Azteca*, the green coffee scale, and *Lecanicillium* described above, or the higher attack rate of the parasitoid fly *Pseudacteon* sp. on *Azteca* when nest density is higher (Philpott et. al 2009). Endogenous ecological processes tend to lead to spatial self-organization and contrast

with patchiness resulting from exogenous environmental factors by their spatial signature, namely the fitting of cluster size distributions to a power law (Pascual et. al 2002). Previous research in the particular coffee agroecosystem of this study suggest that the coffee agroecological matrix creates a homogenous environment that is conducive to the expression of spatial patterns of self organization, and that the clustered distribution of the nests of *Azteca instabilis* does indeed follow a power law distribution (Perfecto and Vandermeer 2008, Vandermeer et. al 2008).

However, ant spatial distribution may also be influenced by environmental and abiotic factors, such as habitat patchiness, that reflect topographical or microclimate variation (Soares and Schoerder 2000). Ant nest distribution has been shown in other systems to be a combination environmental factors and interspecies relationships, i.e. exogenous and endogenous factors (Theunis et. al 2005). The focus of this modeling project is on understanding the exogenous factors that could also explain *Azteca* nest clustering. Doing so would help create a more robust understanding of what drives the *Azteca* system of relationships, and how the ecosystem service of biological control that it confers is related to the environmental conditions on the farm. This knowledge would be of value to managers of agroecosystems, through an understanding of what landscape conditions, either inherent in abiotic factors such as topography or climate, or through active ecosystem management, is associated with *Azteca*'s ecosystem service.

Methods

Study Area

Two farms were the subject of this modeling study: Finca Hamburgo, a conventional low-shade farm, and Finca Irlanda, a historically organic high shade farm. Low-shade coffee farms such as Hamburgo support less-populated and less-diversified assemblages of shade trees which can be used by *Azteca* as nest sites. Organic farms, such as Finca Irlanda in 2004 (the time of collection of the farm's dataset in this study), have shade tree assemblages that closely resemble the density and richness found in natural forests (Moguel and Toledo 2001). These diversified assemblages have been shown to be associated with richer, more robust ecological networks, which include ant interactions (Philpott et. al 2006). Finca Irlanda has since transitioned to a more conventional form of management by introducing pesticide use and reducing shade tree richness and abundance. This presents possible modeling opportunities with later datasets which are described in the discussion section of this paper.

For this study, a 30-ha plot was chosen in Finca Hamburgo for mapping shade trees and *Azteca* nest distribution. The dataset was designed to be comparable to an ongoing spatial dataset that had been collected from a 45-ha plot in Finca Irlanda since 2004. The Finca Irlanda dataset was mapped on an unreferenced coordinate system through on-the-ground surveying, while the plot in Finca Hamburgo was mapped using GNSS technology.

Data Acquisition

The 30-ha conventional agroecosystem comparison plot was mapped in the summer of 2012 using a handheld GNSS unit (2003 Trimble GeoXT Pocket PC), with a reported maximum accuracy of 0.5 to 2 m in open-canopy conditions, and 2 to 10 m in closed canopy conditions (Trimble 2004, Chamberlain 2002). All trees over 10 cm in girth at breast height (GBH) were exhaustively identified, GPS-mapped, tagged, and checked for *Azteca* presence.

Previously mapped ant nest data in a 45-ha plot were available from the years 2004 to 2012 as points in an unreferenced coordinate system. Trees in the plot had been tagged and *Azteca* nest presence recorded as part of an ongoing long-term study. Tree locations were determined by their distances from rows of transects laid along a compass bearing. A small systematic sample of control point trees were geo-referenced with GNSS and used to estimate the location of all the trees of the plot, using the "spatial adjustment" tool in ArcGIS (ESRI 2011).

Point data from both farms were converted to 20m raster grids using R statistical software (R core team 2012). The *Azteca* nest density response grid was calculated as the number of nests in each cell, while the presence/absence response was simply determined by whether the cell contained a nest. Two environmental predictor variables, nest density and tree richness, were also calculated from the tree datasets. Both variables were measured in terms of proximity to a focal tree, by calculating the number of nests or number of species within a 20m radius of every tree. Values were assigned to each cell as the mean total tree or species value of all the trees falling within the cell's boundaries. This produced a variable measure that was more relevant to the perspective of an ant nest, because neighborhood measurements were centered on potential nest locations rather than arbitrary cell centers.

All other environmental predictors were abiotic variables calculated with ArcGIS from a 20m DEM layer. These included elevation, percent slope, topographical wetness, an index of southern aspect, and an index of eastern aspect. All the grids, including biotic predictors, were aligned to the DEM grid's location and resolution.

Predictor variables were chosen based on hypothesized roles they could play in determining *Azteca* distribution. Tree density and richness may have a positive relationship with nest number or presence, because greater density and richness could provide more potential nesting sites and a robust system of ecological relationships, respectively. Elevation may correlate with microclimate differences while slope may be related to wind exposure. Topographical wetness identifies potential site moisture. Hill aspect, both in relation to south or east, serve as a proxy for a site's exposure to sunlight. This may be especially important during the wet season when daily afternoon showers limit sun exposure to mornings. South aspect has traditionally been assumed to receive the most sunlight, but in areas nearer to the equator, east may actually be more important.

Model Construction

This study used two forms of generalized linear models (GLM) to test the relationship between environmental predictors and *Azteca* distribution. A logistic regression link was used to model binary ecological states of *Azteca* presence or absence in the 20m cells because it is able to output probabilities limited between 1 (occurrence) and 0 (no occurrence). The logistic regression takes the form:

$$\text{logit}[\pi(x)] = \ln\left(\frac{\pi(x)}{1 - \pi(x)}\right) = \alpha + \beta_1 X_1 + \cdots + \beta_P X_P$$

where $\pi(x) = \Pr(Y=1)$, or probability of a positive outcome (Y), X_P is the predictor variable, and β_P is the model coefficient for the predictor variable. *Azteca* abundance was modeled using a negative binomial distribution because of this link's appropriateness for modeling biological counts, especially when data is overdispersed (Bliss 1953, Dalthorp 2004). The negative binomial distribution is defined as the probability of observing a specific value of x so that:

$$\Pr(X = x) = \binom{k + x - 1}{k - 1}\left(\frac{m}{k}\right)^x \left(1 + \frac{m}{k}\right)^{-(k+x)}$$
$$m, k > 0, x = 0, 1, 2, \ldots$$

where m is the arithmetic mean (the expected value of x), and k is a parameter that measures the distribution's dispersion.

The backwards elimination method was used to select the most parsimonious model while retaining all significant model variables. As described in Guisan and Zimmerman (2000) and Franklin (1998), backwards elimination model fitting begins with all predictor variables included and systematically removing non-significant variables, testing the model for significance at each step. Other comparative measures of model fit used to choose the best model were the pseudo R^2 and Akaike's information criterion. Separate logistic and negative binomial models were created for Finca Hamburgo and Finca Irlanda, in order to test the hypothesis that the same environmental factors are driving the nest distributions in each farm.

In order to successfully apply a mathematical model to ecological data, the data must meet the assumptions that observations are independent, the residuals of the data are normally distributed, and that the variance of the response is constant and not dependent on the expected value (Dalthorp 2004).

Model Analysis

Logistic models were assessed for their predictive power by classification tables, receiver operating characteristic (ROC) curves, and by mapping model predictions in GIS. The predictive accuracy of negative binomial models was more difficult to assess because the output was in the form of estimated value. Expected value was compared against actual value to see if greater expected value correlated with areas of higher nest density. Expected value was mapped in order to visually compare actual abundances and expected values.

Spatial autocorrelation of model residuals were visually assessed by mapping Pearson residuals in GIS and looking for clustering. This was important in determining whether the models were successful in accounting for spatial autocorrelation. Because no corrective measures were taken in model building, e.g. through autocovariate modeling or spatial eigenvector mapping (Dormann et. al 2007), spatial autocorrelation would have to be accounted for through choosing an appropriate scale of analysis.

Results

Exploratory Analysis

An important consideration in choosing between a Poisson distribution and a negative binomial distribution for abundance count modeling is whether the data is overdispersed (Bliss and Fisher 1953). This is determined through comparing the mean and variance of the count data. The variance is greater than the mean for both the Hamburgo and Irlanda datasets, indicating that a negative binomial distribution should be used to model abundance (Table 1).

Table 1: Summary statistics of *Azteca* nest counts per 20m grid in Finca Hamburgo and Finca Irlanda.

	mean	variance
Hamburgo	0.8398058	1.713356
Irlanda	0.2681159	0.6341938

Pairwise correlations between predictor variables were examined by plotting (Figure 1) and calculating pairwise Pearson's correlation coefficients (Tables 2 and 3). No significant correlations were found among predictors, although east and south aspect indices showed a nonlinear relationship because of their related derivations.
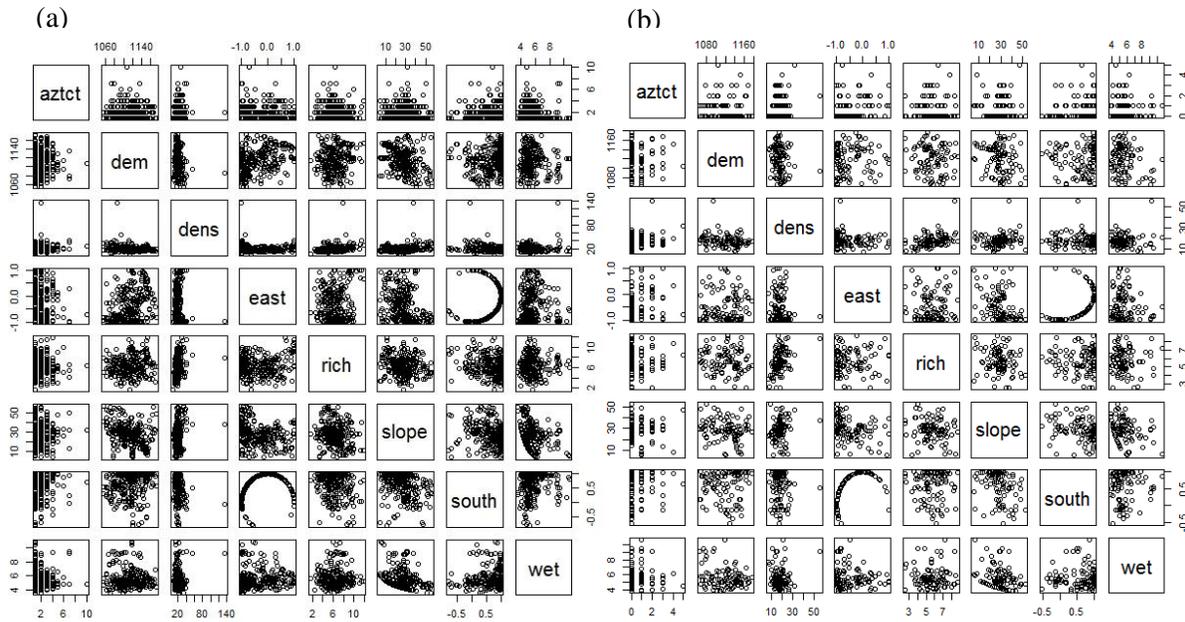

Figure 1: Pairwise plots of predictor variables and nest density for (a) Finca Hamburgo and (b) Finca Irlanda. The nonlinear relationship between east and south aspect is the result of the geometric relationship between the two indices. Only cells with *Azteca* present were plotted. 'aztct' = *Azteca* abundance; 'dem' = elevation; 'dens' = tree density; 'east' = east-facing index; 'rich' = tree species richness; 'slope' = percent slope; 'south' = south-facing index; 'wet' = topographical wetness.

Table 2: Pairwise Pearson's correlation coefficients for predictor variables in Finca Hamburgo. 'aztct' = *Azteca* abundance; 'dem' = elevation; 'dens' = tree density; 'east' = east-facing index; 'rich' = tree species richness; 'slope' = percent slope; 'south' = south-facing index; 'wet' = topographical wetness.

	aztct	dem	dens	east	rich	slope	south
dem	-0.06						
dens	0.12	-0.2					
east	0	0.33	-0.05				
rich	-0.02	0.12	0.3	0.18			
slope	0.05	-0.36	0.22	-0.3	-0.17		
south	0.05	0.12	-0.22	0.37	-0.21	-0.24	
wet	-0.03	-0.07	0.14	-0.01	0.03	-0.28	0.08

Table 3: Pairwise Pearson's correlation coefficients for predictor variables in Finca Irlanda. 'aztct' = *Azteca* abundance; 'dem' = elevation; 'dens' = tree density; 'east' = east-facing index; 'rich' = tree species richness; 'slope' = percent slope; 'south' = south-facing index; 'wet' = topographical wetness.

	aztct	dem	dens	east	rich	slope	south
dem	0.07						
dens	-0.02	0.18					
east	0.04	-0.03	0.32				
rich	0.03	0.2	0.65	0.3			
slope	-0.03	-0.19	-0.07	0.06	-0.23		
south	0.01	-0.16	0.11	0.3	0.11	-0.31	
wet	-0.07	-0.18	-0.26	0.09	-0.01	-0.33	0.2

Logistic Model Results

Fitting the logistic model of *Azteca* presence/absence determined two significant predictors for each farm. Both farm models retained elevation ('dem') as a significant predictor, while Hamburgo retained east aspect index ('east') and Irlanda retained slope as an important factor (Tables 4 and 5). The fit for the Hamburgo model was better, with a pseudo-R^2 of 0.058 (McFadden R^2), while Irlanda had a pseudo-R^2 of 0.018.

Table 4: Nest presence/absence prediction model summary for Finca Hamburgo data. Pseudo R^2 = 0.058. Residual deviance: 791.82 on 613 degrees of freedom. 'dem' = elevation; 'east' = east-facing index.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	12.79595	3.583734	3.571	0.000356 ***
dem	-0.01142	0.003192	-3.577	0.000348 ***
east	0.863198	0.157355	5.486	4.12e-08 ***

Table 5: Nest presence/absence prediction model summary for Finca Irlanda data. Pseudo R^2 = 0.018. Residual deviance: 791.82 on 613 degrees of freedom. Residual deviance: 672.72 on 825 degrees of freedom. 'dem' = elevation, 'slope' = percent slope.

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-10.5263	3.813417	-2.76	0.00577 **
dem	0.009147	0.003711	2.465	0.01370 *
slope	-0.02019	0.009611	-2.101	0.03567 *

Classification tables were calculated to assess the accuracy of the model when the probability threshold was set to p=0.5 (Tables 6 and 7 for Hamburgo and Irlanda respectively). Both models had high specificity, i.e. they successfully predicted areas without *Azteca*, but much lower sensitivity, with the Hamburgo model predicting only 30% of true occurrences and the Irlanda model predicting none. In fact, the Irlanda model predicted no occurrence in its model, although this still allowed it to classify 86% of the area correctly, compared to 62% correct by the Hamburgo model. This reflects a lack of training presence data for Irlanda, since Irlanda has relatively fewer *Azteca*-inhabited cells than Hamburgo. A more informative comparison between the two are the receiver operating characteristic (ROC) curves. Finca Hamburgo (Figure 2a) and Irlanda (Figure 2b) show that the Hamburgo model has slightly better discrimination, with a slightly higher area under curve (AUC) value. The mapped true presence, predicted presence, and standardized Pearson's residual are shown in Figure 3.

Table 6: Classification table of Hamburgo logistic model results with threshold at p=0.5. Sensitivity = 30.50%, specificity = 84.12%, total correctly classified = 61.65%

	True positive	True negative	Total
Classified positive	79	57	136
Classified negative	180	302	482
Total	259	359	618

Table 7: Classification table of Irlanda logistic model results with threshold at p=0.5. Sensitivity = 0%, specificity = 100.00%, total correctly classified = 85.51%

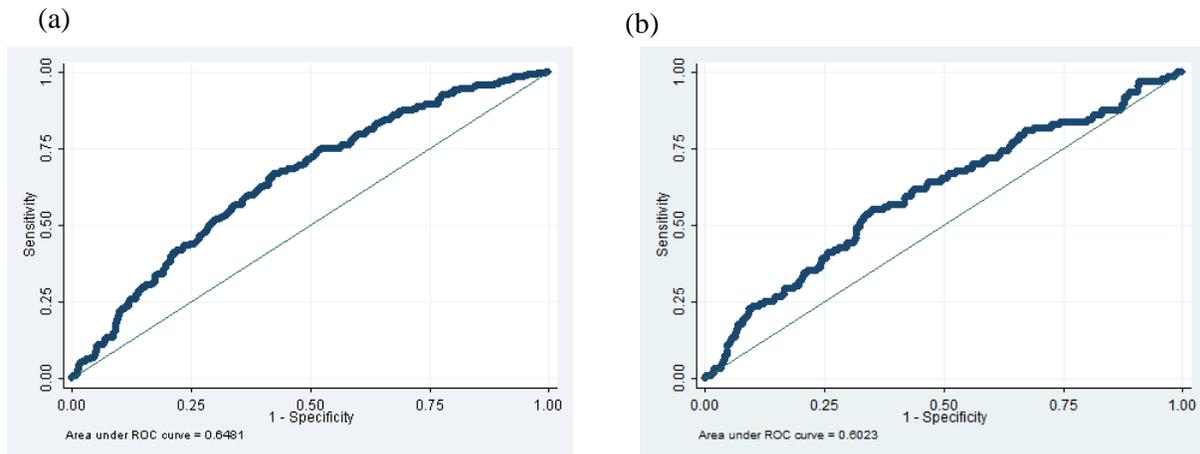|	True positive	True negative	Total
Classified positive	0	0	0
Classified negative	120	708	828
Total	120	709	828

(a) (b)

Figure 2: The receiver operating characteristic (ROC) curves of the Finca Hamburgo (a) and Finca Irlanda (b) models. Area under curve (AUC) of the Hamburgo model is 0.6481, AUC of the Irlanda model is 0.6023.
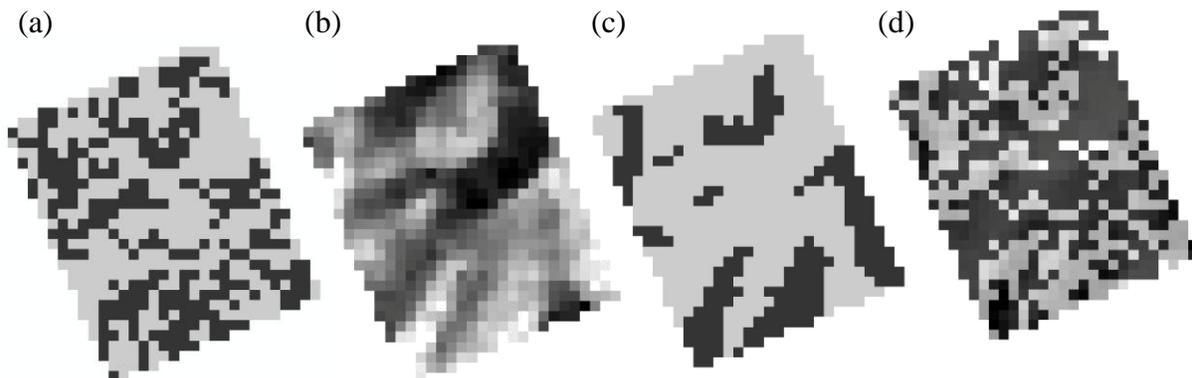
(a) (b) (c) (d)

Figure 3: (a) Actual *Azteca* presence in Hamburgo, (b) probability surface predicted by the model, (c) classified probability at threshold P=0.5, and the standardized Pearson's residuals.

Negative Binomial Model Results

For predicting nest density of Finca Hamburgo, three significant predictors emerged from model fitting: elevation ('dem'), south aspect index ('south'), and tree density ('dens'). However, the model fit was not very good, with a pseudo-R^2 (McFadden R^2) value of 0.022. Finca Irlanda only had one significant predictor variable, elevation. Pseudo-R^2 was very low, about 0.007. Tables 8 and 9 summarize negative binomial results for Hamburgo and Irlanda respectively.

Table 8: Summary of nest density prediction model using negative binomial regression on Finca Hamburgo data. Residual deviance = 562.88 on 614 degrees of freedom. Pseudo R^2 = 0.022

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	5.493286	2.573528	2.135	0.0328 *
dem	-0.00588	0.002301	-2.555	0.0106 *
south	0.738344	0.151322	4.879	1.06e-06 ***
dens	0.023303	0.005473	4.257	2.07e-05 ***

Table 9: Nest density prediction model with negative binomial regression on Finca Irlanda data. Residual deviance = 344.71 on 826 degrees of freedom. Pseudo R^2 = 0.0072

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.54404	0.129229	-4.21	2.56e-05 ***
dens	0.018448	0.005574	3.31	0.000934 ***

The negative binomial model outputs a probability for each possible number of nests that can be observed, taken from the actual range of observed nests per grid cell. The predicted values of *Azteca* nests can be expressed as an expected value by summing the product of each probability to its corresponding count, for the set of predictor variables found in a grid cell. The actual nest counts and expected nest counts are plotted in Figure 4. It is clear that the expected values do not match the actual values, but there is a weak trend associating greater expected values with higher nest counts. The actual and expected values of nests are mapped in Figures 5a and b, respectively. Figure 5c maps the Pearson's residuals, which illustrates the amount of variability not accounted for by the model. Clearly, the spatial structures of the residuals are dominated by the actual nest counts rather than any predictor variable. Figure 6 shows the Pearson's residuals plotted against component predictor variables of each model and the actual nest counts. The only relationship that is evident is between the residuals and the nest counts. This suggests that the deviance of the negative binomial models are not shaped by any one predictor, so spatial autocorrelation may not be an important issue for these predictors.
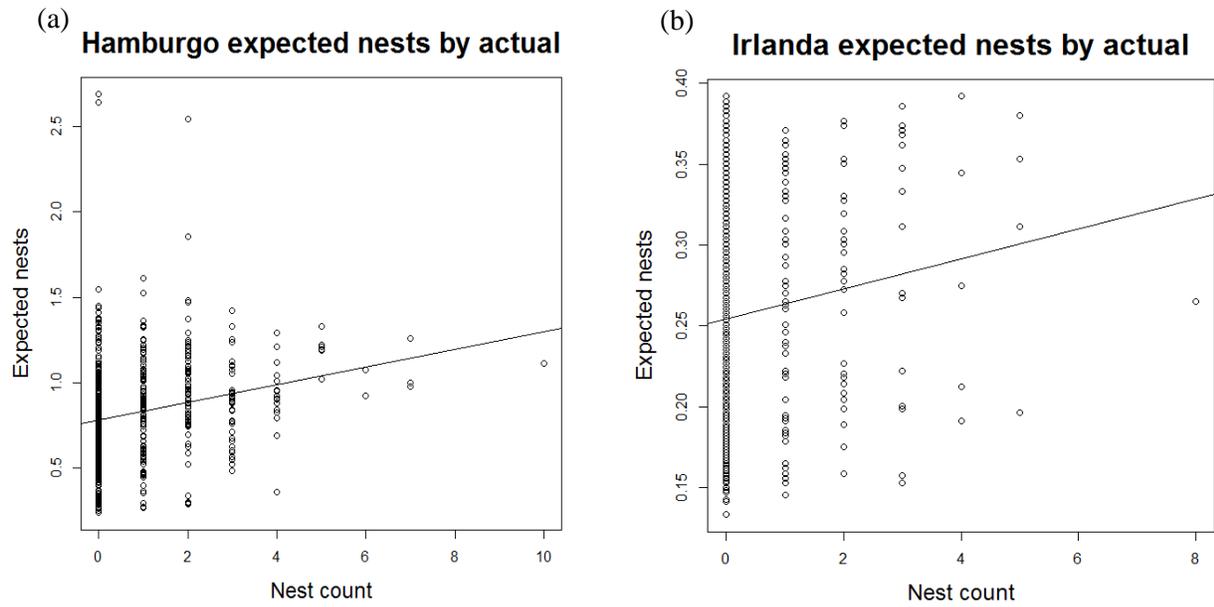
Figure 4: (a) Hamburgo nest count by cell plotted against the expected value of nests predicted by the negative binomial model (adjusted R^2 = 0.05, slope = 0.05), and (b) Irlanda nest count by cell against expected value (adjusted R^2 = 0.01, slope = 0.01).
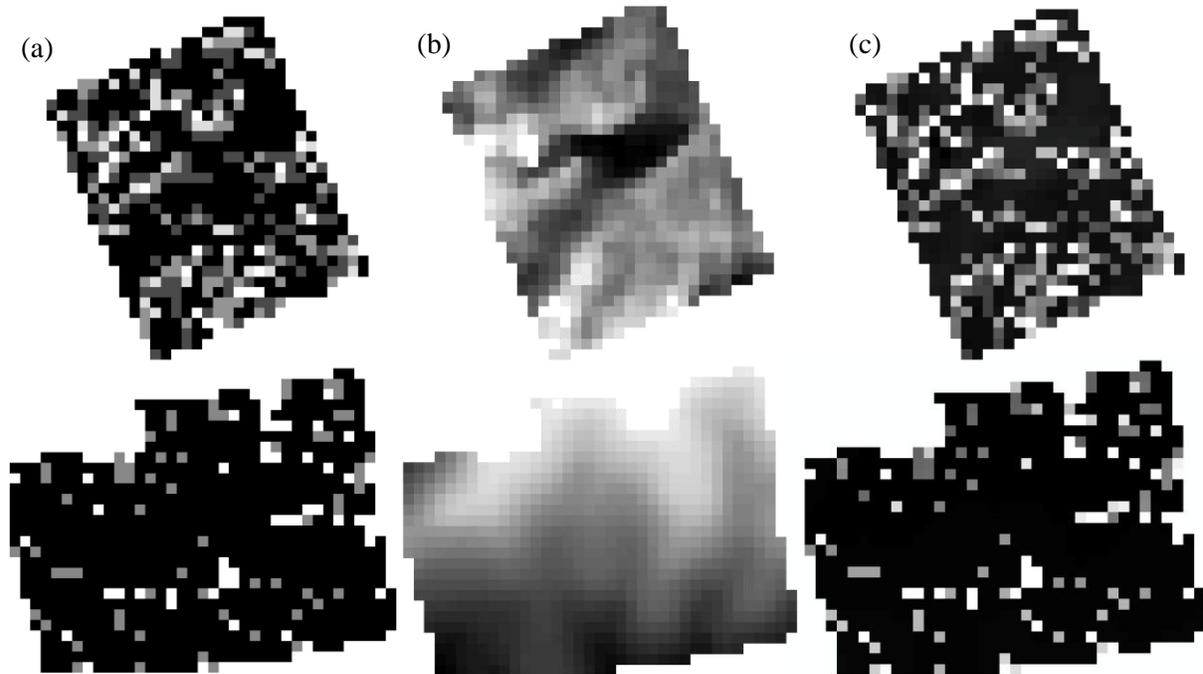

Figure 5: (a) Actual nest counts of Hamburgo (above) and Irlanda (below), (b) model-predicted expected value of nest counts, and (c) mapped Pearson's residual.
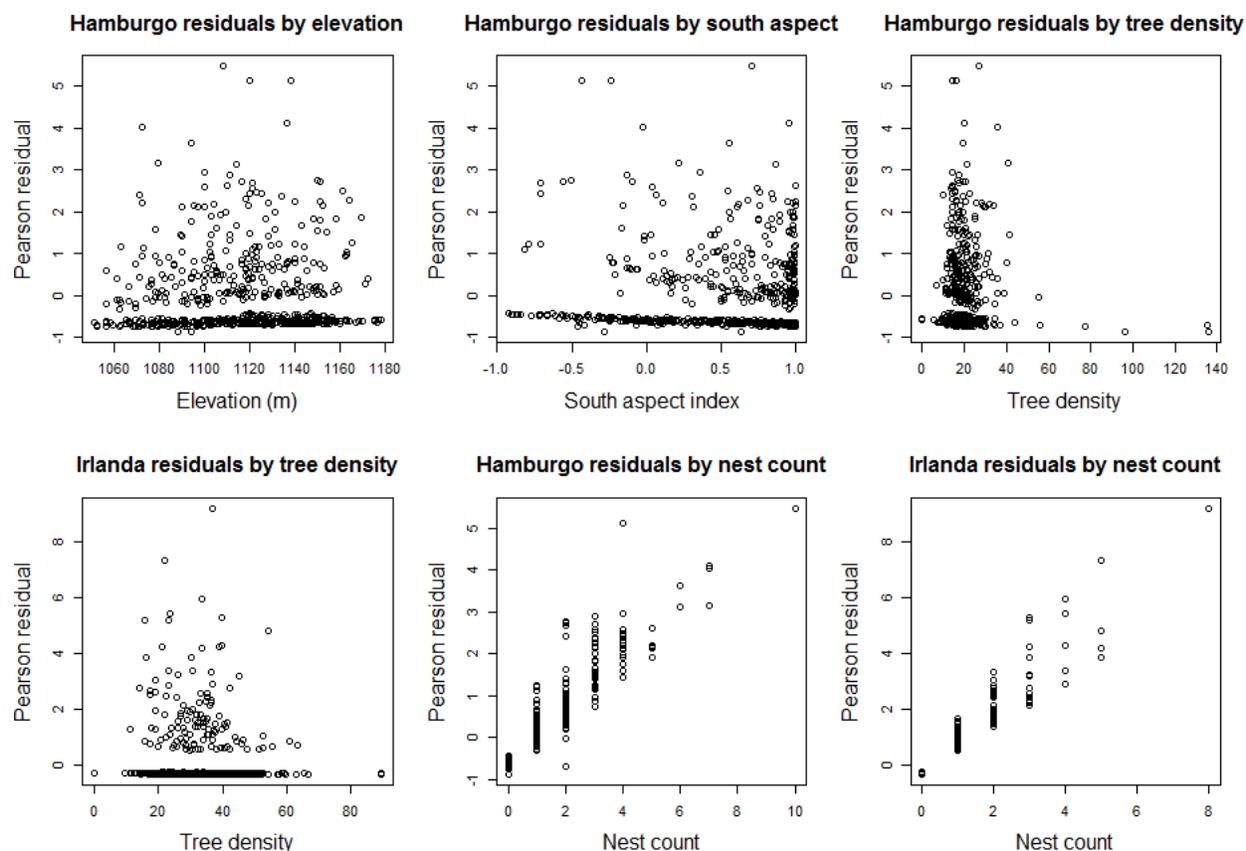
Figure 6: Model residuals plotted by the component predictor variables of the model and the actual nest counts. Correlation is mostly seen between the residuals and nest count, suggesting that most deviance is explained by low predicted values, rather than spatial autocorrelation.

Discussion

Generally, the models presented in this paper are rather weak, with a best fit among them of pseudo-R^2 = 0.05. The Finca Hamburgo dataset performed slightly better in model fitting, perhaps because it contained more cells with *Azteca* to train the data. A brief exploration of the model residuals of the negative binomial model suggests that the fitted data, at least for the negative binomial model, is not strongly influenced by spatial autocorrelation from the predictor variables (see Figure 5). However, the signal of the model may simply be too weak to detect autocorrelation. Further tests of autocorrelation, such as Moran's I could help determine its presence, although if using model residuals, the effect of the training data must be controlled for.

If spatial autocorrelation does exist, one possibility is to scale up the resolution of the model. This could also help the model achieve a better fit, if the processes that determine *Azteca* distribution are operating at a larger scale than the present study's 20m cell size.

Between the negative binomial and logistic regression models, the logistic model did better at fitting for both farms. This could indicate either that the negative binomial model could use more adjustment, through changing the scale or adding interacting or transformed predictors, or that simply the abundance of *Azteca instabilis* is not as strongly determined by environmental variables as its presence. This would fit well with the current understanding of how *Azteca* expands spatially in the farm, which is through a self-organized, density-dependent process that does not need exogenous environmental factors to influence its spatial pattern. It could be that

Azteca presence, perhaps determined at a larger scale than 20m, is influenced by environmental factors, but whether it is successful in creating a large cluster from an initial seed is determined by endogenous processes.

However, further work is necessary to clarify the importance of the role of environmentally-driven species distribution models before this possibility can be explored. This includes testing for correlation at a different scale, transforming predictor variables, and exploring other possible predictor variables. For example, the pairwise correlation comparisons (Figure 1 and Tables 1 and 2) reveal that there is little correlation between *Azteca* abundance and any predictor variable. Testing different predictor transformations is necessary to strengthen any conclusions about the predicting power of these variables. Once all plausible possibilities are exhausted, the next step would be to test whether endogenous, density-dependent processes are capable of creating the observed nest distribution patterns.

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