SPATIAL PATTERN AND ECOLOGICAL PROCESS
IN THE COFFEE AGROFORESTRY SYSTEM

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Abstract. The coffee agroforestry system provides an ideal platform for the study of spatial ecology. The uniform pattern of the coffee plants and shade trees allows for the study of pattern generation through intrinsic biological forces rather than extrinsic habitat patchiness. Detailed studies, focusing on a key mutualism between an ant (Azteca instabilis) and a scale insect (Coccus viridis), conducted in a 45-ha plot in a coffee agroforestry system have provided insights into (1) the quantitative evaluation of spatial pattern of the scale insect Coccus viridis on coffee bushes, (2) the mechanisms for the generation of patterns through the combination of local satellite ant nest formation and regional control from natural enemies, and (3) the consequences of the spatial pattern for the stability of predator–prey (host–parasitoid) systems, for a key coccinellid beetle preying on the scale insects and a phorid fly parasitoid parasitizing the ant.

Key words: Azia orbigeria; Azteca instabilis; Coccus viridis; coffee agroforestry; mutualism; predator–prey interactions; self-organization; spatial pattern.

INTRODUCTION

Some of the earliest forays into ecology were concerned at least implicitly, with the spatial distribution of organisms (Turner 1989). Yet it was not until the 1990s that the study of spatially explicit models became popular (Dunning et al. 1995) and today it is one of the more vibrant growth areas of the discipline, effectively joining forces with the traditional field of landscape ecology (Tilman and Kareiva 1997, Turner et al. 2001). The study of space in ecology ranges from the description of movement of individuals from cell to cell in cellular automata models, to spatially explicit multispecies interactions at the local level described by Lotka-Voterra or Nicholson-Bailey models, to self-organization and the formation of large-scale spatial patterns in the distribution of organisms. A substantial body of ecological theory shows that (1) spatial pattern can spontaneously arise from the dynamic interactions among components in the system and (2) spatial pattern can determine the consequences of biological interactions. Thus, for example, local spread of a population coupled with regional control, the so-called Turing mechanism, can easily lead to a patchy spatial distribution (Turing 1952, Murray 1991). On the other hand, spatial heterogeneity per se is well known to be a potential stabilizing mechanism for biological interactions that are unstable at a local level (Steel 1974, May 1978, Tilman and Kareiva 1997). Finding field data that speak to these theoretical ideas has been difficult (Rohani et al. 1997). Spatial patterns of populations in nature are most often observed in the context of habitat patterns, with patches of individuals associated with patches of habitat determined by abiotic or exogenous factors. Less common are cases in which a spatial pattern observed in nature can unequivocally be shown to be a consequence of biological interactions. One reason that such biologically determined spatial pattern is not often observed is that almost all habitats are patchy, thus automatically confounding the results of biological interactions with the patchiness of the environmental background.

Agroforestry systems, by design are almost always more uniform than natural systems. For this reason, they provide an excellent model system for studying the patterns of the distribution of organisms in space and the forces that generate them. Because of their underlying uniformity, they are ideal systems for studying three general areas in spatial ecology: (1) the quantitative evaluation of spatial pattern, (2) the mechanism of pattern generation, and (3) the consequences of spatial pattern. We treat each of these questions in turn, highlighting results from our own research in the coffee agroforestry system of Mesoamerica.

THE SYSTEM

In Mesoamerica, as well as other regions in Latin America, coffee is produced in an agroforestry system with shade trees interspersed with the coffee bushes that grow in the understory. Because the understory is uniformly planted with coffee and the canopy consists of a small number of species with a planted dominant...
shade “backbone” of a single species or genus of even-aged trees, the coffee agroecosystem is spatially homogeneous relative to natural forest. Even so, this tropical managed system is highly diverse compared with other human managed systems (Perfecto et al. 1996, Moguel and Toledo 1999, Perfecto and Armbracht 2003) and contains highly complex ecological interactions (Vandermeer et al. 2002, Armbracht and Perfecto 2003, Armbracht et al. 2004, 2005, Philpott et al. 2004a, b, 2005, Philpott 2005, Philpott and Armbracht 2006). In this complex agroforestry system, we have identified a subsystem in which ecological interactions determine spatial pattern and that spatial pattern influences, even determines, key aspects of the ecological interactions.

The system consists of an arboreal ant, its scale insect mutualist, the natural enemies of the scale, the natural enemies of the enemies of the scale, and a phorid parasitoid of the ant (Fig. 1). The ant, Azteca instabilis, is an aggressive arboreal ant that nests in the shade trees. The trees with colonies are spatially aggregated (Vandermeer et al. 2008). The ant has a mutualistic relationship with Coccus viridis, a scale insect and an herbivore in coffee. Azteca protects C. viridis from its natural enemies and in turn harvests the honeydew that the scales produce. The natural enemies of C. viridis include the coccinellid beetle, Azya orbiger, and at least two parasitoids in the family Encyrtidae, however, the coccinellid beetle appears to be the main natural enemy in this system (H. Liere, unpublished data). Furthermore, the beetle larva, which is a voracious predator of the scale, is covered with waxy filaments that render it immune to the attack by the ants. Thus, clusters of trees with Azteca represent high quality patches for this myrmecophilic coccinellid larva since there is a high availability of food (scale insects) and indirect protection from predators and parasitoids by the harassment action of the ants (Liere and Perfecto, in press). A fly parasitoid (Pseudacteon sp., Phoridae) attacks the Azteca workers while they are foraging and tending scales, dramatically reducing their foraging activity (Philpott et al. 2004b, Philpott 2005). Finally, a fungal pathogen (Verticillium lecanii) attacks the scale insects, seemingly only when they reach a critical density, which only happens under the protection of ants.

The Quantitative Evaluation of Spatial Pattern

The earliest evaluations of spatial patterns focused on the simple question of whether a population had a random, uniform or aggregated distribution (Morisita 1959, Lloyd 1967), a focus that continues today only with far more sophisticated statistical analyses (Roberts 1987, Wackernagel 2003). However, questions of a more theoretical statistical nature have surfaced in recent years. Chief among them is the distribution of cluster sizes in a spatially patterned population (Pascual et al. 2002), noted in theoretical studies to frequently follow a power law (i.e., if $f(x)$ is the frequency of clusters of size $x$, then $f(x) = ax^b$ where $a$ and $b$ are constants).

Taking advantage of the highly replicated and spatially uniform distribution of coffee plants in the coffee agroecosystems, we examined the pattern of distribution of the scale insect, C. viridis associated with individual coffee bushes in the relatively homogeneous sea of coffee found in the understory. In particular, we examined how this pattern might vary in the presence or absence of Azteca, the key mutualist of the scale. Estimating population densities on over 600 coffee bushes, we observed that the spatial pattern did, indeed, reflect an underlying power law (Vandermeer and Perfecto 2006a), with significant deviations at large cluster sizes (those encountered in Azteca patches [Vandermeer and Perfecto 2006a]), and with systematic deviations also at smaller cluster sizes. Scale insect distribution provides an example of a spatial distribution governed by simple biological rules associated with birth, death, and immigration rates within subpopulations (Alonso and Pascual 2006). Kendall (1948) long

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**Fig. 1.** Diagram of the Azteca system showing the anti-scale mutualism and the higher-level trophic interactions. The system consists of an arboreal ant (A. instabilis), its scale insect mutualist (Coccus viridis), the natural enemies of the scale, the natural enemies of the enemies of the scale, and a phorid parasitoid of the ant. Arrows represent positive effects; solid circles represent negative effects; solid lines represent direct interactions; dashed lines represent indirect interactions; and the × indicates an interaction that is affected by a third species (i.e., the arrows with solid circles represent predator–prey interactions and parasite–host interactions, and the double arrow represents a mutualistic interaction).
ago noted that depending upon these rates, the statistical
distribution of subpopulations would follow either
Fisher’s log series distribution or a negative binomial.
Alonso and Pascual (2006) found a close fit to the
negative binomial, thus explaining what we had
characterized only as deviations from a power series,
and also reinforced the conclusion that high density
deviation from the power law was a consequence of the
ant mutualism. Thus we see an overall pattern in which a
metapopulation is an example of Kendall’s hypothesis in
which the lognormal, negative binomial, and logseries
can be seen as part of the same general theory, the
lognormal being the expected final state when subpop-
ulations have positive growth rates, but either the
negative binomial or logseries when subpopulations
have negative growth rates with the entire metapopula-
tion maintained by the migration coefficients (Vander-
meer and Perfecto 2006b).

THE MECHANISM OF PATTERN GENERATION

Distinguishing between the importance of intrinsic
(density-dependent) and extrinsic (density-independent)
factors in governing population processes has a long
history in ecology (May 1984, Borcard et al. 1992,
Legendre 1993). A similar dichotomy has emerged in the
study of spatial pattern, usually referred to as self-
organized (intrinsic) or not (Hassell et al. 1994, Rohani
et al. 1997, Reitkerk et al. 2004). A large theoretical
literature demonstrates that a variety of intrinsic
arrangements can give rise to complex, and sometimes
beautiful, spatial patterns (Czarán and Bartha 1992,
Wilson et al. 1993, Gurney and Veitch 2000, Camazine
et al. 2003). However, spatial patterns of populations in
nature are often attributed to underlying habitat
patterns, with patches of individuals associated with
patches of habitat, which, in turn, are determined by
extrinsic factors such as type of soils, humidity, and so
on. Spatial pattern in nature that can be shown to be a
consequence of biological interactions (e.g., Maron and
Harrison 1997, Wootton 2001, Reitkerk et al. 2004), are
far less common, even though many theoretical formu-
lations suggest this should frequently be the case
(Rohani et al. 1997).

Here again, the coffee agroforestry system offers an
excellent opportunity to empirically distinguish between
these two alternatives, because of the underlying habitat
uniformity. Since in this system, Azteca nests occurred in
some sort of non-uniform pattern, we tested the
hypothesis of self-organization (Vandermeer et al. 2008).

A map of all A. instabilis nests on a 45-ha plot shows a
clear clumped pattern (Fig. 2A), providing initial
support for the hypothesis of intrinsic control of spatial
pattern (Vandermeer et al. 2008). While it is conceivable
that some underlying habitat variable (tree species or
size, for example) provides an extrinsic forcing to create
the pattern, we found no evidence for that (Vandermeer
et al. 2008; I. Perfecto and J. Vandermeer, unpublished
data). It is not completely clear what intrinsic forces are
involved. However, based on the natural history and
ancillary studies of the species, we hypothesize that
Azteca clumps are formed by the local establishment of
satellite colonies, followed by control from a natural
enemy that responds to local population density
(Vandermeer et al. 2008). Thus, local clusters are formed
by the process of local satellite nest expansion, but then
a density responsive natural enemy is especially effective
at high local densities, the basic idea of the Turing
mechanism of pattern formation in which local activa-
tion is balanced by regional repression (Ellner and
Guckenheimer 2006).

Formulating a simple stochastic cellular automata
model based on local activation and regional repression,
we were able to reproduce the qualitative features of the
spatial distribution of the ant colonies (Fig. 2B), within
the range of parameters estimated from five field surveys
of the ants. The precise parameter estimates did not, in

Fig. 2. (A) Map of the 45-ha plot in a coffee plantation
showing all trees >10 cm circumference (in gray) and all trees
that contain an Azteca instabilis nest (black) as of August 2005.
(B) An example model simulation plotted on a background of
the actual distribution of trees in the natural plot, for parameter
settings \( m_0 = 0.13 \) and \( m_1 = 0.036 \) (parameters of phorid attack),
and \( s_0 = 0.0035 \) and \( s_1 = 0.035 \) (parameters of satellite nest
expansion). The simulation is based on a 120 × 90 lattice; \( N =
261\), mean variance ratio = 0.43.
fact, reproduce the pattern observed. However, we found a set of parameter values that fell within the range determined by the extreme estimates of all parameters that gave a qualitatively similar pattern to the one we observed in nature (Vandermeer et al. 2008).

The Consequences of Spatial Pattern

The theoretical literature on the effects of space on biological interactions is large (Tilman and Kareiva 1997). Of particular interest is the situation in which the nature of local biological interactions can be altered when casting the problem spatially. Perhaps the simplest example is that of source–sink dynamics. A complication that is not often acknowledged is when the patchiness that permits source/sink dynamics is itself generated by intrinsic biological properties. An excellent example of this occurs in the coffee agroforestry system in which *Azteca* forms clusters and acts as a predator within those clusters.

For example, the most important current insect pest in coffee in Mesoamerica is the coffee berry borer (*Hypothenemus hampei*), a small scolitid beetle that burrows into the ripening coffee fruit, causing considerable economic damage (Damon 2000). It is now well established that ants can be important predators of this pest (Philpott and Armbricht 2006). In the case of spatial patchiness, we have a clear example of a possible sink (within patches of the predator ant) and a source (the rest of the coffee farm). Because *Azteca* tends scale insects, some farmers consider it a pest in coffee. Yet, *Azteca* also creates sink habitats for the borer (Perfecto and Vandermeer 2006), which clearly represent a sort of spatially induced biological control (Vandermeer et al. 2002). Thus this example of potential “control from above” can be fully understood only if the biological interactions (mutualism, herbivory and predation) are cast in their spatially explicit framework.

A more complicated case involves the coccinellid beetle *A. orbignyae*, a voracious predator of the scale insects. As mentioned earlier, the larva of this beetle is protected from the harassment activity of the ants, while the adults are not. Furthermore, the ant incidentally harasses the natural enemies of the beetle larvae, inadvertently protecting the larvae much as it protects the scale insect mutualists (Liere and Perfecto, *in press*). Thus, the extended spatial system confronts a situation in which there are patches (those with ants) in which the adult coccinellids are virtually excluded from eating but the larvae is protected from natural enemies and has ample food resources, and other patches (the areas without ants) in which scale density is very low and the coccinellid larvae probably are unable to survive. Given these conditions, it is not difficult to imagine a two-patch situation in which the predator/prey system is unstable (or non persistent) in both patches: in one patch the adult beetle is unable to feed, while in the other patch the larvae cannot find enough food to sustain itself. A collection of such patches, if isolated from one another would obviously result in the elimination of the predator from the system. However, linking the two patches together by means of interpatch migration could result in persistence over the whole space. The idea is effectively a metapopulation with two patch types where the population is expected to go extinct in each of the patches, but each patch is continually “rescued” (Gotelli 1991) from permanent extinction by migration from the other patch.

Circumstantial evidence exists that the beetle *A. orbignyae* and its prey, *C. viridis*, the scale insect, exist in just such a situation in the coffee agroecosystem (H. Liere, unpublished data). In the absence of *Azteca*, the beetle larvae are attacked at a high rate by at least three species of parasitic wasps, rendering their effective intrinsic rate of mortality extremely high. Add to this the fact that in the absence of ants the scale insects, which are their main prey, have extremely low population densities. In the presence of *Azteca*, the abundance of the prey (*C. viridis*) is high due to protection provided by the ants, and the beetle larvae are indirectly protected from their natural enemies by the ants, such that the ants effectively enrich the environment of the beetle predator. It thus appears that the beetle exists in two environments, both of which would normally lead to its extinction.

Adult beetles must migrate between patches with and without *Azteca* in order to maximize the tradeoff between egg laying and feeding. To increase larval survival the adults must place their offspring in habitats with abundant food and under the protection of the ants. Yet adults cannot feed in *Azteca* patches because of harassment from ants, and must migrate to patches without *Azteca* in order to feed. Migration from patch to patch thus appears to stabilize this inherently unstable situation (H. Liere et al., unpublished data).

Another host–parasitoid system that seems to be stabilized when spatially extended is the *Azteca–Pseudacteon* system mentioned earlier. The theoretical literature identifies two potential stabilization mechanisms that have to do with the response of the parasitoid to spatial pattern. One of them is a behavioral response that occurs at a very local level (Murdoch and Stewart-Oaten 1989) and the other is a demographic response that occurs at a much larger spatial scale with heterogeneous patches of host concentrations (Hassell et al. 1994, Maron and Harrison 1997, Wooton 2001). In the coffee agroforestry system, where the habitat is divided into *Azteca* patches and patches without *Azteca* we find that Pseudacteon attacks vary with distance from *Azteca* colony within a patch and are significantly higher in *Azteca* patches than in patches without *Azteca* (Vandermeer et al. 2008). What is particularly interesting of this system is that the spatial heterogeneity is hypothesized to be caused, at least in part, by the phorid fly through the Turing mechanism. Thus we have a situation where a host–parasite system may be stabilized.
because of the spatial heterogeneity that it, itself, is partially responsible for creating.

CONCLUSION

The coffee agroforestry system has proven useful for the study of spatial ecology. The uniform pattern of the coffee plants and shade trees has allowed researchers to search for spatial patterns generated through biological interactions. In particular the detailed studies we have conducted in a 45-ha plot in a coffee agroforestry system have provided insights into the quantitative evaluation of spatial patterns, the mechanisms for the generation of patterns, and the consequences of the spatial pattern for the stability of predator–prey (host–parasitoid) systems. Thus far, three main insights into spatial ecology have been elucidated by studying the coffee agroforestry system. (1) Metapopulations can be conceived as Kendall’s birth, death, immigration process, leading to the overall interpretation that the lognormal, negative binomial, and logseries distributions can be seen as part of the same general theory (Vandermeer and Perfecto 2006a, h). (2) Spatial pattern may form in a homogenous background as a result of intrinsic factors operative at a large scale. More specifically, clusters of Azteca ants are self-organized, mediated by satellite colony expansion followed by a natural control agent, and show a density-dependent response (Vandermeer et al. 2008). (3) The spatial heterogeneity generated by these intrinsic factors may lead to the stabilization of host/parasite systems. As an example, the scale-coccinellid system, which is unstable within each habitat patch (with and without Azteca) in isolation, is stabilized when these two types of patches are connected (H. Liere, unpublished data). Further, the Azteca–Pseudacteon system, appears to be stabilized due to a demographic response in an heterogeneous landscape that causes the phorids to have higher attack rates in Azteca patches than in patches without Azteca (Vandermeer et al. 2008).

Traditionally, ecologists have avoided working in managed ecosystems because of the inherent human manipulation to which they are subjected and the somewhat artificial nature of the systems. Ironically, it is precisely because of these attributes that the coffee agroforestry system has yielded some novel insights in spatial ecology.

ACKNOWLEDGMENTS

The research described in this article is the result of a collective effort between us (I. Perfecto and J. Vandermeer) and our graduate students and colleagues at the University of Michigan and the Colegio de la Frontera Sur-Tapachula. In particular, we acknowledge H. Liere, S. Uno, S. Philpott, and D. Jackson, J. Maldonado, B. Estaban Chiel, and G. López-Bautista performed the bulk of the field censuses. We thank the Peters Foundation for permission to establish the plot on Finca Irlanda, and for considerable logistic support. El Colegio de la Frontera Sur (ECOSUR), and especially G. Ibarra Núñez and A. Garcia-Ballinas provided critical logistical support. This work was supported by an NSF grant DEB 0349388 to I. Perfecto and J. Vandermeer.

LITERATURE CITED


