Habitat structure and population persistence in an experimental community


Understanding spatial population dynamics is fundamental for many questions in ecology and conservation. Many theoretical mechanisms have been proposed whereby spatial structure can promote population persistence, in particular for exploiter-victim systems (host-parasite/pathogen, predator-prey) whose interactions are inherently oscillatory and therefore prone to extinction of local populations. Experiments have confirmed that spatial structure can extend persistence, but it has rarely been possible to identify the specific mechanisms involved. Here we use a model-based approach to identify the effects of spatial population processes in experimental systems of bean plants.

Figure 1 Experimental layouts and results. a, The single-island system consisted of a Syzgoea sheet with 30 embedded plants (filled circles) floating in a shallow tray of water. b, The metapopulation subdivided the sheet into 8 islands (10 plants per island) connected by cord bridges, with the space for 10 plants being lost. Replicate systems were housed simultaneously in the same environmental chamber, and given identical initial inoculations of mites. c, Fluctuations in total density of prey (open circles) and predatory (filled triangles) mites in the single-island experiment. d, Fluctuations in total density of prey (open circles) and predatory (filled triangles) mites in the two replicates of the metapopulation experiment.

Figure 2 Examples of mite population dynamics on a single plant, from run B of the metapopulation experiment. a, A prey outbreak (plant 1, island 5) that was not discovered by predators. The three successively larger peaks in this prey density (days 125, 137 and 144) are the original colonizers, their offspring (counted when they become adults at age 10 d), and offspring of the offspring. The rapid collapse of the outbreak is primarily due to emigration after exhaustion of the resource. b, A prey outbreak (plant 1, island 2) colonized by predators after several on-plant prey generations. Predators arrived too late to prevent growth of the prey population, and the outbreak terminated through exhaustion of the resource and prey emigration. c, A prey outbreak (plant 8, island 2) colonized by predators when prey densities were still low. The outbreak terminated through predators consuming all prey and then emigrating.
(Phaseolus lunatus), herbivorous mites (Tetranychus urticae) and predatory mites (Phytoseiulus persimilis). On isolated plants, and in a spatially undivided experimental system of 90 plants, prey and predator populations collapsed; however, introducing habitat structure allowed long-term persistence. Using mechanistic models, we determine that spatial population structure did not contribute to persistence, and spatially explicit models are not needed. Rather, habitat structure reduced the success of predators at locating prey outbreaks, allowing between-plant asynchrony of local population cycles due to random colonization events.

Plants (P. lunatus) were grown in individual pots in arrays that were initially free of mites (Fig. 1). Experiments began by placing individual prey mites (T. urticae) onto several plants, followed by predatory mites (P. persimilis) on the same plants. Mite populations on an individual plant collapse either through the prey exhausting the resource or by predators colonizing the plant, consuming all prey and then starving or emigrating (Fig. 2). The individual plant dynamics did not differ between the single-island (unstructured habitat) and metapopulation (subdivided habitat) systems (Fig. 1a, b), therefore the differencing dynamics must result from effects of habitat structure. The factors are present in the metapopulation system for two distinct but non-exclusive stabilizing mechanisms.

The first mechanism is that spatial subdivision produces differing dispersal scales in predators and prey. In the single-island system, both species dispersed throughout the system, but in the metapopulation system only predators dispersed throughout the system while prey mainly colonized plants on the same or nearby islands. Such differences in dispersal can create spatial patterns where different locations act as source habitat for prey and predators, and total densities are stabilized. We tested for such clumped distributions using Moran's I, and found significant (P < 0.05) spatial correlation (I > 0) among plants on the same island for both mite species on most census dates (85 and 81% for prey; 93 and 92% for predators, in the two metapopulation experiments). The second mechanism is that spatial subdivision reduces the discovery rate of prey outbreaks by predators. Nearly 90% of prey outbreaks were attacked by predators in the single-island experiments, but only 68 and 78% in the two metapopulation experiments. This mechanism has two components, neither involving spatial pattern: reduced average predator success, and the resulting between-plant asynchrony, meaning that not all plants are simultaneously exploited by prey and not all prey outbreaks are simultaneously discovered and extinguished. Hence a non-spatial model for total numbers of plants occupied by each species can describe the system.

To determine which mechanism accounts for the observed dynamics, we developed and tested models that allowed us to simulate experiments that would be infeasible in the actual systems. The models consist of colonization probabilities, and nonlinear stage-structure models for the predator—prey—plant interactions occurring on the plant. We assigned parameters to the on-plant interaction models (Box 1) using independent data. These were identical for the metapopulation and single-island systems. The equations for colonization probabilities (Box 2) give each plant's daily chance of colonization as a function of the abundance and

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**Box 1**

**Structured population models for mite dynamics on a plant**

We combined a stochastic description of plant colonization (Box 2) with a deterministic growth model for mite populations on occupied plants. The stochasticity of individual mites colonizing suitable plants is essential for generating between-plant asynchrony in the model, but the on-plant dynamics involve many individuals and can be modelled deterministically.

We used nonlinear, stage-structured matrix models with a 1-d time step for the mite populations on each occupied plant. We classified mites by life stage and assigned stage-specific vital rates (described below) derived from empirical age- and sex-specific vital rates. Male adults are much smaller than female adults in both species; we give male adults the same feeding and survival rates as juvenile females (who are similar in size), and assigned a fixed male : female ratio in all stages (1:4 in predators; 1:3 in prey) rather than explicitly tracking males. Because pre-adult prey require much less food and rarely experience food shortages, we assumed predation to be the only cause of pre-adult

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**Box 1 Figure**

Life stages of prey and predatory mites in the model. Solid arrows indicate survival and fecundity. Dashed arrow indicates predation (other mortality rates are omitted for clarity). We assumed constant durations for pre-adult stages. Adult stages have indefinite duration, with a constant background mortality rate (0.1 d⁻¹ for prey; 0.04 d⁻¹ for predators). The resulting models are coupled, nonlinear Leslie matrices of sizes 11 x 11 and 6 x 6 for prey and predators, respectively.
Box 2

**Colonization probability models**

The colonization models are regression models for the conditional probability of an available plant being colonized, given the current and recent mite abundances on each plant, and the state of each plant. Plant states are as indicated in Fig. 2: empty; prey only; prey donor (plant is exhausted and prey are emigrating); predator–prey; and predator donor (all prey consumed and predators emigrating). Either of the donor states is followed by the refractory state, ending with replacement by a fresh plant (following the experimental protocol). Small prey outbreaks (number of adults is always ≤ 10) were not scored as colonization events or prey-only state: we interpret these as mites exploring a plant without settling. However one adult female of each species was sufficient for the predator–prey state, because a few predators arriving early in an outbreak can consume prey before they mature.

We used logistic regression with stepwise and backward variable selection (as in ref. 18) to identify significant ‘risk factors’ affecting colonization. Plants were classified by distance from the focal plant (single-island: nearest neighbour, the next nearest neighbour, the next, next-nearest neighbour, and non-neighbour; metapopulation: same island, adjacent island, or non-adjacent island; adding within-island distance classes did not improve the final model). The potential risk factors were the mean conspecific densities within each distance class, the decrease in density between current and previous censuses on donor state plants for the species (an indicator of emigration rate), and prey density on the focal plant for predator colonization. We pooled the two metapopulation experiments and did not consider time-lagged densities because mites tend to find new plants quickly or not at all. As an example, the fitted predator colonization probability (between now and the next census) for a prey-only plant in the metapopulation is:

\[
\logit(P(x_1 - P)) = -2.7 + 0.074 (\text{prey density on plant})^{39} \\
+ 0.024 (\text{total predator density on same island}) \\
+ 0.036 (\text{total predator decrease on same island predator donor plants}) \\
+ 0.021 (\text{total predator decrease on adjacent island predator donor plants}) \\
+ 0.011 (\text{total predator decrease on non-adjacent island predator donor plants})
\]

spatial distribution of predator and prey mites; these were estimated from the modelled experiments and differed between the metapopulation and single-island systems. However, neither mean colonization rates (number of plants colonized each day) nor their patterns of temporal variation were fitted to the data. Rather, they are predicted by the model from the interaction between on planta dynamics and the equations for colonization probabilities.

The model dynamics match the experimental results. Nearly all model runs of the single island system exhibit rapid increase of prey and then predators, followed by extinction (Fig. 3a, b). Extinction of both species occurred within 1yr in over 99% of 3,000 simulation runs. Replicate runs are highly variable because small chance differences in the success of the predators at detecting the initial prey outbreaks have a large effect on the peak densities reached by prey and then predators. Similarly, the single-island experiment (Fig. 1c) persisted longer than typical model runs (Fig. 3a, b) owing to two late prey outbreaks that started at about day 50, but escaped predation until days 65 and 78.

The metapopulation model, although differing only in its equations of colonization probability, showed long-term persistence much more frequently (Table 1 and Fig. 3c, d), corresponding to the experiments (Fig. 1d, e). Measures of temporal averages (Table 1) and patterns of temporal variation (Fig. 4) were close to those for the experiments. The model also produced spatial correlations similar to those in the experiments (within-island I was significantly positive on 63–90% of sample dates [mean = 74%] for prey; 83–97% of sample dates [mean = 89%] for predators, in 25 model runs with both species persisting). These are strong tests because we did not use any of these summary statistics in assigning parameters to the models. However, the model over-predicts slightly the number of plants occupied by prey while under-predicting the prey colonization rate; the coefficients of variation of population fluctuations were low (possibly because the on-plant population

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**Table 1 Summary statistics for metapopulation experiments and models with and without spatial pattern at different scales**

<table>
<thead>
<tr>
<th></th>
<th>Experiments (run1, run2)</th>
<th>Metapopulation (spatial model)</th>
<th>Island shuffle</th>
<th>Plant scramble</th>
<th>Global dispersal</th>
<th>Blair plants on island</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Prey</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Mean no.</td>
<td>610, 567</td>
<td>696</td>
<td>695</td>
<td>699</td>
<td>650</td>
<td>260</td>
</tr>
<tr>
<td>CV (%)</td>
<td>56.8</td>
<td>(612, 782)</td>
<td>(612, 779)</td>
<td>(611, 781)</td>
<td>(702, 740)</td>
<td>(112, 420)</td>
</tr>
<tr>
<td>Plants occupied</td>
<td>7.6, 8.1</td>
<td>8.7</td>
<td>(7.7, 8.8)</td>
<td>(7.6, 8.6)</td>
<td>(7.2, 9.2)</td>
<td>(19.6, 4.4)</td>
</tr>
<tr>
<td>Colonization rate/(plant d−1)</td>
<td>0.83, 0.84</td>
<td>(0.56, 0.67)</td>
<td>(0.55, 0.67)</td>
<td>(0.55, 0.67)</td>
<td>(0.55, 0.67)</td>
<td>(0.55, 0.67)</td>
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<tr>
<td><strong>Predators</strong></td>
<td></td>
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<td></td>
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<tr>
<td>Mean no.</td>
<td>42.47</td>
<td>(34.54)</td>
<td>44</td>
<td>46</td>
<td>47</td>
<td>61</td>
</tr>
<tr>
<td>CV (%)</td>
<td>87.104</td>
<td>(80.80)</td>
<td>(81.66)</td>
<td>(82.56)</td>
<td>(82.56)</td>
<td>(82.56)</td>
</tr>
<tr>
<td>Plants occupied</td>
<td>7.0, 7.8</td>
<td>6.6</td>
<td>(5.7, 7.7)</td>
<td>(5.7, 7.6)</td>
<td>(5.7, 7.6)</td>
<td>(5.7, 7.6)</td>
</tr>
<tr>
<td>Colonization rate/(plant d−1)</td>
<td>0.52, 0.59</td>
<td>(0.42, 0.54)</td>
<td>(0.42, 0.54)</td>
<td>(0.43, 0.55)</td>
<td>(0.44, 0.56)</td>
<td>(0.43, 0.55)</td>
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<tr>
<td><strong>Persistence</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Prey (% of runs)</td>
<td>yes, yes</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>1.8</td>
</tr>
<tr>
<td>Both species (% of runs)</td>
<td>yes, yes</td>
<td>81</td>
<td>81</td>
<td>81</td>
<td>81</td>
<td>0.08</td>
</tr>
</tbody>
</table>

Values for the models are mean values (9th and 95th percentiles in parentheses) from 1,000 runs (50,003 for plant blur, averaging over runs in which both species persisted for 400 d). Model runs in which one or both species go extinct are not comparable to the experiments, in which both species persisted. Data from the first 30 d of the experiments and simulations were omitted to eliminate transients. Plants were scored as occupied by prey for model output and experimental data only when ten or more adults were present, to eliminate the frequent counts of a few stray prey in the experimental systems not associated with a prey outbreak on a plant. CV, coefficient of variation.
models are deterministic; and the time lags between changes in prey abundance and the resulting changes in predator abundance and colonization rate were under-predicted by roughly 3 d.

The differing temporal autocorrelations between the two metapopulation experiments (Fig. 4c–f) are also consistent with the model. The first wave of predator colonizations was much smaller in the second experiment (Fig. 1e) than in the first (Fig. 1d), resulting in higher prey densities and a deeper subsequent crash by both species. This pattern also occurred in about 15% of model runs where initial predator growth was restricted.

We determined which aspects of spatial dynamics were responsible for persistence in the metapopulation by systematically eliminating different aspects of spatial pattern in simulations. Under the first mechanism, eliminating spatial pattern at the island and metapopulation levels should produce dynamics similar to those observed in the single-island system. Under the second mechanism, reducing local between-plant asynchrony should have this effect. In 'island shuffling' simulations, the sequence of islands in the ring (Fig. 1b) was randomly shuffled each day, but plants remained on their home island. This preserves within-island correlation but eliminates pattern at the metapopulation level. In 'plant scrambling' simulations the location of all plants was randomized each day, and in 'global dispersal' simulations, all colonization probabilities were calculated from system-wide average densities rather than local densities. These simulations eliminate spatial pattern at the island and metapopulation level, but retain between-plant asynchrony. In 'plant blurring' simulations, the age-specific mite densities on each plant were replaced daily by the average density over all plants on the same island. This eliminates within-island asynchrony but preserves pattern at the metapopulation level.

Island shuffling, plant scrambling and global dispersal had only small effects on the dynamics (Table 1, Figs 3 and 4). Plant scrambling eliminated within-island autocorrelations because each island is reassembled daily at random, but autocorrelations of total densities were unaffected (Fig. 4). In contrast, plant blurring produced extinction similar to the single-island experiment (Fig. 3j) with predators finding all prey outbreaks because of the rapid within-island dispersal. The reduced system size with blurring (8 islands versus 80 plants) still allows enough asynchrony for prey persistence in the absence of predators (81% of 1,000 runs).

These results indicate that the first stabilizing mechanism is not responsible for long-term persistence in the metapopulation.
is consistent with this conclusion (Supplementary Information). Comparison of alternative mechanistic models is a powerful approach for testing hypotheses regarding processes responsible for patterns in ecological dynamics. By comparing models with different assumptions about the effects of habitat subdivision, we have shown that the one essential process allowing persistence of the metapopulation was one of the earliest and simplest hypotheses about spatial dynamics: isolation by distance[21,24]. Habitat subdivision increased the effective distance between plants from the viewpoint of the predators, giving prey a moving refuge from their enemies.

Methods
Experimental design
We counted adult female mites on each plant twice a week. After all mites had left a plant (three consecutive samples without prey or four without predators, whichever occurred last), it was replaced with a 1-week-old plant pruned to two leaves. We regularly pruned plants and replaced uncolonized plants with 1-week-old plants, to standardize conditions and eliminate direct connections among plants. Mites dispersed only by walking from one plant to another. Because the bridges between islands in the metapopulation were positioned below the island rim, mites often missed these connections, reducing inter-island movements. See ref. 15 for further experimental details. Initial prey inoculations in the models were identical to the experiments, matching the day, plant and number of individuals added. Predator inoculations in the models corresponded in the same way to successful predator inoculations in the experiments (where the founding predator reproduced and established a local population).

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21. Nisbet, R. M. & Gurney, W. S. C. Modelling Fluctuating Populations (Ch. 10 (Wiley, New York, 1982).
The end of world population growth

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There has been enormous concern about the consequences of human population growth for the environment and for social and economic development. But this growth is likely to come to an end in the foreseeable future. Improving on earlier methods of probabilistic forecasting, we show that there is a 5 per cent chance that the world's population will still growing before the end of the century. There is a 50 per cent probability that the world's population will not exceed 10 billion people before 2100, and around a 15 per cent probability that the world's population at the end of the century will be lower than it is today. For different regions, the date and size of the peak population will vary considerably.

Figure 1 shows the probability that the world population size would reach a peak at or before any given year. It indicates that there is around a 20 per cent chance that the peak population would be reached by 2050, around a 55 per cent chance that it would be reached by 2075, and around an 85 per cent chance that it would be reached by the end of the century.

There is around a 75 per cent chance that the peak population of the European portion of the former USSR has already been reached in 2000, an 88 per cent probability that it will be reached by 2025, and over a 95 per cent chance by the end of the century. For the China region, the probability of reaching a peak within the next two decades is still low owing to its relatively young age structure. By 2040 the probability becomes greater than half. In sub-Saharan Africa, despite the prevalence of HIV, there is a low probability of peaking before the middle of the century. The probability reaches 25 per cent by 2070, 50 per cent by 2085, and almost 75 per cent by 2100, owing to assumed reductions in fertility.

Figure 2 shows the distribution of simulated world population sizes over time. The median value of our projections reaches a peak around 2070 at 9.8 billion people and then slowly decreases. In 2100, the median value of our projections is 8.4 billion people with the 80 per cent prediction interval bounded by 5.6 and 12.1 billion. The medium scenario of the most recent United Nations long-range projection is inserted in Fig. 2 as a white line. It is almost identical to our median until the middle of the century, but is higher thereafter owing to the United Nations assumption of universal replacement-level fertility, that is two surviving children per woman.

Table 1 shows the median population sizes and associated 80 per cent prediction intervals for the world and its 13 regions, indicating major regional differences in the paths of population growth. While over the next two decades the medians are already declining in eastern Europe and the European portion of the former Soviet Union, the populations of north Africa and sub-Saharan Africa are likely to double, even when we take into account the uncertainty about future HIV trends.

The China region and the South Asia region, which have approximately the same population size in 2000, are likely to follow very different trends. Owing to an earlier fertility decline, the China region is likely to have around 700 million fewer people than the South Asia region by the middle of the century. This absolute difference in population size is likely to be maintained over the entire second half of the century and illustrates the strong impact of the timing of fertility decline on eventual population size.

Our findings concerning the timing of the end of world population growth are robust to plausible changes in parameter assumptions. A detailed sensitivity analysis is provided as Supplementary Information. The forecasts of the Word Bank, the US Census Bureau, and the medium variant of the United Nations are based on independent assumptions; the median trajectory of our world forecasts is almost identical to these up until 2045. Of these three forecasts, only the UN long-range projections provide scenarios of the world’s population to the end of the century. If we define the end of population growth slightly less literally and take it to correspond with annual population growth of one-tenth of one per cent or less, the United Nations medium projection also shows the end of population growth during the second half of the century. Their medium scenario predicts that world population growth will first fall below one-tenth of one per cent at around 2075.

A stabilized or shrinking population will be a much older population. At the global level the proportion above age 60 is likely to increase from its current level of 10 per cent to around 22 per cent in 2050. This is higher than it is in western Europe today. By the end of the century it will increase to around 34 per cent, and extensive population ageing will occur in all world regions. The most extreme levels will be reached in the Pacific OECD (mostly Japan), where half of the population is likely to be age 60 and above by the end of the century, with the 80 per cent uncertainty interval...