



# Hysteresis and critical transitions in a coffee agroecosystem

John Vandermeer<sup>a,b,1</sup> and Ivette Perfecto<sup>c,1</sup>

<sup>a</sup>Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109; <sup>b</sup>Program in the Environment, University of Michigan, Ann Arbor, MI 48109; and <sup>c</sup>School for Environment and Sustainability, University of Michigan, Ann Arbor, MI 48109

Edited by Mercedes Pascual, The University of Chicago, Chicago, IL, and accepted by Editorial Board Member Ruth S. DeFries June 10, 2019 (received for review February 15, 2019)

**Seeking to employ ecological principles in agricultural management, a classical ecological debate provides a useful framing. Whether ecosystems are controlled from above (predators are the limiting force over herbivores) or from below (overutilization of plant resources is the limiting force over herbivores) is a debate that has motivated much research. The dichotomous nature of the debate (above or below) has been criticized as too limiting, especially in light of contemporary appreciation of ecological complexity—control is more likely from a panoply of direct and indirect interactions. In the context of the agroecosystem, regulation is assumed to be from above and pests are controlled, a way of using ecological insights in service of an essential ecosystem service—pest control. However, this obvious resolution of the old debate does not negate the deeper appreciation of complexity—the natural enemies themselves constitute a complex system. Here we use some key concepts from complexity science to interrogate the natural functioning of pest regulation through spatially explicit dynamics of a predator and a disease operating simultaneously but distributed in space. Using the green coffee scale insect as a focal species, we argue that certain key ideas of complexity science shed light on how that system operates. In particular, a hysteresis pattern associated with distance to a keystone ant is evident.**

complexity | agroecosystem | criticality | hysteresis | biocontrol

**C**alls for utilizing ecological knowledge to improve environmental functioning of agricultural ecosystems have become common. Recent work suggests that land use, especially pesticides in intensive agriculture, are partially responsible for dramatic losses in insect abundance, even in protected areas (1), giving sustenance to those who argue that more sophisticated ecological understanding should drive future developments in agriculture (2). However, some critics argue that the popular magic-bullet approach (e.g., one pest, one pesticide; one pest, one natural enemy) cannot be a sound philosophical basis for employing ecological science any more than it was in more conventional management—ecology is too complex. They argue that ideas associated with complex adaptive systems may provide a useful theoretical framework (3–5). Pest control is an evident example. Linking to the science of ecology, effecting or failing to effect pest control is parallel with the historical debate as to whether herbivores are regulated from “above” or “below” (6–8). In a strictly agricultural context, regulation from above is strongly linked with pest control (natural enemies such as predators and diseases regulate from a trophic level above), while regulation from below would imply crop losses due to pest outbreak (the plants—crops—having lost much of their tissue to the herbivores—pests—thus “regulate” from a trophic level below, although complications such as plant defensive compounds certainly complicate this picture considerably). However, presuming control is mainly from above does not relieve us from the inevitability of complexity—the collection of predators, parasites, and diseases that naturally attack the pests are themselves a complex system. In this paper we employ core ideas of complexity science to contribute to the understanding of several dynamic patterns involved in this real-world application

of a basic ecological principle: pest regulation as a complex adaptive system.

The threat of pest outbreaks, not only in agriculture but also in other managed systems (e.g., forestry, fish farming, and wildlife management), is palpable, especially in today’s world of climate change (9). In 1997 a group of entomologists (10) opined that “long term resolutions [of pest management] can be achieved only by restructuring and managing [agroecosystems] in ways that maximize the array of ‘built-in’ preventive strengths,” and in the subsequent call for “autonomous ecosystem services” the ecosystem service of pest control occupies center stage (11). Autonomous, in this usage, clearly implies the “control from above” of pure ecology. Furthermore, the ecological community of natural enemies is assumed to exhibit the kind of multiple interactions that result in patterns now familiar in the science of complex systems. Here, we use some key concepts in complexity science—chaos, critical transitions, hysteresis, basin boundary collision, and higher-order interactions—to tell the natural history story of the green coffee scale insect, a pest of coffee throughout the world. We trust more general applications will be obvious.

We propose a general theory that emerges naturally in this and other pest systems from 3 elementary observations: 1) For most examples of autonomous regulation (control from above) one or more refuges are likely to exist for at least the pest (12); 2) dispersion away from that (those) refuge(s) is met with effective control of the pest in nonrefuge areas (13); and 3) excessive

## Significance

**As farmers seek solutions to perceived problems on their farms, agroecologists rightly wish to use the science of ecology to help. Unfortunately, basic research required to understand some of the vexing problems the farmers face is in its infancy. Yet, ecology is complicated. Normative rules of thumb extrapolated from a few experiments or local traditions frequently fail in the face of such complications. Only through acknowledgment of the agroecosystem as a complex system may we gain full knowledge of the relevant ecological principles which in turn can aid agroecosystem management. Here we take a significant pest, the green coffee scale insect, as a model system and explore the utility of several concepts from complexity science to understand its regulation.**

Author contributions: J.V. and I.P. designed research; J.V. and I.P. performed research; J.V. analyzed data; and J.V. and I.P. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. M.P. is a guest editor invited by the Editorial Board.

Published under the PNAS license.

Data deposition: Raw data from this study have been deposited at Zenodo, <https://zenodo.org/record/3269844#XR-QBxt7ndR>.

<sup>1</sup>To whom correspondence may be addressed. Email: [jvander@umich.edu](mailto:jvander@umich.edu).

This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1902773116/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1902773116/-DCSupplemental).

Published online July 9, 2019.

population growth within the refuge creates conditions for a pathogen to become locally epidemic (epizootic) (14). The theory, formulated in a spatial context, suggests a basic hysteresis as the system moves between refuge and nonrefuge and, under some conditions, it suggests that the extreme boundary of a meandering chaotic attractor will intersect the separatrix of the basin in a “basin boundary collision” (15). Thus, the more traditional bifurcation in which a stable and unstable point suddenly emerge is coupled with the basin boundary bifurcation fixing boundaries of hysteretic zones within the constraints of these 2 distinct forms of bifurcation, as elaborated below.

The green coffee scale (*Coccus viridis*) (Fig. 1A) is a common herbivore in many crops, especially important in coffee and citrus. It is well known to be eaten by several predators, in particular the coccinellid beetle, *Azya orbigera* (Fig. 1C). In addition, like all known organisms, it is susceptible to disease, in particular the white halo fungal disease caused by *Lecanicillium lecanii* (Fig. 1B). The combination of a predator and disease has been suggested as an important ecological structure for maintaining this regulatory system (16). The scale insect is commonly tended by ants, in this case *Azteca seriaseasur*, which provide a “refuge” for the scale insect. When under protection by the ant, the early-stage nymphs have higher survival and the adults produce more offspring (17), effectively creating a zone of high scale density providing the larvae of the beetle with substantial food. While the larva of the beetle contains protective structures (Fig. 1C) against the ants (18), the adult beetle is unprotected. Thus, the adult beetle predator is dissuaded from entering too closely into this “refuge” (19), the area where *A. seriaseasur* ants are active, in which the risk of predation by adults is dramatically reduced (i.e., near an ant nest) and survival and reproduction of scales is enhanced. Additionally, the white halo fungal disease regularly attacks the scale insects. As in most disease systems, the success of this disease dramatically increases above a critical population density of the scale, which is frequent when the scale is under ant protection.

The system can be modeled dynamically (*SI Appendix*) with very general predictions as to its qualitative structure as a whole and, by extension, the many other ecosystems that contain these basic features. We here present a simplified version of that dynamic approach (justified in *SI Appendix*), capturing its basic structure with only a few simple analytical details. In particular, because of the behavior of mutualistic ants, scale populations exhibit an indirect Allee effect: At low population densities they do not attract ant protectors and are thus especially susceptible to the predatory activities of the beetle. At some critical scale population density the ants discover them, begin tending them, and their population consequently begins to increase dramatically (see *SI Appendix* for more details) (20). Furthermore, we presume the scale population has an upper limit on its population size (i.e., it will have a correction to its population size when too large, either from the predator or the disease), the form of which can lead to a “boom and bust” situation frequently seen in disease systems (21). A simple model resulting from these assumptions (effectively a heuristic way of representing the more complete dynamic approach as presented in *SI Appendix*, sections I–III) is

$$N_i(t+1) = r_i [N_i(t) - N_{i,crit}] [1 - N_i(t)]; \text{ for } N(t) < 0 \quad [1]$$

$$N_i = 0 : \text{ for } N(t) < 0,$$

where  $N_i(t)$  is scale population density removed  $i$  spatial points from the refuge at time  $t$ ,  $r_i$  = per capita population growth rate, and  $N_{i,crit}$  = the Allee point (population below which no growth will occur). We presume that  $N_{i,crit}$  decreases within the refuge zone (as  $i$  decreases) and  $r_i$  increases within the refuge zone (we do not treat  $i$  explicitly and only propose to understand the

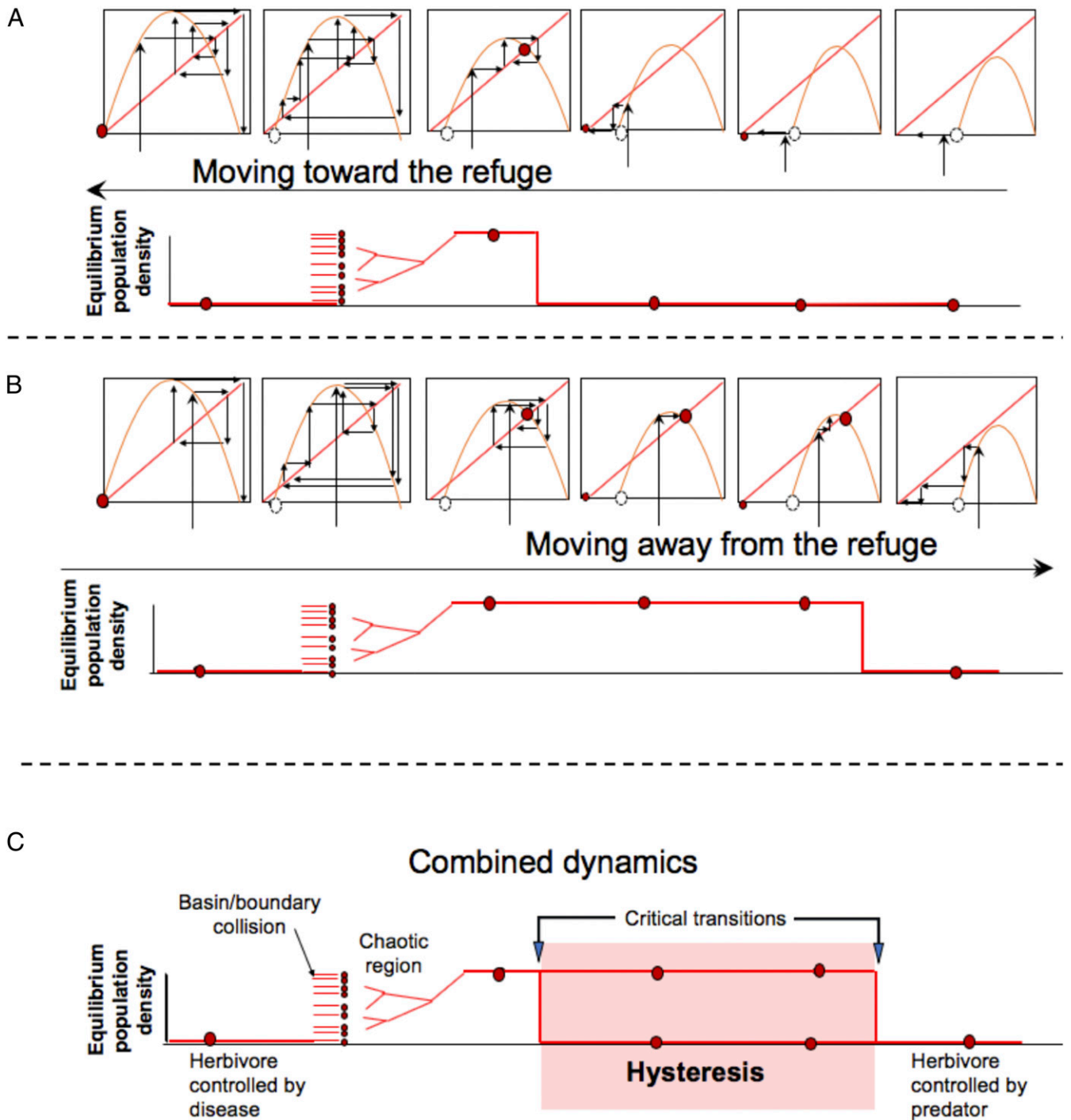


**Fig. 1.** Two key natural enemies of the green coffee scale (*C. viridis*) on coffee leaves in Mexico. (A) Healthy scales. (B) Scales with the white halo fungal disease (caused by *L. lecanii*), showing infected scales on both a leaf and on a coffee bean. (C) Larva and adult of the coccinellid *A. orbigera* consuming the green coffee scale.

spatial component from a modification of  $r_i$  and  $N_{i,crit}$  as the population is positioned at various points in space related to the refuge). Classical chaotic patterns are easily formed as  $r_i$  increases (but note that the combined relationship between  $N_{i,crit}$  and  $r_i$  determine the exact dynamics; *SI Appendix*, section IV). In Fig. 2 we illustrate the basic dynamics of hysteresis generation in this model. Note that as one moves away from the refuge (the model graphical representation on the left of Fig. 2A and







**Fig. 2.** The elementary form of critical transition and hysteresis generation with the iterative model (Eq. 1). (A) As the pests move toward the refuge, their predators “follow” them, until they are well within the refuge, and thus the control over them is effected by said predators over a broad range. Note that the population remains at the value of zero until a critical point (where the initiation point, indicated by small vertical arrow, is larger than the point at which the function intersects the 45° line) wherein it jumps to its maximum value. (B) As the pests move away from the refuge, they are not discovered by the predators until they are some distance away from the refuge, and thus control over them by the predators occurs at a further distance from the refuge. As it gradually is moved away from the refuge, the population retains the upper population density over a broad range of parameter values (note that both  $r$  and  $N_{crit}$  change as the distance from the refuge increases). However, suddenly, as the model undergoes a saddle/node bifurcation, the equilibrium population drops to zero. In A, B, and C, moving toward the refuge eventually results in a chaotic region, represented by a stylized bifurcation sequence leading to a basin boundary collision (seen more clearly in Fig. 3). (C) Combining the move toward and the move away from the refuge, we see the emergence of the hysteretic zone.

B is meant to represent the refuge) the equilibrium value remains high until a critical point at which it declines to zero; Fig. 2A). This occurs at the point where the function no longer intersects the 45° line in the iterative map (Fig. 2A). In contrast,

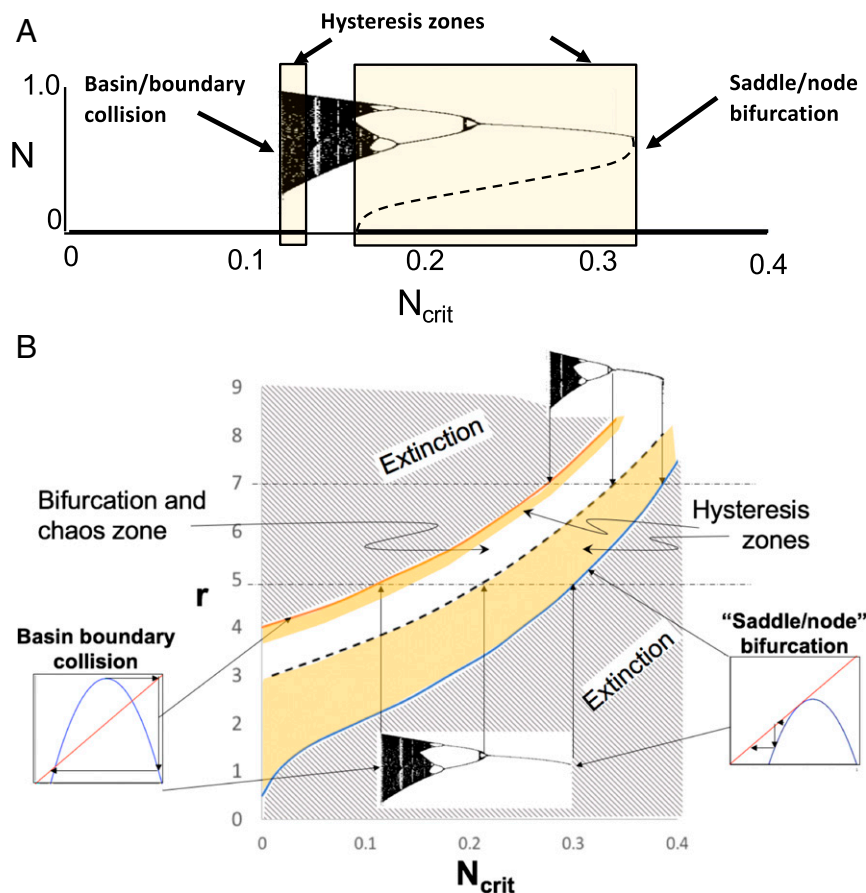
as one moves toward the refuge the population equilibrium remains zero until a critical point after which it remains high (Fig. 2A). This occurs at the point where the function intersects the 45° line in the iterative map (Fig. 2A). Putting these 2

scenarios together (Fig. 2C) illustrates the basic idea of hysteresis generation.

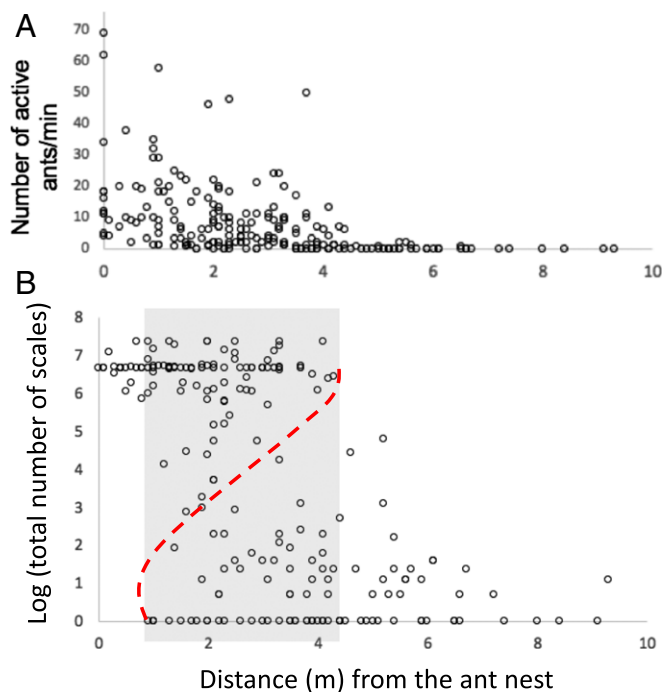
Although the generation of hysteresis is elementary, some complications are involved. Taking the definition of a high-quality refuge as an increased value of  $r_i$  and a decreased value of  $N_{i, \text{crit}}$ , the model generates period-doubling bifurcations to chaos and, under appropriate parameter combinations, a basin boundary collision (15). Thus, at one extreme when the model generates a single equilibrium point at the origin (zero population density), when either  $r_i$  increases or  $N_{i, \text{crit}}$  decreases (i.e., as the refuge is approached), a saddle/node bifurcation is encountered wherein 2 stable points emerge, separated by an unstable point—clearly the origin of the hysteretic pattern (as in Fig. 2). However, continuing the process toward the high-quality refuge, period-doubling bifurcations are encountered, eventually leading to chaos and ultimately to a basin boundary collision. This means that the refuge can, effectively, be “too good,” leading to the irony of extinction within the “refuge,” and the possibility of hysteresis moving into the area of the refuge. While the basic structure emerges naturally from the dynamics of the model, we note that the frequent occurrence of empirical boom and bust dynamics in disease systems reflects this basic theoretical picture. The overall dynamic story can be represented in a combined bifurcation diagram with the 2 parameters, as illustrated in Fig. 3.

This model is intended as a qualitative generalization, in the traditional sense of allowing “mathematics to inform our intuition,” and thus should not be viewed as a Newtonian-like

parameterizable model. Our expectation is that the qualitative pattern it suggests will be seen in many contexts where the only information available is natural historical. We here present such a context, the biological “control” of a pest of coffee through the spatially segregated joint dynamics of a predator and a disease. Relevant field work was undertaken at a site in southern Mexico, Finca Irlanda, the characteristics of which have been described elsewhere (22). In a contiguous 45-ha plot of shaded organic coffee, we sampled 20 sites, each containing a shade tree with an *Azteca* nest, selected so as to sample the range of positions available within the plot (*SI Appendix, section V*). We selected an average of 10 coffee bushes per site (sample size varied based on the local concentrations of coffee bushes) for a total of 211 coffee bushes. The nature of the refuge was taken to be related to a bioassay of ant activity, wherein it is evident that most ant activity is concentrated in an area less than about 4 m from the nesting shade tree (Fig. 4A). We censused all coffee bushes within a 4-m radius of the location of each of the 20 ant nests and then added bushes at further distances to reach an average of 10 coffee bushes per site. At each coffee bush ant activity was established by counting the number of ants crossing a fixed point on an arbitrary branch for 60 s. The bush was then examined for a total of 2 min, counting all scales encountered while searching among all branches. When the count reached 400 we stopped counting and simply recorded “more than 400.” Scales were counted as either alive and healthy or infected by the fungal pathogen (*L. lecanii*). In addition, all bushes were searched for



**Fig. 3.** Bifurcation pattern of the basic model. (A) simple one-parameter bifurcation on  $N_{\text{crit}}$  with  $r = 5$ , illustrating the basic dynamic types as discussed in the text. (B) Two-dimensional bifurcation diagram in the  $(r, N_{\text{crit}})$  parameter space, illustrating hysteresis sandwiched between saddle/node bifurcations and basin boundary collisions. The dotted line represents the locus of the initial bifurcation from a single equilibrium to a 2-point cycle, to the left of which are various stages of period doubling, until reaching the orange (upper) curve. The orange (upper) curve is the locus of basin boundary collisions. The blue (lower) curve is the locus of the initial saddle/node bifurcation.



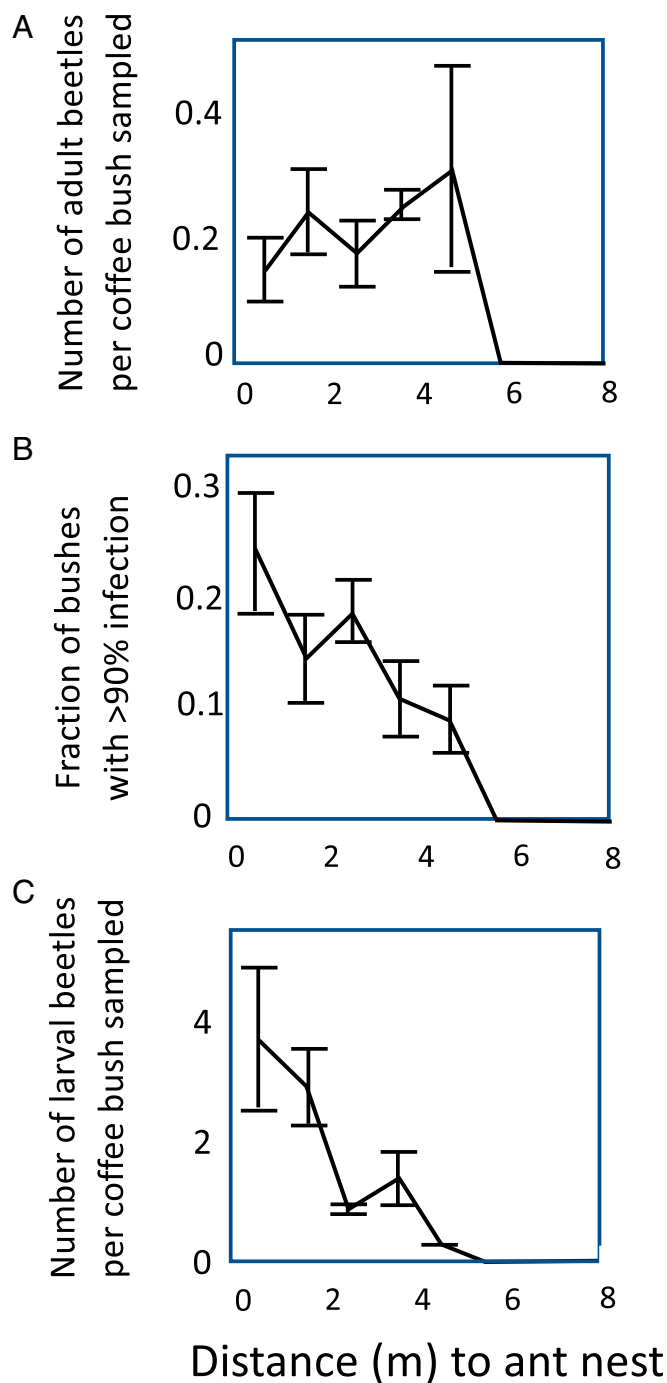
**Fig. 4.** (A) Ant activity (as bioassay of refuge “quality”) as a function of distance from nesting tree (nests are in the shade trees of the system). (B) Log of number of scale insects per coffee bush (left ordinate) as a function of distance to an ant [*Azteca*] nest. Shaded area indicates hysteresis zone and dashed curve the location of the unstable points, both drawn by eye.

larvae and adults of the predacious beetle (*A. orbiger*) and numbers of individuals encountered recorded. The total number of scales encountered (both with and without infection from *L. lecanii*) are presented in Fig. 4B, where the existence of alternative concentrations of scales (either near zero or above 400) strongly suggests a broad hysteretic zone with implied critical transitions at either end (corresponding to the theory summarized in Fig. 3B).

The spatial pattern of the 2 natural enemies supports our mechanistic interpretation of the overall hysteretic pattern (Fig. 5). In particular, the adult beetle is both attracted to the refuge area (where the food for its larvae is located) and repelled by the activity of the ants, producing a generally increasing number from near the nest toward the edge of the refuge (i.e., the edge of effective ant activity at about 4 m), after which it becomes very rare within our sampling scheme (Fig. 5A). The fungal disease, contrarily, is at its highest when closest to the refuge and declines rapidly toward the edge of the refuge (Fig. 5B). Larvae of the beetle are basically immune to the attacks of the ants (18) and thus show a strong tendency to be located within the refuge (Fig. 5C). The expected basin boundary collision associated with the second critical transition (at distances near to the refuge) is not a pattern that lends itself conveniently to empirical verification, especially in a study that is effectively a snapshot of a dynamic process. Nevertheless, a qualitative analysis of the data suggests such a pattern, as described in *SI Appendix, section III*.

In conclusion, 2 natural enemies closely approximate what is expected from qualitative theory (part of which is gleaned through qualitative mathematics; see *SI Appendix, sections I–IV*), suggesting a simplified way of understanding complexity in so-called control from above. Thus, concepts borrowed from complexity science can be marshalled to interpret patterns obtained from simple field surveys. Using this framework, we argue that the particular system of regulation of a common pest, the green coffee scale, can be characterized as a balance between 2 independent natural enemies, combining control in a spatially patterned

environment. The spatial pattern is conceived of as including a refuge for the pest, wherein it escapes the control of the predator, but, because of that escape, increases local density to the point that a pathogen can become epidemic. The area in space between these 2 dynamic situations represents an indirect balance of the 2 controlling factors, maintaining both natural enemies in the system and ensuring long-term persistence of the desired “control from above.”



**Fig. 5.** Distribution of the natural enemies of the scale insects with respect to the distance from the refuge (ant nest). Data bootstrapped within each bin, sampling 90% of the points 10 times to estimate a stabilized SD. Main lines are binned data by 1-m intervals. Indicated interval is twice the SD above and below the bootstrapped average. (A) Adult coccinellid beetles. (B) White halo fungal pathogen. (C) Larval coccinellid beetles.

Exploration of the literature reveals many situations in which this general mechanism might be operative, although not specifically cited as such. The coral *Acropora cervicornis* is simultaneously visited by a snail predator and a disease (23) in a spatially explicit context. The cabbage pest *Pieris rapae* is simultaneously attacked by several predators and at least one disease and is reported (24) to show a spatial signature that is similar to what one would expect from the dynamics we propose. Sea otters in the north Pacific prey on kelp-eating sea urchins, such that in areas with low sea otter populations “urchin barrins” tend to form, creating a spatial pattern in which these high-density areas attract urchin diseases (25). The interactions of aphids with their diseases and predators is quite complicated (26), yet the sessile nature

produced by crops fixed in space suggests the precise mechanism here proposed may occur (27). Given that all organisms must face both predators and diseases and most organisms have a spatial component to their existence, we suspect our proposed pattern is likely to be found in many other systems.

Raw data from this study have been deposited at Zenodo (<https://zenodo.org/record/3269844#.XR-QBXt7ndR>) (28).

**ACKNOWLEDGMENTS.** We thank Gustavo Lopez-Bautista for technical coordination of this entire project and Finca Irlanda for permission to engage in the study. Much gratitude is due to several anonymous reviewers for important suggestions that improved the manuscript considerably. We also thank Theresa Ong for a careful reading of the manuscript, especially the *SI Appendix*. This work was supported by NSF Grant DEB-1853261.

1. C. A. Hallmann *et al.*, More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One* **12**, e0185809 (2017).
2. F. Sánchez-Bayo, K. A. Wyckhuys, Worldwide decline of the entomofauna: A review of its drivers. *Biol. Conserv.* **232**, 8–27 (2019).
3. J. Vandermeer, I. Perfecto, Ecological complexity and agroecosystems: Seven themes from theory. *Agroecol. Sustain. Food Syst.* **41**, 697–722 (2017).
4. J. Vandermeer, I. Perfecto, Ecological complexity in the Rosennean framework. *Ecol. Complex.* **35**, 45–50 (2018).
5. J. Vandermeer, I. Perfecto, *Ecological Complexity and Agroecology* (Routledge, 2017).
6. G. A. Polis, Food webs, trophic cascades and community structure. *Aust. J. Ecol.* **19**, 121–136 (1994).
7. D. R. Strong, Are trophic cascades all wet? Differentiation and donor-control in sparse ecosystems. *Ecology* **73**, 747–754 (1992).
8. S. R. Carpenter, J. F. Kitchell, Consumer control of lake productivity. *Bioscience* **38**, 764–769 (1988).
9. C. Bjorkman, P. Niemela, Eds., *Climate Change and Insect Pests* (CABI, 2015).
10. W. J. Lewis, J. C. van Lenteren, S. C. Phatak, J. H. Tumlinson, 3rd, A total system approach to sustainable pest management. *Proc. Natl. Acad. Sci. U.S.A.* **94**, 12243–12248 (1997).
11. J. Vandermeer, I. Perfecto, S. Philpott, Ecological complexity and pest control in organic coffee production: Uncovering an autonomous ecosystem service. *Bioscience* **60**, 527–537 (2010).
12. Z. Ma *et al.*, Effects of prey refuges on a predator-prey model with a class of functional responses: The role of refuges. *Math. Biosci.* **218**, 73–79 (2009).
13. B. A. Hawkins, H. V. Cornell, Eds., *Theoretical Approaches to Biological Control* (Cambridge University Press, 2008).
14. J. B. Collings, Bifurcation and stability analysis of a temperature-dependent mite predator-prey interaction model incorporating a prey refuge. *Bull. Math. Biol.* **57**, 63–76 (1995).
15. J. Vandermeer, P. Yodzis, Basin boundary collision as a model of discontinuous change in ecosystems. *Ecology* **80**, 1817–1827 (1999).
16. T. W. Y. Ong, J. H. Vandermeer, Coupling unstable agents in biological control. *Nat. Commun.* **6**, 5991 (2015).
17. S. Jha, D. Allen, H. Liere, I. Perfecto, J. Vandermeer, Mutualisms and population regulation: Mechanism matters. *PLoS One* **7**, e43510 (2012).
18. H. Liere, I. Perfecto, Cheating on a mutualism: Indirect benefits of ant attendance to a coccidophagous coccinellid. *Environ. Entomol.* **37**, 143–149 (2008).
19. H. Liere, A. Larsen, Cascading trait-mediation: Disruption of a trait-mediated mutualism by parasite-induced behavioral modification. *Oikos* **119**, 1394–1400 (2010).
20. J. Vandermeer, I. Perfecto, A keystone mutualism drives pattern in a power function. *Science* **311**, 1000–1002 (2006).
21. O. Diekmann, H. Heesterbeek, T. Britton, *Mathematical Tools for Understanding Infectious Disease Dynamics* (Princeton University Press, 2012).
22. I. Perfecto, J. Vandermeer, The effect of an ant-hemipteran mutualism on the coffee berry borer (*Hypothenemus hampei*) in southern Mexico. *Agric. Ecosyst. Environ.* **117**, 218–221 (2006).
23. D. E. Williams, M. W. Miller, Coral disease outbreak: Pattern, prevalence and transmission in *Acropora cervicornis*. *Mar. Ecol. Prog. Ser.* **301**, 119–128 (2005).
24. R. E. Jones, V. G. Nealis, P. M. Ives, E. Scheermeyer, Seasonal and spatial variation in juvenile survival of the cabbage butterfly *Pieris rapae*: Evidence for patchy density-dependence. *J. Anim. Ecol.* **56**, 723–737 (1987).
25. J. A. Estes, C. H. Peterson, R. S. Steneck, “Some effects of apex predators in higher-latitude coastal oceans” in *Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature*, J. Terborgh, J. A. Estes, Eds. (Island Press, 2010), pp. 37–53.
26. H. E. Roy, J. K. Pell, Interactions between entomopathogenic fungi and other natural enemies: Implications for biological control. *Biocontrol Sci. Technol.* **10**, 737–752 (2000).
27. T. W. Y. Ong, D. Allen, J. Vandermeer, Huffaker revisited: Spatial heterogeneity and the coupling of ineffective agents in biological control. *Ecosphere* **9**, e02299 (2018).
28. J. Vandermeer, I. Perfecto, Basic data *Coccus Viridis*. Zenodo. <https://zenodo.org/record/3269844#.XR-QBXt7ndR>. Deposited 5 July 2019.