ENDOGENOUS AND EXOGENOUS SPATIAL DYNAMICS OF THE KEYSTONE ANT

*AZTECA SERICEASUR* IN AN INTENSIFYING COFFEE AGROECOSYSTEM

by

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**Abstract**

*Azteca sericeasur* is a keystone tropical arboreal ant species whose ecological interactions with mutualists and natural enemies are believed to determine a self-regulating (endogenous) spatial process. We inferred ecological processes from the spatial patterns of *A. sericeasur* in a 45-ha coffee farm plot from 2004 to 2012 using three types of analysis: (1) clustering statistics describing the range of significant spatial clustering; (2) stochastic spatial process models of cluster formation; and (3) tree-level logistic regressions predicting ant nest formation and disappearance. We fitted the latter two models with endogenous and exogenous (habitat and environmental) variables to investigate whether endogenous processes sufficiently explained nest clustering, or whether other exogenous variables also played a role. We found that nest clusters were predicted by nest density from the previous year and not consistently by any exogenous variables except tree density in later years.

Nests were clustered to a scale of about 40m and new nests occurred within clusters of existing nests to a scale of approximately 30m. These patterns most likely reflected budding colonies, suggesting the ant's preferred maximum dispersal range. Nest formation was positively related to measures of nest density and proximity, but nest disappearances could not be predicted by any combination of variables. Nest disappearances also had no significant clustering pattern with other nests. These results support our hypothesis that the *A. sericeasur* system is endogenously driven, although mainly through effects on new nests rather than nest disappearance. Tree density became a consistently significant predictor of nest clustering after the farm shifted toward more intensive agricultural management. Intensification resulted in thinning of host trees, which caused new nests to be spaced farther apart. This would have counteracted negative density-dependent interactions with natural enemy species if those species had a shorter dispersal range than *A. sericeasur*. These results have implications in coffee agroecological management, as this system provides important biocontrol ecosystem services.

**Acknowledgements**

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# 1. Introduction

Spatial patterns in ecology may represent a combination of interacting exogenous and endogenous processes (Fortin and Dale, 2005). Endogenously-driven spatial distributions are determined by local interactions with conspecific or other species, and are expected to be density-dependent on the distribution they influence. Exogenously-driven spatial distributions are determined by environmental heterogeneity that can be abiotic, such as slope or elevation, or biotic, such as extrafloral nectar resources for ants (Yitbarek et al., 2011) or trees for nesting. Exogenous processes are expected to be density-independent of the distribution they influence.

The coffee agroecosytem is ideal for examining spatial patterns and process in ecology because of its relatively uniform managed environment and its well-documented complex ecological interactions (Perfecto and Vandermeer, 2008; Vandermeer et al., 2010). These systems exist on a scale of intensification that controls shade tree diversity and density. Diversified coffee farms are structurally similar to natural forests, while more intense farms have fewer species of shade trees in the canopy above the coffee understory (Moguel and Toledo, 1999). Shade trees contribute to ecosystem services by providing habitat for natural enemies of pests, such as bird and bats species that prey on arthropods (Bael et al., 2008; Perfecto et al., 2004; Williams-Guillén et al., 2008) and the arboreal ant *Azteca sericeasur* (previously *Azteca instabilis*, Longino, pers. com.), which provides several different biological control services (Gonthier et al., 2013; Perfecto and Vandermeer, 2006; Vandermeer et al., 2010).

## 1.1 The spatial ecology of the *A. sericeasur* system

Previous research in a 45-hectare plot of a shaded coffee farm in Chiapas, Mexico, suggests that *A. sericeasur* nest locations are influenced by several interactions that create opposing forces of growth and repression (Vandermeer et al., 2008, 2010). Colony growth results from nest 'budding,' whereby new nests split off from existing nests to colonize new trees. Colony repression results from attack by natural enemies including parasitoid flies (*Pseudacteon spp.*) that parasitize the ant; and a beetle (*Azya obigera*) and fungus (*Lecanicillium lecanii*) that attack the ant's scale mutualist (*Coccus viridis*). Ants tend the mutualist scales, which produce sugar-rich waste product that the ants collect as a resource. Natural enemies attack scales, hampering resource collection by the ants. Field and experimental evidence suggest that intensity

of beetle, fly, and fungus attacks are density-dependent, and attacks increase at higher concentrations of ant nests (Liere et al., 2014; Philpott et al., 2009; Vandermeer et al., 2009).

This system can be understood within the reaction-diffusion framework (Turing, 1952). Turing presented these interactions as an explanation of autonomous pattern formation between activating and repressing 'chemicals,' but the concept has applications in biology and ecology (Kondo and Miura, 2010; Vandermeer and Goldberg, 2013). Applied to the ecology of the *A. sericeasur* system, ant colony growth and budding acts as the activation process; but when a cluster of nests becomes too large, it attracts natural enemies that inhibit the continuous expansion of the ant nests and act as the repressing process. Thus, ant nest clusters tend to form due to budding, but cannot become overly large without increasing exposure to natural enemies.

## 1.2 Spatial analysis of endogenous and exogenous ecological forces

The uniform distribution of the trees within the 45-hectare plot (Perfecto and Vandermeer, 2008) as well as evidence of a negative density-dependent relationship of *A. sericeasur* clusters (Liere et al., 2012; Vandermeer et al., 2008) suggest the role of endogenous processes in determining the spatial distribution of *A. sericeasur* nests. However, environmental heterogeneity can play an important role in spatial distribution, and if left unaccounted for, may potentially distort the results of spatial analysis (Birkhofer et al., 2010; Waagepetersen and Guan, 2009). Using a 'space as surrogate' inference approach (McIntire and Fajardo, 2009), we formed a priori hypotheses in spatial analysis to decompose the nest spatial patterns into component processes. This allowed us to compare the relative importance of endogenous and exogenous ecological forces.

Certain management decisions and ecological interactions may act as exogenous factors to the processes hypothesized to control the spatial pattern of *A. sericeasur* nests, which we have considered in our hypotheses: (1) Increased tree spacing could allow new nests to escape the density-dependent repression effect. Agricultural intensification within the 45-hectare plot reduced tree density by approximately one third but despite this drastic decrease in potential nest sites, *A. sericeasur* nests increased notably (Jackson et al., 2014). Jackson and colleagues proposed that this was due to a mismatch between the effective dispersal ranges of repressing natural enemies and budding nests: new nests could perhaps more readily move farther from their source nest than the natural enemies concentrated at that source. (2) Nest distribution may

be associated with the exogenous variable of *Inga* genus tree distribution. The extra-floral nectaries of *Inga* trees are a known food source for some arboreal ants (Koptur, 1984). Additionally, because intensification increased the prevalence of *Inga* trees, *A. sericeasur* may have been more easily able to switch to *Inga* as its primary food resource. (3) Abiotic environmental variables, such as elevation and sun exposure, could have also affected microclimate and other nest site conditions.

Our three interacting hypotheses of nest spatial distribution were: (a) if *A. sericeasur* nests were influenced by density-independent exogenous processes, they would correlate with environmental heterogeneity; (b) if endogenous processes played an important role, nests and nest activity would have density-dependent interactions over space and time; and (3) intensification (tree density reduction) would result in an observable change in the relative strength of these relationships, e.g. an increased importance of *Inga* trees, or the emergence of a correlation between lower tree density and decreased nest mortality, reflecting a shift in ecological dynamics.

## 2. Methods

### 2.1 Study plot

We conducted our study in a 45-hectare plot established in 2004 within an organic shaded coffee plantation located in the Soconusco region of Chiapas, Mexico. The farm is located at approximately 92° 20' 29" West and 15° 10' 6" North, ranging between 917 to 1079m above sea level. Like many areas of the tropics, this region experiences annual wet and dry seasons. The study farm is historically an organic, traditional polyculture coffee farm (see Moguel and Toledo (1999) classification), but began a shift to more intensified management (shade tree reduction) in 2007, which continued to the end of the data collection period in 2012.

### 2.2 Nest and tree points

We mapped the locations and recorded the species of trees on the plot that were greater than 10 cm in circumference, in annual transect surveys from 2004 to 2012. Transect locations were later georectified using GPS (Trimble GeoXT) and a geographic information system (ESRI, 2013). Because *A. sericeasur* only nests within trees, tree coordinates also served as nest locations, which could be determined during the tree surveys. Between each year, some trees were removed from the dataset because they died or were cut down, and some trees were added because they had grown large enough to be included in the tree survey.

We interpreted basic life history stages from changes in annual presence/absence data. Trees without nests in year $t$ that subsequently contained a nest in year $t + 1$ were considered to have a 'new' nest. Trees with a nest in $t$ but no nest in $t + 1$ were considered a 'disappeared' nest, although it was not possible to tell from the data whether the colony moved to another tree or died. Trees which contained a nest in consecutive years were assumed to host the same persistent nest.

### 2.3 Environmental covariates

We used spatial grids of continuous environmental data to inform site conditions at tree point locations (Table 1). Four abiotic environmental covariates – elevation (elev), slope, south-facing index (south), and topographical wetness index (wet) – were derived from a 20m resolution digital elevation model. The slope grid was calculated as a function of the neighboring values of each 20m cell of the digital elevation model using a GIS (ESRI, 2013). Topographical

wetness index, an approximation of water accumulation based on upstream catchment area and slope, was calculated by the function $\ln(A_c/s)$ for each cell, where $A_c$ is the catchment area, and $s$ is slope (Beven and Kirkby, 1979; Hjerdt et al., 2004). South-facing index quantifies the relative deviation of each cell's aspect from due south on a linear scale (Beers et al., 1966).

Biotic environmental covariates were density surfaces based on point densities of tree and ant nest surveys. Covariates included: trees (trees), *Inga* trees (Inga), forest edges (edge), tree cutting (cut), and ant nests (nest). Density surfaces were based on a Gaussian kernel using a biologically-relevant bandwidth. For tree density, this bandwidth was estimated by a cross-validation procedure to minimize mean-square error. We chose 15m, based on the mean optimal bandwidth across all nine years. For 'Inga,' 'cut,' and 'nest' density surfaces, we used a bandwidth of 30m, approximately the mean maximum distance of significant clustering of new nests, obtained from the clustering analysis. Forest edge was calculated as the standard deviation of a 9-cell ($300m^2$) moving window of forest density. We created dummy variables representing five categories of nest density (cat1 - cat5) to allow our models to capture non-linear effects of nest density. The highest and lowest levels of these categories were open-ended, and the middle levels represented equal-interval ranges that were common through all years of the study. For the tree-level logistic regression, we also differentiated pre- and post-intensification data with a categorical variable (intens).

**2.4 Analyses**

We took three approaches to analyzing and modeling ant nest spatial distributions: (1) we described significant clustering patterns of nests and nest events (nest formation and disappearance) over a range of clustering scales; (2) using information from the clustering analysis, we modeled the nest cluster process with a stochastic model that also considered endogenous and exogenous spatial covariates; and (3) we modeled nest formation and disappearance probability at the tree level, using endogenous and exogenous covariates in logistic regressions. For the clustering analysis (1) and subsequent cluster process modeling (2), we modeled point distribution of nests or nest events separately for each year. For the tree-level models of nest formation and disappearance (3), we combined all years together, but distinguished between before and after intensification with a categorical variable.

**2.4.1 Spatial point clustering analysis with Pair Correlation Function (PCF)**

We used the pair correlation function (PCF, Perry et al., 2006; Wiegand and A. Moloney, 2004) to quantify nest clustering within each year and a bivariate variant (Harkness and Isham, 1983) to quantify clustering around nest events between consecutive years. The PCF test is similar to the Ripley's *K* test (Ripley, 1976), but it quantifies clustering only at a specific radius *r* (i.e. a 'ring'), rather than the cumulative clustering from 0 to *r* (i.e. a 'disc'). The maximum *r* for our analyses was 100m. We performed four PCF analyses, which either compared within a point distribution (univariate) or between two point distributions (bivariate). These included analyses of: (1) clustering of existing nests within a year; (2) clustering of nests in one year to the sites of the next year's new nests; (3) clustering of neighboring nests to disappeared nests, in the year before they disappeared; and (4) clustering of new nests to disappeared nests in the same year.

To test for significance, we compared the observed PCF values at each distance of *r* to Monte Carlo simulations representing random nest or nest event placement. We generated null nest patterns by randomly sampling without replacement from a pool of 'available' locations to account for any spatial patterns within these locations themselves. When simulating all existing nests (not differentiating between new and persistent nests), the simulation placed random nests by selecting within all existing trees. For randomizing new nests, the simulation drew from the unoccupied trees of the previous year that were not cut the next year. For randomizing disappeared nests, it selected from all nests that were occupied in the previous year. We estimated a 95% confidence envelope based on 1000 simulations.


**2.4.2 Modeling nest clusters with a stochastic cluster model and environmental factors**

We fitted annual nest point distributions to stochastic models based on the Thomas process (Thomas, 1949), a multi-level clustering process that has been used to quantitatively describe and model the clustering of seed dispersal in forest studies (Cheng et al., 2012; Seidler and Plotkin, 2006; Wang et al., 2011; Wiegand et al., 2007). It involves an initial placement of 'mother' points that are subsequently replaced by 'offspring' clusters (Waagepetersen, 2007), which mirrors the budding process by which *A. sericeasur* forms new nests. Having this spatial process built into the stochastic model allowed us to account for spatial autocorrelation from nest colony spreading and better identify underlying spatial trends.

In the Thomas process 'mother' points (i.e. cluster centers) are placed randomly as spatially independent Poisson distributions of base intensity κ. Each distribution of 'offspring' points replacing the cluster centers has an isotropic Normal shape with standard deviation σ and mean intensity μ. We fit the data to a theoretical Ripley's *K* function of the Thomas process using the method of minimum contrast (Diggle and Gratton, 1984) in the R package 'spatstat' (Baddeley and Turner). The function is defined by the clustering parameters κ and σ:

$$K(r) = \pi r^2 + \frac{1}{\kappa}\left(1 - \exp\left(-\frac{r^2}{4\sigma^2}\right)\right)$$

where *r* is the radius of the *K* analysis. The intensity of the fitted Thomas process, λ, is the product of the mother (κ) and offspring (μ) intensities. Assuming an inhomogeneous Thomas process (Waagepetersen, 2007), we estimated λ as a function of environmental covariates in a Poisson point process model, where probability of a nest at point x was defined by a Poisson distribution with the log intensity function:

$$\log\lambda(x) = \sum_{j=1}^{p} \beta_j z_j(x)$$

where $\beta_j$ is the fitted coefficient of environmental covariate $z_j(x)$, $j = 1, \ldots, p$ (Bivand et al., 2013). Following Waagpeterson and Guan (2009), we used a backwards stepwise model reduction at alpha = 0.05 to select models for the years 2005 to 2012.

When parameterizing the cluster models, we always included the previous year's nest density as a predictor to account for the fact that some of the nests in the year being modeled were persistent from a previous year. This was because a majority of nests persisted between years, so nest density was expected to always be significant, with a positive linear relationship. We were interested in whether any of the levels of nest density dummy variables would also be significant, as this would indicate an additional effect of particular density levels over the expected linear relationship from year to year. This was defined against a baseline at the least dense areas (density category 1: < 5 nests/ha). We then assessed the ability of the cluster process models to recreate the observed spatial patterns using Monte Carlo goodness-of-fit tests to compare the nearest-neighbor statistic (*G*) of 1000 simulations of the predicted nest to the observed nest distribution.

**2.4.3 Modeling nest events with logistic regressions**

Conceptualizing nest events as binary outcomes allowed us to model them as two independent logistic regressions. We treated nest formation as a positive outcome for empty trees within 30m of existing nests (the negative outcome being trees remain empty), and nest disappearance as the positive outcome for trees occupied by a nest. All available sites for each event were included for every year that they remained available as negative outcomes for the model's dataset; so all nearby empty trees were included in the nest formation regression for all years they were empty, and likewise for occupied trees in the nest disappearance regression. Positive events (nest formation or nest disappearance) were included in their respective dataset on the year they occurred, but were not repeated for subsequent years. All the years were used for the regressions except 2004, which did not have prior data to define new and disappeared nests.

Since the logistic regressions modeled nests at the level of the individual tree, we also considered point-based covariates: a binary factor identifying each tree as *Inga* or non-*Inga* (treeID), the distance of each tree to the nearest occupied tree in the past year (nn), and the nest cluster size that the tree fell within in the previous year, using a 30m radius cluster definition (prclus). We built the models over the entire study period's dataset and created a factor for pre- and post-intensification periods (intens). We added an interaction between pre- and post-intensification and nearest past neighbor (intens:nn) for the hypothesized effect of tree thinning on ant and natural enemy dispersal, and an interaction between intensification and *Inga*/non-*Inga* variables (intens:treeID) to account for a possible effect of intensification on *A. sericeasur* use of *Inga* trees.

We performed backwards and forwards-stepping model fitting to select the best model for nest formation and disappearance, using the Bayesian Information Criterion (BIC) to gauge performance. BIC, as opposed to Akaike's Information Criterion (AIC), was chosen as a more conservative standard for comparing models by parsimony and explaining power (Weakliem, 1999). Model fit was assessed with the area under curve (AUC) value of receiver operator characteristic (ROC) plots, which are a measure of model fit for logistic regression that is independent of a probability threshold (Manel et al., 2001). We created stochastic nest event distributions based on the predicted probabilities for the available sites of each year, using the logistic regression models. Goodness-of-fit of these simulated distributions was evaluated with

Monte Carlo tests that compared the PCF statistic of the observed distributions to the 95% envelope of 1000 realizations of the simulated patterns and to simulations of random patterns of new nests placed within 30m of existing nests.

# 3. Results

## 3.1 General population patterns

Tree population remained constant for the three-year period before intensification, followed by a period of tree thinning. Larger culls occurred every other year, with the initial cull in 2007 as the largest. A simple linear regression confirmed that the total number of nests increased significantly over the study period (slope=46 nests/year, p<0.001, $R^2$=0.85). Analyzing the new nests, persistent nests, and disappeared nests within the total population for each year in their own linear regression, we saw that persistent nests had the strongest and most significant trend of 27 more persistent nests every year ($p$<0.001, $R^2$=0.86). The number of new nests also had an increasing trend, although it was only marginally significant (slope=10 new nests/year, $p$=0.07, $R^2$=0.34). The trend of disappeared nests had an increasing slope of 10 disappeared nests per year, but this was not significant ($p$>0.10, $R^2$=0.27). Note that disappeared nests were not simply the difference of persistent nests from total nests, because we did not include nests that were destroyed from tree cutting. Annual per capita birth, death, and survival rates did not have significant non-zero linear trends ($p$>0.10). Tree populations are tabulated in Appendix 1 and *A. sericeasur* nest populations are tabulated in Appendix 2.

## 3.2 Clustering analysis results

The univariate PCF (Fig. 1) showed that nests were clustered, with ranges of significant clustering extending from 30 to 60m from each nest, depending on the year. Other portions of the range of analysis crossed the threshold for significance for some years, but the general qualitative trend was that nest distribution patterns became closer to random beyond a range of 30m.

New nest clustering around the existing nests in the previous year (Fig. 2a) had a clear trend of significant clustering within 30-40m of existing nests for every year. Nest patterns beyond this distance of analysis were not significant or were very close to random for all years. Nests that disappeared (Fig. 2b) did not have any consistently significant patterns of nest clustering around them prior to disappearing. New nests were significantly clustered around disappeared nests for all years, but the strength of clustering decreased in the last three years to be much closer to a random nest distribution (Fig. 2c).

## 3.3 Stochastic cluster modeling results

Coefficients of significant predictor variables are plotted graphically in Fig. 3 and tabulated in Appendix 3. The cluster models did not select abiotic environmental variables as significant predictors, except elevation in 2005 and south-facing index in 2010. Tree density was the only biotic exogenous variable that was significant, with a positive effect on nests in the latter four years (2009-2012); however, the magnitude of this effect was small (Fig. 3). Density of *Inga* was not a significant predictor in any year.

We always used the continuous variable of the previous year's nest density as a predictor representing persistent nests, so dummy density category variables showed whether certain categories deviated from the expected linear relationship between nest densities. Several years had multiple nest density category dummy variables that were significant. All significant density category coefficients were positive, with overlapping confidence intervals. Most commonly, areas of 10-15 nests/ha (category 3) were significant. All significant categories predicted more nests than expected from the previous year's nest alone, but never decreased the expected number of nests.

The estimated Thomas clustering parameters, $\kappa$ (cluster center Poisson distribution intensity) and $\sigma^2$ (standard deviation of offspring cluster size), for the selected models had increasing trends over the course of the study (Appendix 3). When fit to a linear regression, $\kappa$ increased significantly at a rate of 0.0002 nests/m$^2$ a year ($p<0.003$, R$^2$=0.77) and $\sigma^2$ increased significantly by 3m a year ($p<0.02$, R$^2$=0.57). These trends indicated that the clustering process created larger and more numerous nest clusters over time, which aligned with our observations of the changes in nest population and spatial distribution.

Monte Carlo nearest neighbor (*G*) goodness-of-fit tests comparing the observed data to the selected model (Appendix 4) indicated that there was a range of spatial clustering that the fitted inhomogeneous Thomas process models could not replicate in years 2005 to 2007. For these years, predicted patterns were too clustered at scales less than 10m. After 2007, however, this unaccounted clustering was reduced and became largely insignificant by 2010. After 2007, empirical *G* values remained within or close to the 95% confidence interval of model predictions.

**3.4 Logistic regression results**

The new nest model performed better than the disappeared nest model in receiver operator characteristic (ROC) fit assessments (Appendix 6). ROC plots of the predicted new

nests by year had an average area under curve (AUC) of 0.76 (sd = 0.06). In contrast, the yearly nest disappearance models had an average AUC of 0.56 (s.d. = 0.03). Values of AUC over 0.7 indicate that the model has "useful applications" while values closer to 0.5 indicate little difference from random predictions (Manel et al., 2001). Thus, we only report results from the nest formation model in this text, though nest disappearance results can be accessed in Appendices 5, 6, and 7.

The significant variables of the nest formation logistic regression are plotted in Figure 4 and tabulated in Appendix 5. Among the significant covariates, a closer nest in the previous year (lower nn) increased new nest probability (Fig. 4). There was a positive interaction between distance to nearest nest and before and after intensification, which suggested that following intensification, the negative effect of nearest nest distance (i.e. the positive effect of closer nests) became weaker. Post-intensification (intens(after)) was significant and had a negative relationship with new nests, suggesting that the probability of a new nest was lower per tree in the post-intensification period, all other variables being equal. The square of the previous year's cluster size (prclu^2) was also a significant negative predictor of new nests. New nest formation was predicted by lower tree density (tree) and greater standard deviation of tree density (edge), i.e. in sparser and more variably-forested areas.

Monte Carlo simulations of new nests based on the logistic regression do not account for clustering under 20m, but above this distance the observed clustering appears within or very near the predicted envelope (Appendix 7a). Comparing these predictions to randomly-selected new nests within 30m of existing nests (dotted envelope in Appendix 7) suggests the logistic regression does perform better than random. Not surprisingly, the disappeared nest logistic regression predicted distributions that were nearly identical to random selections of nests (Appendix 7b).

# 4. Discussion

*Azteca sericeasur* spatial distribution appears to be driven mainly by its own budding activity and suppression by natural enemies (endogenous forces), rather than in response to environmental drivers (exogenous forces). Spatial distribution was most commonly predicted by variables related to the previous year's distribution; an exception to this was that tree distribution also played a significant, but limited role. This is most logically explained by the ant's use of trees as nest hosts, but there was also evidence to support the hypothesis that trees mediated the endogenous interactions between ant colonies and natural enemies through inter-nest spacing. No other exogenous variable consistently predicted the occurrence of ant nests, including *Inga* trees, which were hypothesized to be an alternative resource due to its extrafloral nectaries. We were also unable to identify any useful model for nest disappearances; they appeared to occur randomly or were not strongly determined by any endogenous or exogenous variables considered in this study.

## 4.1 Clustering analysis conclusions

The spatial relationship of new nests to existing nests (clustering up to a scale of about 30m, Fig. 2a) reflected the pattern of overall nest clustering (Fig. 1). This suggested that the process of budding was the main driver of spatial distribution, as opposed to more random forms of dispersal, such as reproductive alate flights. Nests on a whole were clustered at a greater scale than new nests to existing nests because clustering analysis of all nests would have included multi-year persistent nests, whose inter-generational offspring may have dispersed farther away than a single budding event distance.

There was no significant pattern of nest clustering that preceded disappearance the next year (Fig. 2b). This suggested that nest disappearance was not different from our null hypothesis of random occurrence. This conclusion was the same as our logistic regression of disappeared nests, and the implications of this conclusion will be discussed later. Decreased clustering between new nests and disappeared nests (Fig. 2c) may have reflected greater spacing between nests due to tree cutting, as well as the higher number of new nests over disappeared nests, which would have decreased the likelihood of one of the former being located near the latter, especially when nests were spaced farther apart.

Previous work has shown that nest distributions are clustered at a 20m scale of inter-nest distance (Vandermeer et al., 2008). This distance was thought to be the maximum distance that new nests could form from a source nest based on informal natural history observations, but subsequent Ripley's *K* analysis demonstrated that clustering extended to 75m (Jackson et al., 2014). Our use of the PCF instead of the Ripley's *K* is likely the reason that our conclusions differed from previous results. Because the PCF is not cumulative over distance (PCF uses 'rings' instead of 'discs'), it is more sensitive to changes in clustering behavior than the Ripley's *K* (Perry et al., 2006). It is likely that the very strong local nest clustering in the plot often exceeded the expected mean random number of nests assumed by Ripley's *K* discs out to much greater radii than would be significant for the PCF. Another advantage of our approach was that we judged significance against null distributions based on actual tree positions, which allowed us to account for the inherent clustering of nest host sites.

## 4.2 Stochastic clustering model conclusions

When accounting for nest aggregation using the Thomas cluster process, nest clusters correlated consistently with the preceding year's nest distribution. The spatial relationship of nests between years was consistent with the known biology of nest budding and persistence, which again emphasized the importance of endogenous interactions between nests. Beyond a linear relationship of nests existing and growing from one year to the next, areas with a medium nest density had an additionally higher probability of having nests the following year, suggesting that these areas had a greater rate of survival, nest formation, or both.

Once intensification began, higher local tree density significantly raised the probability of nest occurrence. Two other exogenous variables were significant for single years, but the uniqueness of their significance suggested that they only played an incidental role or were a result of a spatial coincidence. That tree density was only significant following intensification suggested that once intensification reduced the number of trees below a certain threshold, trees became a limiting resource and could positively influence the number of nests in the area. This was most likely through their role as a host site for nests, but also possibly as foraging sites.

*Inga* tree density was not a significant factor for nest probability, despite evidence that *Inga* trees can act as a resource for this guild of ants (Koptur, 1984). However, during the intensification cuttings, *Inga* trees were often spared for their nitrogen fixing services, so their

relative numbers may not have been reduced enough to act as a limiting resource, as trees generally did for nesting sites; alternatively, the ants may have been indifferent to their proximity to *Inga* and did not have to depend on this resource when it was not nearby.

**4.3 Logistic regression conclusions**

The local nature of budding was evident in the higher probability of new nests for trees that were closer to existing nests. New nest probability decreased with the square of the size of the nearby nest cluster, which could be explained by a higher natural enemy presence in larger nest clusters (Philpott et al., 2009; Vandermeer et al., 2009). Following intensification, new nests became more likely to occur farther away from the nearest existing nest, reflecting the increased spacing between trees.

From the exogenous variables, decreased tree density and increased tree variability were related to higher nest formation probability in the model. These relationships applied to all years of data (there was no interaction between the intensification period and tree variables), but would have become more prevalent once intensification reduced tree density. The negative relationship between tree density and nest formation probability does not conflict with the positive relationship between tree density and nest probability in the latter years of the stochastic cluster model because these models describe different processes. The stochastic cluster models were fit to each year independently and modeled all nests rather than only new nests.

We could not show that the nest disappearance logistic regression model performed any better than random, so these results did not signify very strong trends. In addition, the new nest logistic regression could not account for all spatial clustering, especially at close (<20m) distances (Appendix 7a). This could be because the model did not account for spatial interactions between new nests. These interactions could be due to especially productive nests that sent out multiple budding nests within the same year. As in the stochastic cluster model, *Inga* did not play a significant role; in this case, *Inga* trees were no more or less likely to host a new nest, or have an existing nest disappear.

**4.4 How trees affect endogenous nest processes**

Prior to our analyses, the paradoxical observation of increased *A. sericeasur* nests following a gross reduction of their host trees was attributed to increased nest spacing due to fewer trees, which reduced connectivity for the natural enemies of the ants and their associated

mutualists (Jackson et al., 2014). Our results support this hypothesis, but we observe the effect in terms of increasing new nests rather than decreasing disappeared nests, which may stem from the limited temporal resolution of our data. Between the available annual time points, budding nests may have already been established and disappeared as a result of suppression by natural enemies, and the 'new' nests we observed may have largely represented successfully established nests. Thus, the nests that were most susceptible to density-dependent effects may have already perished between data collections, so nest 'deaths' actually represent a longer-term process of senescence that is less density dependent. That the number of nest disappearances does not have a significant trend over time, that disappearances are not correlated with higher nest clustering, and that it had no strong relationship with any of our endogenous or exogenous variables appears to support this idea.

Through thinning the trees, the coffee farmer has inadvertently forced more budding nests to travel farther, increasing the survival rate of new nests by placing them outside of the range of natural enemies. Since nests can only occur in host trees, and because of the presence of natural enemies, the offspring nests were in effect subject to a Janzen-Connell effect (Connell, 1971; Janzen, 1970), whereby the mother nest is also a source of natural enemies. If we assume that budding nests typically travel from the mother nest to the nearest tree, we would expect most new nest attempts to fail in very dense coffee agro-forests with closely-spaced trees. Data collection at a finer temporal resolution is needed to confirm whether the increase we have observed is due to higher rates of survival of new nest propagules. Further stochastic point process-based and theoretical modeling of this proposed spatial process could also provide a better understanding of its anticipated spatial structure and verify it against our observations.

## 4.5 Implications and conclusions

Understanding the endogenous and exogenous interactions of spatial processes of *A. sericeasur* is relevant to biocontrol in the coffee agroecosystem. The interaction between *A. sericeasur* and its mutualist green coffee scale (*Coccus viridis*) allows the beneficial fungi *L. lecanii* to reach epizootic levels, which in turn reduces the outbreak intensity of its alternate host, the coffee rust (*Hemileia vastatrix*) in the proximity of scale aggregations (Jackson et al., 2009, 2012; Vandermeer et al., 2009, 2014). Furthermore, the ant aggressively patrols the coffee bushes where it tends *C. viridis*, indiscriminately removing intruders including the coffee berry

borer, *Hypthenemus hampei* (Vandermeer et al., 2010). The beetle, *Azya orbigera*, can provide effective biological control over *C. viridis*, which is also a pest of coffee. However, the beetle's effectiveness is conditioned on a complex interaction network that is also dependent on *A. sericeasur* nest clusters (Hsieh and Perfecto, 2012; Liere and Larsen, 2010; Liere and Perfecto, 2008). Given the biocontrol services of *A. sericeasur* and its associates, understanding the ecological drivers of this system's spatial distribution is important for supporting diversified farming systems, which aim to decrease reliance on external inputs (Kremen et al., 2012).

We have demonstrated that this endogenous system of interactions is also connected to the exogenous management of the agroecosystem through the spatial structure of the agro-forest. As a dynamical system, the ecological interactions surrounding *A. sericeasur* must be understood to be at a state that is the result of a balance of processes (Scheffer, 2009). By changing the underlying spatial structure that we propose helped regulate the system previously, this system could enter into a critical transition towards another unknown steady state. Other research in intensification and biodiversity suggest that simplification of agriculture leads to increased pest species and decreased biodiversity (Matson et al., 1997; Tscharntke et al., 2005). It is unclear how this complex system of relationships between pest and beneficial biodiversity will change as a result of intensification, and whether this change will allow the system to continue providing its ecosystem service of biocontrol.

# 5. Tables & Figures

**Table 1:** Descriptions of model covariates. Covariates of type 'grid' were continuous surface grids. 'Point' type covariates were calculated only at nest and tree points. Grid covariates were used to parameterize stochastic cluster models, while grid and point covariates were used to parameterize logistic regressions.

| *Variable* | *Type* | *Description* |
|---|---|---|
| **trees** | grid | Tree density surface, bandwidth standard deviation = 30m |
| **Inga** | grid | *Inga spp.* tree density surface, bandwidth standard deviation = 30m |
| **edge** | grid | Standard deviation of tree density in a 5 cell ($300m^2$) window |
| **cut** | grid | Density of thinned trees, bandwidth standard deviation = 30m |
| **elev** | grid | Elevation of 20x20m pixel (m above sea level) |
| **slope** | grid | Slope of 20x20m pixel (%) |
| **wet** | grid | Topographical wetness index |
| **south** | grid | South-facing index |
| **nest** | grid | Nest density surface at *t*-1, bandwidth standard deviation = 30m |
| **cat1-cat5** | grids | Dummy categories of nest density at *t*-1: |
| | | **cat1** $<=$ 5 $<$ **cat2** $<=$ 10 $<$ **cat3** $<=$ 15 $<$ **cat4** $<=$ 20 $<$ **cat5** (nests/ha) |
| **nn** | point | Distance to nearest neighboring nest at *t*-1 |
| **treeID** | point | Whether or not a tree is in genus *Inga* |
| **prclu** | point | Size of attached nest cluster (30m radius cluster definition) |
| **intens** | time | Categorical variable indicating before or after start of intensification |

**Figure 1:** PCF statistic for nest annual nest distributions, plotted as the difference from the theoretical value based on the average expected value given random placement. Dotted line represents the observed PCF – theoretical PCF. The gray areas represent the 95% confidence envelope from 1000 random nest allocations. The colored bars below each panel indicate significance at that distance (green = clustered, red = dispersed, grey = not significant).
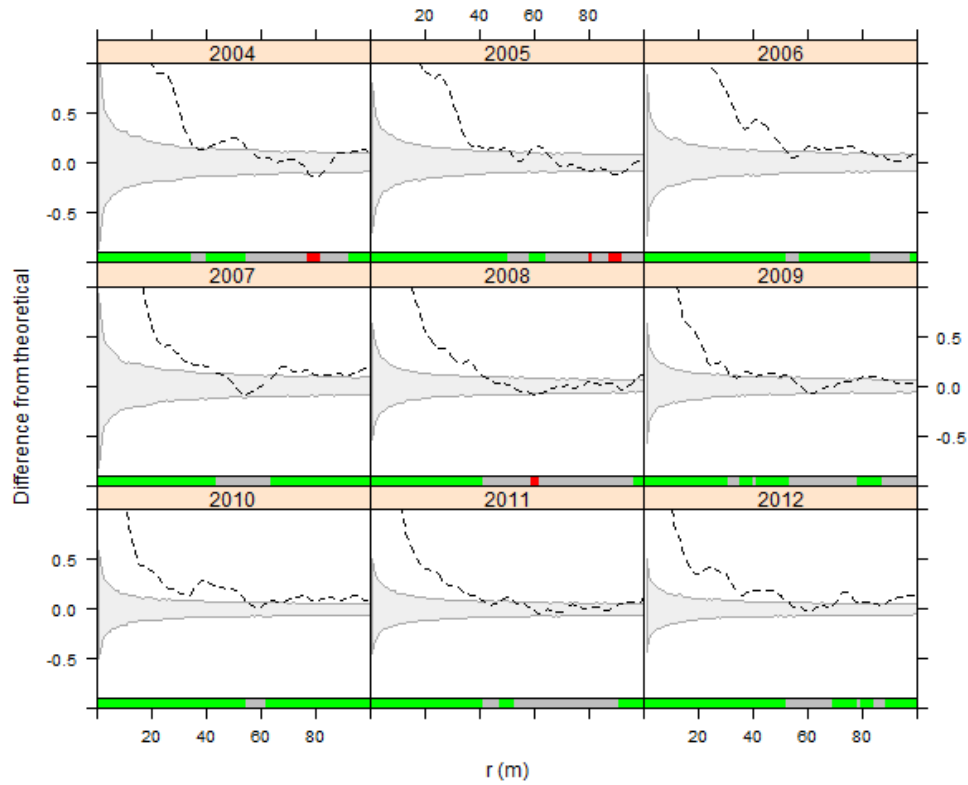
**Figure 2**: Bivariate PCF between nest event locations and the previous year's nest distribution compared to random nest allocation. Bivariate comparisons are: **(a)** spatial association of new nests in year *t* around existing nests in year *t*-1, **(b)** association of nests in *t*-1 around the nests that disappeared by year *t*, and **(c)** association between new nests and disappeared nests in year *t*. Year *t* is identified at the top of each panel. Plotting conventions are the same as Figure 1.
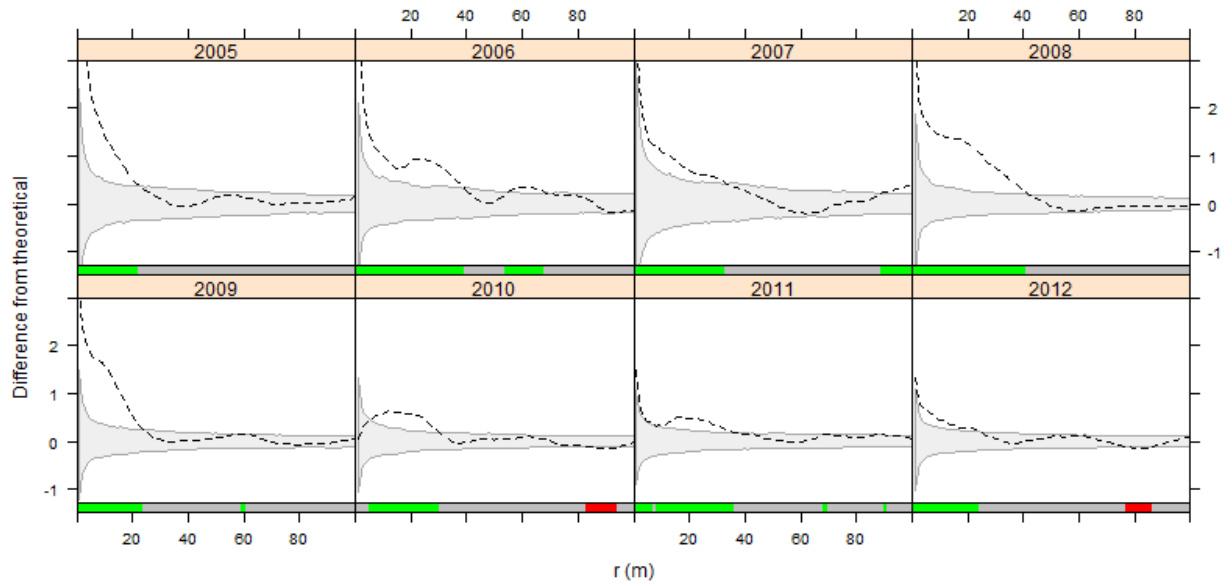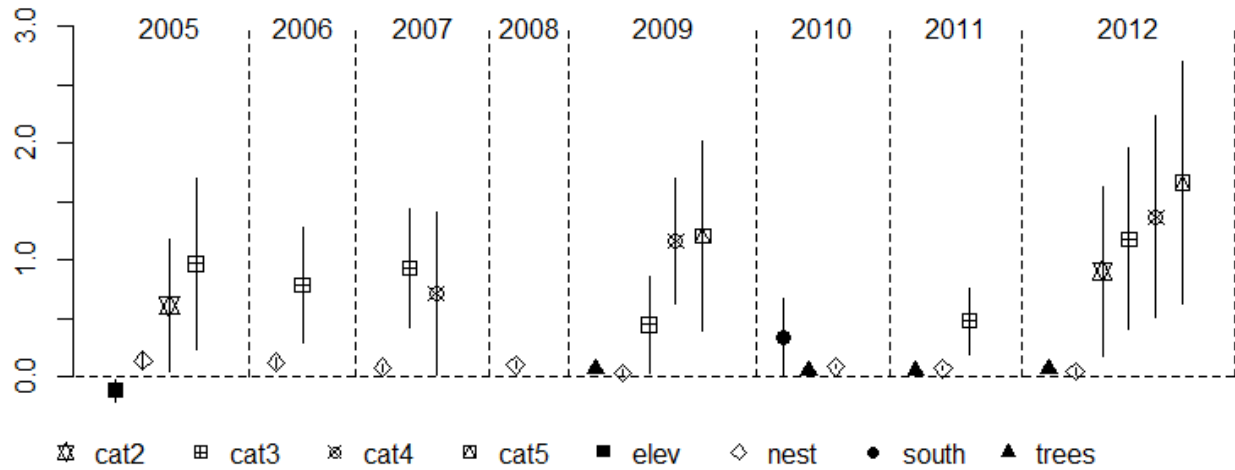
**Figure 2a**
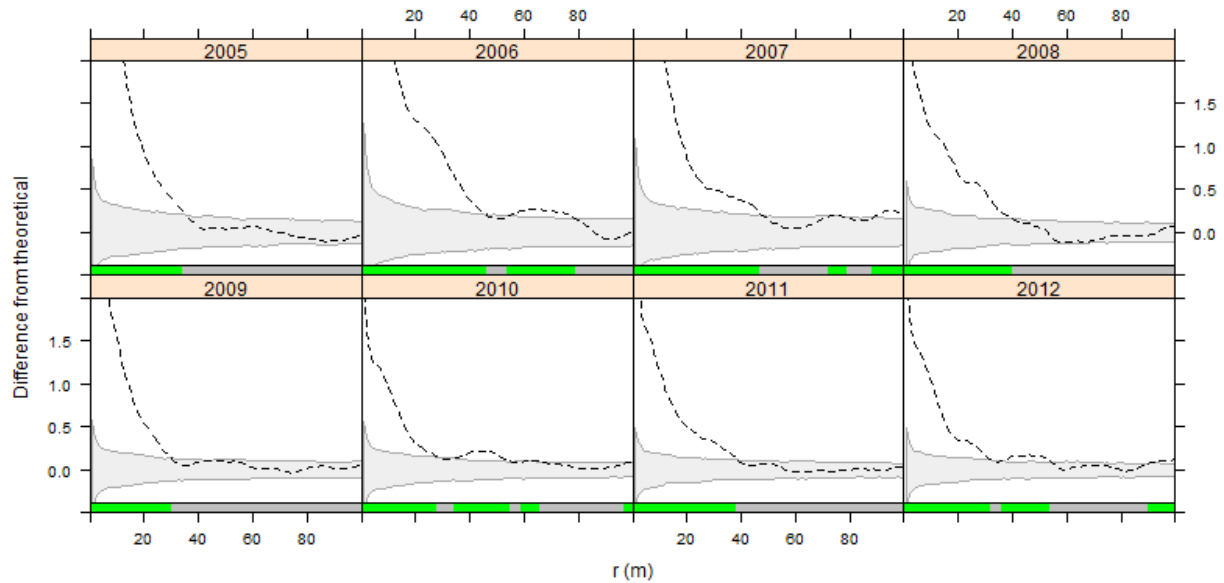


**Figure 2b**
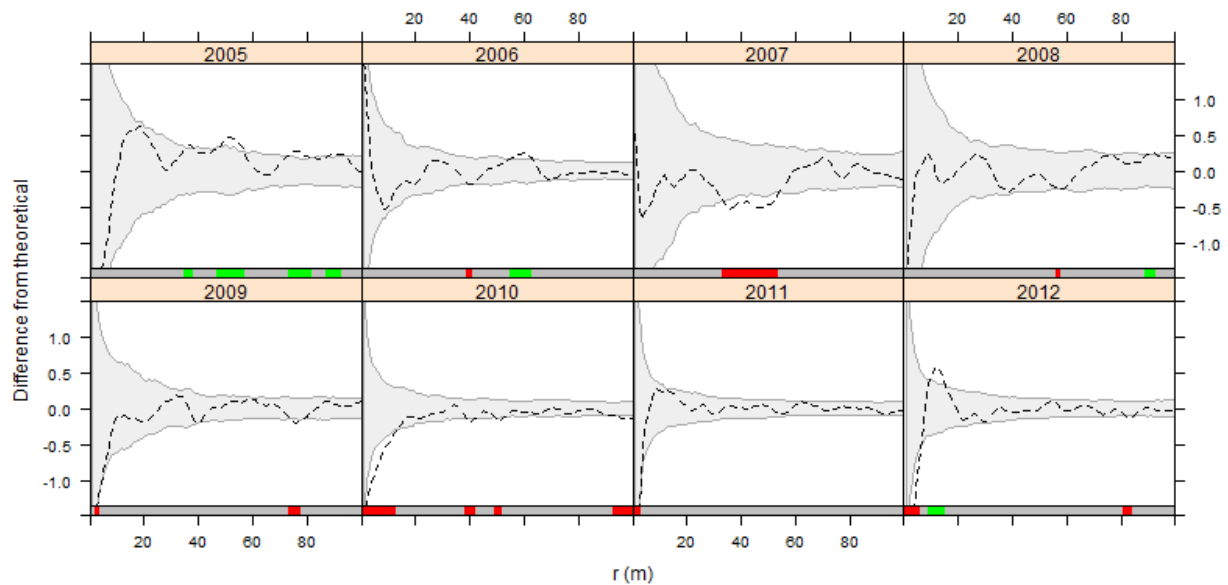
**Figure 2c**

**Figure 3:** Significant predictors of annual nest distributions, 2005-2012, with 95% confidence intervals. Endogenous variables are represented by empty shapes while exogenous variable are represented by solid shapes. Elevation (elev) and tree density (trees) are multiplied by a factor of 10 to for clarity. Parameter fit statistics are in Table 2.

**Figure 4:** Significant regression coefficients of new nest logistic regression model. Model was chosen through backwards and forwards selection procedures based on the Bayes Information Criterion (BIC). Parameter fit statistics are in Table 3.
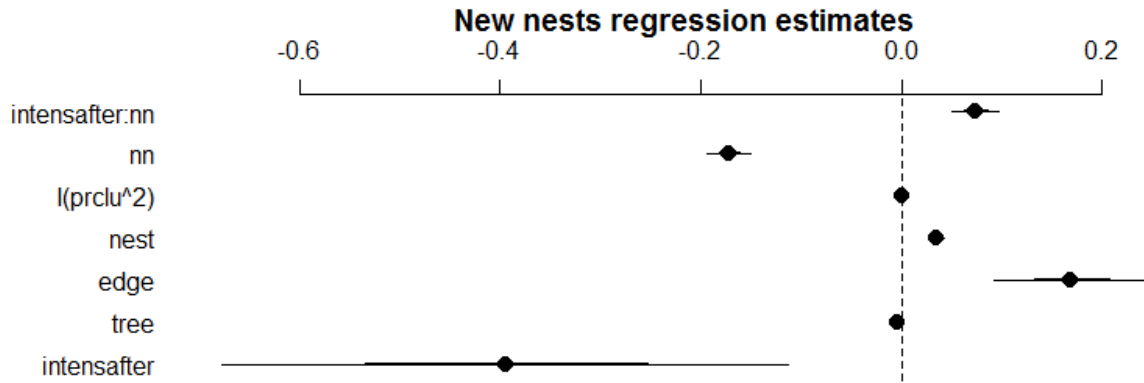
## 6. Appendices

**Appendix 1:** Population of trees (all species), *Inga spp.*, and trees thinned since the previous census, >10cm circumference at breast height. No changes in tree population were observed from 2004 to 2006 because no thinning occurred.

| Year | trees | Inga | cut |
|------|-------|------|-----|
| 2004 | 10595 | 6009 | NA |
| 2005 | 10595 | 6009 | 0 |
| 2006 | 10595 | 6009 | 0 |
| 2007 | 8834 | 4950 | 2690 |
| 2008 | 8560 | 4820 | 274 |
| 2009 | 6425 | 3533 | 2135 |
| 2010 | 7294 | 3960 | 183 |
| 2011 | 6145 | 3505 | 1149 |
| 2012 | 5876 | 3420 | 554 |

**Appendix 2:** *A. sericeasur* annual nest populations and population change. Shown are total nests, new (i.e. nest formation), disappeared, persistent nests, per capita 'birth' rate, and per capita survival rate. Disappeared nests numbers do not include nests lost due to tree thinning. Nests lost due to thinning account entirely for the difference between the total 'nest' column and the 'new', 'disappeared,' and 'persistent' subsets.

| Year | nests | new | disap. | persist | birth rate | survival rate |
|------|-------|-----|--------|---------|-----------|---------------|
| 2004 | 282 | NA | NA | NA | NA | NA |
| 2005 | 378 | 152 | 56 | 226 | 0.54 | 0.80 |
| 2006 | 350 | 92 | 120 | 258 | 0.24 | 0.68 |
| 2007 | 322 | 107 | 54 | 215 | 0.31 | 0.61 |
| 2008 | 513 | 254 | 54 | 258 | 0.79 | 0.80 |
| 2009 | 506 | 199 | 91 | 306 | 0.39 | 0.60 |
| 2010 | 624 | 192 | 148 | 330 | 0.38 | 0.65 |
| 2011 | 581 | 211 | 153 | 367 | 0.34 | 0.59 |
| 2012 | 644 | 222 | 110 | 412 | 0.38 | 0.71 |

**Appendix 3:** Fitted stochastic clustering coefficients and 95% confidences intervals for inhomogeneous Thomas cluster models of nests in years 2005-2012. Clustering parameters κ and $\sigma^2$ give the fitted Poisson process intensity of the 'mother' points and the standard deviation of offspring cluster size (m), respectively.

| Year | Endogenous variables | Exogenous variables | κ | $\sigma^2(m)$ |
|---|---|---|---|---|
| 2005 | **nest:** 0.142 (0.076, 0.208) | **elev:** -0.012 (-0.022, -0.003) | 0.00036 | 8.26 |
| | **cat2:** 0.608 (0.042, 1.173) | | | |
| | **cat3:** 0.970 (0.239, 1.700) | | | |
| 2006 | **nest:** 0.122 (0.084, 0.161) | | 0.00045 | 1.06 |
| | **cat3:** 0.785 (0.295, 1.276) | | | |
| 2007 | **nest:** 0.079 (0.045, 0.112) | | 0.00051 | 9.00 |
| | **cat3:** 0.932 (0.426, 1.437) | | | |
| | **cat4:** 0.714 (0.016, 1.413) | | | |
| 2008 | **nest:** 0.105 (0.073, 0.136) | | 0.00056 | 2.58 |
| 2009 | **nest:** 0.035 (0.000, 0.069) | **trees:** 0.007 (0.004, 0.010) | 0.00113 | 16.7 |
| | **cat3:** 0.448 (0.038, 0.857) | | | |
| | **cat4:** 1.163 (0.626, 1.700) | | | |
| | **cat5:** 1.208 (0.391, 2.025) | | | |
| 2010 | **nest:** 0.089 (0.071, 0.107) | **trees:** 0.005 (0.003, 0.008) | 0.00153 | 15.5 |
| | | **south:** 0.343 (0.020, 0.666) | | |
| 2011 | **nest:** 0.074 (0.059, 0.090) | **trees:** 0.005 (0.002, 0.008) | 0.00182 | 14.4 |
| | **cat3:** 0.482 (0.200, 0.763) | | | |
| 2012 | **nest:** 0.048 (0.012, 0.084) | **trees:** 0.006 (0.003, 0.010) | 0.00133 | 30.6 |
| | **cat2:** 0.907 (0.180, 1.635) | | | |
| | **cat3:** 1.182 (0.406, 1.958) | | | |
| | **cat4:** 1.369 (0.507, 2.231) | | | |
| | **cat5:** 1.663 (0.627, 2.698) | | | |

**Appendix 4:** Nearest neighbor (*G*) function of nest distributions, shown as the difference from the theoretical *G* function of a random distribution of points. Plotting conventions are the same as Figures 1 and 2. Where the observed *G* value is outside the envelope indicates that the spatial structure of the estimated cluster process does not account for the observed nest distribution at that scale.
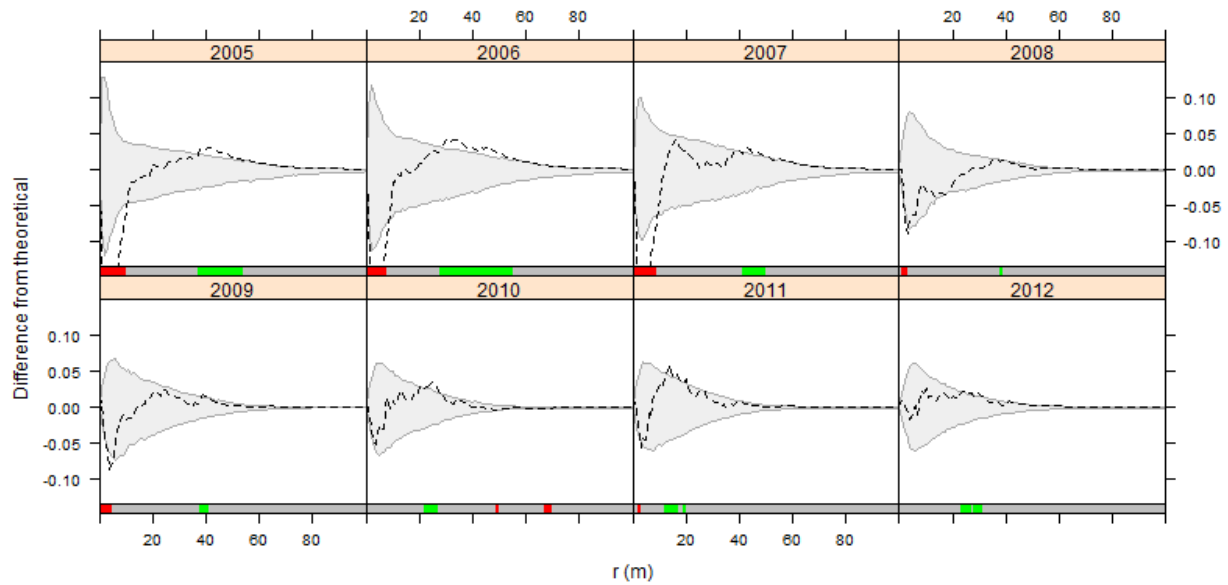
**Appendix 5:** Significant coefficients of final nest formation and disappearance logistic regression model.

| | *Estimate* | *Std. Error* | *z value* | *Pr(>|z|)* |
|---|---|---|---|---|
| *New nests* | | | | |
| **intens(after)** | -0.395 | 0.141 | -2.798 | 0.005 |
| **tree** | -0.004 | 0.001 | -7.707 | < 0.001 |
| **edge** | 0.169 | 0.038 | 4.424 | < 0.001 |
| **nest** | 0.034 | 0.004 | 8.912 | < 0.001 |
| **prclu^2** | -0.00003 | 0.00001 | -3.363 | < 0.001 |
| **nn** | -0.172 | 0.011 | -16.030 | < 0.001 |
| **intens(after):nn** | 0.073 | 0.012 | 6.163 | < 0.001 |
| *Disappeared nests* | | | | |
| **intens(after)** | -0.310 | 0.125 | -2.488 | 0.013 |
| **slope** | 0.013 | 0.004 | 3.285 | 0.001 |
| **prclu^2** | 0.00003 | 0.00001 | 3.717 | < 0.001 |
| **nn** | -0.013 | 0.008 | -1.607 | 0.108 |
| **intens(after):nn** | 0.027 | 0.010 | 2.791 | 0.005 |

**Appendix 6:** The receiver operator characteristic (ROC) plots of logistic regression model predictions for **(a)** new nests and **(b)** disappeared nests by year. ROC plots compare the true positive rate (sensitivity) to the false positive rate (specificity) of the prediction model over the entire range of discrimination thresholds. Models are assessed by the area under curve (AUC) value, with AUC > 0.7 indicating a useful prediction and AUC = 0.5 indicating no better than random prediction. AUC values are shown in the lower right corner of each graph.
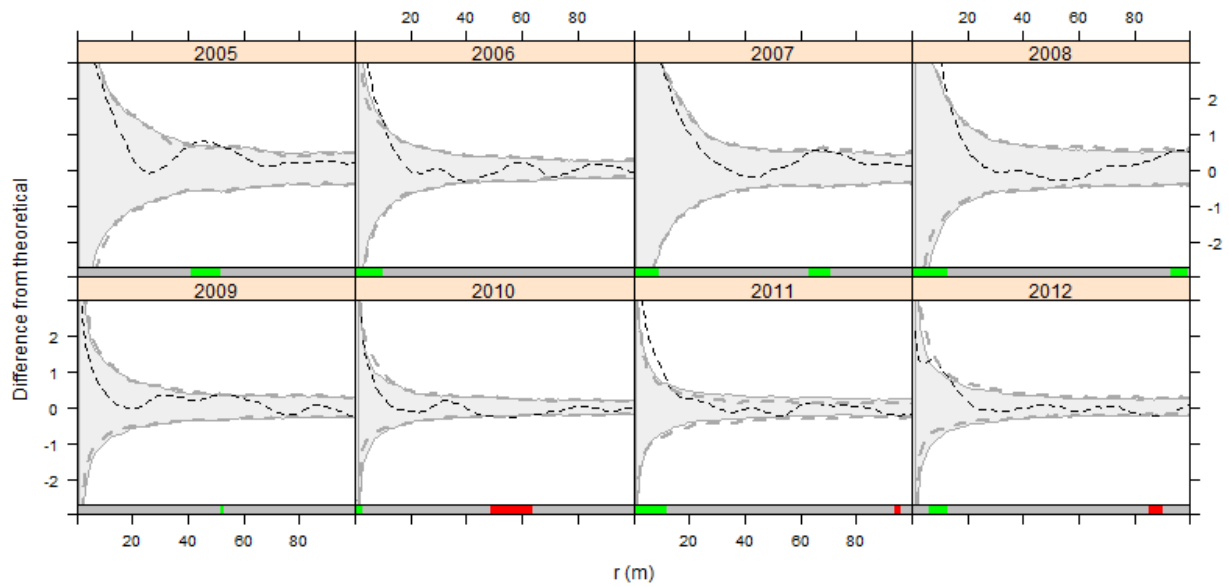
**Appendix 6a**
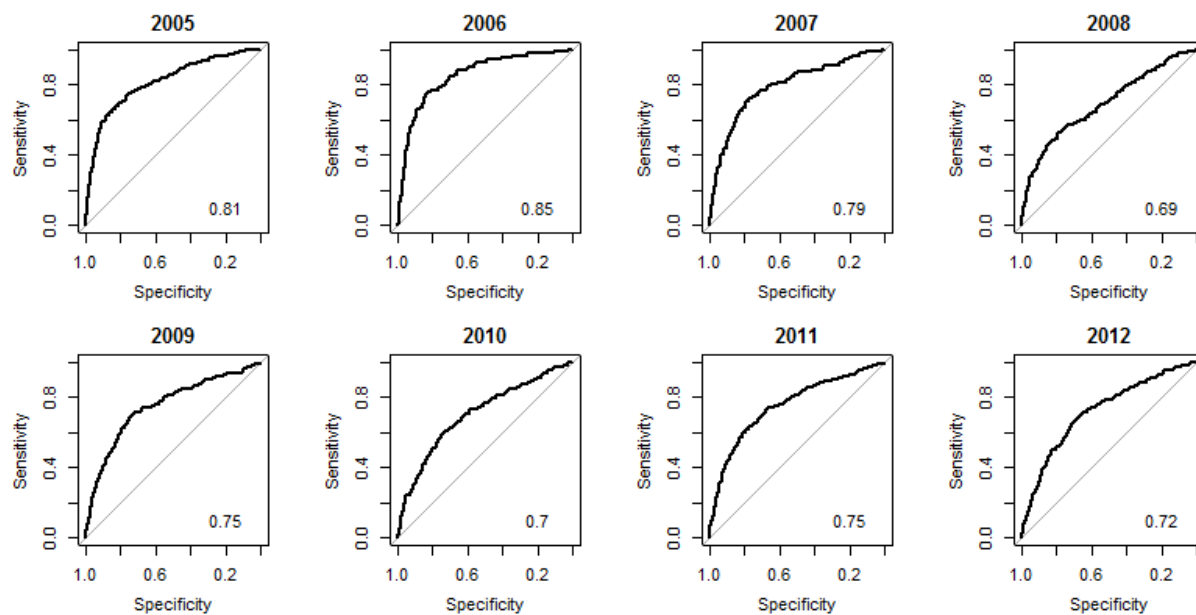


**Appendix 6b**
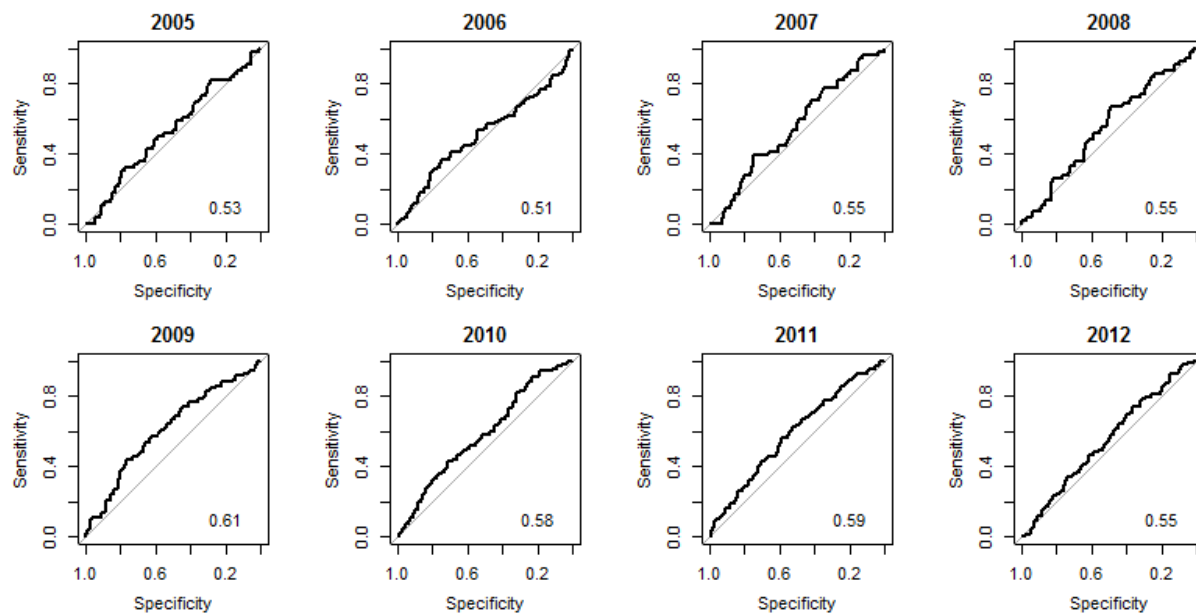
**Appendix 7:** Pair correlation function of predicted nest events based on logistic regressions of (a) new and (b) disappeared nests. Dotted line represents the observed PCF – theoretical PCF. The gray areas represent the 95% confidence envelope from 1000 simulations based on selecting from available sites with the logistic regression model. The colored bars below each panel indicate significant deviation of spatial structure from the model predictions at that distance (green = clustered, red = dispersed, grey = not significant). Dark gray dotted lines indicate an envelope of 1000 nest distributions selected at random.
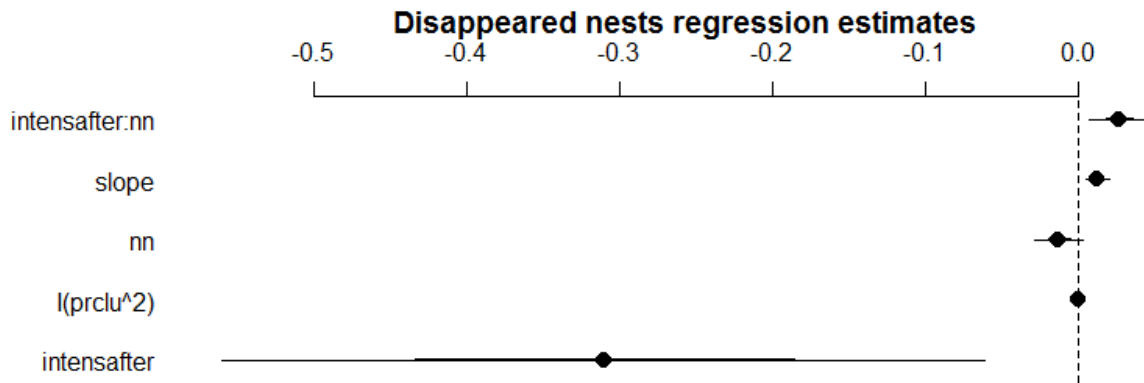
**Appendix 7a**
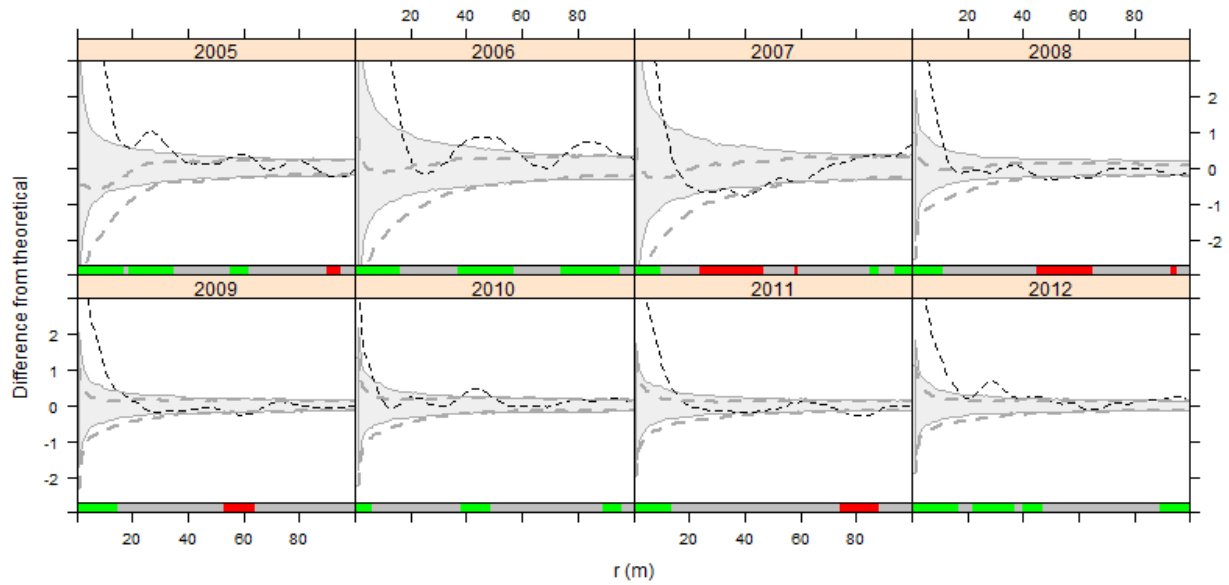


**Appendix 7b**

**Appendix 8:** Significant regression coefficients of disappeared nest logistic regression model. Models were chosen through backwards and forwards selection procedures based on the Bayes Information Criterion (BIC). Parameter fit statistics are in Appendix 6.

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