

Additionally, he said, there are about 40 percent more ticks on each mouse.

The researchers tested the effect of acorns by manipulating the population of mice and the availability of acorns in forest plots along the Hudson River. Jones said the work, extended over several seasons, proved the theory that mice and tick populations rise and fall based on the availability of acorns.

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*How could a key factor analysis be used to pinpoint the phases of importance in determining risk of human disease?*

## 9.3 Dispersal, patches and metapopulation dynamics

dispersal is ignored at the ecologist's peril

In many studies of abundance, the assumption has been made that the major events all occur within the study area, and that immigrants and emigrants can safely be ignored. But migration can be a vital factor in determining and/or regulating abundance. We have already seen, for example, that emigration was the predominant reason for the loss of summer adults of the Colorado potato beetle, which was both the key phase in determining population fluctuations and one in which loss was strongly density-dependent.

habitable sites and dispersal distance

Dispersal has a particularly important role to play when populations are fragmented and patchy – as many are. The abundance of patchily distributed organisms can be thought of as being determined by the properties of two features: the ‘habitable site’ and the ‘dispersal distance’ (Gadgil, 1971). Thus, a population may be small if its habitable sites are themselves small or short-lived or only few in number; but it may also be small if the dispersal distance between habitable sites is great relative to the dispersibility of the species, such that habitable sites that go extinct locally are unlikely to be recolonized.

To discover the limitations that the accessibility of habitable sites places on abundance, though, it is necessary to identify habitable sites that are not inhabited. This is possible, for example, for a number of butterfly species, because their larvae feed only on one or a few species of patchily distributed plants. Thus, by identifying habitable sites with these plants, whether or not they were inhabited, Thomas et al. (1992) found that the silver-studded blue butterfly *Plebejus argus* was able to colonize virtually all habitable sites less than 1 km from existing populations, but those further away (beyond the dispersal powers of the butterfly) remained uninhabited. The overall size of the population was determined as much by the accessibility of this patchy resource as by the total amount of the resource. Indeed, the habitability of some of these isolated sites was established when the butterfly was successfully introduced there (Thomas & Harrison, 1992). This, after all, is the crucial test of whether an uninhabited ‘habitable’ site is really habitable or not.

metapopulations

A radical change in the way ecologists think about populations has involved combining patchiness and dispersal in the concept of a *metapopulation*, the origins of which are described in Box 9.3. A population can be described as a



## 9.3 HISTORICAL LANDMARKS

### 9.3 Historical landmarks

#### The genesis of metapopulation theory

A classic book, *The Theory of Island Biogeography*, written by MacArthur and Wilson and published in 1967, was an important catalyst in radically changing ecological theory. They showed how the distribution of species on islands could be interpreted as a balance between the opposing forces of extinctions and colonizations (see Chapter 10) and focused attention especially on situations in which those species were all available for repeated colonization of individual islands from a common source – the mainland. They developed their ideas in the context of the floras and faunas of real (i.e. oceanic) islands, but their thinking has been rapidly assimilated into much wider contexts with the realization that patches everywhere have many of the properties of true islands – ponds as islands of water in a sea of land, trees as islands in a sea of grass, and so on.

At about the same time as MacArthur and Wilson's book was published, a simple model of 'metapopulation dynamics' was proposed by Levins (1969). The concept of a *metapopulation* was introduced to refer to a subdivided and patchy population in which the population dynamics operate at two levels:

- 1 The dynamics of individuals within patches (determined by the usual demographic forces of birth, death and movement).
- 2 The dynamics of the occupied patches (or 'subpopulations') themselves within the overall metapopulation (determined by the rates of colonization of empty patches and of extinction within occupied patches).

Although both this and MacArthur and Wilson's theory embraced the idea of patchiness, and both focused on colonization and extinction rather than the details of local dynamics, MacArthur and Wilson's theory was based on a vision of mainlands as rich sources of colonists for whole archipelagos of islands, whereas in a metapopulation there is a collection of patches but no such dominating mainland.

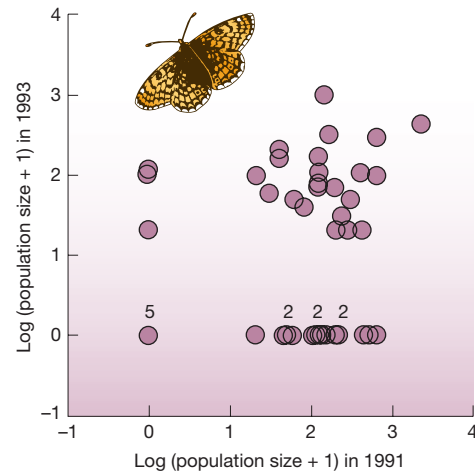
Levins introduced the variable  $p(t)$ , the fraction of habitat patches occupied at time  $t$ . Note that the use of this single variable carries the profound notion that not all habitable patches are always inhabited. The rate of change in  $p(t)$  depends on the rate of local extinction of patches and the rate of colonization of empty patches. It is not necessary to go into the details of Levin's model; suffice to say that as long as the intrinsic rate of colonization exceeds the intrinsic rate of extinction within patches, the total metapopulation will reach a stable, equilibrium fraction of occupied patches, even if none of the local populations is stable in its own right.

Perhaps because of the powerful influence on ecology of MacArthur and Wilson's theory, the whole idea of metapopulations was largely neglected during the 20 years after Levins's initial work. The 1990s, however, saw a great flowering of interest, both in underlying theory and in populations in nature that might conform to the metapopulation concept (Hanski, 1999).

metapopulation if it can be seen to comprise a collection of subpopulations, each one of which has a realistic chance both of going extinct and of appearing again through recolonization. The essence is a change of focus: less emphasis is given to the birth, death and movement processes going on within a single subpopulation; but much more emphasis is given to the colonization (= birth) and extinction (= death) of subpopulations within the metapopulation as a whole. From this

**Figure 9.8**

Comparison of the subpopulation sizes in June 1991 (adults) and August 1993 (larvae) of the Glanville fritillary butterfly (*Melitaea cinxia*) on Åland Island in Finland. Multiple data points are indicated by numbers. Many 1991 populations, including many of the largest, had become extinct by 1993.



AFTER HANSKI ET AL., 1995

perspective, it becomes apparent that a metapopulation may persist, stably, as a result of the balance between extinctions and recolonizations, even though none of the local subpopulations is stable in its own right. An example of this is shown in Figure 9.8, where within a persistent, highly fragmented metapopulation of the Glanville fritillary butterfly (*Melitaea cinxia*) in Finland, even the largest subpopulations had a high probability of declining to extinction within 2 years.

Aspects of the dynamics of metapopulations can be illustrated in a study of a small mammal, the American pika, *Ochotona princeps*, in California (Figure 9.9). The overall metapopulation could itself be divided into northern, middle and southern networks of patches, and the patch occupancy in each was determined on four occasions between 1972 and 1991. These data (Figure 9.9a) show that the northern network maintained a high occupancy throughout the study period, the middle network maintained a more variable and much lower occupancy, while the southern network suffered a steady and substantial decline.

The dynamics of individual subpopulations were not monitored, but these were simulated using models based on the principles of metapopulation dynamics and on general information on pika biology. When the three networks were simulated in isolation (Figure 9.9b), the northern network remained at a stable high occupancy (as observed in the data), but the middle network rapidly and predictably crashed, and the southern network eventually suffered the same fate. However, when the entire metapopulation was simulated as a single entity (Figure 9.9c), the northern network again achieved stable high occupancy, but this time the middle network was also stable, albeit at a much lower occupancy (again as observed), while the southern network suffered periodic collapses (also consistent with the real data).

This all suggests that within the metapopulation as a whole, the northern network acts as a net source of colonizers that prevent the middle network from suffering overall extinction. These in turn delay extinction in, and allow recolonization of, the southern network. The study therefore illustrates how whole metapopulations can be stable when their individual subpopulations are not. Moreover, the comparison of the northern and middle networks, both stable but at very different occupancies, shows how occupancy may depend on the size

metapopulation dynamics:  
the American pika

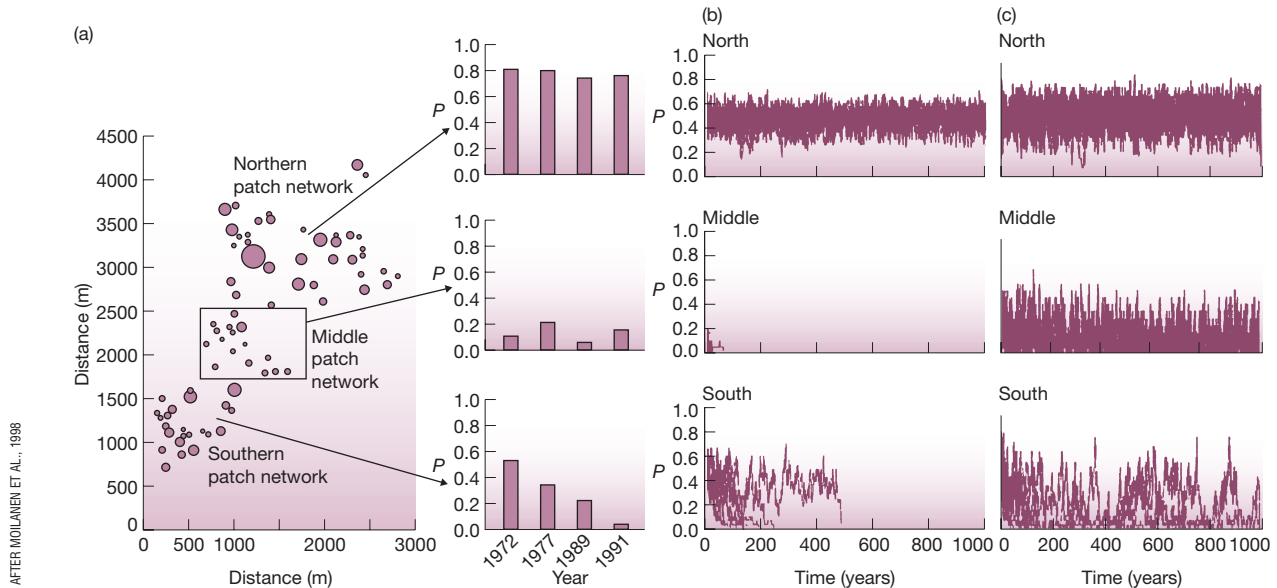


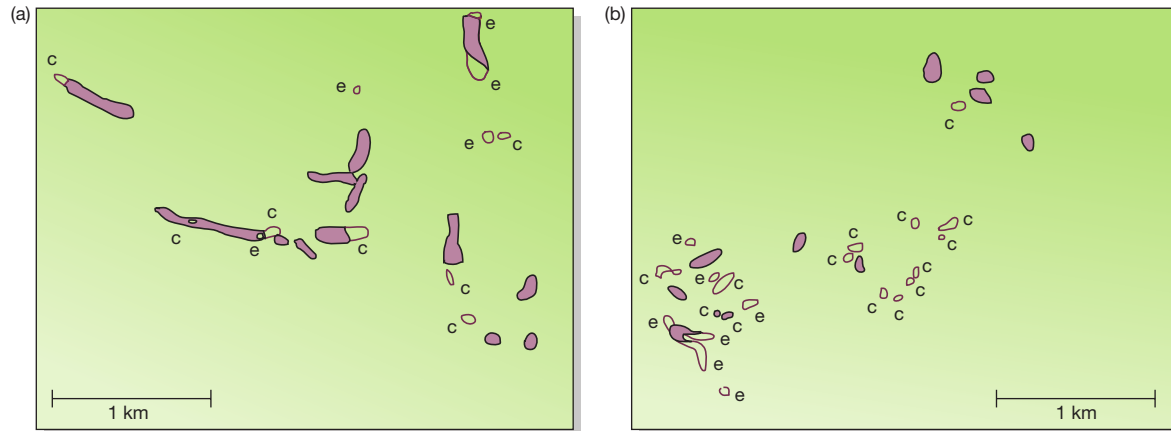
Figure 9.9

The metapopulation dynamics of the American pika, *Ochotona princeps*, in Bodie, California. (a) The relative positions (distance from a point southwest of the study area) and approximate sizes (as indicated by the size of the dots) of the habitable patches, and the occupancies (as proportions,  $P$ ) in the northern, middle and southern networks of patches in 1972, 1977, 1989 and 1991. (b) The simulated temporal dynamics of the three networks, with each of the networks simulated in isolation. Ten replicate simulations are shown, overlaid on one another, each starting with the actual data in 1972. (c) Equivalent simulations to (b) but with the entire metapopulation treated as a single entity.

of the pool of dispersers, which itself may depend on the size and number of the subpopulations.

Finally, the southern network in particular emphasizes that the observable dynamics of a metapopulation may have more to do with ‘transient’ behavior, far from any equilibrium. To take another example, the silver-spotted skipper butterfly (*Hesperia comma*) declined steadily in Great Britain from a widespread distribution over most calcareous hills in 1900, to 46 or fewer refuge localities (local populations) in 10 regions by the early 1960s (Thomas & Jones, 1993). The probable reasons were changes in land use – increased plowing of grasslands, reduced stocking with grazing animals – and the virtual elimination of rabbits by myxomatosis with its consequent profound vegetational changes. Throughout this non-equilibrium period, rates of local extinction generally exceeded those of recolonization. In the 1970s and 1980s, however, reintroduction of livestock and recovery of the rabbits led to increased grazing, and suitable habitats increased again. This time, recolonization exceeded local extinction, but the spread of the skipper remained slow, especially into localities isolated from the 1960s refuges. Even in southeast England, where the density of refuges was greatest, it is predicted that the abundance of the butterfly will increase only slowly – and remain far from equilibrium – for at least 100 years. Thus, it seems that around a century of ‘transient’ decline in the dynamics of the metapopulation is to be followed by another century of transient increase – except that the environment will no doubt alter again before the transient phase ends and the metapopulation reaches equilibrium.

transient dynamics may be as important as equilibria



**Figure 9.10**

Two metapopulations of the silver-studded blue butterfly (*Plebejus argus*) in North Wales: filled outlines, present in both 1983 and 1990 ('persistent'); open outlines, not present at both times; e, present only in 1983 (presumed extinction); c, present only in 1990 (presumed colonization). (a) In a limestone habitat, where there was a large number of persistent (often larger) local populations among smaller, much more ephemeral local populations (extinctions and colonizations). (b) In a heathland habitat, where the proportion of smaller and ephemeral populations was much greater.

a continuum of  
metapopulation types

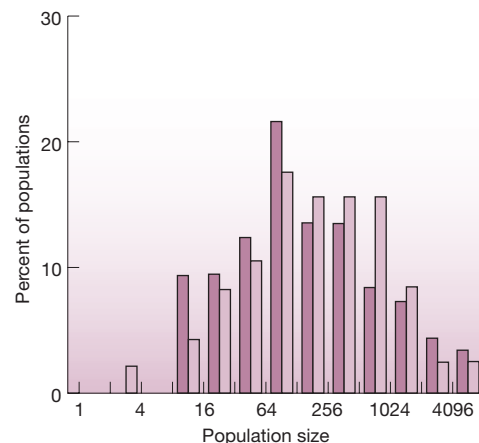
metapopulations of plants?  
remember the seed bank

In reality, moreover, there is likely to be a continuum of types of metapopulation: from collections of nearly identical local populations, all equally prone to extinction, to metapopulations in which there is great inequality between local populations, some of which are effectively stable in their own right. This contrast is illustrated in Figure 9.10 for the silver-studded blue butterfly (*Plebejus argus*) in North Wales, UK.

Finally, we must be wary of assuming that all patchy populations are truly metapopulations – comprising subpopulations, each one of which has a measurable probability of going extinct or being recolonized. The problem of identifying metapopulations is especially apparent for plants. There is no doubt that many plants inhabit patchy environments, and apparent extinctions of local populations may be common. This is shown in Figure 9.11 for the annual aquatic plant *Eichhornia paniculata*, living in temporary ponds and ditches in arid regions

**Figure 9.11**

Of 123 populations of the annual aquatic plant *Eichhornia paniculata* in northeast Brazil observed over a 1-year time interval, 39% went extinct, but the mean initial size of those that went extinct (dark bars) was not significantly different from those that did not (open bars). (Mann-Whitney  $U = 1925$ ,  $P > 0.3$ ).



AFTER THOMAS & HARRISON, 1992

AFTER HUSBAND & BARRETT, 1996

in northeast Brazil. However, the applicability of the idea of recolonization following a genuine extinction is questionable in any plant species that has a buried seed bank (see Section 5.2.2). In *E. paniculata*, for instance, the heavy seeds almost always drop in the immediate vicinity of the parent rather than being dispersed to other patches. ‘Extinctions’, then, are typically the result of the catastrophic loss of habitat (note in Figure 9.11 that the chance of extinction has effectively nothing to do with the previous population size); and ‘recolonizations’ are almost always simply the result of the germination of seeds following habitat restoration. Recolonization by dispersal, a prerequisite for a true metapopulation, is extremely rare.

## 9.4 Temporal patterns in community composition

### 9.4.1 Founder-controlled and dominance-controlled communities

From the perspective of environmental patchiness, the metapopulation concept is important for our understanding of population dynamics, but when community organization is the focus of attention we usually refer to the *patch dynamics* concept. The concepts are closely related. Both accept that a combination of patchiness and dispersal between patches can give rise to dynamics quite different from those that would be observed if there was just one, homogeneous patch.

Disturbances that open up gaps are common in all kinds of community. Gaps are simply patches within which many species suffer local extinction simultaneously. In forests, high winds, elephants or simply the death of a tree through old age may all create gaps. In grassland, agents include frost, burrowing animals and cattle dung. On rocky shores, gaps may be formed as a result of severe wave action during hurricanes, battering by moored boats or the action of predators.

Two fundamentally different kinds of community organization can be recognized (Yodzis, 1986). When all species are good colonists and essentially equal competitors, communities are described as *founder controlled*; when some species are strongly superior competitively, communities can be described as *dominance controlled*. The dynamics of the two are quite different, and we deal with them in turn.

In founder-controlled communities, species are approximately equivalent in their ability to invade gaps and can hold the gaps against all comers during their lifetime. Hence, the probability of competitive exclusion in the community as a whole may be much reduced where gaps are appearing continually and randomly. This can be referred to as a ‘competitive lottery’. On each occasion that an organism dies (or is killed) a gap is opened for invasion. All conceivable replacements are possible, and species richness is maintained at a high level in the system as a whole. For example, three species of fish co-occur on the upper slope of Heron Reef, part of the Great Barrier Reef off eastern Australia: *Eupomacentrus apicalis*, *Plectroglyphidodon lacrymatus* and *Pomacentrus wardi*. Within rubble patches, the available space is occupied by a series of non-overlapping territories, which individuals hold throughout their juvenile and adult life, defending them against individuals of their own and other species.

disturbances and the patch dynamics concept of community organization

founder-controlled communities: competitive lotteries