

***Azteca sericeasur* nest patterns in a conventional and organic coffee farm**

By

Teresa Dorado

A thesis submitted in partial fulfillment of the requirements for the degree of
Master of Science (Ecosystem Science and Management)
School for Environment and Sustainability
University of Michigan, Ann Arbor
August 2021

Thesis Committee:

Dr. Ivette Perfecto
Dr. John Vandermeer

Acknowledgements

I would like to thank my advisors Ivette Perfecto and John Vandermeer for their insights and useful advice throughout my work. A special thanks to Kevin Li for his help with the code and spatial analysis, and the Perfectomeer lab for all the thoughtful comments and suggestions. I would also like to thank Gustavo López Bautista and everyone who has gathered data at both Finca Irlanda and Finca Hamburgo throughout the years. I would like to thank my family and friends for all their encouragement and support.

Table of Contents

	Page
Acknowledgements	ii
Abstract	1
Introduction	2
Methods	3
Results	6
Discussion	8
References	11

Abstract

Spatial patterns in ecology have an important role in the temporal dynamics of a system. Here, I analyze the arboreal nesting keystone species', *Azteca sericeasur*, dynamic clustering patterns over time in a conventionally managed coffee farm and a certified organic coffee farm. *A. sericeasur* exhibits self-organized dynamics due to its density dependence and interactions with natural enemies. Environmental heterogeneity, in this case tree availability, also contributes to the nest distribution patterns.

I explore the spatial patterns of *A. sericeasur* through cluster analyses to determine the impact of nest clustering on nest mortality over time. Using Ripley's K analysis, I find there is clustering of ant nests at both farms but only at a small spatial scale ($r < 100$ m) in the conventionally managed farm and at all spatial scales analyzed ($r < 150$ m) in the organic farm. In addition, older nests in the conventional farm that died were observed to be more isolated from live nests. This study has implications for coffee farm management, as this system contains a biological control agent. Understanding the nesting patterns of *A. sericeasur* can guide farm managers in utilizing their ecosystem services more effectively.

Introduction

In ecology, it is generally accepted that environmental heterogeneity impacts species distribution across a landscape (Deblauwe 2008). Variability in soil nutrients and water availability are some examples that result in non-random spatial patterns (John et al. 2007, Villalobos-Vega et al. 2014). However, sometimes species demonstrate self-organizing patterns under uniform environmental conditions (Vandermeer et al. 2008). Alan Turing's concepts of diffusion (i.e. activation) and restriction (i.e. repression) in chemical reactions offer a process through which self-organizing patterns could emerge (Turing 1952). This Turing mechanism has been used in theoretical ecology to demonstrate non-random patterns over space and time (Bolker 2003). Observations in nature are found in semiarid vegetation (Klausmeier 1999) and mussel beds (van de Koppel 2008) where species demonstrate non-random spatial patterns.

The distribution of nesting ant species can reveal an example of a Turing mechanism in tropical ecosystems. *Azteca sericeasur* is an arboreal nesting ant species common in coffee agroecosystems in Mesoamerica that nests in shade trees planted among coffee bushes (Vandermeer et al. 2010) in shaded coffee farms. *A. sericeasur* has been shown to form clustering spatial patterns following a Turing process involving instances of activation and repression (Vandermeer et al. 2008, Li et al. 2016). As the colony grows, it may 'bud out' and form a new colony in a nearby tree, which represents the activation process (Vandermeer et al. 2008). Density dependent attacks from natural enemies, such as parasitoid phorid flies, can limit the expansion of nests, representing the Turing repression process (Philpott et al. 2009, Perfecto and Vandermeer 2008, Pardee and Philpott 2011, Hsieh et al. 2012). Phorid flies cause a decline in ant foraging activity limiting the amount of honey dew from hemipteran mutualists that the ants can bring back to feed the colony (Perfecto and Vandermeer 2006). Proximity to a nest attack by phorid flies may impact the ant behavior of nearby nests (Mathis et al. 2011).

Understanding the spatial distribution of *A. sericeasur* ants is important to farmers as they provide important biological control services (Vandermeer et al. 2010, 2019). *A. sericeasur* is considered a keystone ant species in Mexican coffee farms due to their multitude of interactions with other organisms that result in pest control. One of those interactions is their mutualistic association with the green coffee scale, *Coccus viridis*, where they offer protection to the scale

insects in return for a food resource. As they forage and protect scale insects on coffee plants, they exhibit aggressive behavior towards many other insects, including the coffee berry borer, a common pest of coffee. As a result, *A. sericeasur* is considered an important biological control agent in coffee farms (Morris et al. 2015).

Extensive work has focused on ant communities in a large certified organic and shaded farm (Jackson et al. 2009, Liere et al. 2012, Perfecto and Vandermeer 2008, Vandermeer et al. 2008, Vandermeer et al. 2010) where a 45 hectare plot allows for spatial analyses to be conducted. But less is known about the dynamics that influence nest distribution in a more intensive and conventionally managed farm. Here, I analyze the spatial distribution of *A. sericeasur* in the 45 hectare plot in Finca Irlanda, the organic shaded farm, and compare it to the spatial distribution on a 30 hectare plot in Finca Hamburgo, a conventional farm with much lower density of shade trees. A previous study showed that the impact of phorid flies in reducing ant foraging activity was stronger in low shade sites than in sites with higher shade levels (Pardee and Philpott, 2011). For this reason, I expect that the clustering pattern would be stronger in the conventional farm with low shade level than in the organic shaded farm. I hypothesize that (1) nest distribution is significantly clustered in both farms, but the conventional farm has a stronger clustering, and (2) that there is a significant clustering of live nests surrounding dead nests due to the density dependence dynamics between ants and phorid flies.

Methods

Study site

The study was conducted in the Soconusco region of Chiapas, Mexico. Finca Irlanda (15° 11'N, 92° 20'W), is a 280 ha certified organic coffee farm, with a high diversity and density of shade trees (for a description of the farm see, Perfecto and Vandermeer 2002; Philpott and Bichier 2012). In 2004 a 50 ha plot was established in Finca Irlanda. Trees larger than 10 cm in circumference were tagged, georeferenced and identified to species. A census of the location (individual tree) of *A. sericeasur* nests is conducted on a yearly basis (Vandermeer et al. 2008, Li et al. 2016). Finca Hamburgo (15° 10'N, 92° 19'W) is a 300 ha conventionally managed coffee farm with low density of shade trees (for a description of the farm see, Perfecto and

Vandermeer 2002). In 2012, a 30 ha plot was established in Finca Hamburgo using the same methodology as the 45 ha plot in Finca Irlanda. Yearly data on *A. sericeasur* nest location was also collected from 2012 to 2015, and then sporadically. For this reason I only used data from 2012 to 2015 for Finca Hamburgo.

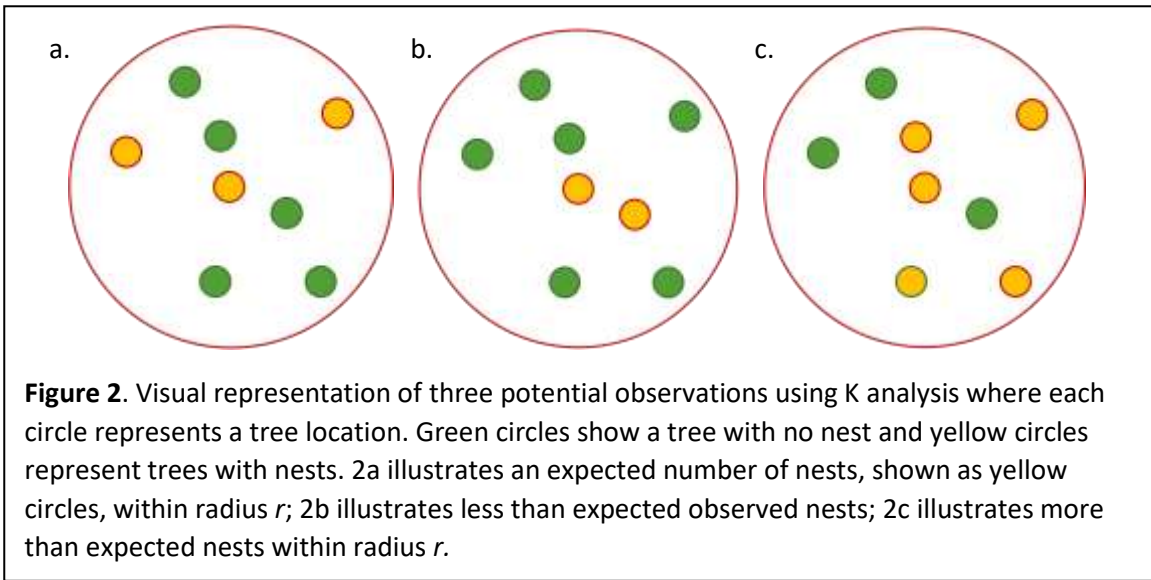
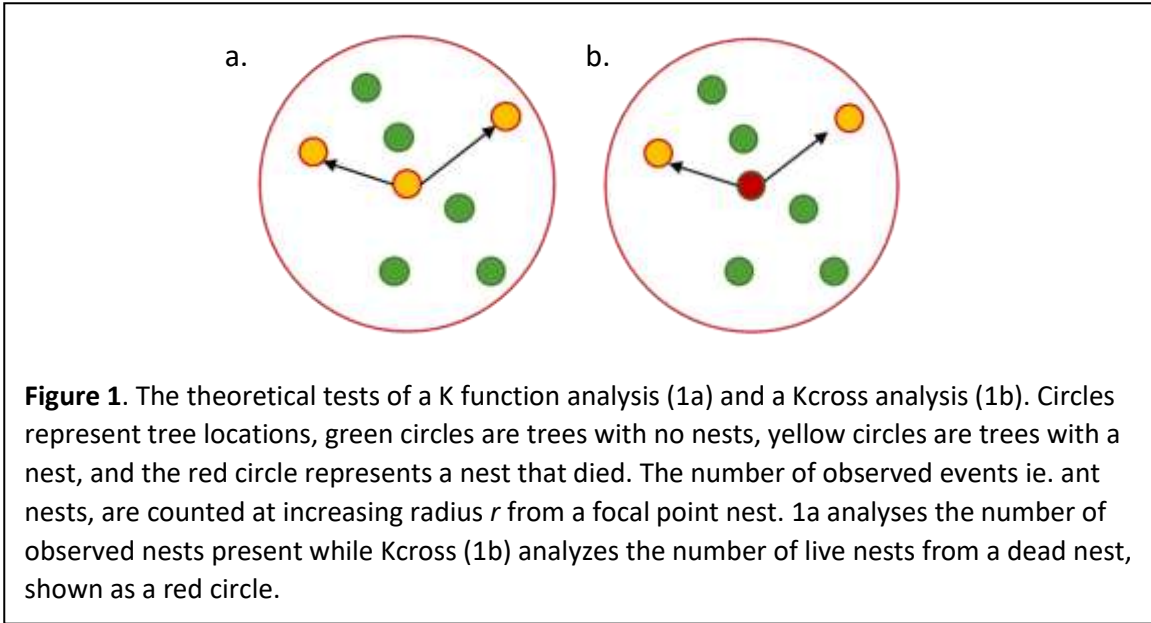
Cluster analysis

I analyze *A. sericeasur* nest distribution in 2015 for both farms using Ripley's K analysis in the spatstat package in R (Baddeley and Turner 2004). Ripley's K is used to analyze the clustering of observed events (i.e. nests) at circles of radius r (see Fig. 1a) against a homogeneous Poisson process (Dixon 2014). To achieve a 95% confidence interval, we compared the observed patterns with 100 randomly-generated patterns based on the type of event (Table 1). This analysis gives the expected number of points of event j from event i (see Table 1) within radius r to determine distribution and clustering (see Fig. 2) patterns (Haase 1995).

Mortality

To examine the repression component in the Turing-like process, I analyzed the spatial arrangement of nest mortality for the year 2015 (i.e. nests that were present in previous census but were not present in the 2015 census). To achieve this, I performed a Ripley's Kcross function (Dixon 2014) analysis to determine potential clustering of live nests around nests that died in 2015. Each data point contained "marks" which represent qualitative or quantitative characteristics (Penttinen et al. 1992), in this case marks represent live or dead nest information (Fig. 1b).

To further understand the activation and repression dynamics, I separated nests that died in 2015 by their relative age and performed a Kcross function analysis based on nest age at death. For example, a new nest present in 2013 and 2014 that was no longer present in 2015 would be classified as a mortality of a two year old nest. In Hamburgo, two year old nests will consist of nests that were two years or older since we had no nest data prior to 2012 when the research plot was established.



K_{ij}	Pattern i (from)	Pattern j (to)	Null pattern rule
K_r	All nests in 2015	none (univariate)	Random relabeling of occupied and empty trees
$K_{0,1}$	Nests alive in 2014 that died in 2015	Nests alive in 2014 and 2015	Random relabeling of nests that died
$K_{1,0}$	1 year old nests that died in 2015	Nests alive	Random relabeling of one year old nests that died and live nests
$K_{2,0}$	2 year old nest that died in 2015	Nests alive	Random relabeling of two year old nests that died and live nests

Table 1. Variables used in the Ripley's K and Kcross spatial analyses. Clustering patterns from i to j are compared with null patterns created with specific rules.

Results

2015 Nest Clustering

Both farms showed clustering of *A. sericeasur* nests (Figure 3a and 3b) as the observed curve falls above the theoretical envelope of the random distribution curve. In Hamburgo, however, above a radius distance $r = 100\text{m}$ clustering decreases as shown by the observed curve falling within the theoretical envelope of the random distribution curve (Fig. 3b).

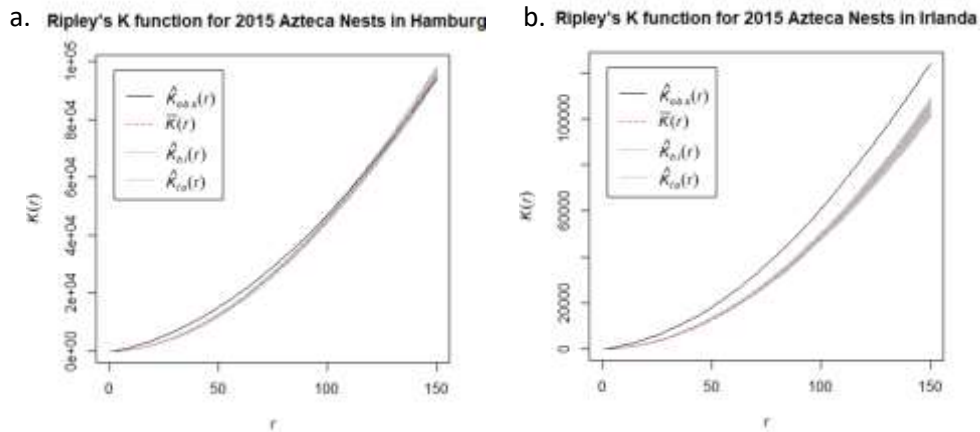


Figure 3. Ripley's K analysis for *Azteca sericeasur* ant nests present in 2015 for Finca Hamburgo (a) and Finca Irlanda (b).

Mortality

In Hamburgo, the conventionally managed farm, there is no observed clustering of live nests around nests that died in 2015 (Fig. 4a). The observed curve falls within the envelope of expected nests present at a random distribution. In Irlanda, however, there were less live nests than expected at random around nests that died at all radius distances r (Fig.4b).

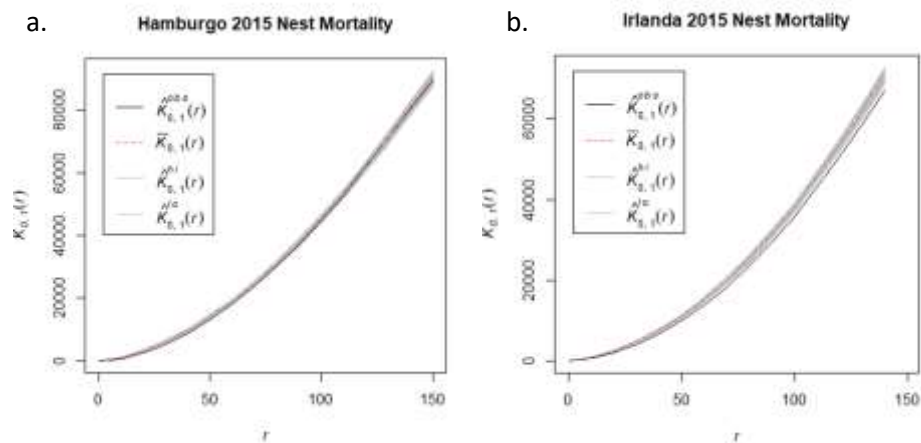


Figure 4. Kcross function measuring clustering of live nests around nests that died in 2015 for Finca Hamburgo (a) and Finca Irlanda (b).

Relative Age

In Hamburgo, there was no significant clustering of live nests around one year old nests that died in 2015. In fact, the distribution of live nests surrounding dead nests was no different than random (Fig. 5a). However, there were less live nests than expected around two year old (or older) nests that died at all distances considered (Fig. 5c). Similarly, in Irlanda, there was no clustering of live nests around dead nests. Rather, there were less live nests than expected from a random distribution around one year old nests that died, at a scale of up to 40 meters (Fig. 5b). However, for the 2 year old nests this pattern is reversed, with less live nests than expected

from a random distribution around one year old nests that died in 2015, at a scale of more than 30 meters (Fig. 5d).

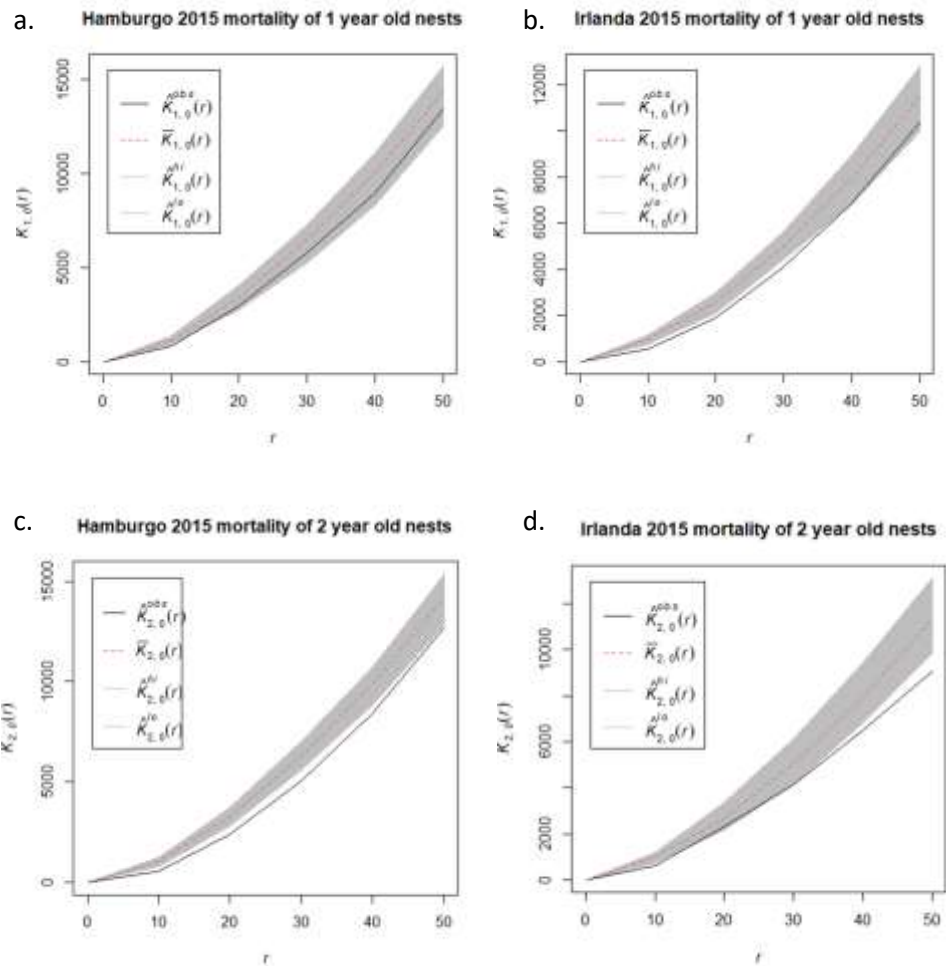


Figure 5. Kcross function measuring clustering of live nests surrounding dead nests for one year old nests in Hamburgo (a), one year old nests in Irlanda (b), two years old (or older) nests in Hamburgo (c) and two year old nests in Irlanda (d) 2015.

Discussion

Clustering

The Ripley's K analysis demonstrates that the spatial distribution of *A. sericeasur* nests distribution is significantly clustered in both farms (Fig. 3). However, rather than finding a stronger clustering in Finca Hamburgo, due to higher phorid attacks in less shaded farms

reported earlier (Pardee and Philpott, 2011), the clustering is less strong and it disappears at scales of 100 m and higher for Finca Hamburgo (Fig. 2b). Since phorid attacks were not measured between 2012 and 2015, we cannot assume that phorid attacks were indeed stronger in Finca Hamburgo than in Finca Irlanda for those years. The reported differences in phorid attacks between high shade and low shade habitats were based on a study conducted in 2009, six years before the collected data was used for the overall ant nest distribution. The lower density of shade trees in the low shade farm (Finca Hamburgo) do not explain these results either since the analysis takes into account the overall density of trees in each plot (as the comparison is with a random spatial distribution based on the same number of trees). However, these results (Fig. 3a and 3b) suggest tree location may impact the clustering of ant nests at a larger spatial scale due to ant's potential difficulty to go from one cluster of trees to the next. Because Hamburgo is a conventionally managed farm with less shade tree density, it represents a low-quality matrix in which the agricultural landscape is less suitable and contains less opportunity for species habitats (Perfecto and Vandermeer 2002, Liere et al. 2012).

Mortality

In the conventionally managed farm (Finca Hamburgo), there is no clustering of live nests around dead nests at any radius. However, in the organic farm (Finca Irlanda), there are less live nests around nests that died compared to a random distribution. This may indicate the nests that died that year are isolated from most other nests since tree location is accounted for. When separating the relative age of the dead nests in Hamburgo, there were less live nests than expected around two year old (or older) nests that died at all distances (Fig. 5c) suggesting relatively older nests are more isolated. Although density dependent attacks from natural enemies, can limit the expansion of nests (Philpott et al. 2009, Perfecto and Vandermeer 2008, Pardee and Philpott 2011), this does not fully explain why older nests that died in Hamburgo were more isolated compared to a random distribution. In Finca Irlanda, where there are more shade trees, the clustering of live nests around a nest that died was less compared to a random distribution, potentially due to the higher availability of habitat (shade trees) throughout the study site. Furthermore, if there are fewer nests around nests that died in Finca Irlanda, this

may indicate less activity among a nest colony complex across multiple trees resulting in abandoned nests (ie. dead nests).

The distribution of nesting ant species in this tropical ecosystem can reveal an example of a Turing mechanism. Density dependent attacks from natural enemies, such as parasitoid phorid flies, can limit the expansion of nests, representing the Turing repression process (Philpott et al. 2009, Perfecto and Vandermeer 2008, Pardee and Philpott 2011, Hsieh et al. 2012). Although an earlier study reported higher phorid attacks in less shaded farms (Pardee and Philpott, 2011), this did not explain the spatial distribution observed in Finca Hamburgo, a conventionally managed farm with less shade trees. This analysis assumes phorid attacks are the main cause of nest deaths throughout the years of this study. However, future studies observing the intensity of phorid attacks on nest clusters and on varying nest ages is necessary to test the assumptions of this study. Collecting phorid attack data at observed clusters in both farms would be useful to determine the impact of phorid attacks on the clustering of live nest around nests that die.

This study offers a comparison of observed *A. sericeasur* nest patterns over time in a certified organic farm and a conventionally managed farm. Finca Hamburgo represents a low-quality matrix in the agricultural matrix as it is a conventionally managed farm with less shade tree density, therefore contains less habitat opportunity for *A. sericeasur* (Perfecto and Vandermeer 2002). On the other hand, Finca Irlanda is an organic farm with higher shade tree density and as a result, more opportunities for ant nests to establish. *A. sericeasur* is an important biological control agent in coffee farms (Morris et al. 2015, Vandermeer et al. 2010, 2019). Understanding the spatial distribution of *A. sericeasur* ants over time is important to farmers as it can guide farm managers in utilizing their ecosystem services more effectively.

References:

- Baddeley, Adrian J., and Rolf Turner. "Spatstat: An R package for analyzing spatial point patterns." (2004): 1-42.
- Bolker, Benjamin M. "Combining endogenous and exogenous spatial variability in analytical population models." *Theoretical Population Biology* 64.3 (2003): 255-270.
- Klausmeier, Christopher A. "Regular and irregular patterns in semiarid vegetation." *Science* 284.5421 (1999): 1826-1828.
- Deblauwe, Vincent, Nicolas Barbier, Pierre Couteron, Olivier Lejeune, and Jan Bogaert. "The global biogeography of semi-arid periodic vegetation patterns." *Global Ecology and Biogeography* 17, no. 6 (2008): 715-723.
- Dixon, Philip M. "R iple's K function." *Wiley StatsRef: Statistics Reference Online* (2014).
- Haase, Peter. "Spatial pattern analysis in ecology based on Ripley's K-function: Introduction and methods of edge correction." *Journal of vegetation science* 6.4 (1995): 575-582.
- Hsieh, Hsun-Yi, and Ivette Perfecto. "Trait-mediated indirect effects of phorid flies on ants." *Psyche* 2012 (2012).
- Jackson, Doug, John Vandermeer, and Ivette Perfecto. "Spatial and temporal dynamics of a fungal pathogen promote pattern formation in a tropical agroecosystem." *The Open Ecology Journal* 2, no. 1 (2009).
- John, Robert, James W. Dalling, Kyle E. Harms, Joseph B. Yavitt, Robert F. Stallard, Matthew Mirabello, Stephen P. Hubbell et al. "Soil nutrients influence spatial distributions of tropical tree species." *Proceedings of the National Academy of Sciences* 104, no. 3 (2007): 864-869.
- Li, Kevin, John H. Vandermeer, and Ivette Perfecto. "Disentangling endogenous versus exogenous pattern formation in spatial ecology: a case study of the ant *Azteca sericeasur* in southern Mexico." *Royal Society open science* 3.5 (2016): 160073.
- Liere, Heidi, Ivette Perfecto, and John Vandermeer. "Stage-dependent responses to emergent habitat heterogeneity: consequences for a predatory insect population in a coffee agroecosystem." *Ecology and evolution* 4.16 (2014): 3201-3209.
- Liere, Heidi, Doug Jackson, and John Vandermeer. "Ecological complexity in a coffee agroecosystem: spatial heterogeneity, population persistence and biological control." *PloS one* 7.9 (2012): e45508.
- Mathis, Kaitlyn A., Stacy M. Philpott, and Rayane F. Moreira. "Parasite lost: chemical and visual cues used by *Pseudacteon* in search of *Azteca instabilis*." *Journal of insect behavior* 24, no. 3 (2011): 186-199.
- Morris, Jonathan R., John Vandermeer, and Ivette Perfecto. "A keystone ant species provides robust biological control of the coffee berry borer under varying pest densities." *PloS one* 10.11 (2015): e0142850.

Pardee, G.L. and Philpott, S.M., 2011. Cascading indirect effects in a coffee agroecosystem: effects of parasitic phorid flies on ants and the coffee berry borer in a high-shade and low-shade habitat. *Environmental Entomology*, 40(3), pp.581-588.

Penttinen, Antti, Dietrich Stoyan, and Helena M. Henttonen. "Marked point processes in forest statistics." *Forest science* 38.4 (1992): 806-824.

Perfecto, Ivette, and John Vandermeer. "Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico." *Conservation biology* 16.1 (2002): 174-182.

Perfecto, Ivette, and John Vandermeer. "The effect of an ant-hemipteran mutualism on the coffee berry borer (*Hypothenemus hampei*) in southern Mexico." *Agriculture, Ecosystems & Environment* 117.2-3 (2006): 218-221.

Perfecto, Ivette, and John Vandermeer. "Spatial pattern and ecological process in the coffee agroforestry system." *Ecology* 89.4 (2008): 915-920.

Perry, J. N., A. M. Liebhold, M. S. Rosenberg, J. Dungan, M. Miriti, A. Jakomulska, and S. Citron-Pousty. "Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data." *Ecography* 25, no. 5 (2002): 578-600.

Philpott, Stacy M., and Peter Bichier. "Effects of shade tree removal on birds in coffee agroecosystems in Chiapas, Mexico." *Agriculture, ecosystems & environment* 149 (2012): 171-180.

Philpott, Stacy M., Ivette Perfecto, and John Vandermeer. "Effects of management intensity and season on arboreal ant diversity and abundance in coffee agroecosystems." *Biodiversity & Conservation* 15.1 (2006): 139-155.

Philpott, Stacy M., Ivette Perfecto, John Vandermeer, and Shinsuke Uno. "Spatial scale and density dependence in a host parasitoid system: an arboreal ant, *Azteca instabilis*, and its *Pseudacteon* phorid parasitoid." *Environmental Entomology* 38, no. 3 (2009): 790-796.

Turing, A. M. "The Chemical Basis of Morphogenesis." *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*. 237 (1952):37-72.

van de Koppel, Johan, Joanna C. Gascoigne, Guy Theraulaz, Max Rietkerk, Wolf M. Mooij, and Peter MJ Herman. "Experimental evidence for spatial self-organization and its emergent effects in mussel bed ecosystems." *Science* 322, no. 5902 (2008): 739-742.

Vandermeer, John, Ivette Perfecto, and Stacy M. Philpott. "Clusters of ant colonies and robust criticality in a tropical agroecosystem." *Nature* 451.7177 (2008): 457-459.

Vandermeer, John, Ivette Perfecto, and Stacy Philpott. "Ecological complexity and pest control in organic coffee production: uncovering an autonomous ecosystem service." *BioScience* 60.7 (2010): 527-537.

Villalobos-Vega, Randol, Ana Salazar, Fernando Miralles-Wilhelm, Mundayatan Haridasan, Augusto C. Franco, and Guillermo Goldstein. "Do groundwater dynamics drive spatial patterns of

tree density and diversity in Neotropical savannas?." *Journal of vegetation science* 25, no. 6 (2014): 1465-1473.

Vandermeer, J., Armbrrecht, I., De la Mora, A., Ennis, K.K., Fitch, G., Gonthier, D.J., Hajian-Forooshani, Z., Hsieh, H.Y., Iverson, A., Jackson, D. and Jha, S., 2019. The community ecology of herbivore regulation in an agroecosystem: Lessons from complex systems. *BioScience*, 69(12), pp.974-996.

Yitbarek, Senay, John H. Vandermeer, and David Allen. "The combined effects of exogenous and endogenous variability on the spatial distribution of ant communities in a forested ecosystem (Hymenoptera: Formicidae)." *Environmental entomology* 40.5 (2011): 1067-1073.