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.

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

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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

spatial synchrony in population fluctuations may not be time-invariant and that prominent and regular population cycles at the local scale may temporarily give way to stable dynamics, a phenomenon that has been noted in real data without full explanation (7). We also show that synchrony in population fluctuations can have a very simple explanation in the spatial structure of the environment.

We began with a set of population data from the Canadian lynx, *Lynx canadensis*. Figure 1 illustrates a 68-year time series of lynx population sizes from eight Canadian provinces (8), which we identify as "populations." It is well known (1, 8) that all of the populations exhibit 10- to 11-year cycles, although the cycle is not pronounced in every province. Details of the time series analysis of North American

lynx cycles, as well as other regular population cycles, are reported elsewhere (1, 8). We first note that the synchrony between populations varies with distance between them (Fig. 1C), that is, populations from nearby provinces tend to fluctuate hand-in-hand, whereas populations farther apart are increasingly out of phase with each other. Moreover, the synchrony between populations varies considerably over time (Fig. 1D). The sliding time-window analysis reveals that the synchrony between any population pair (for example, Northwest Territory versus Quebec Province) at some period of time may either be strongly positive, strongly negative, or zero. Thus, depending on which section of the time series is studied, the conclusion about synchronous population fluctuations may vary tremendously.

Although spatially segregated populations cannot be decisively delimited, it is safe to say that most populations are spatially subdivided (patchy). Most models of patchily distributed populations assume a regular grid of either cellular automata (4) with limited dispersal between patches or globally interconnected patches with or without internal dynamics (5). Given the uncertainties of real population delimitation and deviating from the special case of regular grid structure, we built a single-species model in an n by n matrix of arbitrarily located subpopulations (9). This was achieved by randomly dislocating the initially regularly spaced populations in the x and y direction. We let the population renewal within each patch be governed by Moran-Ricker dynamics with time-lag two. The parameters were chosen such that the internal dynamics exhibited cyclic fluctuations with an 11-year period. We let dispersal between patches be distance-dependent in an exponential fashion and fixed the fraction of migrants leaving each patch each generation at 10%. The synchrony in population fluctuations varies with distance between patches in this model system (Fig. 1E). The results from the simulations of the model system are markedly similar to the long-term data from the Canadian lynx populations. Identical patterns are found in a number of long-term data sets from a variety of animal taxa (1, 3, 8). The model also recovers the fact that the synchrony between any population pair is time-dependent (Fig. 1F). The amplitude of the cross-correlation (10) coefficients (measuring the sign and magnitude of the synchrony) fluctuate widely between −1 (fluctuations in opposite phase) and +1 (fluctuations hand-in-hand). In the lynx data and in the simulated data, the maximum amplitude is 1.67.
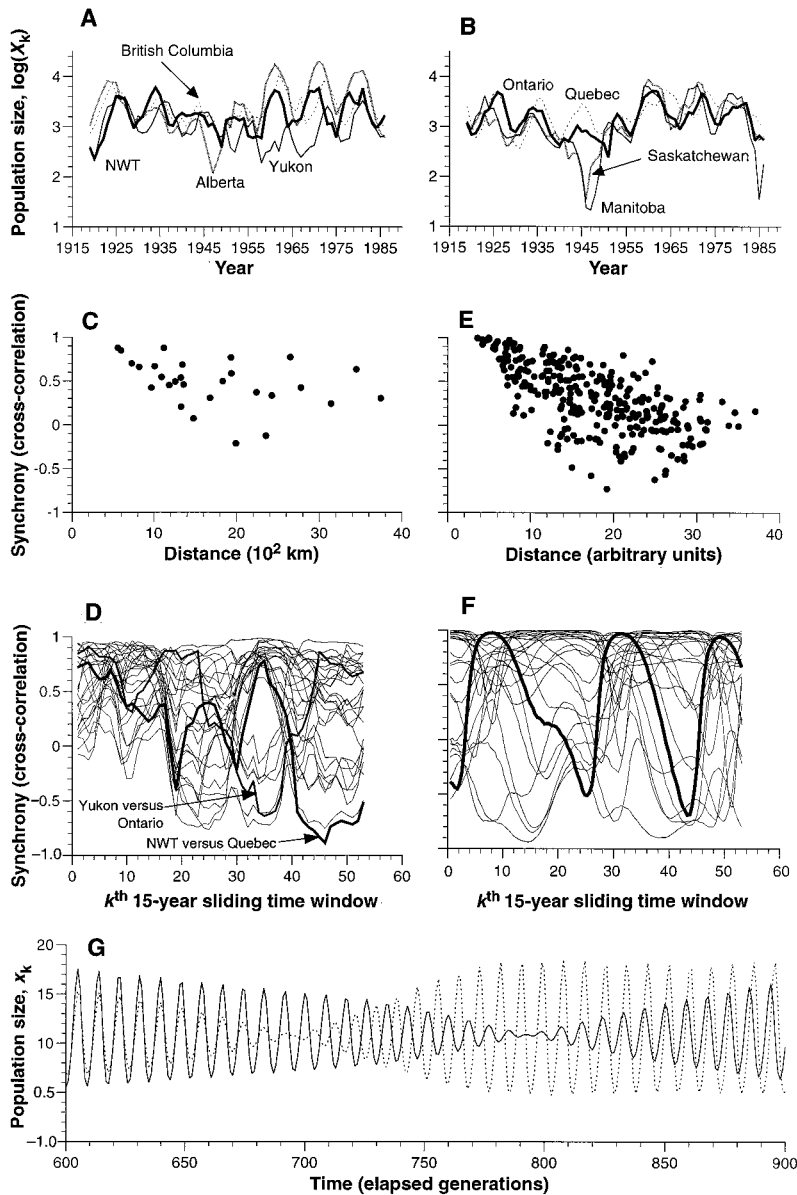
Fig. 1. (**A** and **B**) Long-term records of the Canadian lynx (8). (**C**) Synchrony among all pairs of lynx series scored by the cross-correlation coefficient (10) with time-lag zero and graphed against distance between geographical midpoints of the eight provinces. Synchrony across Canada is obvious (most of the correlations are above zero), but its level tends to reduce with distance. (**D**) The lynx display 11-year cyclic dynamics (1, 8), thus a 15-year sliding time window (covering about 1.5 cycles) was applied throughout the 68 years of records to assess dynamics of the synchrony. (**E** and **F**) The data after (9) were subjected to similar analyses as the lynx data in (C) and (D). (**G**) To further illustrate some properties of the dynamics of the 25 populations during the 1500 generations, we selected a pair displaying (*k* ranging from 600 to 900) a drift from synchrony to asynchrony and again back to synchrony. Both populations showed disappearance of the cyclic dynamic and its reappearance some tens of generations later.

The irregular patch distribution also produces another phenomenon noted in real populations (7). The endogenous regular oscillations in our model, together with the exponentially decaying dispersal between patches, generally maintains rather regular cycles. This explains why a wide range of cross-correlation values is observed for pairs of populations. The cycles thus produced are not necessarily persistent. Pronounced and regular population cycles may gradually fade away and subsequently recover (Fig. 1G). Hence, both the amplitude of population fluctuations and the spatial synchrony between pairs of populations changes considerably over time, without any other source of randomness than the spatial location of the interconnected subpopulations. The dispersal is probabilistic because of the assumption of an exponential distribution of dispersal distances, but a regular grid of patches with exactly the same kind of dispersal did not generate the pattern we observed in this model or in the data.

Thus, we conclude that the spatial structure may be of great importance for the dynamics of populations. Most previous studies have concentrated on either the internal dynamics within patches or the rules for dispersal between them (4, 5) in order to explain large-scale spatial dynamics. Here, we used a simple, albeit realistic model for which the assumptions are well substantiated. Delayed density-dependence seems to be the rule rather than exception for a wide range of taxa (8, 11), the exponential distribution of dispersal distances is well established (12), and the irregular distribution of patches is true for all natural environments. These are the simple building blocks on which important analyses of spatial population dynamics can rest.

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9. In an arena of 30 units by 30 units, 25 populations were randomly placed (median and interquartile distances were 10.3, 7.4, and 14.2 units). They renewed after

$$X_i(k + 1) = (1 - m)F[X_i(k), X_i(k - 1)]$$
$$+ \sum_{s = 1, s \neq i}^{n} M_{si}(k)$$

$i = 1, \ldots, n, k = 1, 2, 3, \ldots,$

where $F[X_i(k), X_i(k - 1)] = X_i(k) \exp[r + a_1 x_i(k) + a_2 X_i(k - 1)]$, r is an intrinsic rate of increase, and a_1 and a_2 are parameters. M_{si} is the number of immigrants from patch s to patch i after (3)

$$M_{si}(k) = mF[X_s(k), X_s(k - 1)] \frac{\exp(-cd_{si})}{\sum_{j, j \neq s} \exp(-cd_{si})}$$

(d_{si} is the distance between patches s and i and $m = 0.1$ and $c = 0.75$ are parameters telling the proportion emigrating and distance emigrated, respectively). The other parameter values used, $r = 0.47$, $a_1 = 0.056$, and $a_2 = -0.1$, yield deterministic cyclic dynamics with a 10.8-year period. The populations were initiated in phase ($X_{i,1} = X_{i,2} = 10$) and left to renew for 1000 generations. From the next 1500 generations, a 68-year sequence was randomly selected for further analyses. Experimentation suggests that the outcome, as we report, is achievable by cyclic dynamics alone or with damped or chaotic dynamics when superimposed with correlated disturbances (3, 6). Thus, the feature we report (Fig. 1, E through G) is not unique for the selected parameters.
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Requirement for V$_\alpha$14 NKT Cells in IL-12–Mediated Rejection of Tumors

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A lymphocyte subpopulation, the V$_\alpha$14 natural killer T (NKT) cells, expresses both NK1.1 and a single invariant T cell receptor encoded by the V$_\alpha$14 and J$_\alpha$281 gene segments. Mice with a deletion of the J$_\alpha$281 gene segment were found to exclusively lack this subpopulation. The V$_\alpha$14 NKT cell–deficient mice could no longer mediate the interleukin-12 (IL-12)–induced rejection of tumors. Although the antitumor effect of IL-12 was thought to be mediated through natural killer cells and T cells, V$_\alpha$14 NKT cells were found to be an essential target of IL-12, and they mediated their cytotoxicity by an NK-like effector mechanism after activation with IL-12.

V$_\alpha$14 NKT cells, originally defined as NK1.1$^+$ T cells (1), are a distinct lymphoid lineage expressing several characteristics that demarcate them from T cells, natural killer (NK) cells, and B cells. First, V$_\alpha$14 NKT cells develop outside of the thymus at an early stage of embryogenesis (2) and belong to the CD4$^-$CD8$^-$ or CD4$^+$CD8$^-$ populations that express heat-stable antigen and the B220$^+$, Mac-1$^+$, CD44$^+$, CD45RB^{dim}, and Mel-14^{dim} phenotypes (3–5). Second, V$_\alpha$14 NKT cells express a single invariant T cell receptor α chain (TCRα) encoded by the V$_\alpha$14 and J$_\alpha$281 segments (4, 6, 7), mostly in association with V$_\beta$8 (3, 5), which is not expressed on conventional T cells (8). Because of the unique expression of in-

variant V$_\alpha$14 TCR, transgenic (tg) mice that only express the invariant V$_\alpha$14 TCR and no endogenous TCRα (TCRα$^{-/-}$ V$_\alpha$14^{tg}) preferentially develop V$_\alpha$14 NKT cells and block conventional αβ$^+$ T cell development (8). Therefore, we speculated that disruption of the genes encoding the invariant V$_\alpha$14 TCR would generate mice lacking V$_\alpha$14 NKT cells while leaving the other lymphoid lineages intact.

IL-12 is known to mediate antitumor effects and was originally hypothesized to interact with NK cells or CD8$^+$ cytotoxic T lymphocytes (CTLs) (9). However, recent studies indicate that the systemic administration of IL-12 activates NK1.1$^+$ TCR^{intermediate} cells (which are similar to V$_\alpha$14 NKT cells) and inhibits the hepatic metastasis of tumor (10). It is thus unclear whether IL-12 interacts with NK, T, or V$_\alpha$14 NKT cells. It is possible that V$_\alpha$14 NKT cells may be responsible for functions that have been reported for NK cells, because purifications were difficult and the studies were done with a mixture of NK and V$_\alpha$14 NKT cells. We investigated

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