Dynamics of metapopulations: habitat destruction and competitive coexistence

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Summary

1. We take a previously studied model for two species — one of which is competitively inferior — coexisting in a patchy environment, and examine the effects of removing patches (that is, of decreasing the amount of available habitat).

2. Habitat destruction or patch removal reduces the number (and proportion) of patches occupied by the superior competitor, but can result in an increase in the total number of patches occupied by the inferior competitor (even though there are fewer patches in total).

3. It has long been appreciated that disturbance and destruction of habitat can create edge effects and other ecological changes favouring ‘weedy’ species. The present study suggests that patch removal can by itself favour such species, even in the absence of other, concomitant changes.

4. An implication relevant to conservation biology is that habitat loss can bring about changes in community composition in remaining patches, even if such patches themselves undergo no intrinsic changes whatsoever.

Key-words: competition, conservation biology, habitat loss, metapopulations.

Introduction

Many species exist as metapopulations in a fragmented world, facing inevitable extinction in any occupied patch, but persisting regionally by dispersal into unoccupied patches. It has long been recognized that two species may coexist as metapopulations even if one is competitively superior within a patch, as long as the inferior competitor either disperses more effectively or has a lower patch extinction rate (Skellam 1951; Hutchinson 1951; Levins & Culver 1971; Horn & MacArthur 1972; Slatkin 1974; Hastings 1980; Hanski & Ranta 1983; Hanski 1983, 1987), or even in the absence of these off-setting advantages if the superior competitor’s distribution is sufficiently clumped (Atkinson & Shorrocks 1981, 1984; Shorrocks, 1990; Ives & May 1985).

In this paper we analyse the effect of patch removal on the regional abundances of two such species. We find that patch thinning decreases both the number of patches occupied by the superior competitor and the number of empty patches, i.e. patches occupied by neither species. At the same time, the number (and, of course, the proportion) of patches occupied by the inferior competitor initially increases. Thus, patch removal or habitat destruction can actually increase the regional abundance of inferior competitors. We discuss the implications of these results for understanding biodiversity changes in a changing world.

Model

For simplicity, we make the extreme assumption that the inferior competitor, B, is unable to invade a patch occupied by the superior competitor, A. Furthermore, if A invades a patch occupied by B then B is immediately extinguished. The analysis can clearly be extended to less extreme cases where the difference in competitive ability between the two species is at some intermediate level (with results that are qualitatively similar); we choose not to pursue such elaborations. A and B have colonization rates $c_A$ and $c_B$ respectively, and extinction rates $e_A$ and $e_B$. We will consider an environment consisting of a large number of patches, of which a fraction $h$ (for ‘habitable’) is suitable for occupancy by the species, although some may actually be empty at any particular time. If we let $x$, $y$ and $z$ denote the proportion of empty patches, A-only patches and B-only patches respectively in the environment, the following equations correspond to the kinetic diagram in Fig. 1.

\[
\frac{dx}{dt} = -c_A xy + e_A x - c_B xz + e_B z, \quad \text{eqn 1a}
\]
Habitat destruction

\[
\begin{align*}
\frac{dy}{dt} &= c_A xy - e_A y + c_A z y, \quad \text{eqn 1b} \\
\frac{dz}{dt} &= c_B x - e_B z - c_A z y. \quad \text{eqn 1c}
\end{align*}
\]

This is actually a two-dimensional system because \(x + y + z = h\).

Subject to the feasibility constraint that \(x, y, \text{ and } z\) are all greater than zero, these equations have the equilibrium solution

\[
\begin{align*}
x^* &= \frac{1}{c_B} (hc_A - e_A + e_B) \quad \text{eqn 2a} \\
y^* &= h - \frac{e_A}{c_A} \quad \text{eqn 2b} \\
z^* &= \frac{e_A(c_A + c_B)}{c_Ac_B} \frac{e_B}{c_B} - \frac{hc_A}{c_Ac_B} \quad \text{eqn 2c}
\end{align*}
\]

In this system, feasible equilibria are locally stable and species with feasible equilibria can increase when rare.

A necessary condition for the inferior competitor to persist in this system is

\[
\frac{e_B}{c_B} > \frac{e_A}{c_A} \quad \text{eqn 3}
\]

This may be satisfied if the inferior competitor has a fugitive life style characterized by a high colonization rate: our typical notion of a ‘weed’. But the inferior competitor may also persist if it has a lower colonization rate, provided it has an even lower extinction rate as well. This case corresponds to, among other things, a species which uses its local resources in a frugal fashion and may fall victim to a profligate glutton of depletable resources.

We can immediately see from the equilibrium solutions that patch removal, i.e. lowering \(h\), actually:

1. increases the total number of patches occupied by the inferior competitor (i.e. increases the proportion of all patches, destroyed plus still existing, occupied by this inferior competitor);
2. lowers the number of patches occupied by the superior competitor; and
3. lowers the number of empty (but not destroyed) patches.

If the inferior competitor is a superior colonizer, then the overall number of occupied patches falls. If it is an inferior colonizer, then the overall number of occupied patches rises. When \(h\) falls below a critical value of its extinction/colonization ratio \((h < e_A/c_A)\), the superior competitor can no longer persist. Beyond this point, only the inferior competitor is found and the number of patches it occupies declines as \(h\) decreases further. Finally, as patch removal or destruction continues \((h\) decreases still further), the inferior competitor also disappears \((h < e_B/c_B)\).

Fig. 2 illustrates these numbers (or frequencies, expressed in relation to the pristine number of patches) as functions of \(h\), for the special case in which both species have the same extinction rate, but the inferior competitor has a higher colonization rate. Fig. 3 explains the result.

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\[
\begin{align*}
\text{Fig. 1.} \quad \text{The structure of the model analysed in the text. See text for an explanation of the symbols.}
\end{align*}
\]

\[
\begin{align*}
\text{Fig. 2.} \quad \text{Illustrating the relative proportions of empty ( ), species A-only ( ) and species B-only ( ) patches (}, x^*, y^*, z^*, \text{ respectively) as functions of the fraction of all patches (}h\text{) that are habitable or have not been destroyed. The figure shows the stable equilibrium solutions of equations 1 in the simplified case when extinction rates are equal (}e_A = e_B = e). \text{ For } 1 > h > e/c_A, \text{ both species coexist in the proportions given by equation 2; for } e/c_A > h > e/c_B, \text{ only the more vagile but competitively inferior species } B \text{ can persist (}z^* = h - e/c_B, x^* = e/c_B); \text{ and for } h < e/c_B \text{ all patches are empty.}
\end{align*}
\]

\[
\begin{align*}
\text{Fig. 3.} \quad \text{The direct effect of patch removal on both species is negative, lowering the number of new patches they colonize per unit time. The direct effect of the superior competitor on the inferior is negative in two ways: first, it raises its overall extinction rate and, secondly, lowers the number of patches available for colonization by the inferior competitor. So patch removal indirectly benefits the inferior competitor by lowering the frequency of patches occupied by the superior competitor.}
\end{align*}
\]
Discussion

As Lande (1987) has emphasized in a single species context, we do not have to destroy all patches to extinguish a metapopulation that persists by virtue of a balance between local extinctions and recolonizations in a mosaic environment. Vaccination programmes that eradicate infection without having to reach every individual host (or ‘patch’) provide concrete illustrations of this principle (Anderson & May 1985). The present note goes beyond earlier work to emphasize the counter-intuitive effects that patch removal can have on populations of competing species. Inferior competitors persist by virtue of colonizing empty patches, so it is surprising that removing patches increases their regional abundance. It is often observed that habitat fragmentation or patch destruction can favour ‘weedy’ species over those that are more commonly of concern to conservationists, and this phenomenon is usually attributed to disturbance and/or edge effects favouring such weedy species. While these conventional explanations undoubtedly explain much of what is observed, the present work emphasizes that patch removal per se can favour weedy species and extinguish other species even in the total absence of edge-effects or other forms of habitat disturbance within the remaining habitats.

Weedy species are not the only kind to be favoured by patch removal. Inferior competitors may be organisms with lower colonization rates but which consume local resources in a slow, more sustainable fashion and can be starved by overconsuming weedy species. Focusing only on competitive relationships of this sort, our results show that patch removal can actually increase the biodiversity in the remaining patches, as the number of patches that are occupied by neither species declines. Obviously, this result should not induce complacency about the consequences of the habitat removal that is occurring around the world. Rather, it serves to highlight the fact that the consequences of patch removal for biodiversity may be non-obvious. Understanding these consequences is a challenging goal for pure, as well as applied, research in ecology.

The notion that environmental degradation may have counter-intuitive consequences receives further support from a theoretical analysis of Hastings (1980). His study explores the effects of changes in patch extinction rates (e, in Model 1) on the number of co-existing competitors. In a model in which all the species in a competitive hierarchy have the same patch extinction rate, e, Hastings finds that as e increases, the number of species that coexist does not necessarily change in any simple fashion, but can rise and fall several times.

One study that is explicitly relevant to our work is of the patterns of occurrence of *Daphnia* species in rock pools on islands with different numbers of pools (Hanski & Ranta 1983; for a re-analysis, see Bengtsson 1991). They showed that coexistence between competing species which differ in competitive and dispersive ability is facilitated by a larger number of patches. This foreshadows our work, the purpose of which is to provide simple, qualitative insights into the effects of patch removal on equilibrium species abundances. Such questions are enjoying a surge of interest in today’s green intellectual climate and are readily addressed with this sort of phenomenological modelling (MacArthur & Wilson 1967; Levins 1969). We will explore the more complex consequences of patch removal on predator–prey relationships elsewhere.

The model can be looked at from viewpoints other than those adopted here. The consequences of patch addition may be of more relevance to European ecology, if the farmland that is being removed from agriculture over the next decades is not simply paved over.

References


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