Habitat fragmentation, percolation theory and the conservation of a keystone species

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Many species survive in specialized habitats. When these habitats are destroyed or fragmented the threat of extinction looms. In this paper, we use percolation theory to consider how an environment may fragment. We then develop a stochastic, spatially explicit, individual-based model to consider the effect of habitat fragmentation on a keystone species (the army ant *Eciton burchelli*) in a neotropical rainforest. The results suggest that species may become extinct even in huge reserves before their habitat is fully fragmented; this has important implications for conservation. We show that sustainable forest-harvesting strategies may not be as successful as is currently thought. We also suggest that habitat corridors, once thought of as the saviour for fragmented environments, may have a detrimental effect on population persistence.

Keywords: habitat fragmentation; habitat corridors; conservation; extinction; tropical rainforest; percolation theory

1. INTRODUCTION

The tropical rainforests are the most important ecosystems of all in terms of biodiversity (May 1990) and they are being destroyed at an increasing rate (Gradwohl & Greenberg 1988; Laurance & Bierregaard 1997). Because habitat destruction is the major cause of species extinction (Ehrlich & Ehrlich 1981; Wilson 1992; Lawton & May 1995), this is the greatest conservation crisis. There have been many studies on the effect of habitat loss for mammals, but there have been comparatively few studies for insects (but see Laurance & Bierregaard 1997). This lack of attention to invertebrates is surprising given that invertebrates are more species-diverse than vertebrates in tropical forests by several orders of magnitude (Fittkau & Klinge 1973; May 1990). Indeed, as far as we are aware, ours is the only work that provides long-term conservation guidelines for any of the tropical rainforest insect species (see also Partridge *et al.* 1996).

The army ant, *Eciton burchelli*, is a keystone species in certain neotropical rainforest ecosystems; many species of vertebrates and invertebrates associate with them and would surely face extinction if the army ants disappeared (Willis 1967, 1974; Willis & Oniki 1978; Ray & Andrews 1980; Stouffer & Bierregaard 1995). Their near-daily raids create a mosaic of habitat patches in different stages of ecological succession, therefore promoting species diversity (Franks 1982*a,b*). Moreover, in Central and South America 50 bird species 'professionally' follow army ant raids: they depend almost entirely on the ants to flush insect prey out of the leaf litter (Willis & Oniki 1978).

To understand the population dynamics of the army ants, we have developed a stochastic individual-based

model which deals with space explicitly. For other examples of individual-based models see DeAngelis & Gross (1992). Our model is stochastic in the sense that the movement of colonies is random and this in turn leads to a stochastic birth and death process (Nisbet & Gurney 1982; Renshaw 1993). The individual-based approach allows us to keep track of both individual colony size and the number of colonies. Owing to the nature of individual-based models, multiple realizations are necessary to examine the variance and sensitivity of the system. Our model strongly suggests that there are critical thresholds both in the size of habitat islands and in the number of degraded patches within such habitat islands, beyond which the population becomes extinct. Even with appeal to results from percolation theory, which deals with fragmentation under the random removal of sites (Stauffer 1985; With & Crist 1995), the results we obtain are both surprising and counterintuitive. Our approach enables us to question future management strategies, not only with regard to *Eciton burchelli* but for many other species exposed to habitat fragmentation. In particular, we will consider in general the cost and benefits of habitat corridors and their role in conservation.

2. NATURAL HISTORY

Eciton burchelli army ants live in colonies that can number in excess of 500 000 individuals (Schneirla 1971; Franks 1985). Their raids have a massive impact. In the course of a day's raiding, a single colony captures some 30 000 prey items, mainly other social insect species (Franks 1982*b*). These raids also flush out larger arthropods, some of which are quickly devoured by ant-following birds (Willis 1967, 1974; Willis & Oniki 1978; Stouffer & Bierregaard 1995). Colonies exhibit a 35-day

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Figure 1. The raiding trails laid out during two statary phases and one intervening nomadic phase. The length of the raids are, on average, 90 m during the statary phase and 116 m during the nomadic phase. The mean direct distance migrated between two successive statary phases is 530 m (Willis 1967; Franks & Fletcher 1983).

activity cycle (Willis 1967; Schneirla 1971; Franks 1989). For 20 days, a colony resides in a fixed bivouac (nest) from which raids emerge nearly every other day (figure 1). During this so-called statary phase, the colony's single queen lays around 100 000 eggs (Rettenmeyer 1963; Franks 1985). At the end of the 20-day period, the eggs hatch into larvae and there are now more mouths to be fed so the raiding becomes more frequent and intense. The colony now enters the nomadic phase, where a new bivouac is formed at the end of each day's raiding trail (figure 1). This behaviour lasts for about 15 days, until the larvae pupate, and a new statary phase begins. At the end of each statary phase, the pupae become new callow workers (Schneirla 1971; Franks 1989).

Such 35-day cycles continue relentlessly through wet and dry seasons. Colonies die either through queen death or simply by the colonies becoming too small (Rettenmeyer 1963; Franks 1982*b*, 1985; Partridge *et al.* 1996). The largest colonies reproduce by rearing a sexual brood and then by splitting in half (Schneirla 1971). The daughter colonies are then headed either by the existing queen or by one of the new queens reared prior to the binary fission of the original colony (Franks & Hölldobler 1987).

3. THE MODEL

Our model is consistent with that of Britton *et al.* (1996) whereby we approximate the area raided by *Eciton burchelli* as a square of side 180 m, roughly the area raided during the statary phase. We assume the effects of nomadic-phase raiding are relatively small since the colony briefly passes through an area, rather than occupying it for a considerable time (figure 1). We model time discretely, one time-step representing the 35-day activity cycle. Thus we are dealing with a discrete-time stochastic cellular automata model, also known as a patch-occupancy model (Durrett & Levin 1994; Rand & Wilson 1995). For our simulations, we chose the habitable world to be 2500 patches (i.e. 50 cells $\times$ 50 cells, or an area of rainforest 9 km $\times$ 9 km). A number of patches are then randomly removed from the lattice, with reflecting boundary conditions imposed on these patches and on the edge of the lattice. The system is then allowed to change subject to several transition rules.

1. Each colony chooses to move to any of the 24 patches at the edge of a 7 $\times$ 7 square, the centre of which is the current position (Britton *et al.* 1996). This fixes the distance a colony moves and is roughly equal to 530 m,

the direct overland distance between successive statary bivouacs (Willis 1967; Franks & Fletcher 1983). Hence, a colony can move from one square to any of the eight adjacent cells. Movement rules such as these have been used in numerous other models (Durrett & Levin 1994; Dytham 1995; Travis & Dytham 1998).

2. It moves in that direction until it hits a removed patch or the edge of the lattice at which point it reflects, like a beam of light reflected by a mirror.
3. The colony stops moving when it has migrated the distance determined in step 1.

When a colony moves onto a young patch, one that has recently been occupied and depleted of prey, it decreases in size, whereas when it lands on an old patch with plenty of prey, it increases in size. This approach is used to emulate the time it takes for an area of land to recover from the effects of raiding by army ants (Partridge *et al.* 1996). A maximum colony size is introduced and any colony exceeding this size splits into two colonies of equal size. This mimics natural behaviour (Franks 1985; Franks & Hölldobler 1987).

The reflecting boundary conditions imposed on the removed patches are consistent with observations made in Panama and elsewhere, whereby *Eciton burchelli* colonies do not move for a prolonged time into areas that have no canopy cover (Willis & Oniki 1978; Stouffer & Bierregaard 1995; N. R. Franks, personal observations).

We define a young patch to be one that has been occupied in the last six time steps (because patch recovery time is 200 days (Franks 1982*b*), a time step is 35 days and 200/35 is approximately six). Queen death is included and is assumed to occur via a Poisson process. Therefore, with probability $1/(Q \times (365/35))$ the queen, and hence the entire colony, would die during the time-step, Q being the queen's average lifespan in years (Partridge *et al.* 1996). We took $Q=6$, a not unreasonable figure (Franks 1985).

Several simulations were conducted with various numbers of removed patches, the average number of colonies only being recorded once the system had settled down to a quasi-steady state (figure 2*a*).

4. RESULTS

Our simulations yield some surprising results, particularly highlighting the importance of habitat accessibility. As the proportion of randomly removed patches approaches 0.45, the number of colonies approaches zero, i.e. extinction (figure 2*a*). What is surprising here is that extinction occurs well before the lattice is broken up into separate clusters.

Percolation theory predicts that for an infinite lattice there is a critical percolation value where the expected cluster size goes from being infinite to being finite. A finite lattice having a finite cluster size will simply smooth this transition (figure 3). Extinction is to be expected for values above this phase transition value since none of the clusters of the fragmented space would support even one colony at equilibrium. For our choice of neighbourhood—eight adjacent cells—this critical value occurs when 0.5928 of the cells have been randomly removed (Stauffer 1985). (Note, for nearest-neighbour models—the four

Figure 2. A proportion of habitat is randomly destroyed starting from 0 and changing in small increments (typically 0.04). One-tenth of the remaining habitat is then populated by colonies and the simulation is allowed to run for 500 cycles with only the last 300 iterations being recorded; this allows a quasi-steady state to be reached. The habitat is removed in various ways, (a) 1×1 blocks, (b) 2×2 non-overlapping blocks, (c) 3×3 non-overlapping blocks and (d) 4×4 non-overlapping blocks. Each such simulation is repeated ten times and the mean and standard deviation is shown. In (d) it becomes impossible to remove a 4×4 block once a certain amount of habitat is removed because the remaining habitat is of such a complex shape that it rarely contains a single block of that shape (see also figure 5). In (a), a linear decline in colony numbers is to be expected since we are not close to the critical percolation value.

closest cells—the critical value is 0.4072.) Our results show that, unexpectedly, the populations go extinct well before this threshold. We repeated the simulation using a hexagonal lattice (G. P. Boswell, unpublished data) and observed the same pattern, namely the critical extinction-causing threshold of habitat removed was significantly less than the critical percolation value.

This phenomenon occurs because even though it is not impossible for a colony to get from one site in the cluster to any other, it may be very difficult (figures 4 and 5a). Hence a colony will predominantly occupy a region of a cluster and not necessarily the whole cluster. So a habitat that appears to be continuous may be unable to support a population of *Eciton burchelli*. One way of emphasizing this finding is to remove 0.45 of the habitat as a single block and leave the remaining habitat as a single large square. This will be able to support 100 colonies almost indefinitely (Britton *et al.* 1996; Partridge *et al.* 1996).

From this perspective, it would be better to remove large square clumps of forest than long strips to lessen the fragmentation. We tested this prediction by removing the habitat as non-overlapping blocks consisting of 2×2 , 3×3 and 4×4 patches, although the blocks themselves are still removed at random (figure 5). By removing habitat as progressively larger blocks, the degree of fragmentation decreases and the army ants' ability to persist increases (figure 2). For example, by removing 50% of the habitat as single patches, persistence is impossible. However, if the same amount of habitat is removed, but as 4×4

Figure 3. The size of the largest remaining cluster plotted as a function of the fraction of patches removed (where patches are removed totally at random). Two patches are neighbours of one another, and hence in the same clusters in the sense of nearest and next-nearest neighbours. Notice that even when half the patches are removed, the lattice still often consists of just one cluster or one large and a few very small clusters. (Hence it is possible to get from almost any one habitable patch to almost any other habitable patch.) In fact, the critical percolation value in this instance occurs when 0.4072 of the patches exist, i.e. when 0.5928 are removed (Stauffer 1985).

Figure 4. A snapshot of the lattice with 1000 patches removed. The red squares are those patches currently occupied: the darker the shade, the larger the colony. The white squares represent the removed patches. The blue squares are the young patches: the darker the shading, the more recent the raiding. The green squares represent the old patches, recovered forest. Finally, notice that the lattice basically consists of a single cluster, but is not far short of completely fragmenting.

blocks, some 70 colonies are able to persist at the quasi-steady state.

5. DISCUSSION

The importance of these results can be seen when one considers so-called sustainable forest management

Figure 5. The effect of 'randomly' removing 40% of the habitat from a 50×50 lattice. The black patches represent the removed habitat; the white patches represent forested areas. (a) The patches are removed totally at random. (b) The patches are removed in blocks of four patches (i.e. 2×2). (c) The patches are removed in blocks of 3×3 . (d) Patches removed in blocks of 4×4 .

strategies, which involve felling long strips of woodland (Hartshorn 1989, 1995) so that a large forest is broken up into strips. These forested strips are internally fragmented by streams, roads, tree-fall gaps, etc., so that the actual cluster size may be a great deal smaller than one might be first led to believe. Our simulations predict that if the clusters are too small, or too inaccessible, then (at the very least) the army ant *Eciton burchelli* will become locally extinct.

A number of other authors have examined the effect of habitat removal on population persistence (Dytham 1995; With & Crist 1995; Bascompte & Solé 1996). For example, Dytham (1995) examined the effect of habitat removal on two interacting populations but did not interpret his results using percolation theory. He investigated how two species in competition fared in a fragmented environment where one was a superior disperser. His neighbourhood rules were the same as ours, namely direct movement into the eight adjacent cells. The poorer disperser went extinct while the habitat was still connected; the better disperser persisted until the percolation critical value was achieved, at which point there was a sudden shift in the abundance of this species. These results are entirely to be expected with the use of percolation theory (see also With & Crist 1995; Bascompte & Solé 1996).

Our results suggest that a better sustainable forest-harvesting strategy is to remove reasonably large square-like clumps. Of course, this is a very one-sided view. It is going to take less time for the forest to recover if felling is in the form of a long strip than a square clump. However, the value of faster recovery would be diminished because it would involve a cost: species reduction.

These results also raise questions about habitat corridors between reserves. For species that possess no 'long-term memory', that is to say they do not remember how they arrived at some point in space—as is the case for army ants—corridors between reserves have to be sufficiently large so that first the corridors can be found, and second they can be negotiated successfully. It is hard to lay down any figures on minimum corridor size, since differently shaped lattices and different models for local movements will yield different answers. However, these results certainly suggest that there is a minimum corridor width between small reserves to ensure the persistence of a population, because we observed persistence to be impossible if pockets of habitat are hard to find.

We have seen that geometrically complicated reserves are of little use to this keystone species: a colony becomes trapped in a small pocket of rainforest, depleting its local resources and thus facing starvation. It could be possible for this situation to be repeated in a habitat corridor and an individual (with poor or no navigational skills) enters a corridor, wanders back and forth, depleting its resources, and therefore leading to starvation. Given that the characteristics of habitat corridors are species-specific (Hobbs 1992), we could design a corridor that would suit one species but might be detrimental to others. In other words, habitat corridors may not be a solution to species loss through fragmentation, but could escalate the problem further. We are currently investigating this possibility.

Of course the equilibrium number of colonies does not tell the whole story. Almost surely any population will eventually become extinct (MacArthur & Wilson 1967; Mangel & Tier 1994). However, the time to extinction depends very strongly on the equilibrium number of colonies (Partridge *et al.* 1996), and this emphasizes the importance of not allowing the equilibrium number of colonies to fall too low.

We conclude that any future strategy for tropical rainforest management is going to have to take a great many issues on board: to look not only at short-term solutions but at more long-term effects as well. Conservationists must examine the trade-off between quicker forest recovery and an increased risk of extinction of certain species.

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