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Endogenous spatial pattern formation from two intersecting ecological mechanisms: the dynamic coexistence of two noxious invasive ant species in Puerto Rico

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Endogenous (or autonomous, or emergent) spatial pattern formation is a subject transcending a variety of sciences. In ecology, there is growing interest in how spatial patterns can 'emerge' from internal system processes and simultaneously affect those very processes. A classic situation emerges when a predator's focus on a dominant competitor releases competitive pressure on a subdominant competitor, allowing coexistence of the two. If this idea is formulated spatially, two interesting consequences immediately arise. First, a spatial predator/prey system may take the form of a Turing instability, in which an activator (the dispersing prey population) is contained by a repressor (the more rapidly dispersing predator population) generating a spatial pattern of clusters of prey and predators, and second, an indirect intransitive loop (where A beats B beats C beats A) emerges from the simple fact that the system is spatial. Two common invasive ant species, *Wasmannia auropunctata* and *Solenopsis invicta*, and the parasitic phorid flies of *S. invicta* commonly coexist in Puerto Rico. Emergent spatial patterns generated by the combination of the Turing mechanism and the indirect intransitive loop are likely to be common here. This theoretical framework and the realities of the natural history in the field could explain both the long-term coexistence of these two species, and the highly variable pattern of their occurrence across a large landscape.

1. Introduction

In ecology as in all science, simplifications are needed to generate theory. One of ecology's historical simplifications is to ignore spatial structure even when it is known to be important, by formulating mean-field models, or assuming complete mixture in a panmictic population. Relaxation of this simplification requires a look at spatial pattern, something that has become standard in recent decades (e.g. [1]). Studying the nature of that pattern, whether exogenously stipulated or endogenously generated, is challenging with, for example, landscape ecology contributing useful and extensive methodological programmes for doing so [2]. However, we suggest that a more general framing is possible from a simple categorization of pattern-forming mechanisms, enabling a bipartite classification depending on those mechanisms. First, when a reaction–diffusion process is evident, patterns of clusters are generally formed, the most well-known example being the mechanism proposed by Alan Turing [3–5], in which a controlling agent diffuses faster than the agent it controls. Second, when an intransitive structure is evident (e.g. the rock–paper–scissors game), spiral spatial patterns may emerge [6–8]. Clusters versus spirals, then, is a useful simplification for studying spatial pattern, perhaps especially useful since they are based on well-known underlying mechanisms. Relevant
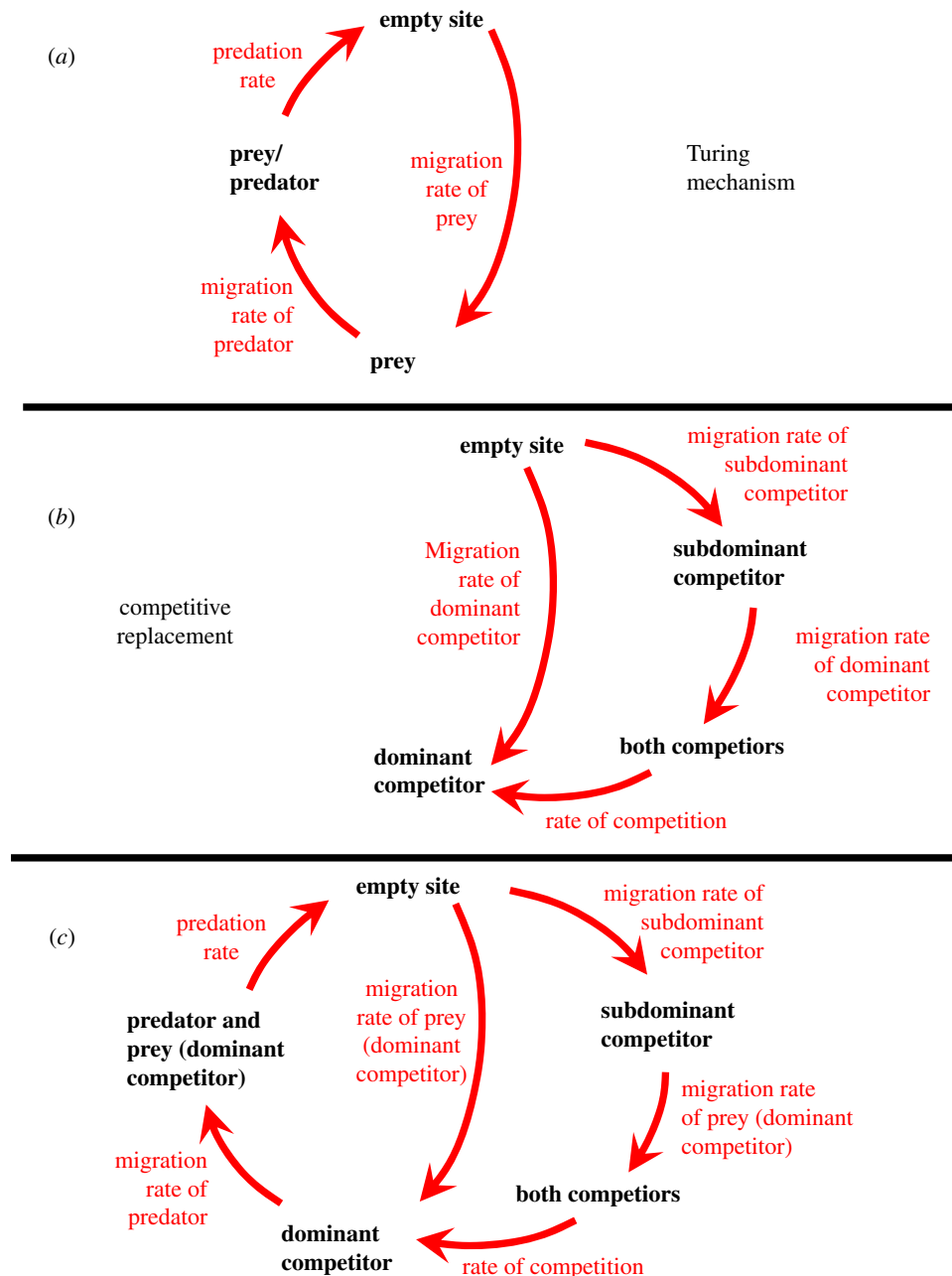
Figure 1. Illustration of the basic theoretical argument of the paper, with states in black bold and rates in red. (*a*) predator and prey in a spatial context create spatial patterns of clusters when the dispersion of the predator is sufficiently large with respect to that of the prey. (*b*) Strong asymmetric competition results in ultimate takeover of the site by the dominant competitor species. (*c*) combining a spatial predator–prey relationship with a strong asymmetric competition results in a mixed spatial pattern, but also an indirect intransitive loop where predator replaces prey (by eating it), prey (dominant competitor) competitively replaces the competitor (subdominant competitor), and competitor replaces empty site (by migrating into it). (Online version in colour.)

to spatial pattern formation, the effect of predators on the coexistence of competitors is thought to be common in nature [9,10]. As Darwin described one of his most well-known experiments:

> If turf which has long been mown, and the case would be the same with turf closely browsed by quadrupeds, be let to grow, the more vigorous plants gradually kill the less vigorous … (Darwin, 1859 [11], pp. 67–68)

Such a simple observation led to a canonical ecological idea that a predator (herbivore, parasite) specializing on a competitively dominant species can result in the persistence of one or more competitively inferior species. This well-known framework, known variously as the keystone species concept or predator-mediated coexistence, can generate surprising results when framed in a spatially explicit fashion, a

consequence of the conflation of two generalizations—one associated with the formation of spatial clusters, the other with the formation of spatial spirals. First, a spatial predator–prey system may take the form of a Turing instability, thus generating a spatial pattern of clusters of prey and predators (figure 1*a*) [4,5,12–15]. Second, competitive displacement, if unchecked, leads to the complete domination of a superior competitor, which then is attacked by the predator, thus providing relief to the subdominant competitor. When operative in space, an indirect intransitive loop may emerge wherein: (1) an empty space gives rise to (2) a space occupied by the weak competitor, which gives rise to (3) a space occupied by the strong competitor, which gives rise to (4) a space occupied by the predator/parasite of the strong competitor, which gives rise to (5) an empty space—figure 1*c* [8,16–20].

Characteristic spiral patterns are generally expected from such an intransitivity [21,22] (figure 1c). Without the predator/parasite of the dominant competitor, the outcome would simply be competitive replacement of the weak competitor by the strong competitor (figure 1b). The question naturally arises, what pattern is expected when the clusters resulting from the Turing mechanism are integrated with the spirals resulting from the intransitive loop (figure 1). If predatory control over competitive dominance is common, its spatial counterpart must sometimes take on this spatial complexity, an issue that has yet to be explored.

The many theoretical and empirical studies demonstrating predator-mediated coexistence have generally assumed that the predator (parasite, herbivore, pathogen) must be at least partially specialist on the dominant competitor [23–25]. Furthermore, most such studies have been either direct dynamic models in the panmictic tradition or mean-field models of an assumed spatial component [26,27]. An important exception is Caswell [10], who made the distinction between open and closed systems, noting that 'in open systems local extinction is not an absorbing state' as a defining feature of spatially specific population dynamics. The open system is effectively a spatial system and Caswell seems to be the first to have noted that the spatial component of the predatory behavior could itself be responsible for deterring the competitive exclusion process. Subsequent spatially explicit models have come to similar conclusions [28,29], but none have explored the specific role of the spatial pattern itself in generating the result, as we do here.

The purpose of this paper is to illustrate the spatial pattern generated by the combination of the Turing mechanism with the indirect intransitive loop, as explained above, and as pictured in figure 1c. Given that competitive dominance and specialist predation are both commonly observed in nature, this dynamic framework is perhaps a common form of spatial pattern generation. Although the complicated patterns it may generate (see results below) may be difficult to empirically detect in practice, its basic operation in non-local space nevertheless provides a unique mechanism for the persistence of a system such as this, even if unstable locally or in the mean-field context. The theoretical framework (figure 1) and the realities of the natural history of the system in the field are obviously concordant. We thus hypothesize that an indirect intransitive loop combined with the Turing mechanism could explain both the coexistence of these two species, as well as the highly variable pattern of their occurrence [30].

2. Methods: field study system

Connecting with a real-world case study, this basic arrangement of competitors and predators exists in Puerto Rico, with two invasive ant species, *Wasmannia auropunctata* and *Solenopsis invicta*, and at least two species of parasitic flies in the family Phoridae that attack *S. invicta* but not *W. auropunctata*. Both ant species can be extremely aggressive, have a painful sting, and are listed among the 100 worst invasive species globally [31]. They occupy almost all habitats, and have persisted in Puerto Rico at least since 1981 [32]. In interspecific interactions, in both laboratory experiments and field studies within coffee farms [30], *S. invicta* is able to displace *W. auropunctata*, yet both species remain

common on the island. Furthermore, their distribution on coffee farms, although sometimes extremely abundant locally, is highly variable [30]. The phorid flies are presumably capable of extirpating local populations of *S. invicta*, the fundamental reason driving attempts at employing phorids as biocontrol elements of the species in the southern United States and Puerto Rico [33–37]. Our personal observations, albeit mainly casual at this point, indicate that the occurrence of these flies is highly variable both in time and space.

In sum, the system is composed of a competitively dominant species (*S. invicta*), a competitively subdominant species (*W. auropunctata*) and a specialist predator (the phorid flies) on the competitively dominant.

Both circumstantial and experimental evidence suggest that *S. invicta* will normally dominate *W. auropunctata* in direct competitive interactions, although complete displacement at a particular point in space can be slow [30]. In the laboratory, nest-boxes connected to one another quickly result in the attack of *W. auropunctata* by *S. invicta* and a massive attempt by *W. auropunctata* to escape their invaded nest-boxes, without exception. In the field, sequential baiting with tuna fish at particular points (individual coffee bushes) revealed a slow takeover by *S. invicta*, with a great deal of variability ([30] and results below). Given these experiments and local observations, it is somewhat surprising that both species seem to be well established in coffee farms within the central mountains of Puerto Rico, and the question of the mechanism of their coexistence is of relevance both theoretically as well as practically, given the importance of both as nuisance species.

Previous detailed observations on two coffee farms, Gran Batey and Cítricos Inc. (see [30] for details) suggest the dynamic illustrated in figure 1c. The 'predator' is the phorid flies which seem to 'disperse' extensively, perhaps blown by wind currents, and vigorously attack any concentration of *S. invicta* workers, whether near the nest or far. While some evidence suggests that attacks near the brood mound are more common than far away from the brood mound, the very high variability in phorid attacks militates against precise estimation of the parasitoid dispersion rate (in the sense of figure 1). Nevertheless, the qualitative arrangement of the system is a clear example of the well-known effect of a predator specializing on a dominant competitor and thus releasing pressure on subdominant competitors (in this case, *W. auropunctata*), generally referred to as predator-mediated coexistence.

Ant surveys from 25 coffee farms were undertaken in the central-western Cordillera Central of Puerto Rico, as described elsewhere [30]. On two of the 25 farms in the study, Finca Cítricos Inc. and Finca Gran Batey (codes UTUA 20 and UTUA 2 in [30]), we engaged in more detailed sampling, sampling a total of 550 coffee bushes at Gran Batey and 479 at Cítricos Inc., all at known spatial coordinates (all coffee bushes within a defined area). These samples were taken three times over a 12 month period, twice in the dry season (January/February) and once in the wet season (July), details of which can be found elsewhere [30]. On each coffee bush we recorded which species occurred along with their relative abundance in a six category system (of five tunafish baits placed on the bush, 0, 1, 2, 3, 4 or 5 occupancies were recorded). Being eusocial, the actual number of individual ants at a point in space and time means little with respect to population size and reflects more the recruitment

activity of a colony rather than its population density. We thus take as the best measure of local abundance the number of baits occupied on a bush (ranging from 0 to 5). The relative dynamics of competitive exclusion and new occupations can be estimated for three sampling periods covering two 6-month intervals. Because of clear seasonal effects at Cítricos Inc., we use the 12-month interval only for parameter estimation to explore the dynamics of the model. Gran Batey did not contain sufficient concentrations of *S. invicta* for meaningful parameter estimation, and thus parameters (competition coefficients) were calculated only from the data at Cítricos Inc. All three sampling dates are used for further elaboration of the basic interpretation of the qualitative dynamics in the field for Gran Batey, beyond the model performance.

Part of our methodology relies on a peculiar aspect of the natural history of *S. invicta*. The species is well known for its extreme polymorphism among workers. Yet a detailed study of colony demography (or ontogeny) [38] revealed a common pattern in which 'young' colonies were devoid of the very large workers (called here 'megaworkers'). Only after the colony ages does the queen (or queens) begin producing these megaworkers. This natural history fact permits us to categorize colonies (and particular swarms that emerge from those colonies) as either young or old. Experience revealed that more than 90% of the observed swarms were clearly categorizable as either young or old. It is furthermore well known that this so-called age of the colony is related to the activity of the phorids [39], wherein at least one of the phorid species strongly prefers the megaworkers (J.V. 2020, personal observations).

3. Methods: theory

Computer simulations were based on as simple a set of dynamic assumptions as possible, indicated in figure 1. The model is a cellular automata in the spirit of the 'voting rules' style [40], with governing equations acting at a point in space (i,j) on a torus:

$$W_{i,j}(t+1) = W_{i,j}(t) - \beta_w S_{i,j}(t), \tag{3.1a}$$

$$S_{i,j}(t+1) = S_{i,j}(t) - \alpha P_{i,j}(t) - \beta_s W_{i,j}(t) \tag{3.1b}$$

$$P_{i,j}(t+1) = \alpha S_{i,j}(t) P_{i,j}(t) - \mu P_{i,j}(t) + m + \Phi(P_{i,j}(t) - \beta_p W_{i,j}) \tag{3.1c}$$

where

$$X_{i,j}(t) = \sum_{i-1}^{i+1} \sum_{j-1}^{j+1} X_{i,j}(t)$$

for $X_{ij} = W_{ij}, S_{ij}, P_{ij}$.

Note that the relevant population densities include nine cells, the formal Moore neighbourhood plus the centre cell labelled $\{i,j\}$. Updating the model places in cell $\{i,j\}$; 1) S, if $S_{ij} > W_{ij}$ and $P_{ij} = 0$; 2) W_{ij} if $W_{ij} > S_{ij}$ and $P_{ij} = 0$; 3) P_{ij} if $S_{ij} > W_{ij}$ and $P_{ij} > 0$. Although the spirit of the voting rules model motivates our system, because of the condition on P (that its food, S, must be in the Moore neighbourhood at the same time for it to dominate), the precise number of 'votes' is not the final determinant of the cell occupancy. Updating of the model is synchronous (that is, all X_{ij} are computed for all cells first, then equation set 1 is applied at each cell, and the 'winner' is the one with the most 'votes', under

the constraints of the inequalities above. Corresponding to the dynamic patterns of figure 1, we have α = parasitization rate of the phorids on *S. invicta*, β_w = the competitive effect of *S. invicta* against *W. auropuntata*, β_s = the competitive effect of *W. auropuntata* against *S. invicta*, μ = the death rate of phorids, m = the spontaneous arrival of phorids at the point, Φ and the related β_P are used only in the demonstrative part of the results to illustrate spirals emerging from intransitivity (see below). Note that as long as $m > 0$, the parasitoid effectively disperses more rapidly than its prey (since the latter diffuses only within the Moore neighbourhood), a condition for the diffusive instability of the Turing process. Unless otherwise indicated, all simulations were initiated with 95% of the lattice randomly occupied by each of the species.

Parameters to compare the field data to the model (using data from Cítricos Inc. only) were approximated as follows:

$$\beta_w = E\left[\frac{(W_{i,j}(t+1) - W_{i,j}(t))}{S_{i,j}(t)}\right] = 1.53$$

and

$$\beta_s = E\left[\frac{(S_{i,j}(t+1) - S_{i,j}(t))}{W_{i,j}(t)}\right] = 0.69.$$

4. Results

General results from computer simulations follow the qualitatively expected outcome (figure 2). The system incorporates assumptions of both Turing instabilities (generating fixed patches; figure 2a) and an intransitive loop (generating moving spirals; figure 2b), the latter of which are illustrated with the model in a standard competitive framework (i.e. $\Phi = 1$), for the simple purpose of demonstrating spirals generated by intransitivity. Combining the Turing elements ($\Phi = 0$, $W = 0$) with the indirect intransitivity (figure 1c; $\Phi = 0$), the range of spatial patterns generated by the model (figure 2c) reflects these two well-known mechanisms of pattern formation, but at dramatically different scales. At a relatively small spatial scale the patchwork of *S. invicta* patterns interspersed with the parasitoid forms an effective backdrop to the spiral-like large arms of the *W. auropunctata*, visible mainly at a much larger scale. Note that the patterns displayed in figure 2c are not fixed in time, but change shape both within the Turing-like background (small scale) as well as at the large scale.

If the subdominant competitor (*W. auropunctata*) is absent, the remaining parasite/host interaction produces a patchwork of predator and prey (figure 2a), strongly resembling the patchwork structure so common with the Turing mechanism. This evident pattern is not static, however, but rather the patches continue forming and disappearing, much as has been reported in another context for a different ant species [14,41]. However, recalling figure 1, the intransitivity that arguably occurs can be visualized separately from the parasitoid/prey system. If $\Phi = 0$, which is our intent when modeling the actual system, the parasitoid has no direct effect on *W. auropunctata*. To demonstrate the alternative effect, that is, spirals emerging from the intransitive nature of the system, is not simple since the base structure automatically implies a Turing effect, if the system is spatial. However, by allowing $\Phi = 1$ and setting $\alpha = \beta_W = \beta_P = 2$ we set up a system that reflects the idea that *W. auropunctata* effectively
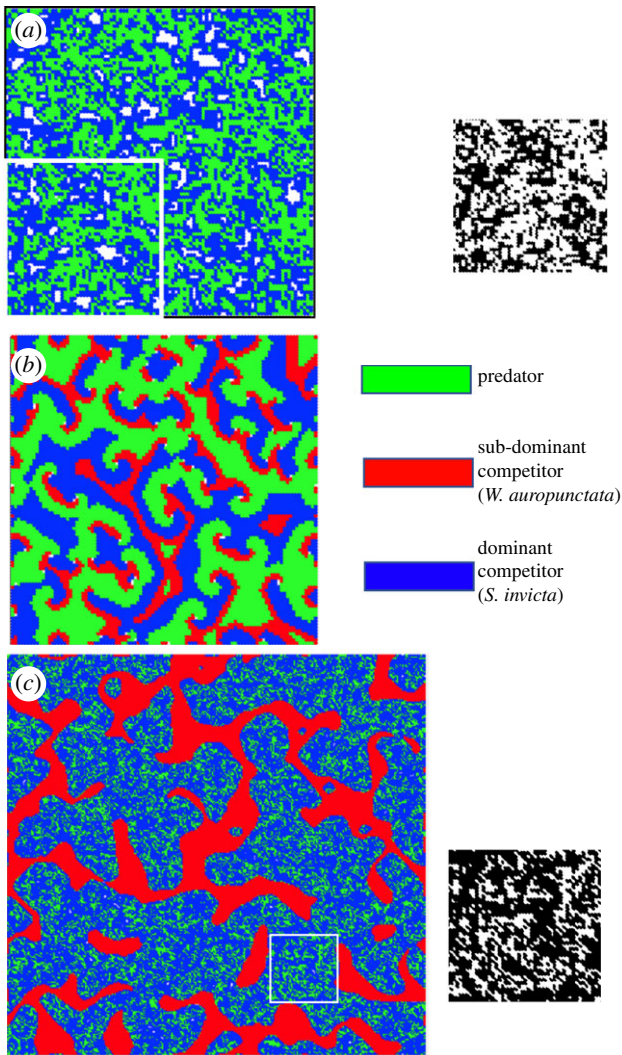
Figure 2. Exemplary simulations with the basic model. (*a*) on a 100×100 lattice over 200 time steps without the subdominant ant species, illustrating the characteristic pattern of a predator and prey patchwork emanating from the Turing mechanism. The 50×50 lattice to the right is a black and white (black = dominant competitor) version of the subquadrat insert in the left plot, highlighting the clumped nature of the system. Parameters are $\alpha = 0.2$, $m = 0.5$, $\Phi = 0$. (*b*) on a 100×100 lattice over 200 time steps, the spiral pattern generated by a direct intransitive loop, obtained by setting $\alpha = \beta_w = \beta_p = 2$, $\beta_s = 0$, $\Phi = 1$; and (*c*) on a 300×300 lattice a combination of a Turing pattern and intransitive loop (based on equation set 1 with $\Phi = 0$), illustrating a background of patches of *S. invicta* interspersed with patches of the phorid parasitoid (predator) from the Turing mechanism with spiral-like penetration of *W. auropunctata*, at a different spatial scale reflecting the indirect intransitivity. To the right a 50×50 black and white version of the subquadrat insert in the left plot, illustrating the similar Turing pattern of the plot in (*a*). Parameters are $\alpha = 0.14$, $\mu = 0.25$, $\Phi = 0$, $\beta_w = 1.53$, $\beta_s = 0.69$. (Online version in colour.)

has a negative effect on the parasitoid (since the parasitoid receives energy from the *S. invicta*, and the *W. auropunctata* exerts a negative competitive effect on the *S. invicta*, there is an indirect effect of *W. auropunctata* on the parasitoid, the so-called 'enemy of my friend is my enemy' structure). This, admittedly artificial, device is used to demonstrate the general expectation of an intransitive loop in this spatial scenario. As expected, if we impose an artificial negative effect of *W. auropunctata* against the parasitoid, moving spirals of the three elements are generated (figure 2*b*).

Most interestingly, when neither mechanism completely dominates, the lattice seems to represent patches as those generated by a Turing mechanism, within zones that are surrounded by patches that resemble spirals, but realized at a much larger scale (figure 2*c*). Qualitatively, the subdominant competitor can be excluded from the system in two ways, either through direct strong competition from the uncontrolled dominant competitor (*S. invicta*), or through the indirect intransitive loop instantiated by a balance between the effect of predation and competition. Consequently, persistence of the subdominant competitor, although it could be because of relatively low competitive pressure from its competitive antagonist (the dominant), could also be due to the oscillatory nature of the predator/prey relationship leading to the intransitive loop in the spatial context.

Beyond the exemplary model results presented in figure 2, the model was explored strictly within the constraints of the field-estimated competition parameters (i.e. $\beta_w = 0.69$ and $\beta_s = 1.53$). In the absence of the parasitoids, the dominant competitor, *S. invicta*, takes over the lattice quite rapidly. Extensive simulations failed to encounter an exception to this uninteresting result. However, adding the parasitoids to the system revealed considerable complications, qualitatively summarizable as a balance between the parasitoid attack rate (α) and the parasitoid migration rate (m), as reported in figure 3.

At the extremes of parasitoid efficiency (large attack rate or dispersal rate) the predator induced competitive coexistence does not operate and the parasitoid simply out strips its food supply, allowing the subdominant competitor (*W. auropunctata*) to take over. The opposite occurs at the other extreme (small attack or dispersal rate). Indeed with competition coefficients of 1.53 and 0.69 one would ordinarily expect an indeterminate situation in which one or the other species wins depending on initial conditions. However, the influence of the parasitoid in effectively reducing the competitive ability of the dominant creates a unique situation in which it is the spatial structure that allows the coexistence. While it is well-known that a predatory effect can reverse competitive outcomes, less well-known is this particular mechanism in which the reduction of competitive efficiency is not the mechanism of coexistence but rather the generation of spatial structure seems to be at least partially responsible.

From the field data, we report that the two farms, Gran Batey and Cítricos Inc, had distinctive patterns, but both fit well within the general narrative of the theoretical considerations here presented (and further discussed in [30]). Cítricos Inc. had numerous coffee bushes occupied by both species and a dynamic pattern of replacement over the year. However, there were very few coffee bushes that were first dominated by one, and then 12 months later by another species [30]. Yet the pattern of change permitted an estimate of both competition coefficients as applied to all the model simulations reported above. Gran Batey, contrarily, had a rather large dominance of *W. auropunctata*, with very little overall change over the three sampling periods. Nevertheless, two small-scale spatial patterns (figure 4) suggest that the underlying dynamics we report herein were operative. In one 30×20 m subplot of the larger sampling area [30] the small number of sampling points occupied by *S. invicta* in January 2019 increased six months later (figure 4*a*,*b*). Then, six months after that, there were virtually no bushes occupied by *S. invicta* (figure 4*c*), consistent with the hypothesis that the phorid flies, encountering this relatively new cluster of
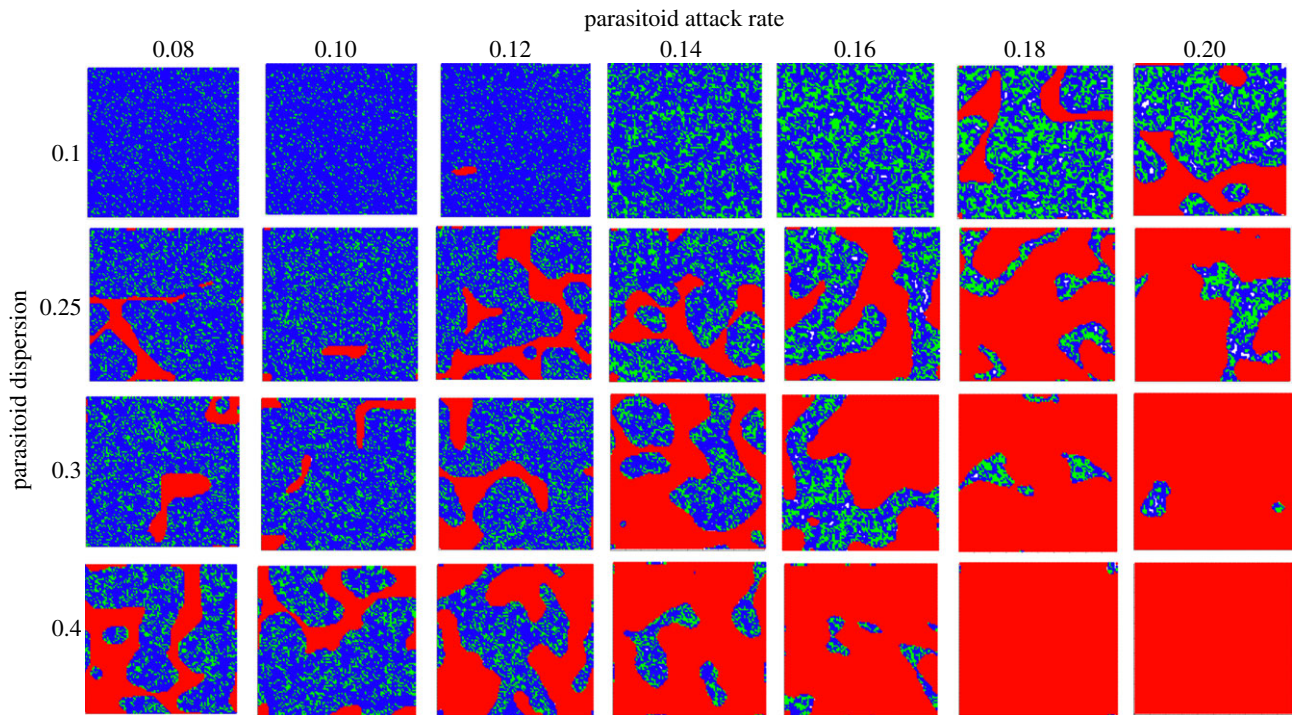
Figure 3. Spatial pattern and species survival as a function of predator attack rate and parasitid dispersion. Parameters for this simulation are $\beta_w = 1.53$, $\beta_s = 0.69$. Red = *W. auropunctata*, blue = *S. invicta*, green = phorid parasitoid. Lattice size is 100×100 for all examples. (Online version in colour.)
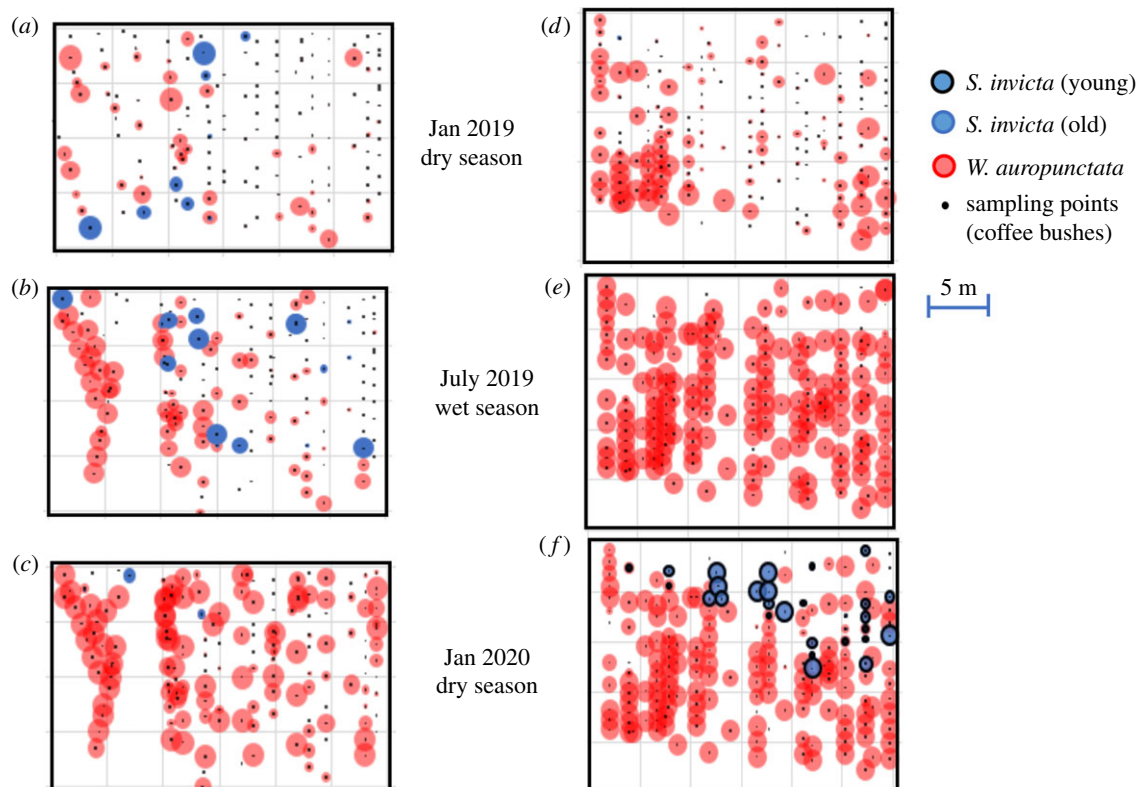
Figure 4. Twelve-month record of two sub plots from the Gran Batey farm, extracted from the larger sampling reported in [30]. Small points indicate presence of a sampled coffee bush, red bubbles indicate *W. auropunctata* occupations, blue bubbles with black outline indicate young *S. invicta* swarms, and blue bubbles with no outline indicate old *S. invicta* occupations. One plot (a–c) records first the expansion of *S. invicta* (old colonies) into the area and its subsequent disappearance and invasion by *W. auropunctata*, consistent with the hypothesis that phorids act to disperse clusters of *S. invicta* colonies, as reported in other literature. The other plot (d–f) records the expansion of *W. auropunctata* between January and July of 2019, with the sudden incursion of *S. invicta* (young colonies) observed in the January 2020 samples. Recorded here are swarms on coffee bushes, where the size of the symbol represents the activity of the species on a bush, occupying 0, 1, 2, 3, 4 or 5 baits on the bush. All *S. invicta* in (f) belong to young colonies. (Online version in colour.)

nests, caused the local nests to either die or relocate. It is notable that all *S. invicta* occupations were judged to be old colonies (figure 4a–c), and thus likely to be subject to high phorid attack. Furthermore, in another plot (30 × 25 m; figure 4d–f), *W. auropunctata* appeared to be in the process of dominating the area completely. But then, in the dry

season of 2020, an invasion of *S. invicta* was evident (figure 4*f*), consistent with the hypothesis that *S. invicta* is competitively dominant, but probably only in areas it had not been before, since the phorid flies had not built up a significant local population. It is notable that all *S. invicta* occupations (figure 4*f*) were judged to be from young colonies (figure 4*f*).

5. Discussion

That a predator (parasite, pathogen, herbivore, etc) can moderate the process of competition such that subdominant competitors are not excluded by dominant ones, is a standard subject in ecology—predator-mediated coexistence. Precisely how such a moderation occurs would seem evident. The predator exerts a reduction in fitness of the dominant competitor thus releasing subdominant competitors from some of the competitive pressure exerted by the dominant [42]. Yet certain complexities emerge when the processes (competition and predation) occur in a spatial context. In particular, the very existence of a predator/prey relationship in space carries with it the implication that a Turing-like process could generate spatial clusters (or permanent patches) of predator and prey. Furthermore, unbalanced competition coupled with predation generates an indirect intransitivity as a potential driving force for the generation of a moving spirals spatial pattern (figure 1). We suggest that the combination of these two phenomena, a competitive hierarchy and predatory pressure on the dominant competitor, when operative in a spatial context, may create an emergent spatial pattern, with clear signals of both pattern formation mechanisms, but at distinctly different spatial scales (figure 2*c*).

More generally, the subject of how spatial patterns are formed in nature has a long history. Two generalizations are of importance in the present work, the combination of which creates a pattern that, if searched for, might be found to be common elsewhere—when a dominant competitor has a broadly dispersing specialist predator. In a spatial context, the predator would be expected to generate a non-random clustered pattern if the predator disperses more rapidly than its prey, roughly in accord with the Turing mechanism. Adding a competitor to the situation changes the spatial dynamics to resemble a spatial intransitive loop—the dominant competitor replaces the subdominant competitor, but is then eventually found by the predator which eliminates it locally, thus creating conditions whereby the subdominant competitor can reoccupy the space (figure 1*c*). We show, theoretically, that the pattern possibly resulting (dependent on parameter values) is recognizable qualitatively as a combination of the Turing mechanism and an intransitive loop (figure 2). Using competition coefficients derived from extensive field surveys, the model qualitatively produces these complicated patterns (figure 3).

Regarding the general problem we seek to engage, multiple invasive species constitute a well-recognized problem worldwide. Especially notable are the many tropical islands on which native faunas have been severely affected [43], a classic situation represented by novel ant communities [44]. Elsewhere [30] we have noted that the most dominant ants on coffee farms in Puerto Rico seem to form a highly variable but consistent community composed of four common invasive species, two of which are especially notable because of their abundance and their position as agricultural pests (*W. auropunctata* and *S. invicta*). Ironically, both of these invasive ant species have also been found to contribute to the biological control of some agricultural pest species [45,46]. However, understanding their population dynamics and how they interact at a landscape level, is relevant not only to their local importance as pests and potential biocontrol agents, but also as an exercise in understanding spatial pattern formation generally, and whether the consequence of moderating unbalanced competition is dependent on that pattern formation.

From various sources of experimental and observational information, it appears that *S. invicta* dominates in the competitive process with *W. auropunctata*, although the strength of this dominance is unknown. As we report above, on one farm over a 12-month period we estimate that *S. invicta* can displace *W. auropunctata* at more than twice the rate that the reverse occurs. However, many observations of individual workers confronting one another on the same branch of a tree did not suggest anything like a competitive dominance through behavior. Upon encountering a *S. invicta* individual, the *W. auropunctata* worker simply lowers its head and remains motionless, whereby the would-be dominant *S. invicta* walks over it, seemingly not noticing its presence. Yet, in laboratory nest box competition, *S. invicta* causes *W. auropunctata* colonies to rapidly abandon their nests completely, seeking to escape the nest-box.

The fact that these two ant species have occupied the island of Puerto Rico extensively, and over at least 40 years, is somewhat unexpected given the apparent competitive dominance of *S. invicta*, and simulations with the model instantiated with field estimates of the competition coefficients show without exception, the dominance of *S. invicta* is complete if the two ant species are directly in competition on the same lattice. It is only through the effect of the phorid fly parasitoids that the model can result in both species being maintained over a long period. However, the effect of the phorids is not what would be expected from, for example, a simple dynamic model of predator/prey(competitor)/competitor [47], in which a simple balance among the population interaction coefficients (here, α, β_S, β_W) determines whether or not competitive coexistence could be realized, or, in a spatial context, whether adding migration will so stabilize the system when space is itself heterogeneous [28]. We suggest that the endogenous formation of spatial pattern, through the combined Turing/intransitive mechanism, can create the spatial heterogeneity that gives rise to this coexistence pattern. It is not simply due to a balance of parameters, nor to the heterogeneity of the background habitat, but rather the codetermination of spatial pattern and coexistence, that is an emergent property of the underlying biology. Thus, beginning a simulation with just the two competitors, *S. invicta* and *W. auropunctata*, the system devolves rapidly into a monoculture of *S. invicta*. However, beginning with all three species together generates a Turing/intransitive pattern in which all three species survive over the long run. Yet the survival appears to be dependent on a spatial pattern that the interaction of the three species itself generates, clearly a self-organized process. The persistence of both competitors depends on the self-organized spatial pattern they, themselves, organize.

In addition to the indications from the basic model that its dynamics are reflected in the natural history of the system,

our detailed observations of the ant community on the Gran Batey farm, while not useful for parameter estimation (due to the overwhelming dominance of *W. auropunctata* there), serve as an example of how we expect the general dynamics of the system to work in space (figure 4). Indeed, it appears that the older colonies of *S. invicta* tend to disappear, presumably because of attack by phorids, and space dominated by *W. auropunctata* can be invaded by younger colonies of *S. invicta*, completely consistent with the general interpretation, and following the general qualitative trends predicted by the model.

It is worth noting that beyond an interesting case of spatial structure in a novel community, both of these ant species are of special practical significance. *W. auropunctata* on coffee farms creates conditions that reduce labour efficiency so as to cause considerable economic damage, according to testimony from many coffee farmers (personal information). As an ant that creates megacolonies [48], this species occupies what are effectively spatial territories, sometimes measured in hectares [42], but, at least in Puerto Rico, more likely in patches of considerably less extent. However, those patches are patches in which the effective yield of coffee is reduced since field workers naturally tend to avoid them or pass through them quickly, leaving most of the berries on the plants. Some farmers with particularly high abundance of *W. auropunctata* on their farms, regard this ant species as the most important pest of coffee in the country, and its indirect economic effects are probably important yet underappreciated [49,50]. Nevertheless, its occurrence is patchy on any given farm. Regionally, *W. auropunctata* dominates local farms only rarely (less than 20%), although it is present on at least 80% of farms [30].

Solenopsis invicta is also regarded as a pest by farmers, and is notorious in the southern United States as a particularly noxious pest, invading lawns and electric boxes, and even killing wildlife [51]. It forms obvious brood mounds, usually in sunny areas, but uses extensive underground foraging trails to forage at least 10 m from the mound (J.V. 2020, personal observations). Regionally, it dominates local farms only rarely (usually less than 10%), although it is extremely common on roads and more open areas in at least 80% of farms [30]. Ironically both of these species have been reported to be biological control agents of some coffee pests [46,50].

Given the evidence both from a field-instantiated theoretical formulation and general observations in the field, we conclude that the underlying mechanism for these two invasive species to coexist over a long period of time is related to the spatial pattern formation they self-organize along with the predatory (parasitoid) element. The formation of a Turing/intransitive pattern sets the stage for the coexistence of the two species over the long run.

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