Metapopulation dynamics

Key concepts

- Patch occupancy

- Two-patch dynamics

- Levins metapopulation model

- Mainland-island metapopulation model

- Metapopulation meltdown

Introduction

We begin this chapter with the observation that species are not ubiquitously distributed. Does population ecology have an explanation for this?

The models we have studied so far allow that a species may not persist in environments where its fitness is low, for instance where the intrinsic rate of increase is less than one. In such cases extinction is the stable state. Of course, habitat (which we may define as environmental conditions such that $r > 0$) is not uniformly distributed. For instance, the Glanville fritillary butterfly (*Melitaea cinxia*) is widely distributed across Europe and Asia, but reproduces only in open meadows. In the Åland islands of Finland the Glanville fritillary is found only in small meadows containing one or both of two plant species, *Plantago lanceolata* and *Veronica spicata*, which serve as hosts to the butterfly in its larval stage.[1] Due to the small size of these meadows, populations of the Glanville fritillary are routinely extirpated and the species exists in a delicate balance between extinction and recolonization from other patches (Figure 2). Thus, for instance, among ≈ 1600 meadows surveyed since 1993 and known to be suitable for growth and reproduction, in any given year only between about 320 and 640 meadows are occupied by the butterfly. That is, the patch occupancy of the Glanville fritillary butterfly is between 20% and 40%.

Figure 1: The Glanville fritillary butterfly (*Melitaea cinxia*).

[1] I.A. Hanski. Eco-evolutionary spatial dynamics in the Glanville fritillary butterfly. *Proceedings of the National Academy of Sciences of the United States of America*, 108(35):14397–404, 2011

The aim of this chapter is to understand such cases of partial habitat occupancy.

Two-patch models

A first step toward understanding the dynamics of species that move among patches is to consider a population comprised of two linked patches. For instance, we may assume that the dynamics in the individual patches are governed by logistic-like density dependence, coupled together by a small amount of migration. Thus, we have the following system of coupled equations

$$dn_1/dt = n_1 r_1 (1 - n_1/k_1) - \epsilon n_1 + \epsilon n_2 \qquad (1)$$

$$dn_2/dt = n_2 r_2 (1 - n_2/k_2) - \epsilon n_2 + \epsilon n_1. \qquad (2)$$

In this model n_1 and n_2 are the sizes of the populations in patches 1 and 2 respectively and r_i and k_i are the intrinsic rate of increase and carrying capacity of the ith population; ϵ is a migration rate. Holt[2] has studied this model in detail, including versions that allow for very different kinds of density dependence.

    We will first investigate this model graphically. To begin we plot the *nullclines*. Recalling that an equilibrium of the system is a state in which the rate of change in zero, we alternately set the two equations to zero and solve for n_2 in terms on n_1. The resulting curves (Figure 3) are the set of points at which each of the equations in 1 is equal to zero. Where they intersect both equations are at zero and the population as a whole is at equilibrium. For comparison, the carrying capacities of the patches considered in isolation are plotted as dashed lines.

[2] Robert D Holt. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology*, 28(2):181–208, 1985
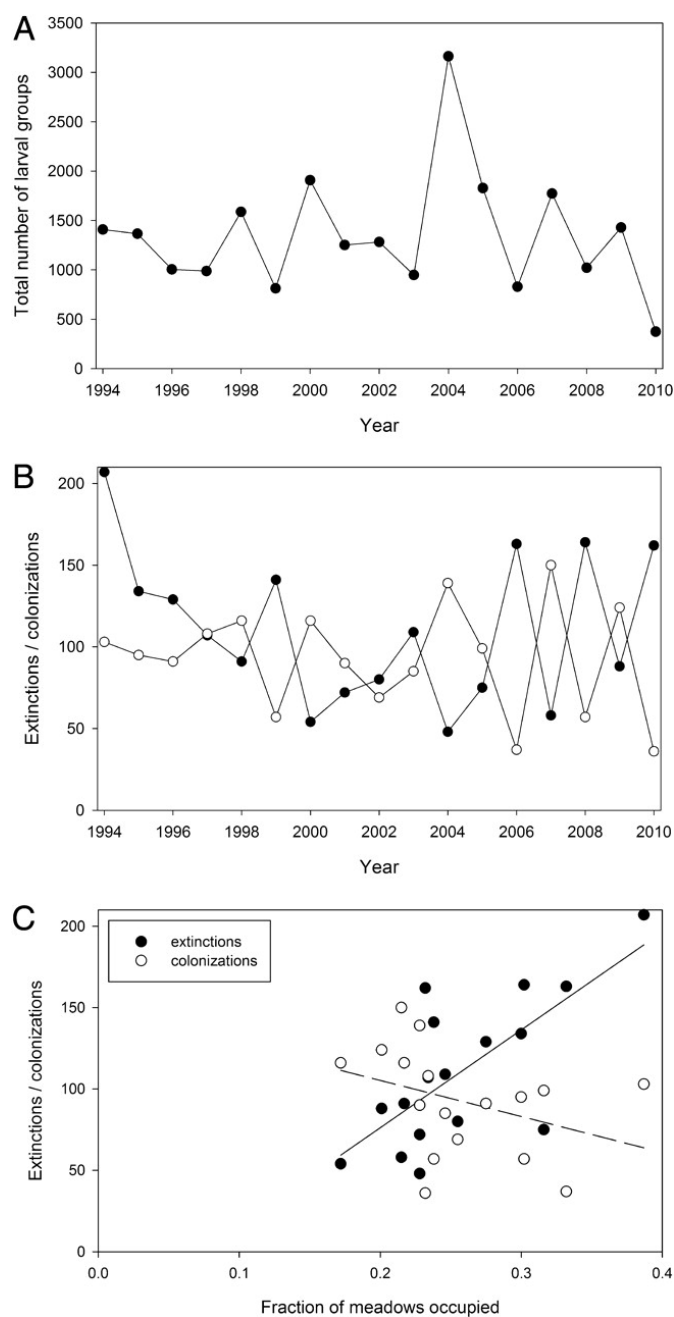
Figure 2: Colonization-extinction balance in The Glanville fritillary butterflies of the Åland Islands. (A) Metapopulation size is sometimes quantified as the number of larval groups where meadows may contain from 1-150 larval groups, each of which is the result of a single clutch of eggs. (B) Number of extinctions and colonizations among ≈ 1600 surveyed meadows in 1993-2010. (C) Extinctions and colonizations from (B) plotted against patch occupancy for the same period. (Figure reproduced from Hanski (2011).)

In the special case of high dispersal (technically the $\epsilon \to \infty$ limit), the equilibrium sizes of the two populations are equal:

$$n_1^* = n_2^* = n^* = \frac{r_1 + r_2}{r_1/k1 + r_2/k_2}. \tag{3}$$

The size of the two populations together is just

$$n_{\text{total}}^* = 2n^* = 2(r_1 + r_2)/(r_1/k1 + r_2/k_2). \tag{4}$$

How is this different than if there had not been any migration between the two populations? To answer this question we recognize that if $\epsilon = 0$ the equations in 1 become decoupled logistic models with equilibrium sizes $n_1^* = k_1$ and $n_2^* = k_2$ for a total of $k_1 + k_2$. The difference in total population size as a result of dispersal may then be calculated as

$$k_1 + k_2 - n_{\text{total}}^* = \frac{(k_1 - k_2)(k_1 r_2 - k_2 r_1)}{k_1 r_2 + k_2 r_1}. \tag{5}$$

This equation is zero if $k_1 = k_2$ because the first term in the numerator will be zero. This means that if the carrying capacities of the two patches are identical, then dispersal has no effect on the total population size. Additionally, if $r_1/k_1 = r_2/k_2$ then the second term in the numerator will be zero and the carrying capacity of the coupled populations will be identical to the sum of the carrying capacities of the isolated populations. Since the per capita growth rate in a logistic model may be written as

$$\frac{1}{n}\frac{dn}{dt} = r - \frac{r}{k}n, \tag{6}$$

we see that the effect of density dependence is to reduce the intrinsic rate of increase r by a factor r/k. Thus, r/k measures the *strength of density dependence* and we conclude that if the strength of density dependence is equal in both patches then the total carrying capacity is unaffected by dispersal. What if neither of these conditions holds? For concreteness, we order the two equations so that $k_1 > k_2$. Then, from equation 5, if $r_2/k_2 > r_1/k_1$ the decoupled populations will have a greater total size than those coupled by dispersal. That is, if the strength of density dependence is greater in the population with a smaller carrying capacity, then dispersal reduces the overall population size. By contrast, if $r_2/k_2 < r_1/k_1$ the effect of dispersal is to increase the total population size. In conclusion, rapid dispersal causes the average size of the two populations $(n_{\text{total}}^*/2)$ to tend toward the carrying capacity of the patch with stronger density dependence. If this is the patch with the greater carrying capacity, dispersal acts
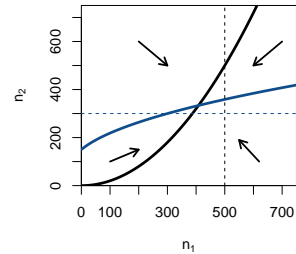

Figure 3: Nullclines of the two-patch model given by equations 1. Black designates the nullcline of n_1 while blue designates the nullcline of n_2. The dashed lines show the corresponding carrying capacities. Since the sizes of the coupled populations at equilibrium are given by the intersection of the solid lines, which lies to the left of the carrying capacity for patch 1 and abive the carrying capacity for patch 2, we conclude that in this population dispersal causes the abundance in patch 1 to be less than would occur if the patch existed in isolation while the abundance in patch 2 is greater than would occur if the patch existed in isolation. The arrows show the net direction that the dynamics will take in the four regions delineated by the intersecting nullclines. Parameters used in this example are $r_1 = 1$, $r_2 = 2$, $k_1 = 500$, $k_2 = 300$, and $\epsilon = 1$.

to increase abundance overall. If this is the patch with the smaller carrying capacity, dispersal acts to decrease abundance overall.

Classical metapopulation dynamics

In this section we seek to "scale up" from the two-patch model developed in the preceding section to consider the dynamics of a population on an arbitrary number of patches. Unfortunately, it is not feasible to simply add more equations to the existing system of two equations. Some simple calculations show why. In general, if the dynamics of a population in one patch require one state variable and h parameters, then the analogous models for an v-patch model will require v state variables and $h \times m$ parameters resulting in a total of $v + vh = v(h + 1)$ quantities overall. Even if we could solve all these equations (for instance, using a computer) the result would be so complicated that it would yield little insight. Besides, such an approach tracks a great deal more information than we actually require. To show why, we make a few assumptions for a species that has the kind of patchy distribution exemplified by the Glanville fritillary butterfly:

- Colonization and extinction of patches is slow compared with the growth of a population in a patch; this means that occupied patches will typically be very close to carrying capacity.

- The average carrying capacity among the v patches is k.

- Population colonization and extinction are not related to properties of the patch, including current population size.

Denoting the number of occupied patches by u, if these assumptions hold, then to a first approximation the total abundance of the population is $(u/v)k$. What's more, for patchily distributed species we are often less concerned with the total abundance than with the number of populations. Finally, patch occupancy, which we will designated by $p = u/v$, will be much more sensitive to factors affecting colonization and extinction than to the growth parameters govering dynamics within a population. Clearly, a different approach will be needed to scale up to the metapopulation level.

The approach we take here was first introduced by Levins.[3] A graphical depiction of the *Levins metapopulation model* is shown in Figure 4. Our objective is an equation for the change in patch occupancy (p) with respect to time. Unoccupied patches (of frequency $v - u$) become occupied through colonization. Occupied patches become unoccupied through extinction. We denote the per patch extinction rate by the parameter γ. Since this rate applies on a per patch basis, to calculate the overall rate of extinction in the population we

[3] R Levins. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, 15(3):237–240, 1969

multiply by the number of occupied patches u yielding total extinction rate γu. Finally, since extinction reduces patch occupancy, the sign on this rate is negative. To derive the colonization rate, we first denote the per patch production of migrating individuals by m. The total production of migrants over all u occupied patches is therefore mu. Colonization by these migrants after dispersal requires that they arrive at an unoccupied patch. Thus, for instance, as patch occupancy gets large finding a vacant patch gets harder and harder. If we assume that migrants arrive at patches irrespective of their occupancy status, then the rate of colonization will be proportional to the fraction of unoccupied patches available to be colonized. Thus, colonization occurs at rate $mu(1 - u/v)$ Together, these considerations give rise to the following equation:

$$\frac{du}{dt} = \overbrace{mu\left(1 - \frac{u}{v}\right)}^{\text{colonization}} - \underbrace{\gamma u}_{\text{extinction}}. \tag{7}$$

Conventionally, we recast this equation in terms of the patch occupancy $p = u/v$). Dividing both sides of equation 7 by the total number of patches v we have

$$\frac{1}{v}\frac{du}{dt} = m\frac{u}{v}\left(1 - \frac{u}{v}\right) - \gamma\frac{u}{v}, \tag{8}$$

which, on recalling our definition of p, may be written as

$$\frac{dp}{dt} = mp(1 - p) - \gamma p. \tag{9}$$

Setting equation 9 to zero and solving for p obtains the equilibrium patch occupancy:

$$mp(1 - p) - \gamma p = 0 \tag{10}$$
$$mp(1 - p) = \gamma p \tag{11}$$
$$m(1 - p) = \gamma \tag{12}$$
$$1 - p = \gamma/m \tag{13}$$
$$p^*_{\text{Levins}} = 1 - \gamma/m. \tag{14}$$

From this equation we can draw two immediate conclusions:

- Since this equation can only equal 1 if $\gamma/m = 0$ we conclude that at equilibrium not all sites are occupied unless $\gamma = 0$.

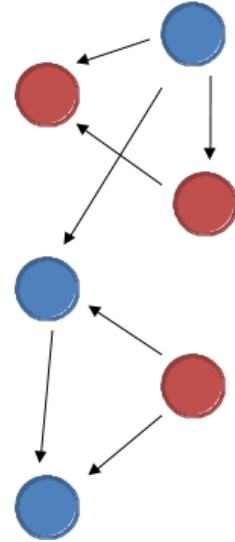- For persistence ($p^* > 0$), m must be greater than γ

Figure 4: Spatial structure of a classical metapopulation. Occupied patches are represented in blue and vacant patches are represeted in red.

Evidently, persistence in such a "classical" metapopulation depends on the delicate balance between extinction and colonization. This is because the entire population exhibits a tentative existense, shifting from patch to patch in a wave of colonization seeking to outrun the tide of extinction that inevitably follows – just as has been observed to occur in the Åland metapopulation of the Glanville fritillary butterfly.

Mainland-island metapopulation dynamics

Not all patchy populations are so precariously positioned. A variation on this model, the *mainland-island model*, supposes that in addition to the ephemeral patches there exists one or more robust populations (Figure 5). By assumption, these populations are large, justifying two additional assuptions:

- Extinction of the mainland population is so unlikely that it may be ignored.

- Production of propagules by the mainland population is so great that this *propagule rain* swamps migration from the patch populations.

If these assumptions hold, then we may replace the term mp in equation 9 by a constant *colonization rate* c, yielding

$$dp/dt = c(1 - p) - \gamma p. \tag{15}$$

This equation is to be interpreted with respect to occupancy only of the patches. That is, the mainland isn't considered in the fraction p. Setting equation 15 to zero and solving for p obtains the equilibrium patch occupancy:

$$c(1 - p) - \gamma p = 0 \tag{16}$$
$$c - cp = \gamma p \tag{17}$$
$$c = cp + \gamma p \tag{18}$$
$$c = p(c + \gamma) \tag{19}$$
$$p^*_{\text{Mainland-island}} = c/(c + \gamma). \tag{20}$$

From this equation we can draw two immediate conclusions:

- At equilibrium, not all sites are occupied unless $\gamma = 0$.

- The population persists for all $c > 0$.

Evidently, only a classical metapopulation may go extinct. However, both classical and mainland-island metapopulations may be far from fully occupied.
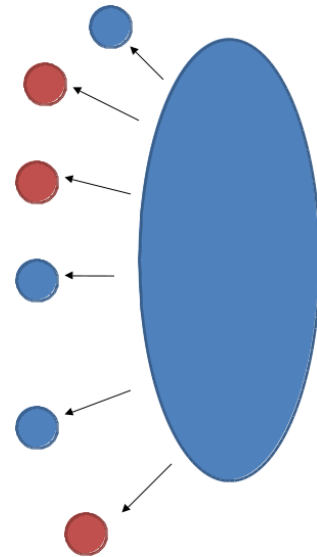

Figure 5: Spatial structure of a mainland-island metapopulation. Occupied patches are reprsented in blue and vacant patches are represeted in red.

Application

What are the implications of metapopulation theory for conservation practice? The main implication is that populations exhibiting a classical metapopulation structure require vacant patches for persistence. That is, just because a patch isn't currently occupied does not imply that it is unimportant to the persistence of the species. It may be important as a site for colonization and subsequent propagation as other, currently occupied sites, face extinction. Consider what happens in a metapopulation when vacant sites are investigated for the presence of species of conservation concern and then permitted for development if the species is not recorded. Starting with some large number of populations, say $v_0 = 1000$, only a fraction of them, p^*, are occupied. Of the remaining $1000 \times (1 - p^*)$ unoccupied patches some fraction $\alpha < 1$ are removed from the metapopulation. Now the entire patch system consists of $v_1 = 1000 - 1000(1 - p^*)\alpha = 1000(1 - \alpha + \alpha p^*)$ patches. Over time the metapopulation re-equilibrates and now $v_1(1 - p^*)$ patches are occupied. Again the metapopulation is censused and a fraction α are removed from the metapopulation, yielding a total of $v_2 = v_1(1 - \alpha + \alpha p^*)$ patches. In the long run the result is complete *metapopulation meltdown* as vacant patches are removed and the metapopulation re-equilibrates in repeated bouts of colonization, extinction, and removal. Assuming that metapopulation dynamics are sufficiently fast that equilibration occurs within each bout of patch removal we may write down a difference equation for the number of occupied patches in the metapopulation,

$$u_{t+1} = p^* v_t = v_t(1 - \alpha + \alpha p^*)p^*, \tag{21}$$

with general solution

$$u_t = (1 - \alpha + \alpha p^*)^t v_0 p^*. \tag{22}$$

This result is plotted in Figure 6 for various values of p^* and α.

For conservation, this means that evaluations of environmental impact should consider not only the species present but also those species in the larger region that may intermittently depend on habitat at the site for long-term persistence. This consequence holds only for classical metapopulations, not mainland-island metapopulations, which persist because of the robustness of the mainland metapopulation and will continue to persist as long as the mainland population is a reliable source of propagules regardless of how many satellite patches are removed from the population.
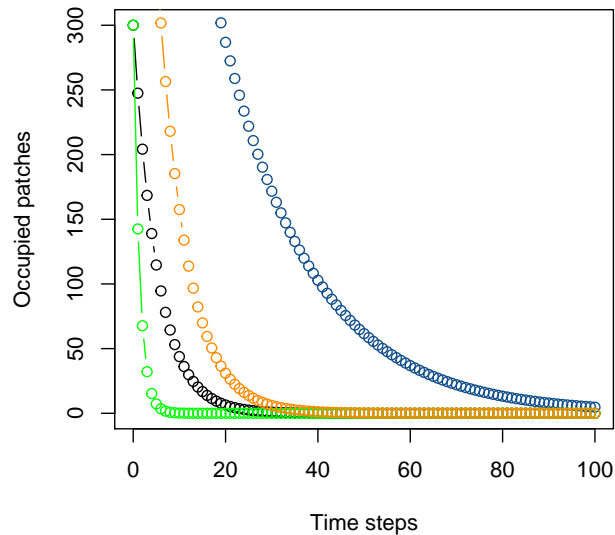
Figure 6: Metapopulation meltdown from removal of unoccupied patches for $v_0 = 1000$ total patches and ($p^* = 0.8$, $\alpha = 0.25$) in blue, ($p^* = 0.8$, $\alpha = 0.75$) in orange, ($p^* = 0.3$, $\alpha = 0.25$) in black, and ($p^* = 0.3$, $\alpha = 0.75$) in green.

Test yourself

- A species exhibits a metapopulation structure if its occupancy depends on the balance of _____ and _____.

- How does the carrying capacity of a two-patch system differ from the sum of the carrying capacities of the component patches?

- What is the condition for a metapopulation to be fully occupied?

- What is a metapopulation meltdown and how does this occur?

Homework

1. Sketch nullclines for a two-patch model with very small ϵ and very large ϵ. How do these plots differ from Figure 3

2. Sketch the curves describing eqilibrium patch occupancy of the classical and mainland-island metapopulations (equations 10 and 16). How does patch occupancy depend on such parameters as m, γ, and c?

3. Are the data in Figure 2 more consistent with a classical or mainland-island metapopulation model?

Bibliography

[1] I.A. Hanski. Eco-evolutionary spatial dynamics in the Glanville fritillary butterfly. *Proceedings of the National Academy of Sciences of the United States of America*, 108(35):14397–404, 2011.

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