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23. For each participant, the mean motion aftereffect durations (with standard deviation given in parentheses) for seven repetitions of low- and high-load conditions, respectively, were 9.3 s (2.0) and 6.4 s (1.0) ($t = 3.26$, $P = 0.01$; one-tailed throughout), 3.4 s (0.9) and 2.5 s (0.4) ($t = 2.74$, $P = 0.02$), 13.73 s (2.2) and 11.7 s (1.8) ($t = 1.92$, $P = 0.05$), and 14.9 s (1.6) and 11.4 s (0.9) ($t = 5.02$, $P = 0.002$). Thus, there was a significant decrease in the motion aftereffect duration under high-load conditions in every participant.
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29. A number of factors make this explanation unlikely. Typically, eye movements do not occur with radial optic flow stimuli [see (*11*) for a full discussion and experimental evidence]. The optic flow display was widely separated from the single words, which were presented foveally for a brief duration, factors that would be further expected to minimize eye movements. Nevertheless, we elected to formally measure eye movements during the experimental paradigm. Technical limitations impede accurate recording of electro-oculography (EOG) while functional images are acquired, so we measured EOG in a single participant performing the experimental paradigm within the experimental apparatus but without acquisition of functional images. The measurement was calibrated and sensitive to saccadic movements of about 1°. During the experimental conditions, no significant eye movements were detected.
30. We thank O. Josephs for his help, R. Turner for FMRI advice, and C. Büchel, J. Driver, R. Frackowiak, and M. Husain for comments on the manuscript. This work was funded by the Wellcome Trust.

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Spatial Pattern Formation in an Insect Host-Parasitoid System

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Spatial models in ecology predict that populations may form patchy distributions within continuous habitats, through strong predator-prey or host-parasitoid interactions combined with limited dispersal. Empirical support of these models is provided. Parasitoids emanating from a population outbreak of tussock moths (*Orgyia vetusta*) suppressed the growth of nearby experimental populations of the moth, while experimental populations farther away were able to grow. This result explains the observed localized nature of tussock moth outbreaks and illustrates how population distributions can be regulated by dynamic spatial processes.

Population ecology has recently seen a surge of interest in spatial phenomena such as limited dispersal, localized species interactions, and habitat geometry. The realization that spatial context may be key to understanding many ecological interactions has been fueled by a profusion of models, and in some cases, a vigorous interplay between theory and empirical research (*1*). For example, metapopulation models are beginning to enjoy success at predicting the behavior of populations in fragmented habitats. But one well-developed branch of spatial theory has still received little empirical attention: the set of models, many of them based on reaction-diffusion equations, that generate the counterintuitive prediction that patchy distributions in population density can arise even within continuous habitats (*2*). Such models combine strong predator-prey interactions (the "reaction") with limited dispersal ("diffusion"). Predators are assumed to control their prey, to disperse farther than do their prey, and to have a partly random element to their dispersal. Under these conditions, the abundant predators supported by a dense patch of prey will spill over at the edges of the prey patch, producing a peripheral zone with a high predator-to-prey ratio that prevents the prey patch from spreading.

These reaction-diffusion (or "activator-inhibitor") models are formally analogous to models of spatial pattern formation in cellular and developmental biology (*3*), as well as in physics. Computer simulations known as cellular automata have recently made the study of spatial pattern formation more detailed and accessible, compared with purely mathematical formulations (*4*). If widely applicable, such models force empirical ecologists to rethink their assumption that species' distributions are usually controlled by extrinsic factors such as climate or competition. We show that theory on spatial pattern formation can explain the observed behavior of a natural insect population.

We have been studying a population of western tussock moths (*Orgyia vetusta*, Lymantriidae) (*5, 6*) that attains high local densities which are spatially stable through time (*7, 8*). Outbreaks of moths remain spatially restricted despite the widespread and continuous availability of their abundant host plants. Unlike in some plant-insect herbivore systems, differences in host plant quality or phenology do not explain the patchiness in tussock moth population density (*7–9*). Rather, poor dispersal of flightless female tussock moths together with low rates of aerial ballooning by young larvae are partly responsible for the restricted nature of tussock moth outbreaks (*7–9*). Tussock moth larvae are attacked by several generalist predators (*10*), and larvae, pupae, and eggs are subjected to heavy parasitism by a variety of parasitoids that are local specialists on the moth (*11*).

Low mobility by the tussock moth and heavy parasitism by its mobile parasitoids suggest that the mechanisms portrayed in models of spatial pattern formation may be operating. Under this hypothesis, rates of parasitism on tussock moths should be highest immediately outside the outbreak and should decline at distances greater than the parasitoids typically disperse. As predicted, recent experiments showed that parasitism was substantially higher on eggs and larvae placed 100 to 600 m from the edge of the outbreak than on those placed within it. Moreover, parasitism increased to 200 m from the edge of the outbreak and then declined (*11*). These results, plus recent simulation and analytical modeling of our system (*12*), provide tantalizing evidence for intrinsic spatial pattern formation in this host-parasitoid system. However, a crucial unanswered question is whether distance-dependent parasitism is strong and consistent enough to suppress incipient new outbreaks near the margins of the existing one.

In our experiment, we created new tussock moth outbreaks on lupine bushes at distances of 0 to 700 m from the edge of the outbreak observed the previous year (1996). Because earlier work suggested a possible role for ants and spiders as important larval and pupal predators (*8, 10*), we simultaneously tested the role of ground-dwelling generalist predators. In February and March 1997, we established two transects emanating from the edge of the

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previous year's tussock moth outbreak. One transect, through dune habitat, extended 450 m; the other transect line through grassland habitat extended 700 m (*13*). We randomly chose two similarly sized lupine bushes every 50 m along each transect and installed around their bases a 30-cm high circular fence topped with sticky Tanglefoot (Tanglefoot Co., Grand Rapids, Michigan) to prevent access by ground-based insect and rodent predators. Fences around control bushes had four 10-cm-wide gates to allow entry by predators. Between 19 March and 7 April 1997, we placed 1000 newly hatched tussock moth larvae on each experimental bush, using larvae from egg masses collected in the outbreak area in July 1996. Starting on 19 April, we performed weekly to biweekly censuses, recording the number of larvae and pupae present and the number of parasitized larvae or pupae. Parasitism by the tachinid fly *Tachinomyia similis* (one of three tachinids that are important parasitoids of *O. vetusta* larvae) is conspicuous, because the fly lays a large white egg on the larval cuticle.

Exclusion of ground-based predators significantly increased the number of *O. vetusta* larvae on experimental bushes at the first census date 2 weeks after the experiment began (Fig. 1) (*14*). At this time, there were no significant main or interactive effects of distance from the edge of the previous year's outbreak, nor of dune versus grassland habitat, on the numbers of larvae. The effect of predator exclusion did not grow through time, as evidenced by the similar slopes of the lines in Fig. 1, indicating that predators had their greatest impact when larvae were small. Later, larval numbers diminished rapidly on predator-exclusion as well as control bushes, both because of parasitism, which we first recorded on 30 April, and because of pupation, which we first observed on 14 May. The strong initial impact of predator-exclusion fences was not the result of larval dispersal; young larvae are not very mobile and do not stray from their host plant except by aerial ballooning, generally only if the plant dies (*7–9*). Larger larvae are somewhat more mobile, but tend to disperse only in response to heavy defoliation of the host plant (which did not happen in this experiment) and during a wandering phase immediately before pupation. To prevent prepupal wandering, we closed the gates on control fences for the 2-week period when pupation was occurring.

As the season progressed, distance from the previous year's outbreak began to have a strong effect, with pupal survival substantially higher at greater distances (Fig. 2, A and B) (*15*). The distance-dependent mortality was evidently due to parasitism, because it was unaffected by the predator-exclusion treatments, and because there was a corresponding spatial pattern in the numbers of parasitized larval corpses found at the bases of experimental bushes (Fig. 2C) (*16*). Numbers of egg masses produced by the experimental moths likewise increased strongly with distance from the edge of the natural outbreak (Fig. 3) (*17*). Because treatments were initiated with 1000 newly hatched larvae, and because the egg masses contained an average of 170 (SE ±10) eggs (*18*), experimental outbreaks could grow only if there were ≥6 progeny egg masses per bush. Population growth was consistently suppressed at distances up to 200 m (dunes transect) or 300 m (grasslands transect) from the natural outbreak (Fig. 3); at greater distances, population growth was sometimes (grasslands) or nearly always (dunes) strongly positive. The stronger effect in the dunes than in the grassland, reflected in a significant distance × location interaction (*17*), may have been caused by different movement behavior of parasitoids in the two habitats. Predator exclusion did not significantly affect the numbers of egg masses per bush (*17*), indicating that distance-dependent parasitism overwhelmed the initially strong effect of predation.

Our results show that parasitoids emanating from a population of host insects suppressed the growth of incipient host populations nearby, while ones farther away were able to increase. This is the

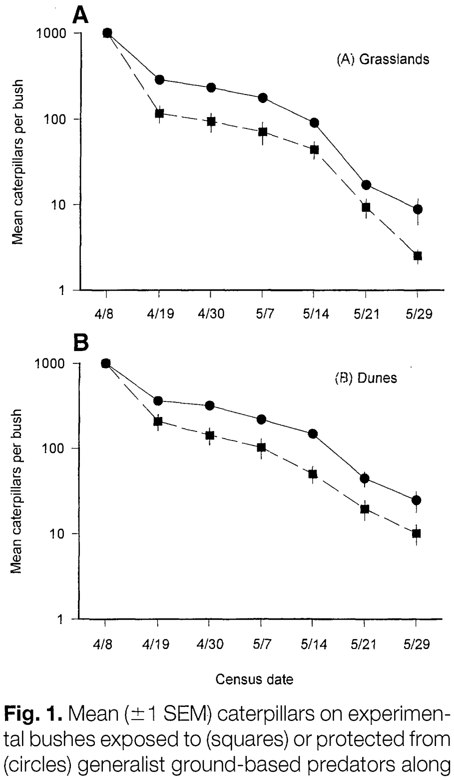

Fig. 1. Mean (±1 SEM) caterpillars on experimental bushes exposed to (squares) or protected from (circles) generalist ground-based predators along (**A**) grassland and (**B**) dune transects.

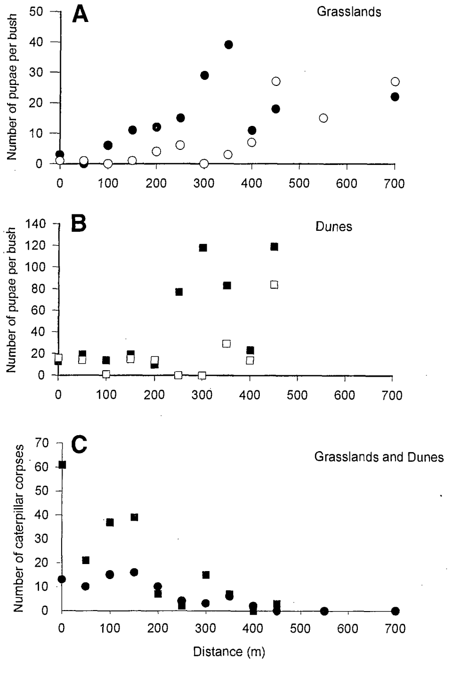

Fig. 2. Numbers of surviving pupae on experimental bushes exposed to (open symbols) or protected from (filled symbols) generalist ground-based predators along (**A**) grassland and (**B**) dune transects and (**C**) numbers of corpses of parasitized larvae and pupae (circles, grasslands; squares, dunes), as a function of distance from the edge of the previous year's tussock moth outbreak.

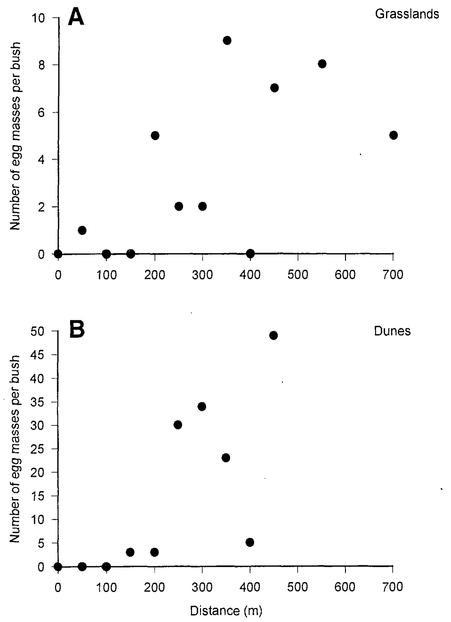

Fig. 3. Numbers of tussock moth egg masses found on experimental bushes in (**A**) grasslands or (**B**) dunes, as a function of distance from the edge of the previous year's tussock moth outbreak. Data are from experimental bushes protected from ground-based predators.

strongest experimental evidence to date for endogenous spatial pattern formation in a population system. System-specific models are now needed to explore more fully the dynamic properties of the interaction, for example, whether spatial pattern formation is an equilibrial or transient phenomenon. Models can also generate further testable predictions. Based on what is known of this system, important model features would include discrete-time host and parasitoid population dynamics, continuous-time spatial dynamics (that is, parasitoid searching), and density dependence in host reproduction and dispersal; space could reasonably be represented as either discrete or continuous. One relatively simple model of this system has already yielded the successful prediction that host densities should be highest near the edge of the host patch (*12*).

Recent observations have also corroborated the role of parasitism in the spatial dynamics of tussock moth outbreaks. The outbreak we studied is now at its lowest size in the last 6 years. In 1996, we discovered a small incipient outbreak approximately 1000 m from the old outbreak. By 1997, this new outbreak had grown tremendously, increasing more than 10-fold in area, and had much lower rates of parasitism than the original outbreak. In contrast, such satellite outbreaks generally failed to become established in previous years, when the original outbreak was much larger and supported a heavy population of parasitoids.

The ecological significance of these results extends beyond the current interest in spatial pattern for its own sake, to broader issues of population dynamics. The western tussock moth is globally far rarer than its abundant food-plant resources would permit it to be. Our results suggest that its populations are not regulated by either "top-down" (predation, parasitism) or "bottom-up" (food quantity or quality) forces acting homogeneously in space. In other words, the controls on this species' abundance would not be revealed by a traditional two-factor manipulative experiment at a single spatial location. Instead, the nature of regulation in this species can only be understood through experiments informed by spatial theory. Whether this is a special case or whether the theory has wide generality can only be revealed by more such experimental work.

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5. Our study site is the University of California's Bodega Marine Reserve (BMR) in central coastal California. Grasslands on the BMR abruptly give way to sand dunes where the Pacific Plate abuts the San Andreas fault zone. Bush lupine are sparser in dunes than in grasslands.
6. Tussock moths are native to the area. At our study site, tussock moth larvae feed exclusively on bush lupine, *Lupinus arboreus*. At other coastal sites to the south, *O. vetusta* feed on another perennial lupine, silver lupine, *L. chamissonis*. Larvae hatch from overwintering egg masses in April and May, and undergo five to six instars before pupation. Eclosion and mating occur 1 to 2 weeks after pupation; flightless females lay a single mass of 100 to 300 eggs on the undersides of lupine bushes. For the past 10 years, a high-density tussock moth population has been located within a 1.5-ha lupine stand at our site.
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13. Use of two transects creates some risk of spatial autocorrelation; an ideal design would be to place our treatments in random directions from the natural outbreak. However, we were constrained by the fact that the outbreak is located on a peninsula.
14. In a three-way analysis of variance (ANOVA) on mean numbers of larvae per bush, the main effect of predator exclusion was statistically significant [$F(1,38) = 24.3$, $P < 0.001$], but the effect of distance, transect location, and interaction terms were not ($P > 0.1$).
15. We used a logit transformation on (1 + pupa number) to equalize the variance between treatments and then performed a three-way ANOVA on transformed data. Main effects of distance and transect location were statistically significant [$F(1,37) = 15.5$ and 5.3, respectively; $P < 0.03$); predator exclusion was marginally significant [$F(1,37) = 5.3$; $P = 0.058$]. No interaction terms were significant.
16. Regressions of number of parasitized larval corpses on distance from the outbreak showed significant negative relationships ($r^2 = 0.733$ and 0.657 for dune and grassland, respectively; $P < 0.004$).
17. In a three-way ANOVA on number of egg masses per bush, the main effect of distance and the distance × location interaction were statistically significant [$F(1,37) = 31.5$ and 17.5, respectively; $P < 0.001$]. No other main effects or interaction terms were significant.
18. We collected one tussock moth egg mass from each experimental bush that had egg masses, dissected it under a dissecting microscope, and counted the number of eggs.
19. We thank M. Greaves and B. Shubin for field assistance. H. C. J. Godfray, A. Hastings, A. R. Ives, K. S. McCann, P. Turchin, and W. G. Wilson provided much theoretical inspiration and M. Holyoak, M. Hoopes, S. Strauss, and D. Strong made helpful comments on the manuscript. Funded by NSF grant DEB-9508546.

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The Spatial Dimension in Population Fluctuations

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Theoretical research into the dynamics of coupled populations has suggested a rich ensemble of spatial structures that are created and maintained either by external disturbances or self-reinforcing interactions among the populations. Long-term data of the Canadian lynx from eight Canadian provinces display large-scale spatial synchrony in population fluctuations. The synchronous dynamics are not time-invariant, however, as pairs of populations that are initially in step may drift out of phase and back into phase. These observations are in agreement with predictions of a spatially-linked population model and support contemporary population ecology theory.

Ecologists have always been interested in population fluctuations, particularly of regular cycles (*1*). Apart from temporal population variability (*2*), populations at different geographical locations may fluctuate in synchrony (*3*). Also, populations in a spatially structured environment may generate a suite of complex dynamics such as spatial chaos, spiral wave, and crystal lattices (*4*). A number of reasons for such patterns has been suggested, including dispersal of both the focal species or its predators or prey (*4, 5*), correlated environmental stochasticity, or other common extrinsic factors (*3, 6*). We show, using population data as well as modeling, that

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