



# Chapter 6

# Movement and Metapopulations

## 6.1 Introduction

All organisms in nature are where we find them because they have moved there. This is true for even the most apparently sedentary of organisms, such as oysters and redwood trees. Their movements range from the passive transport that affects many plant seeds to the apparently purposeful actions of mobile animals. Movement is itself linked directly to the structure of an organism's environment. Patterns of movement will only be favoured by natural selection insofar as they tend to take the individual from a less favourable to a more favourable location.

However, we should not be fooled into thinking that whenever an organism moves away from (escapes) its immediate environment, it has necessarily sensed that the environment is unfavourable and responded to that sensation; or that whenever an organism ceases its movement and arrives in a new location, it has necessarily sensed the attractiveness of its new home. This can often be the case, especially for animals. But there are also many examples where the behaviour has evolved in response to predictable patterns in the environment that the organism need not sense for itself in order for the response to be elicited. Seeds typically escape from their parent plant because the environment around the parent is predictably crowded. The behaviour has evolved over many generations: the seeds do not need to sense this for themselves. Likewise, many birds migrate polewards for the summer to regions with longer day lengths (and hence feeding periods) – but evolution

has taken care of this: the birds typically respond to a proximate cue, probably the changing day length, rather than to diminishing resource availability per se.

A useful distinction in this context is between geographic space and environmental space. Studies of geographic space are focused on the home ranges of individuals or the geographic distributions of species. Studies of environmental space are focused on patterns in the selection and use of resources. Van Moorter *et al.* (2016) characterise individual movements as the glue, binding the two together. Individual movements reflect an immediate or evolutionary response to patterns in the distribution of resources; we observe the consequences in home ranges and species' distributions.

Whatever the precise details in particular cases, it is useful to divide individual movements into three phases: starting (leaving), moving itself, and stopping (South *et al.*, 2002), or, put another way, emigration, transfer and immigration (Ims & Yoccoz, 1997). The questions we ask about the three phases differ both from a behavioural point of view (for example, what triggers the initiation and cessation of movement?) and from a demographic point of view (the distinction between loss and gain of individuals). A broader perspective still proposes a four-part framework onto which all kinds of movement studies can fit (Nathan *et al.*, 2008). The first is the organism's internal state (why move?); the second is the nature of the movement itself; third are the environmental drivers of different patterns of movement (when and where to move?); and last are the ecological

and evolutionary consequences of movement. We touch on all of these in what follows.

### 'dispersal' and 'migration'

*Dispersal* is most often taken to mean the movement of individuals away from others, and is therefore an appropriate description for several kinds of movements: (i) of plant seeds or starfish larvae away from each other and their parents; (ii) of voles from one area of grassland to another, usually leaving residents behind and being counterbalanced by the dispersal of other voles in the other direction; and (iii) of land birds amongst an archipelago of islands (or aphids amongst a mixed stand of plants) in the search for a suitable habitat. A common and somewhat narrower view of dispersal, and one that distinguishes it more clearly from simply 'movement', defines two categories of dispersal: *natal dispersal*, the movement of a prereproductive individual from its site of birth to its site of reproduction, and *postbreeding dispersal*, the movement of individuals between successive sites of reproduction (Matthysen, 2012). Natal dispersal is more common, if for no other reason than it is the only dispersal available to organisms, like plants, with a static reproductive stage, and it has been the main preoccupation of ecologists working on dispersal.

*Migration*, then, is most often taken to mean the movement, frequently directional, either of individuals or of collections of individuals from a starting to a terminal location, which is often predetermined. The term therefore applies to classic migrations (the movements of locust swarms, the intercontinental journeys of birds) but could also be applied, for example, to the to and fro movements of shore animals following the tidal cycle. We deal first here with migration and then move on to dispersal more generally.

### technological advances

Before we do so, however, we should acknowledge the enormous increase there has been recently in our ability to collect and analyse movement data. As Börger (2016) describes, we have been tracking movements for more than 200 years by marking an individual in one location (for example, a leg ring on a bird) so that we can recognise that same individual when we recapture or resight it somewhere else, some time later. But as it has become increasingly easy to monitor resightings without ever capturing an animal – for example, using camera traps linked to photoidentification or non-invasive genetic typing – this approach has become possible in an ever-widening range of cases. Even more profound have been advances in the technology of electronic tags (and decreases in their size and weight) with, for example, signals indicating an individual's location transmittable not simply to a nearby investigator but to satellite systems that can also store the location data

being collected. Note, too, that information on location, alone, is of limited value. It is much better to have this allied to a characterisation of the habitat at that location, and there have been equally significant advances in satellite-based remote-sensing of the environment and in geographical information systems (GIS) able to manage those data and link them, where appropriate, to movement data. Needless to say, these advances in the development of tools to collect data have been paralleled by advances in computing power and software sophistication. As in other sciences, the challenge will be to use these new tools to answer, perhaps for the first time, the most important ecological questions rather than being seduced by them into collecting datasets simply 'because we can'.

## 6.2 Patterns of migration

### migrating to track resources

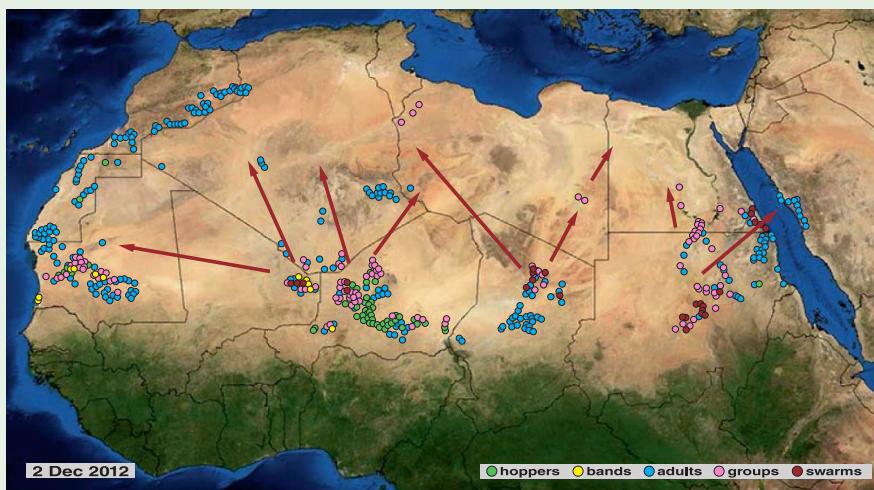
Individuals of many species move *en masse* from one habitat to another and back again repeatedly during their life. The timescale involved may be hours, days, months or years. As we shall see throughout this book, Nature usually defies our attempts to place species' behaviours into neat, water-tight categories, but there is something to be said for dividing migratory movements into those either tracking the same environment or moving between quite distinct environments, or perhaps into being driven either by tracking the environment, finding a breeding site or finding a refuge (Shaw, 2016). The movement of crabs on a shoreline is an example of a tracking migration: they move with the advance and retreat of the tide. Monarch butterflies, *Danaus plexippus*, in North America migrate south to Mexico to overwinter (taking refuge from the harsh northern winters) but then take four generations to migrate northwards again over the summer, tracking the availability of their host plant, the milkweed, *Asclepias* spp.

Not all migrations are easily categorised. American elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) move up into high mountain areas in the summer and down to the valleys in the winter. We can think of this as taking refuge from high altitude winters, but there is also a strong element of their tracking the most favourable supply of food. On a much larger scale, the Arctic tern (*Sterna paradisaea*) travels from its Arctic breeding ground to the Antarctic pack ice and back each year – about 10 000 miles (16 100 km) each way (although unlike many other migrants it can feed on its journey). So this is a breeding migration, and in that sense the terns are deriving something quite different from their Arctic and Antarctic environments. But they are also

## APPLICATION 6.1 Tracking the tracking migrations of locusts

Many locust species also have tracking migrations, following the availability of food, itself driven by patterns of rainfall. However, these migrations, even in those species where they occur, are irregular and complex. The desert locust, *Schistocerca gregaria*, which lives across broad swathes of north Africa and east to India, and which can be devastating to crops throughout this region, is a good example. It passes through a series of wingless nymphal stages before moulting into an adult, and crucially can exist as either of two ‘phases’: the solitary phase, which they display when densities are low, and the gregarious phase, which they transition into and remain in when densities are high. The phases differ morphologically, but most important, their behaviour also differs as the phase names suggest: those in the solitary phase acting as individuals but the gregarious locusts behaving in a concerted way as coherent units. All stages

have voracious (collective) appetites and can destroy crops. Gregarious nymphs form ‘bands’ (having transitioned in their solitary phase through ‘groups’) that then march across the landscape, tracking available vegetation. Gregarious adults form ‘swarms’, also having transitioned through groups, which then take to the skies, sometimes in their hundreds of millions. Crucially, by flying downwind for up to 200 km in a day, these swarms are migrating to where rain (and fresh vegetation) is most likely rather than tracking its current availability. Regardless of whether the migrations are tracking or predictive, though, nymphal or adult, they themselves are tracked by the Food and Agricultural Organization of the United Nations (the FAO), providing farmers and governments throughout the region with early warning alerts through their Desert Locust Watch scheme (Figure 6.1), combining data from satellites, GIS and even drones.



**Figure 6.1 The movements of locusts and their impending threat.** An example from 2 December 2012 of an alert issued by the Food and Agricultural Organization of the United Nations of the impending threat from desert locusts in north Africa. Hoppers (wingless nymphs) and adults are in the solitary phase; groups are transitioning into the gregarious phase; and bands and swarms are the large (often massive) aggregation of nymphs and adults, respectively. The red arrows show the current (2 December 2012) migration paths. *Source:* After FAO (2012).

migrating to maintain a year-round supply of essentially the same kind of food, and taking refuge at both ends of their journey from polar winters that they could not survive. Similarly, many terrestrial birds in the northern hemisphere move north in the spring to breed when food supplies become abundant during the warm summer period, and

move south to savannas in the autumn when food becomes abundant only after the rainy season; while baleen whales in the southern hemisphere move south in summer to feed in the food-rich waters of the Antarctic, and move north in winter to breed (but scarcely to feed) in tropical and subtropical waters.

### migrating between distinct resources

In other cases, migration may involve a more straightforward movement between two distinct environments. For example, many planktonic algae descend to the depths at night to accumulate phosphorus and perhaps other nutrients but move to the surface during the day to photosynthesise. Likewise, but on a very different time scale, many amphibians (frogs, toads and newts) migrate between an aquatic breeding habitat in spring and a terrestrial environment for the remainder of the year, the young developing (as tadpoles) in water with a different food resource from what they later eat on land.

### one-way tickets

Many long-distance migrants, however, make only one return journey during their lifetime. They are born in one habitat, make their major growth in another habitat, but then return to breed and die in the home of their infancy. Eels and migratory salmon provide classic examples. The European eel (*Anguilla anguilla*) travels from European rivers, ponds and lakes across the Atlantic to the Sargasso Sea, where it is thought to reproduce and die (although spawning adults and eggs have never actually been caught there). The

American eel (*A. rostrata*) makes an analogous journey from areas ranging between the Guianas in the south, to southwest Greenland in the north. Salmon make a comparable transition, but from a freshwater egg and juvenile phase to mature as a marine adult. The fish then returns to freshwater sites to lay eggs. After spawning, all Pacific salmon (*Oncorhynchus nerka*) die without ever returning to the sea. Many Atlantic salmon (*Salmo salar*) also die after spawning, but some survive to return to the sea and then migrate back upstream to spawn again.

Most migrations occur seasonally. They are typically triggered by some external seasonal phenomenon (e.g. changing day length), and perhaps also by an internal physiological clock. They are often preceded by quite profound physiological changes such as the accumulation of body fat and represent strategies evolved in environments where seasonal cycles of habitat favourability are reliably repeated from year to year. By contrast, the economically disastrous migration plagues of locusts in arid and semiarid regions, for example, are tactical, forced by events such as overcrowding, and typically have no cyclicity or regularity. These are most common in environments where rainfall is not seasonally reliable.

## APPLICATION 6.2 The conservation of migratory species

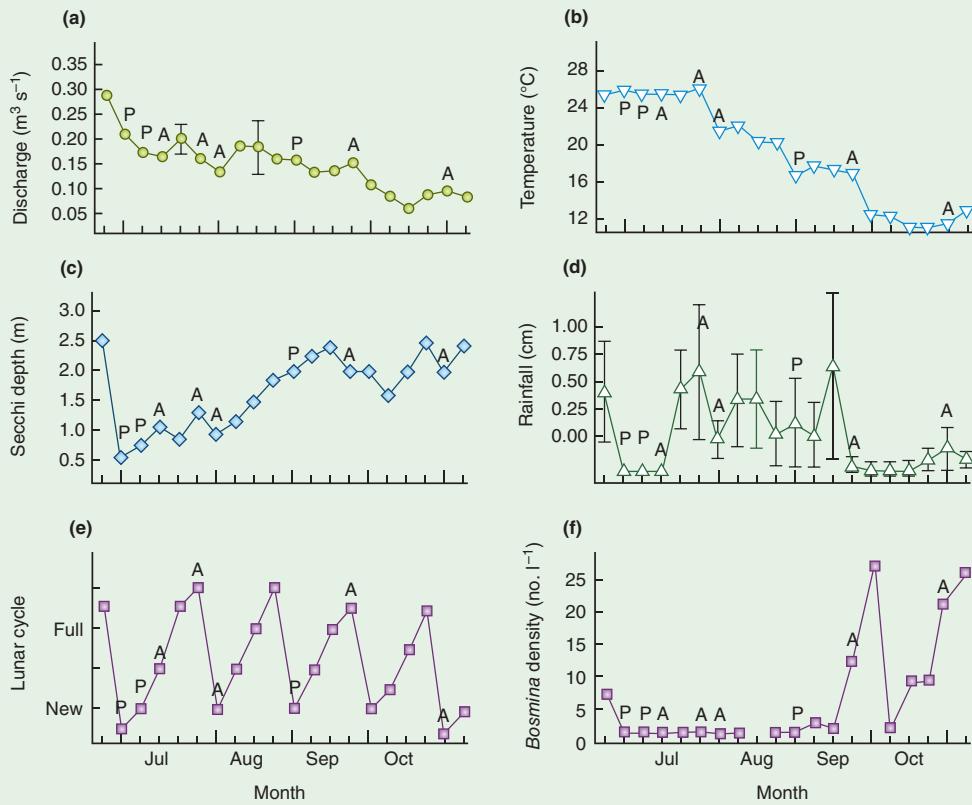
### keeping routes open for commercial fisheries

Species that spend part of their time in one habitat and part in another can be badly affected by human activities that influence the ability to move between them.

The declining populations of river herrings (*Alosa pseudoharengus*, also known as the alewife, and *A. aestivalis*) in the north-eastern USA are a case in point. Adults ascend coastal rivers to spawn in lakes between March and July, and the young fish then remain in fresh water for three to seven months before migrating to the ocean. The species are commercially important as both food and bait, but overfishing, pollution and the construction of dams on their migration paths have prompted the US National Marine Fisheries Service to classify them as a ‘species of concern’. Yako *et al.* (2002) sampled river herrings three times per week from June to December in the Santuit River downstream of Santuit Pond, Massachusetts, USA which contains the only spawning habitat in the catchment. The pond is dammed and discharge of water from it managed – but when are the best times to discharge the

water? To answer this, Yako *et al.* classified periods of downstream juvenile migration as either ‘peak’ (>1000 fish per week) or ‘all’ (>30 fish per week, obviously including the peak), and by simultaneously measuring a range of physicochemical and biotic variables, they aimed to identify factors that could predict the timing of this migration (Figure 6.2). Peak migration was most likely to occur during the new moon (dark nights perhaps reducing the risk from piscivorous fish and birds) and when the density of important zooplankton prey (*Bosmina* spp.) was low, and migration at any level tended to occur when water clarity was low (perhaps because their own ability to forage successfully was impaired and/or because risk from piscivores was lower) and during decreased periods of rainfall. With this information, predictive models could be built to help managers identify periods when river discharge needs to be maintained to coincide with migration. On the other side of the pond, in 2013 a new ‘fish ladder’ was opened (small ascending steps in the river’s profile) to help spawning fish reach the pond from the sea.

## APPLICATION 6.2 (Continued)



**Figure 6.2** Variation in physical and biotic variables in the Santuit River, USA during the migratory period of river herring. (a) Discharge, (b) temperature, (c) water clarity, measured as Secchi disc depth (low values indicate high turbidity), (d) rainfall, (e) lunar cycle and (f) *Bosmina* (prey) density. P denotes 'peak' periods of migration ( $>1000$  fish per week). P and A ( $>30$  fish per week) together denote all periods of migration. Bars are SEs. Source: After Yako *et al.* (2002).

### manipulating the seasonal migration of geese

More broadly, an understanding of the migratory behaviour of species at risk can assist managers in devising conservation strategies.

One example is a scheme to divert the southwards migration route of lesser white-fronted geese (*Anser erythropus*) from arriving in south-eastern Europe, where they tend to get shot, to spending their winters in the Netherlands (Sutherland, 1998). To do this, a captive population of barnacle geese (*Branta leucopsis*) that breeds in Stockholm Zoo but overwinters in the Netherlands was used. Individual barnacle geese were taken from Stockholm to Lapland where they nested and were given lesser white-fronted goose eggs to rear. Then, when the adoptive barnacle goose parents flew to the Netherlands for the winter, the young lesser white-fronted geese flew with them. But

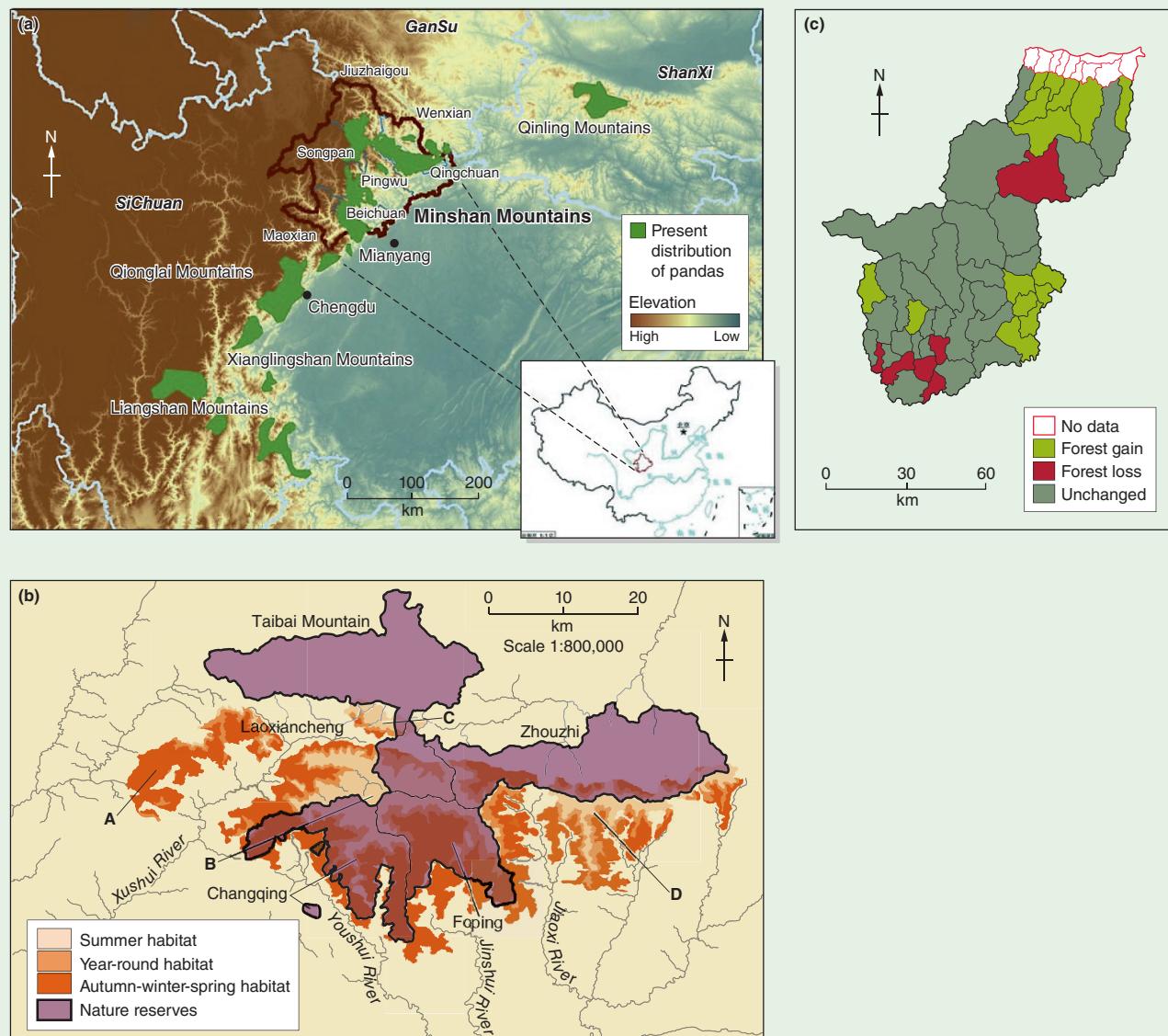
crucially, next spring the young lesser white-fronted geese returned to Lapland and bred with conspecifics there, subsequently returning again to the Netherlands along what was now their accustomed route.

Migratory movements may also play a role in the design of nature reserves. The Qinling Province in China is home to approximately 220 giant pandas (*Ailuropoda melanoleuca*), representing about 20% of the wild representatives of one of the world's most imperilled mammals. The pandas in this region are elevational migrants. They need both low and high elevation habitat to survive. But current nature reserves did not cater for this. Pandas are extreme dietary specialists, primarily consuming a few species of bamboo. In Qinling Province, from June to September, pandas eat *Fargesia*

### designing nature reserves for pandas

*[Continued]*

## APPLICATION 6.2 (Continued)



**Figure 6.3** The optimal location of nature reserves for giant pandas in China must take account of their elevational migrations. (a) The present distribution of the giant panda, *Ailuropoda melanoleuca*, with the location within this of the Qinling Mountains (examined further in this figure) and the Minshan Mountains (see Figure 6.34). (b) Core panda habitats (A–D) in the Qinling Mountains, each of which caters for the year-round needs of the elevational migration of giant pandas. Superimposed are nature reserves as of 2003 (purple) and their names. (c) Subsequent assessment of forest cover change between 2001 and 2008 in the southern section of the Qinling Mountains region – part of the Changqing reserve in (b). Source: (a) After Shen *et al.* (2015). (b) After Loucks *et al.* (2003). (c) After Li *et al.* (2013).

*spathacea*, which grows from 1900 to 3000 m. But as colder weather sets in, they travel to lower elevations, and from October to May they feed primarily on *Bashania fargesii*, which grows from 1000 to 2100 m.

Loucks *et al.* (2003) sought to identify regions of the landscape that would meet the long-term needs of the species.

They first excluded areas lacking giant pandas, forest block areas that were smaller than 30 km<sup>2</sup> (the minimum area needed to support a pair of giant pandas over the short term) and forest with roads, settlements or plantations. Based on this, Figure 6.3b maps summer habitat (1900–3000 m; *F. spathacea* present), autumn/winter/spring

## APPLICATION 6.2 (Continued)

habitat (1400–2100 m; *B. fargesii* present) and a small amount of year-round habitat (1900–2100 m, both bamboo species present). Four areas of core panda habitat (A–D) were identified that provide for the migrational needs of the pandas. Figure 6.3b also shows the location of the current nature reserves. They cover only 45% of the core habitat. Loucks *et al.* (2003) recommend that the four core habitat areas identified should be incorporated into a reserve network. They also note the importance of promoting linkage between these core areas, because extinction in any one area (and ultimately in all combined) is more likely if the populations are isolated from each other (see Section 6.7). Thus, they further identify two important linkage regions for protection, between areas A and B where

steep topography means few roads exist, and between B and D across high elevation forests.

Of course, making recommendations is easier than implementing them, especially when there are conflicting demands being made on the landscape. It is therefore encouraging that a subsequent analysis of forest cover change in the region between 2001 and 2008 showed an overall increase (Figure 6.3c), and that this tended to occur where the Chinese Government had implemented its Grain-To-Green Programme (converting agricultural land to forest), though there was less of an increase (and in some cases decreases), because of the need to grow food, at lower altitudes and where a higher proportion of people were agricultural workers.

## 6.3 Modes of dispersal

### 6.3.1 Passive dispersal

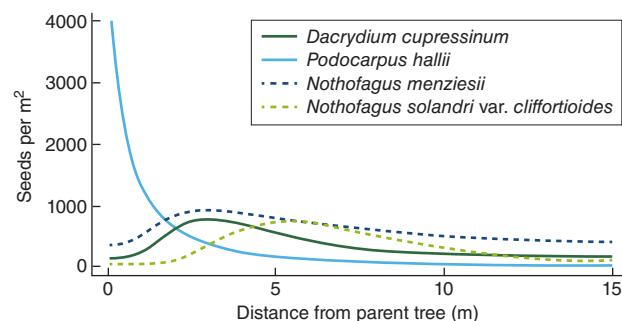
#### seed rains and seed shadows

Much seed dispersal is passive. Most seeds fall close to the parent and their density declines with distance from that parent. This is the case for wind-dispersed seeds and also for those that are ejected actively by maternal tissue (e.g. many legumes). There is a ‘seed rain’ generated by the mother plant that produces a ‘seed shadow’ on the ground. The eventual destination of the dispersed offspring is determined by the original location of the parent and by the relationship between disperser density and distance from parent, but the detailed microhabitat of that destination is left largely to chance. Dispersal is non-exploratory. Some animals have essentially this same type of dispersal. For example, the dispersal of most pond-dwelling organisms without a free-flying stage depends on resistant wind-blown structures (e.g. gemmules of sponges, cysts of brine shrimps).

#### rare but important long-distance dispersal

The density of seeds is often low immediately under the parent, rises to a peak close by and then falls off steeply with distance (Figure 6.4).

However, there are immense practical problems in studying seed dispersal (i.e. in following the seeds), and these become increasingly irresolvable further from the source. Greene and Calogeropoulos (2001) liken any assertion that ‘most seeds travel short distances’ to a claim that most lost keys



**Figure 6.4** The ‘seed rains’ of four tree species from a temperate rainforest in New Zealand. These were standardised for tree size (60 cm diameter at breast height), and combined the estimated total seed production (TSP) and input from outside the immediate area for the study year when TSP was highest. Source: After Canham *et al.* (2014).

and contact lenses fall close to streetlights. Indeed, for seeds, but also more generally, the relatively rare long-distance dispersers may be especially important for the invasion of new habitats or habitat patches (see Section 6.4.1). And when studies have sought evidence for long-distance dispersers they have often found it. For example, the data compiled to estimate the dispersal profiles of the trees in Figure 6.4 were obtained from sites within which the distributions of the four study species had been mapped (and their sizes determined in order to estimate their fecundity) and seeds collected from a network of seed traps within the sites. Spatial models were then fitted to

these data assuming either that all seeds were derived from the known, local trees, or that there was an additional background input of long-distance dispersers that could not be attributed to parent trees within 50 m. In all cases the models with long-distance dispersers were a much better fit to the data. Hence, while there was a fall off within around 5–10 m in the seed rain from individual trees, the tail of that distribution (the outer reaches of the seed shadow) extended, at significant levels, 10 or more times further, as judged by the input from equivalent trees outside the study site (Figure 6.4)

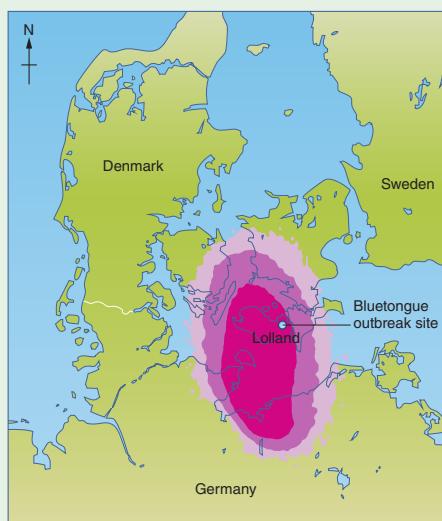
### 6.3.2 An active–passive continuum

The reality, however, is that if we wish to classify the dispersal movements of organisms away from one another, we need a scale from passive to active, and there is often no clear distinction between the two. Young spiders, for example, climb to high places and then release gossamer threads that carry them on the wind where they are at the mercy of air currents, but their ‘starting’ is active even if moving itself is effectively passive. Even the wings of insects are often simply aids to what is effectively passive movement.

## APPLICATION 6.3 Winds predict the arrival of midges carrying bluetongue virus

We see this, for example, in the success with which wind patterns are able to predict the invasion of bluetongue virus into new areas of Europe. Bluetongue is an economically important disease of ruminants (especially sheep and cattle), found in many parts of the world, that since around 1998 has been spreading from north Africa and the Middle East northwards through Europe, carried by its vector: biting midges from the genus *Culicoides*. The midges can, of course, fly, but their powers of flight alone tell us very little about their spreading of the disease. However, a model

that treats midges just as it would any other wind-borne particle does an excellent job of predicting risk areas for new outbreaks, and indeed, linking new outbreaks to their source. This model is the United Kingdom Meteorological Office’s Numerical Atmospheric-dispersion Modelling Environment programme (NAME), modified to incorporate key aspects of midge biology like their daily and seasonal activity cycles. The midges’ wings give them the capacity to be carried by the wind, but the wind plays the major role in determining where they will go. An example is shown in Figure 6.5.



**Figure 6.5 Predicting an outbreak of bluetongue virus.** Results from the modelling programme NAME (see main text) showing the estimated relative likelihood of *Culicoides* midges from northern Germany, to the south, potentially carrying bluetongue virus, reaching the region around the island of Lolland in southern Denmark overnight 22–23 September 2007. The darker the pink, the greater the likelihood. The blue dot shows the actual bluetongue outbreak site. Source: After Burgin *et al.* (2012).

**passive dispersal by an active agent**

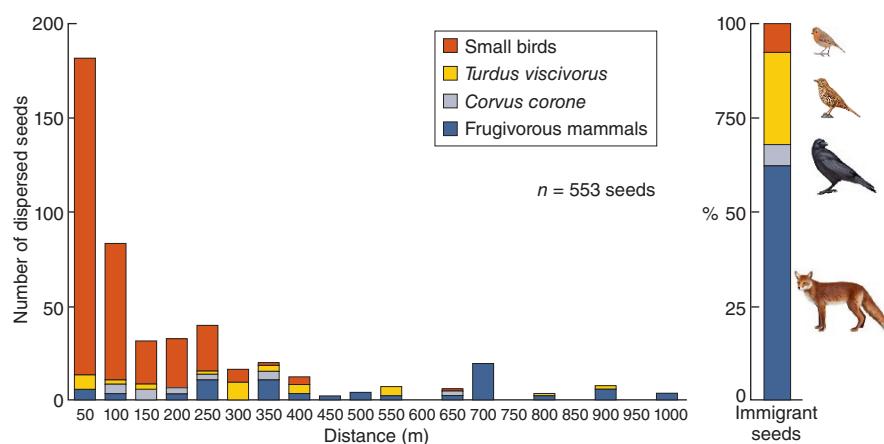
In the case of seed dispersal, too, the role of the seed itself may be passive, but uncertainty as to the destination will be reduced if there is also an active agent of dispersal. The seeds of many herbs of the woodland floor have spines or prickles, increasing their chances of being carried passively on the coats of animals and tending to concentrate their destinations in nests or burrows when the animal grooms itself. The fruits of many shrubs and lower canopy trees are fleshy and attractive to birds, and the seed coats resist digestion in the gut. The destination of the seed then depends on the defaecating behaviour of the bird. With fruits, therefore, the associations are ‘mutualistic’ (beneficial to both parties – see Chapter 13): the seed is dispersed and the disperser consumes the fleshy ‘reward’. There are also important examples in which animals are dispersed by active, mutualistic agents. For instance, many species of mite are taken very effectively and directly from dung pat to dung pat, or from one piece of carrion to another, by attaching themselves to dung or carrion beetles. The mites gain a dispersive agent, and many of them attack and eat the eggs of flies that would otherwise compete with the beetles.

We can see the combination of active and passive processes in the patterns of dispersal of seeds by frugivores (fruit-eaters) in Figure 6.6. Seeds of the St Lucie cherry, *Prunus mahaleb*, at a site in Spain containing 196 cherry trees, were detected and then assigned to a parent tree by DNA-based genotyping and to a frugivore type by noting the faeces in which the seed was found. The frugivore types were mammals (for example foxes and badgers), small birds (including warblers, redstarts and robins) and two medium-sized birds, the mistle thrush (*Turdus viscivorus*) and the

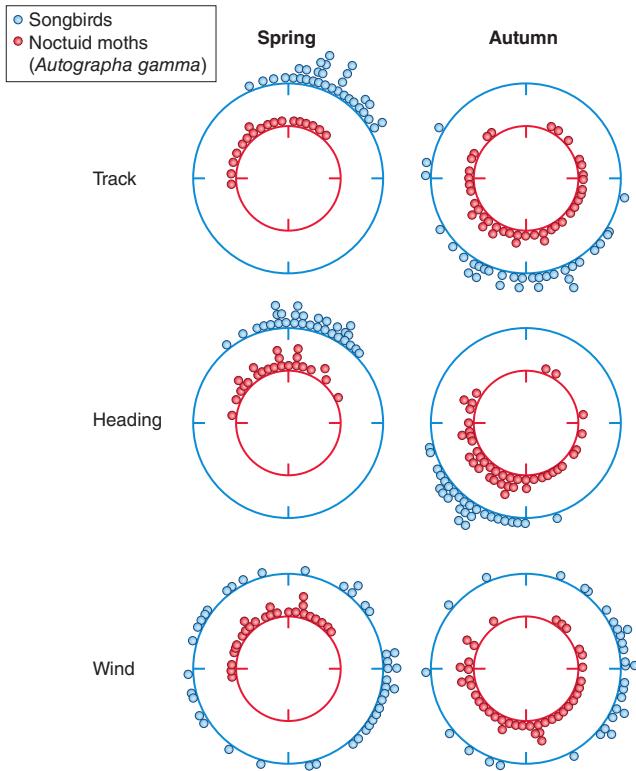
carrion crow (*Corvus corone*). The seed shadows overall were reminiscent of the ‘passive’ patterns for wind-dispersed seeds in Figure 6.4: a rapid decline in numbers close to the source, combined with a long tail (though the distances in this case were much greater). However, there were also important differences in pattern generated by the characteristic activities of the different frugivores. The small birds deposited most seeds only a short distance from the parent tree and did so into covered microhabitats (under cherry trees and various shrubs). These birds, therefore, provided the seedlings with their highest chances of establishing. The mammals and larger birds, on the other hand, were the most important groups in terms of dispersal between cherry populations and in starting new populations (assuming the seeds germinated and established), because they dispersed seeds longer distances and did so selectively into more open habitats (the mammals and crows) or into pine forests (the thrushes).

We can gain further insight into the interplay between active and passive processes in the movements of organisms by turning again to migration and to a study that contrasted the nocturnal movements over Sweden of a species of moth and of small birds, tracked by radar (Figure 6.7). For both groups, and for all flying animals, there is a balance to be struck between, literally, going with the flow – allowing the wind to carry them, expending minimal energy, but having little control over direction or ultimate landing site – and on the other hand, flying actively, and expensively, in a ‘heading direction’ (the way the animal is facing) that combines with the wind direction to carry the animal along a

**active and passive processes interacting in migration?**



**Figure 6.6** Seed dispersal by frugivores can show a variety of patterns. The left panel shows the profile of distances dispersed by seeds of the St Lucie cherry, *Prunus mahaleb*, in Spain carried by four types of frugivore, as indicated in the right panel, which shows the percentage contributions of the four groups to long distance dispersal (>1500 m). Source: After Jordano *et al.* (2007).



**Figure 6.7 Birds and moths reflect contrasting combinations of active and passive processes in their migrations.** Overnight movements for songbirds (blue, outer circle) and noctuid moths, *Autographa gamma* (red, inner circle) in Sweden, in spring and autumn. The compass directions of observed movements (dots) are shown for ‘Track’ movements of the animals (movements in relation to the ground), ‘Heading’ movements (the direction the animal is facing), and also of ‘Wind’ flow while the animals are moving. Source: After Chapman *et al.* (2015).

‘track’ (its movement in relation to the ground) that is its preferred path. Figure 6.7 shows that both the moths and the birds adopted strategies that were somewhere between these two extremes. For the moths this came closer to going with the flow. They were selective in when they set off, limiting themselves to nights with stronger winds and winds blowing in downwind directions that would take them along their preferred track: northwards in the spring and southwards in the autumn. As a result, they tended to move faster across the ground than the birds, despite the birds’ greater intrinsic capacity for fast flight, but they were less accurate than the birds: the moths’ track directions were more affected by the winds. The birds, by contrast, much more frequently compensated for the wind. In the autumn especially, when the winds over Sweden predominantly blow to the east, the birds mostly headed to the south-west

– but doing so took their tracks to the south. The moths flew less often and less accurately than the birds – but more cheaply.

Many other animals, of course, are land-based in their dispersal and control when they leave, where they travel, and when they stop.

### 6.3.3 Clonal dispersal

In almost all modular organisms (see Section 4.2.1), an individual genet branches and spreads its parts around it as it grows. There is a sense, therefore, in which a developing tree or coral actively disperses its modules into, and explores, the surrounding environment. The interconnections of such a clone often decay, so that it becomes represented by a number of dispersed parts. This may result ultimately in the product of one zygote being represented by a clone of great age that is spread over great distances. Some clones of the rhizomatous bracken fern (*Pteridium aquilinum*) were estimated to be more than 1400 years old and one extended over an area of nearly 14 ha (Oinonen, 1967).

We can recognise a continuum of strategies in clonal dispersal (Lovett Doust & Lovett Doust, 1982).

guerrillas and phalanx-formers

At one extreme, the connections between modules are long and the modules themselves are widely spaced. These have been called ‘guerrilla’ forms, because they give the plant, hydroid or coral a character like that of a guerrilla army. Fugitive and opportunist, they are constantly on the move, disappearing from some territories and penetrating into others. At the other extreme are ‘phalanx’ forms, named by analogy with the phalanxes of a Roman army, tightly packed with their shields held around them. Here, the connections between the modules are short, and the organisms expand their clones slowly, retain their original site occupancy for long periods, and neither penetrate readily amongst neighbouring plants nor are easily penetrated by them.

Even amongst trees, it is easy to see that the way in which the buds are placed gives them a guerrilla or a phalanx growth form. The dense packing of shoot modules in species like cypresses (*Cupressus*) produces a relatively undispersed and impenetrable phalanx canopy, whilst many loose-structured, broad-leaved trees (*Acacia*, *Betula*) can be seen as guerrilla canopies, bearing buds that are widely dispersed and shoots that interweave with the buds and branches of neighbours. The twining or clambering lianas in a forest are guerrilla growth forms *par excellence*, dispersing their foliage and buds over immense distances, both vertically and laterally.

## APPLICATION 6.4 Invasive fragmenting aquatic weeds

Clonal growth is most effective as a means of dispersal in aquatic environments. Many aquatic plants fragment easily, and the parts of a single clone become independently dispersed because they are not dependent on the presence of roots to maintain their water relations. The major aquatic weed problems of the world are caused by plants

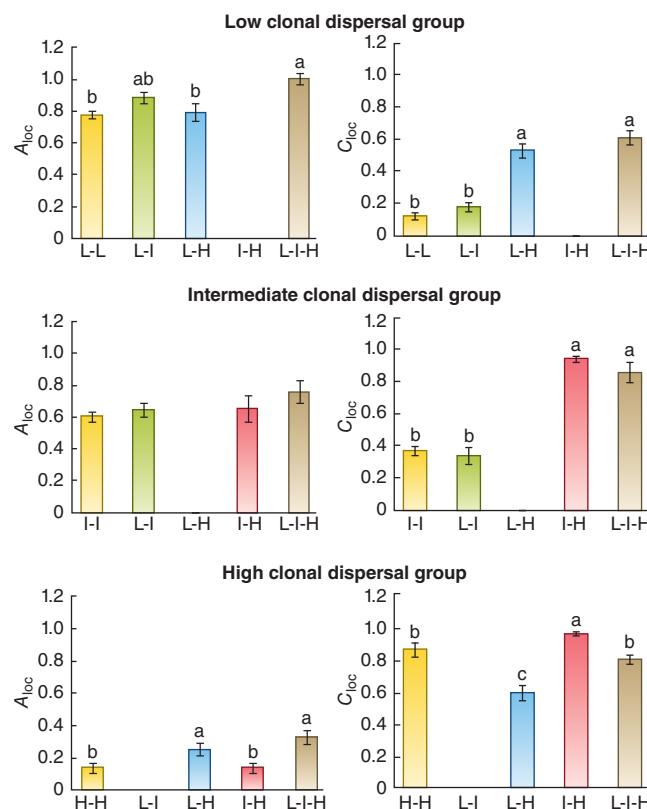
that multiply as clones and fragment and fall to pieces as they grow: duckweeds (*Lemna* spp.), the water hyacinth (*Eichhornia crassipes*), Canadian pond weed (*Elodea canadensis*) and the water fern *Salvinia*. The biological, chemical and mechanical control methods available to counter this threat are reviewed by Hussner *et al.* (2017).

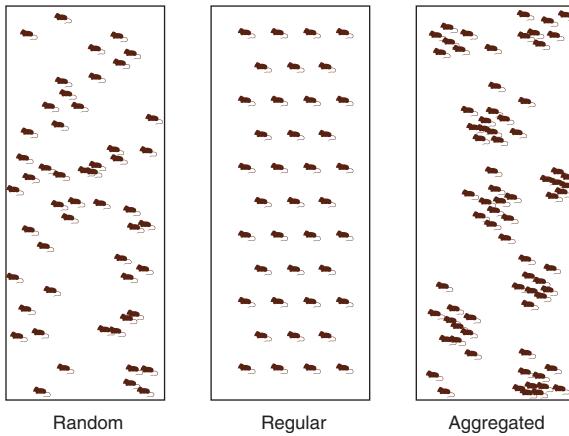
The way in which modular organisms disperse and display their modules affects the ways in which they interact with their neighbours. Those with a guerrilla form will continually meet and compete with other species and with other genets of their own kind. With a phalanx structure, however, most meetings will be between modules of a single genet. We see this, for example, for 12 grassland species in Figure 6.8.

## 6.4 Patterns of dispersion

The movements of organisms, whether we classify them as migration or dispersal, have causes and consequences. The proximate (immediate) causes are the triggers that prompt the movements, but as evolutionary biologists, we take it that the ultimate causes are the forces of natural selection that have favoured the consequences we observe. At the

**Figure 6.8 Phalanx-type plants aggregate locally and co-occur little with other species: guerilla-type plants show high levels of clonal dispersal and co-occur often with other species.** An index of local aggregation ( $A_{loc}$ , left panels) and an index of local co-occurrence ( $C_{loc}$ , right panels) for the interactions of 12 grassland plant species. These are grouped into species with low clonal dispersal, L (four species), intermediate, I (four species), and high, H (four species). They interacted with members of their own or other groups as indicated along the horizontal axis. High levels of local aggregation indicate a tendency to disperse (clonally) into volumes of soil, ‘cells’, nearby. These were observed especially in plants with low clonal dispersal (more phalanx types). High levels of local co-occurrence indicate a tendency to co-occur in cells with other species. These were observed especially in plants with high clonal dispersal (more guerilla types). Standard errors are shown. Bars with different letters above them are significantly different. Source: After Benot *et al.* (2013).





**Figure 6.9** Three generalised spatial patterns that may be exhibited by organisms across their habitats.

individual level, those consequences are the individuals' locations in particular habitats and in relation to other individuals. At the population level, the consequences are the spatial patterns of their distribution – their *dispersion*. We can recognise three main patterns of dispersion, although they form part of a continuum (Figure 6.9).

#### random, regular and aggregated distributions

*Random* dispersion occurs when there is an equal probability of an organism occupying any point in space (irrespective of the position of any others). The result is that individuals are unevenly distributed because of chance events.

*Regular* dispersion (also called a *uniform* or *even* distribution or *overdispersion*) occurs either when an individual has a tendency to avoid other individuals, or when individuals that are especially close to others die. The result is that individuals are more evenly spaced than expected by chance.

*Aggregated* dispersion (also called a *contagious* or *clumped* distribution or *underdispersion*) occurs either when individuals tend to be attracted to (or are more likely to survive in) particular parts of the environment, or when the presence of one individual attracts, or gives rise to, another individual close to it. The result is that individuals are closer to others than expected by chance.

How these patterns appear to an observer, however, and their relevance to the life of other organisms, depends on the spatial scale at which they are viewed. Consider the distribution of an aphid living on a particular species of tree in a woodland. At a large scale, the aphids will appear to be aggregated in woodlands as opposed to other types of habitat. If samples are smaller and taken only in woodlands, the aphids will still appear to be aggregated, but now on their host tree species rather than on trees in general. However, if samples are smaller still ( $25\text{ cm}^2$ , about the size of a leaf) and are taken within the canopy of a single tree, the aphids

might appear to be randomly distributed over the tree as a whole. And at an even smaller scale ( $c.1\text{ cm}^2$ ), we might detect a regular distribution because individual aphids on a leaf avoid one another.

#### 6.4.1 Patchiness

At some scale, at least, all habitats are patchy. Patchiness may be a feature of the physical environment: islands surrounded by water, rocky outcrops in a moorland, and so on. Equally important, patchiness may be created by the activities of organisms themselves; by their grazing, the deposition of dung, or the local depletion of water and mineral resources. It is crucial that we describe dispersion within and across patches at scales that are relevant to the lifestyle of the organisms concerned. MacArthur and Levins (1964) introduced the concept of environmental *grain* to make this point. For example, from the point of view of a bird like the scarlet tanager (*Piranga olivacea*) that forages indiscriminately in both oaks and hickories, the canopy of an oak–hickory forest is *fine grained*. It is patchy, but the birds experience the habitat as an oak–hickory mixture. The habitat is *coarse grained*, however, for defoliating insects that attack *either* oaks *or* hickories preferentially: they experience the habitat one patch at a time, moving from one preferred patch to another (Figure 6.10).

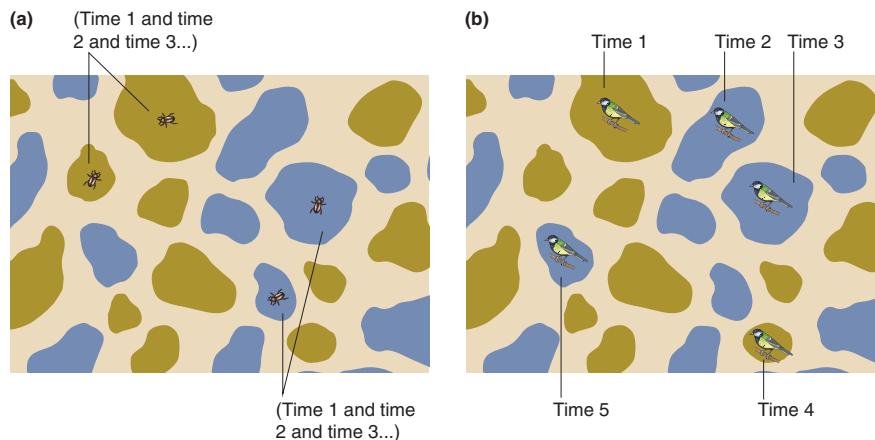
Patchiness, dispersal and scale are tied intimately together. Thus, it is useful to distinguish between *turnover dispersal* and *invasion dispersal* (Bullock *et al.*, 2002) and to do so at local and landscape scales (though what is 'local' to a worm is very different from what is local to the bird that eats it). Turnover dispersal at the local scale refers to the movement of an individual into a gap from occupied habitat immediately surrounding the gap. But that gap may also be 'invaded' by individuals moving in from elsewhere in the surrounding community. Similarly, at the landscape scale, dispersal may be part of an on-going turnover of extinction and recolonisation of occupiable patches within an otherwise unsuitable habitat matrix (see Section 6.7 on metapopulation dynamics), or there may be invasion of an area by dispersal of a 'new' species expanding its range.

#### fine- and coarse-grained environments

#### turnover and invasion dispersal

#### 6.4.2 Forces favouring aggregation

The simplest evolutionary explanation for the patchiness of populations is that organisms aggregate where they find the habitat patches that are most favourable for reproduction and survival. It pays them (and has paid them in



**Figure 6.10** The ‘grain’ of the environment must be seen from the perspective of the organism concerned. (a) An organism that is small or moves little is likely to see the environment as coarse grained: it experiences only one habitat type within the environment for long periods or perhaps all of its life. (b) An organism that is larger or moves more may see the same environment as fine grained: it moves frequently between habitat types and hence samples them in the proportion in which they occur in the environment as a whole.

evolutionary time) to disperse to these patches. There are, however, other specific ways in which organisms may gain from being close to neighbours.

#### aggregation and the selfish herd

A classic theory identifying a selective advantage to individuals that aggregate with others was proposed by Hamilton (1971) in his paper ‘Geometry for the selfish herd’. He argued that the risk to an individual from a predator may be lessened if it places another potential prey individual between itself and the predator. The consequence of many individuals doing this is that they form an aggregation in space. The principle of the selfish herd is also pertinent to the aggregated (synchronous) appearance of organisms in time. We return to this question of so-called ‘mast’ years in Section 10.2.4.

#### philopatry

Individuals may also tend to aggregate, or at least not disperse away from one another, if they exhibit philopatry or ‘home-loving’ behaviour (Lambin *et al.*, 2001). This can come about because there are advantages of inhabiting a familiar environment, or individuals may cooperate with, or at least be prepared to tolerate, related individuals in the natal habitat that share a high proportion of their genes, or dispersers may face intolerance or aggression from groups of unrelated individuals (Hestbeck, 1982). Lambin and Krebs (1993), for example, found in Townsend’s voles, *Microtus townsendii*, in Canada, that the nests of females that were first degree relatives (mother–daughters, littermate sisters) were closer than those that were second degree relatives (non-littermate sisters, aunt–nieces), which were closer than those that were more distantly related, which in turn were closer than those not related at all. *M. townsendii* also

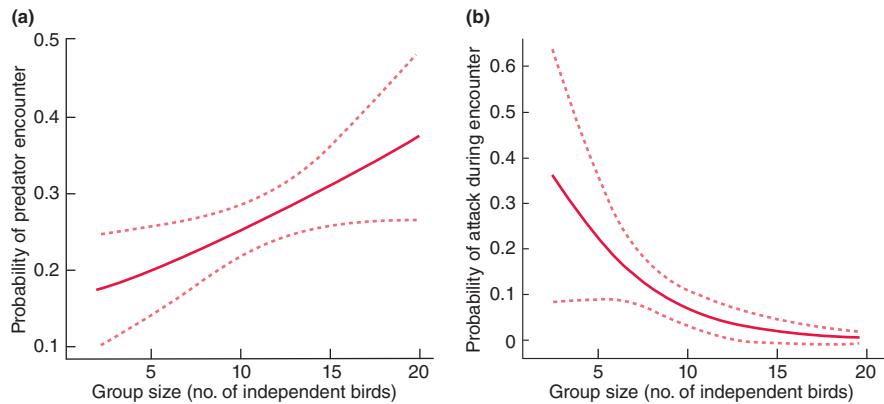
provides an example where the fitness advantages of philopatry have been confirmed. Lambin and Yoccoz (1998) manipulated the relatedness of groups of breeding females, mimicking either a situation where the population had experienced philopatric recruitment followed by high survival ('high kinship'), or where the population had experienced either low philopatric recruitment or high mortality of recruits ('low kinship'). Survival of pups, especially early in their life, was significantly higher in the high kinship than in the low kinship treatment.

Individuals may also gain from living in groups (Krause & Ruxton, 2002) if this helps to locate food, or gives warning of predators, or if it pays for individuals to join forces in fighting off a predator (Figure 6.11); and there are also many species – estimated to be up to 9% of all bird species, for example – that exhibit cooperative breeding, often arising out of philopatry amongst offspring who remain on their natal territory and help their parents raise subsequent broods (Hatchwell, 2009).

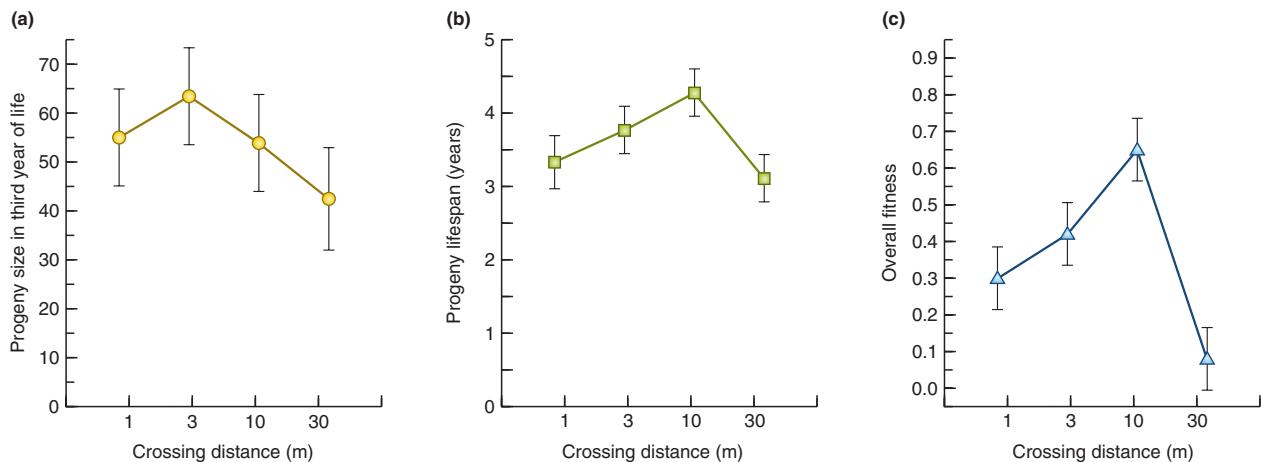
#### sociability and cooperation

### 6.4.3 Forces diluting aggregations: density-dependent dispersal

On the other hand, there are strong selective pressures that can act against aggregation. The foremost of these is undoubtedly the more intense competition suffered by crowded individuals (see Chapter 5) and the direct interference between such individuals even in the absence of a shortage of resources. We see this, for example, in the even spacing that results from territoriality (Section 5.8.4).



**Figure 6.11 Group living protects against predation in the chestnut-crowned babbler, *Pomatostomus ruficeps*, in New South Wales, Australia.** (a) Predators (various falcons and hawks) were more likely to encounter (i.e. be attracted to) larger groups of babblers. (b) But despite this, predators were less likely to attack babblers in larger groups. In each case, lines are from models fitted to the data after other explanatory variables have been taken into account, with standard errors shown by dotted lines. Source: After Sorato *et al.* (2012).



**Figure 6.12 Inbreeding and outbreeding depression in *Delphinium nelsonii*.** (a) Progeny size in the third year of life, (b) progeny lifespan and (c) the overall fitness of progeny cohorts were all lower when progeny were the result of crosses with pollen taken close to (1 m) or far from (30 m) the receptor plant. Bars are SEs. Source: After Waser & Price (1994).

### inbreeding and outbreeding

Another important driver diluting aggregations is not so much ecological as evolutionary. When closely related individuals breed, their offspring are likely to suffer an ‘inbreeding depression’ in fitness (Charlesworth & Charlesworth, 1987), especially as a result of the expression in the phenotype of recessive deleterious alleles. With limited dispersal, inbreeding becomes more likely, and inbreeding avoidance is thus a force favouring dispersal, particularly natal dispersal. On the other hand, many species show local adaptation to their immediate environment (see Section 1.2). Longer distance dispersal may therefore bring together genotypes adapted to different local environments, which on mating give rise to low-fitness offspring adapted to neither habitat. This is called ‘outbreeding depression’, resulting from the break-up of co-adapted combinations of genes – a force acting against dispersal.

The situation is complicated by the fact that inbreeding depression is most likely amongst populations that normally outbreed, since inbreeding itself will purge populations of their deleterious recessives. Nonetheless, natural selection can be expected to favour a pattern of dispersal that is in some sense intermediate – maximising fitness by avoiding both inbreeding and outbreeding depression, though these will clearly not be the only selective forces acting on dispersal. Certainly, there are several examples in plants of inbreeding and outbreeding depression when pollen is transferred from either close or distant donors, and in some cases both effects can be demonstrated in a single experiment. For example, when larkspur (*Delphinium nelsonii*) offspring were generated by hand pollinating with pollen brought from 1, 3, 10 and 30 m to the receptor flowers (Figure 6.12), both inbreeding and outbreeding depression in fitness were apparent.

**avoiding kin competition**

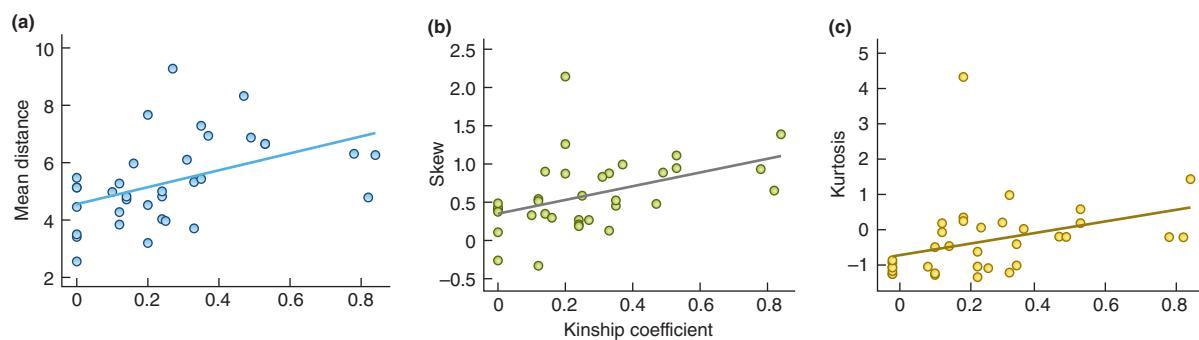
Dispersal of offspring away from their close relatives may also be favoured because it decreases the likelihood of competitive effects being directed at close kin. This was explained in a classic modelling paper by Hamilton and May (1977) (see also Gandon & Michalakis, 2001). In a population of stay-at-home non-dispersers, a rare mutant disperser that keeps some offspring at home but commits others to dispersal will suffer no competition in its own patch from non-dispersers, but it will compete against those non-dispersers in their home patches. Dispersers will thus direct much of their competitive effects at non-dispersing non-kin, while non-dispersers direct all of their competition at their own kin. The propensity to disperse will therefore increase in frequency in the population. On the other hand, if the majority of the population are dispersers, a rare mutant non-disperser will again do worse, since it can never displace any of the dispersers from their patches but has itself to contend with dispersers from outside. Dispersal is therefore said to be an evolutionarily stable strategy (ESS) (Maynard Smith, 1972; Parker, 1984) – it increases when rare but cannot be displaced when common. Hence, the avoidance of both inbreeding and kin competition seem likely to give rise to higher emigration rates at higher densities, when these forces are most intense.

There is indeed evidence for kin competition playing a role in driving offspring away from their natal habitat, but much of it is indirect (Lambin *et al.*, 2001). In some cases, though, it has been demonstrated experimentally, for example in the spider mite, *Tetranychus urticae*, where individuals

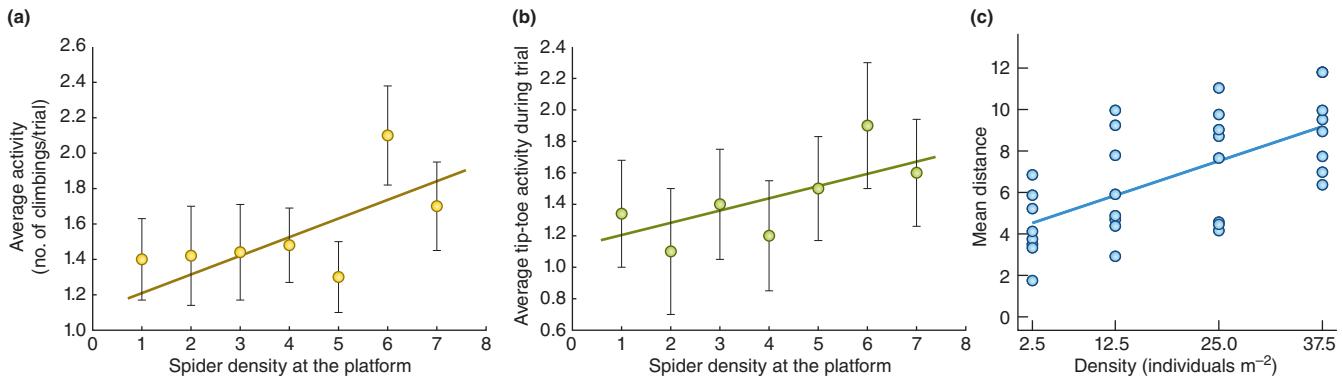
not only dispersed further, on average, when surrounded by more related individuals, but also had a dispersal distribution in which more individuals dispersed the greatest distances (Figure 6.13).

Putting these considerations together, we can see that the types of distribution over available patches found in nature are bound to be evolved compromises between forces attracting individuals towards one another and those provoking them to disperse apart. We return later to the ‘ideal free distribution’ and other spatial distributions that may result from this (Section 10.4.3). We can also see that if dispersal occurs to avoid competition, then it should occur at greater rates at higher densities. That is, we should see density-dependent dispersal. If, however, dispersal occurs to avoid kin competition in particular, then we should especially expect to see density-dependent *natal* dispersal, and we should see it in response to overall kin densities, irrespective of sex. But if density-dependent natal dispersal occurs to avoid inbreeding, then we would expect to see males responding in particular to the densities of females, and females to the densities of males. There are certainly examples of density-dependent emigration, both as regards a tendency to disperse and the distance dispersed (Figure 6.14). But we need to acknowledge the alternative drivers behind such patterns, and to see how these might combine with opposing forces like philopatry, that hold individuals together. Thus, we must recognise the importance of distinguishing between the dispersal patterns of males and females, and of the old and the young, which we do in the next section.

**density-dependent dispersal**



**Figure 6.13 Kin competition may drive offspring away from their natal habitat.** The effect of the relatedness of animals around them (kinship coefficient) on dispersal in the mite, *Tetranychus urticae*. As relatedness increased (a) mean distance dispersed increased ( $F = 8.51, P < 0.01$ ), (b) the distribution was more skewed towards longer distances and fewer near the mean ( $F = 7.94, P < 0.01$ ), and (c) kurtosis was greater: there were more individuals towards the tail of the distribution and less near the mean ( $F = 4.74, P < 0.05$ ). Source: After Bitume *et al.* (2013).

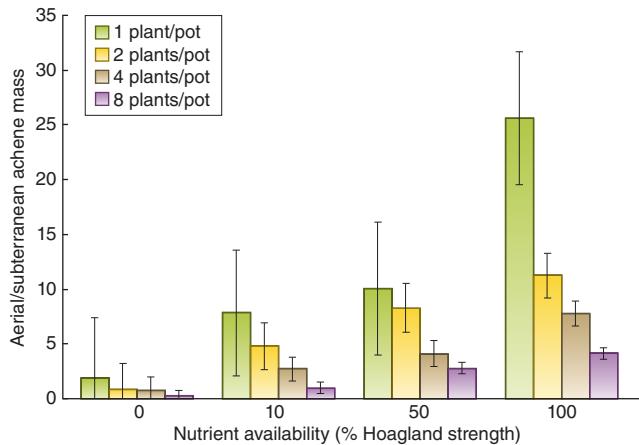


**Figure 6.14 Density-dependent emigration in spiders and mites.** In laboratory experiments, spiders, *Erigone atra*, emigrated from platforms in a wind tunnel, tethered by gossamer threads, at a greater rate at higher densities, as evidenced by (a) their tendency to climb vertical sticks from where the wind carried them away ( $F = 11.27, P < 0.001$ ), and (b) exhibiting ‘tip-toeing’ behaviour which made take-off more likely ( $F = 4.77, P < 0.05$ ). In both cases, standard errors are shown. (c) The mean distance dispersed by the mite, *Tetranychus urticae*, increased with initial density in the experiment also shown in Figure 6.13 ( $F = 9.61, P < 0.001$ ). Source: (a, b) After De Meester & Bonte (2010). (c) After Bitume *et al.* (2013).

## 6.5 Variation in dispersal within populations

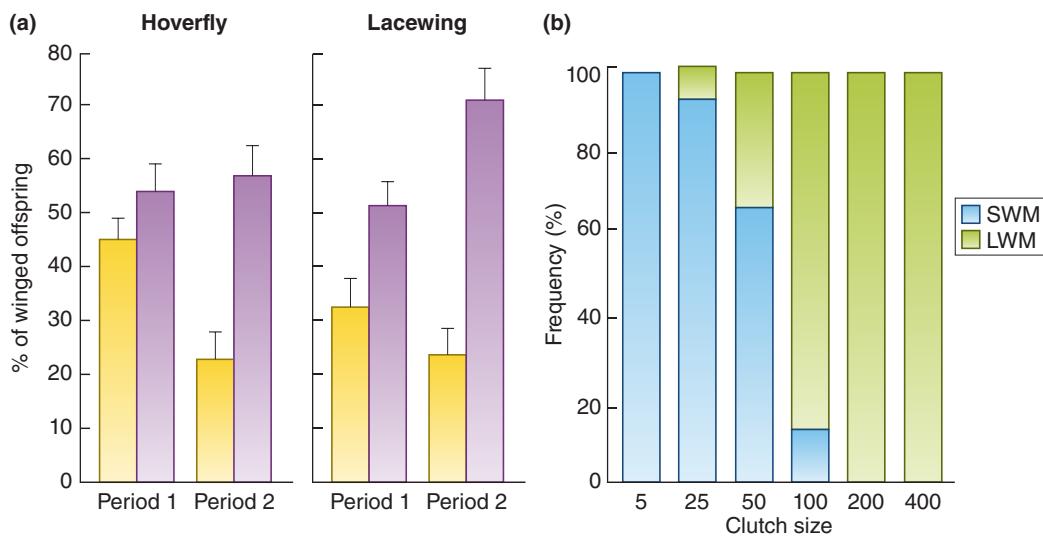
### 6.5.1 Dispersal polymorphism

One source of variability in dispersal within populations is polymorphism ('many types') amongst the progeny of a single parent. This is typically associated with habitats that are variable or unpredictable. A number of plants, for example, produce two different sorts of seed or fruits – *heterocarpy* – one of them dispersive and the other stay-at-home; and worldwide, around 50 of these species exhibit *amphicarpy*, where the same plant may either produce subterranean flowers at its home location that self-pollinate and then germinate underground, usually early in the season, or aerial flowers that cross-pollinate and produce fruits for long-range dispersal. One example is the devil's thorn, *Emex spinosa*, an annual originally from semiarid regions in the Old World that has now spread globally. The dry, aerial one-seeded fruits ('achenes') are spiny, buoyant and light and hence adapted for dispersal by animals, water and wind. The subterranean achenes, by contrast, lack spines and are never shed by the mother but are more competitive than their aerial counterparts. Greenhouse experiments show that the ratio of aerial to subterranean achene mass is greater at lower densities but at higher nutrient concentrations (Figure 6.15). This supports a view of subterranean production as part of a 'bad-year' strategy: when the plants are crowded and short of resources,



**Figure 6.15 Plants staying at home in bad years and dispersing in good years.** Investment by the annual plant, *Emex spinosa*, in dispersive aerial fruits (achenes) as opposed to stay-at-home subterranean ones was greater at lower densities ( $F = 8.59, P < 0.001$ ) and higher nutrient concentrations ( $F = 6.52, P < 0.001$ ). Means and SEs are shown. Source: After Sadeh *et al.* (2009).

they stay at home, investing more of their (scarce) resources safely where the past suggests they may thrive. High investment in aerial achenes, then, constitutes a dispersive, 'good-year' strategy of relatively risky investment that may, however, yield the benefit of the establishment of a new population 'elsewhere'.



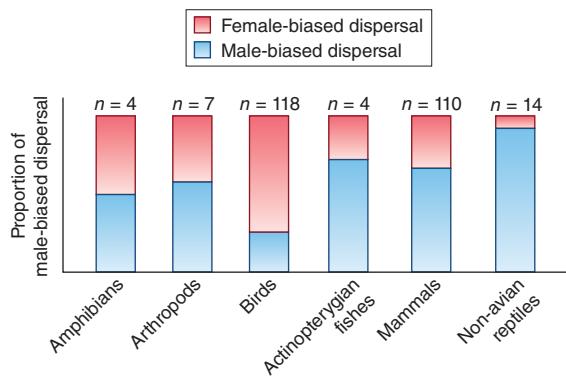
**Figure 6.16 Dispersal polymorphisms.** (a) The mean proportion ( $\pm$  SE) of winged morphs of the pea aphid, *Acyrtosiphon pisum*, produced after two separate periods of exposure to each of two predators: left: hoverfly larvae, and right: lacewing larvae. Purple bars, predator treatment; yellow bars, control. (b) The percentage, in the parasitoid wasp, *Melittobia digitata*, of the relatively dispersive long-winged morph (LWM) at the expense of the short-winged morph (SWM) increased in larger (more crowded) clutches of eggs ( $X^2 = 446.2$ ,  $P < 0.001$ ). Source: (a) After Kunert & Weisser (2003). (b) After Consoli & Vinson (2002).

A dimorphism of dispersers and non-dispersers (winged and wingless progeny), or of more- and less-dispersive offspring, is also a common phenomenon amongst insects. The pea aphid, *Acyrtosiphon pisum*, for example, produces more winged morphs in the presence of predators (Figure 6.16a), presumably as an escape response from an adverse environment; while the parasitoid wasp, *Melittobia digitata*, produces more of its more dispersive long-winged morph from larger, more crowded clutches, again presumably as an escape response (Figure 6.16b).

### 6.5.2 Sex- and age-related differences

We have noted already that much dispersal is natal, involving the movement of an organism from its place of birth to its place of first breeding. This age differential is linked intimately to sex differences in dispersal because the forces shaping dispersal – philopatry, avoidance of kin competition or inbreeding, and so on – often themselves act differently on the two sexes. In a seminal paper that set the scene for much of the subsequent work in this area, Greenwood (1980) contrasted the sex-biased natal dispersal of birds and mammals. He noted that many birds are socially monogamous (pairs breed only with one another, at least

within each breeding season) and that the males establish and defend territories (ideally in areas with which they are familiar) to which females are then attracted. He argued that it was for this reason that females were the dispersive sex far more often than the philopatric males. Many mammals, on the other hand, are polygynandrous (both males and females have multiple mates over the course of a breeding season), with males defending access to groups of females. Hence, here it is the males that disperse more in order to give themselves the opportunity of obtaining this most crucial resource. Of course, the real distinction is not between birds and mammals but between the contrasting lifestyles and selection pressures that they may be said to typify. An entirely equivalent argument can be applied to monogamous and polygynandrous mammals (Dobson, 2013). A review of sex-biased dispersal covering a much wider (animal) taxonomic range (Trochet *et al.*, 2016) confirmed the broad distinction between birds and mammals, but showed that overall, male and female bias are more or less equally common (Figure 6.17). Analysis of the traits associated with sex bias provided some support for Greenwood's hypothesis (an association of the direction of sex bias with the mating system and territoriality) but in fact the link was more strongly related to the type of parental care and sexual dimorphism.



**Figure 6.17** The proportion of male-biased as opposed to female-biased dispersal in studies carried out on different taxonomic groups. Source: After Trochet *et al.* (2016).

The more important, general point, therefore, is that dispersal differentials will reflect differences, however they arise, in the costs and benefits of philopatry, the nature of the key resource being competed for, and so on. These are set against a background of dispersal differences between the sexes being favoured in their own right as a means of reducing inbreeding (Lambin *et al.*, 2001; Dobson, 2013), though of course, if individuals can recognise their own kin, they can avoid breeding with them without the need for differential dispersal. Hence, alongside the common themes there are many apparent ‘special cases’. The superb starling, *Lamprotornis superbus*, for example, studied in Kenya, is a cooperative breeder in which philopatric males remain in the natal territory to help rear their parents’ subsequent broods while their female equivalents disperse, thereby reducing the possibilities of inbreeding but also of cooperation between female kin. In fact, however, 26% of dispersed females occurred in a group with a full sister, and these individuals were significantly more likely to breed, suggesting that the sisters formed some kind of alliance (Pollack & Rubenstein, 2015). In another example, in Tanzania, spotted hyena males, *Crocuta crocuta*, could be either philopatric, remaining with their natal clan, or dispersers, despite the fact that a well-developed female mate-choice in the species would be expected to drive male-biased dispersal in an archetypal mammalian pattern. In practice, though, dispersal decisions appeared much more pragmatic and opportunistic. Males choosing to be philopatric entered the social hierarchy near the top, whereas dispersers had to work their way up over several years. As a consequence, philopatric males mated more often than dispersers did with the highest-ranking females, which compensated for their lower mating rate with other

females, leading to similar fitnesses of the two types overall (Davidian *et al.*, 2016). There is undoubtedly a shared list of drivers of age- and sex-related patterns of dispersal, but an enormous variety of ways in which these drivers can be combined.

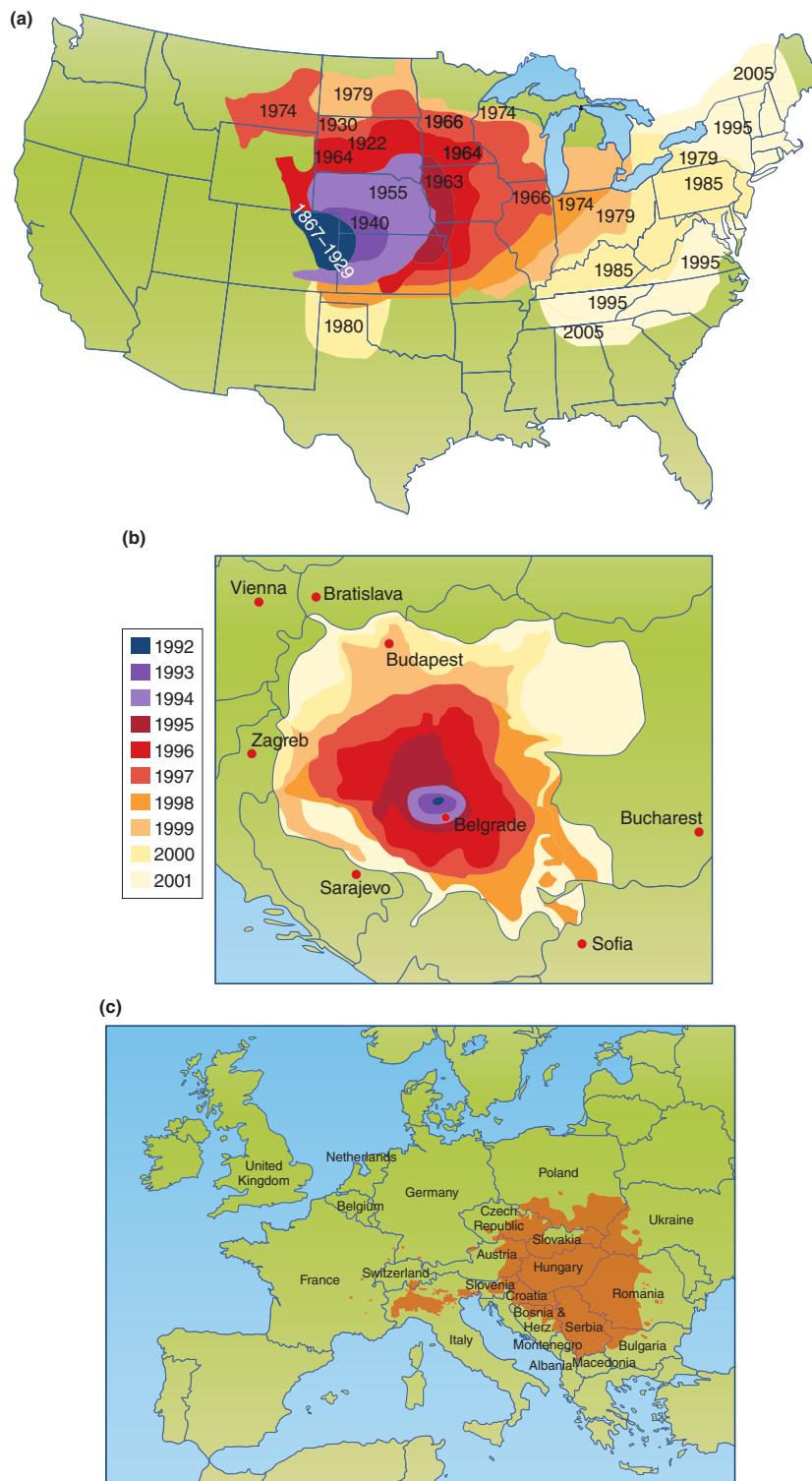
## 6.6 The demographic significance of dispersal

Dispersal can have a potentially profound effect on the dynamics of populations. In practice, however, many studies have paid little attention to dispersal. The reason often given is that emigration and immigration are approximately equal, and they therefore cancel one another out. One suspects, though, that the real reason is that dispersal is usually extremely difficult to quantify.

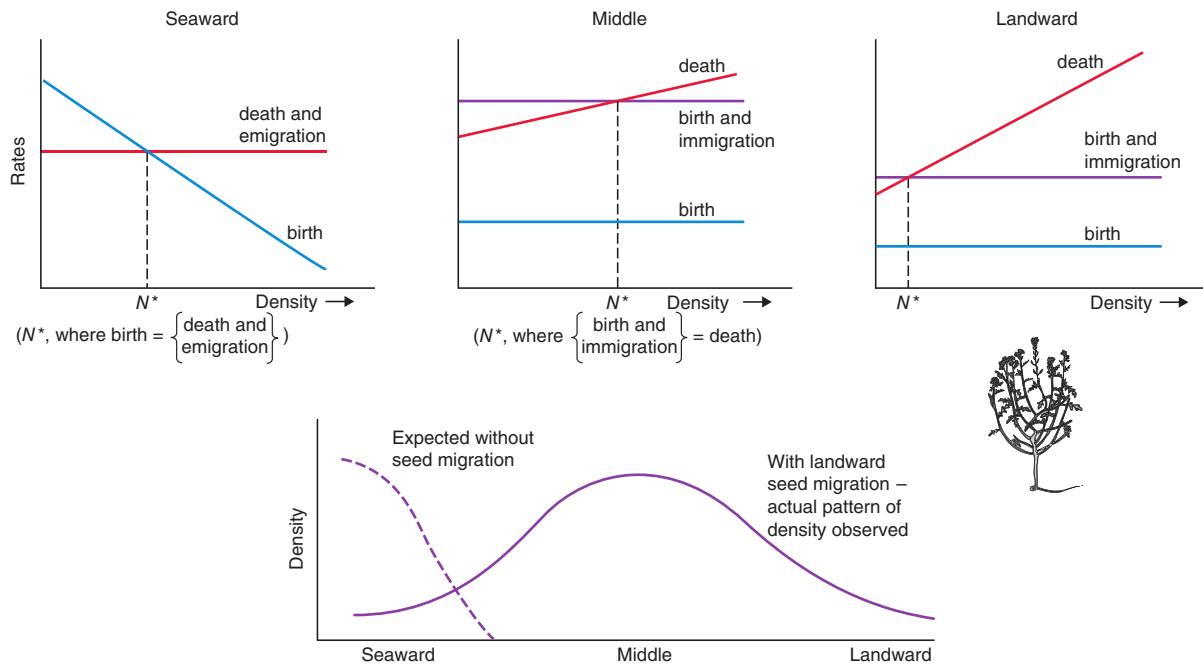
### 6.6.1 Dispersal and the demography of single populations

The studies that have looked carefully at dispersal have tended to bear out its importance. In a long-term and intensive investigation of a population of great tits, *Parus major*, near Oxford, UK, it was observed that 57% of breeding birds were immigrants rather than born in the population (Greenwood *et al.*, 1978). And in many cases the rapid spread of species into new areas, including economically important pests, is a compelling testament to the power of dispersal in determining the abundance we observe (see, for example, Figure 6.18).

A profound effect of dispersal on the dynamics of a population was seen in a study of *Cakile edentula*, a summer annual plant growing on the sand dunes of Martinique Bay, Nova Scotia. The population was concentrated in the middle of the dunes, and declined towards both the sea and the land. Only in the area towards the sea, however, was seed production high enough and mortality sufficiently low for the population to maintain itself year after year. At the middle and landward sites, mortality exceeded seed production. Hence, one might have expected the population to become extinct (Figure 6.19). But the distribution of *Cakile* did not change over time. Instead, large numbers of seeds from the seaward zone dispersed to the middle and landward zones. Indeed, more seeds were dispersed into and germinated in these two zones than were produced by the residents. The distribution and abundance of *Cakile* were directly due to the dispersal of seeds in the wind and the waves.



**Figure 6.18** The rapid spread of the western corn rootworm, *Diabrotica virgifera virgifera*, one of the most important pests of maize worldwide, (a) in the USA following its break-out from a stronghold around eastern Nebraska in the 1940s; (b) in south-eastern Europe, from 1992 to 2001, following its probable introduction from material carried by plane to Belgrade airport; and (c) to elsewhere in Europe by 2007. Source: (a, c) After Gray *et al.* (2009). (b) After European Environment Agency (2002).



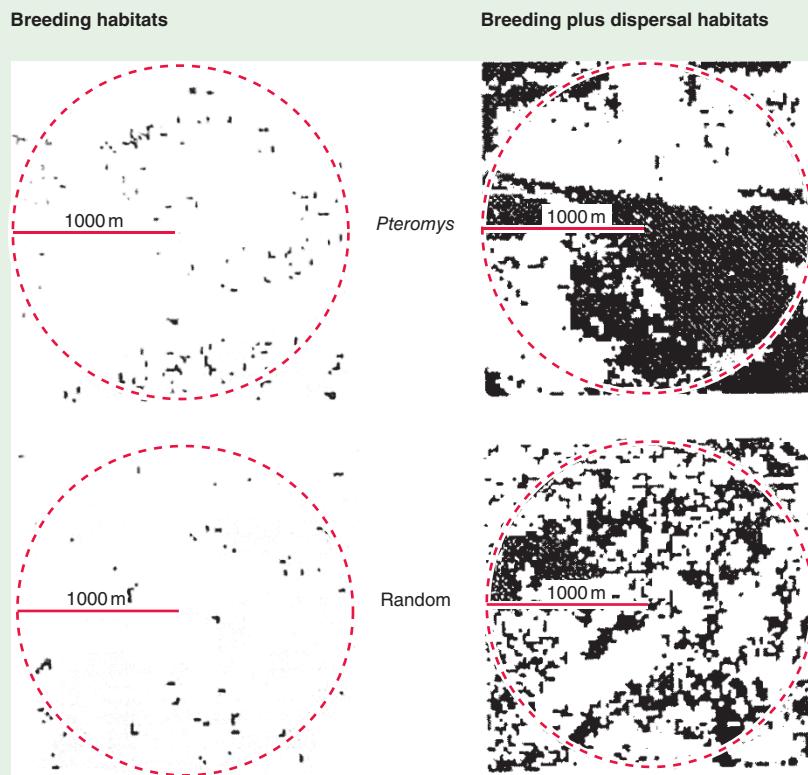
**Figure 6.19 Dispersal drives the local distribution of a sand-dune plant.** Diagrammatic representation of variations in mortality and seed production of *Cakile edentula* in three areas along an environmental gradient from open sand beach (seaward) to densely vegetated dunes (landward). In contrast to other areas, seed production was prolific at the seaward site. Births, however, declined with plant density, and where births and deaths were equal, an equilibrium population density can be envisaged,  $N^*$ . In the middle and landward sites, deaths always exceeded births resulting from local seeds, but populations persisted there because of the landward drift of the majority of seed produced by plants on the beach (seaward site). Thus, the sum of local births plus immigrating seeds can balance mortality in the middle and landward sites, resulting in equilibria at appropriate densities.

### APPLICATION 6.5 Habitat restoration for a declining squirrel population

We can see the importance of dispersal, too, in the development of plans to conserve populations of flying squirrels (*Pteromys volans*), which have declined dramatically since the 1950s in Finland, mainly because of habitat loss, habitat fragmentation and reduced habitat connectivity associated with intensive forestry practices. Areas of natural forest are now separated by clear-cut and regenerating areas. The core breeding habitat of the flying squirrels only occupies a few hectares, but individuals, particularly males, move to and from this core for temporary stays in a much larger ‘dispersal’ area ( $1\text{--}3 \text{ km}^2$ ), and juveniles permanently disperse within this range. Reunanen *et al.* (2000) compared the landscape structure around known flying squirrel home ranges (63 sites) with randomly chosen areas (96 sites) to determine the forest patterns that favour the squirrels. They first established that landscape patch types could be divided into optimal breeding

habitat (mixed spruce–deciduous forests), dispersal habitat (pine and young forests) and unsuitable habitat (young sapling stands, open habitats, water). Figure 6.20 shows the amount and spatial arrangement of the breeding habitat and dispersal habitat for examples of a typical flying squirrel site and a random forest site. Overall, flying squirrel landscapes contained three times more suitable breeding habitat within a 1 km radius than random landscapes. Crucially, however, squirrel landscapes also contained about 23% more dispersal habitat than random landscapes, and significantly, squirrel dispersal habitat was much better connected (fewer fragments per unit area) than random landscapes. Reunanen *et al.* (2000) recommend that forest managers should restore and maintain a deciduous mixture, particularly in spruce-dominated forests, for optimal breeding habitat. But they also need to ensure good physical connectivity between the optimal squirrel breeding and dispersal habitats.

## APPLICATION 6.5 (Continued)



**Figure 6.20 Flying squirrels in Finland preferentially occupy habitat favouring effective dispersal.** The spatial arrangement of patches (dark) of breeding habitat (left hand panels) and breeding plus dispersal habitat (right hand panels) in a typical landscape containing flying squirrels (*Pteromys*) (top panels) and a random forest location (bottom panels). This flying squirrel landscape contains 4% breeding habitat and 52.4% breeding plus dispersal habitat, compared with 1.5% and 41.5% for the random landscape. Dispersal habitat in the squirrel landscape is much more highly connected (fewer fragments per unit area) than in the random landscape. Source: After Reunananen *et al.* (2000).

Probably the most fundamental consequence of dispersal for the dynamics of single populations, though, is the effect of density-dependent emigration in reducing resource over-exploitation (see Section 6.3.3). Locally, all that was said in Chapter 5 regarding density-dependent mortality applies equally to density-dependent emigration. Globally, of course, the consequences of the two may be quite different. Those that die are lost forever and from everywhere. With emigration, one population's loss may be another's gain.

### 6.6.2 Invasion dynamics

#### the importance of eccentric dispersers

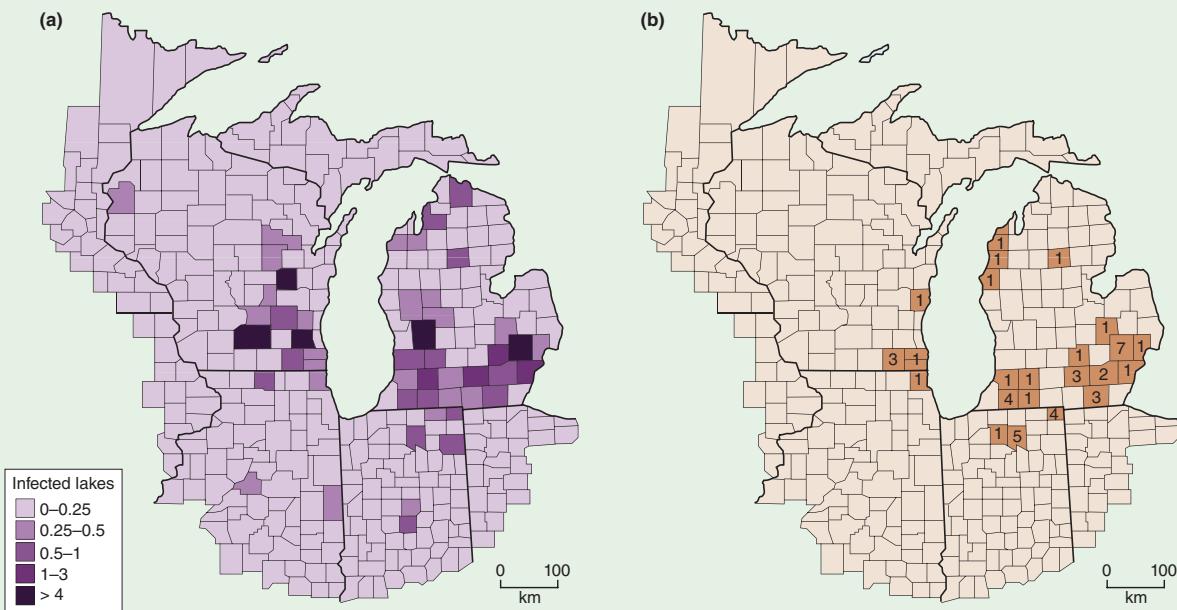
In almost every aspect of life, there is a danger in imagining that what is usual and 'normal' is in fact

universal, and that what is unusual or eccentric can safely be dismissed or ignored. Every statistical distribution has a tail, however, and those that occupy the tail are as real as the conformists that outnumber them. So it is with dispersal. For many purposes, it is reasonable to characterise dispersal rates and distances in terms of what is typical. But especially when the focus is on the spread of a species into a habitat it has not previously occupied, those propagules dispersing furthest may be of the greatest importance. Neubert and Caswell (2000), for example, analysed the rate of spread of two species of plants, *Calathea ovandensis* and *Dipsacus sylvestris*. In both cases they found that the rate of spread was strongly dependent on the maximum dispersal distance, whereas variations in the pattern of dispersal at lesser distances had little effect.

## APPLICATION 6.6 Invaders of the Great Lakes

In many cases, the tail of the dispersal curve is represented by rare individuals that have dispersed by some means that is itself unusual. For example, the Great Lakes of North America have been invaded by more than 170 alien species (Ricciardi *et al.*, 2017), and many of these have arrived as stowaways in ships' ballast water. Ships are filled with ballast water in one location to stabilise them, and suck in organisms with the water, but then transport them to another location where the ballast water and organisms are discharged as heavy cargo is taken aboard. A ballasted ocean freighter, before taking on cargo in the Great Lakes, may discharge three million litres of ballast water that contain various life stages of many plant and animal taxa (and even the cholera bacterium *Vibrio cholerae*) that originate where the ballast water was taken aboard. For example, a whole series of recent invaders (including fish, mussels, amphipods, cladocerans and snails) originated from the other end of an important trade route in the Black and Caspian Seas (Ricciardi & MacIsaac, 2000). One solution is to make the dumping of ballast water in the open ocean compulsory rather than voluntary (this is now the case for the Great Lakes). Other possible methods involve filter systems when loading ballast water, and on-board treatment by ultraviolet irradiation or waste heat from the ship's engines.

The most damaging invaders are not simply those that arrive in a new part of the world; the subsequent pattern and speed of their spread is also significant to managers. Zebra mussels (*Dreissena polymorpha*) have had a devastating effect since arriving in North America via the Caspian Sea/Great Lakes trade route. They threaten native mussels and other fauna, not only by reducing food and oxygen availability but by physically smothering them. The mussels also invade and clog water intake pipes, and millions of dollars need to be spent clearing them from water filtration and hydroelectric generating plants. From the first observations in 1986, range expansion quickly occurred throughout commercially navigable waters, but overland dispersal into inland lakes, mainly attached to recreational boats, has been much slower (Kraft & Johnson, 2000). Geographers have developed so-called 'gravity' models to predict human dispersal patterns based on distance to and attractiveness of destination points, and Bossenbroek *et al.* (2001) adopted the technique to predict the spread of zebra mussels through the inland lakes of Illinois, Indiana, Michigan and Wisconsin (364 counties in all). The model has three steps involving (i) the probability of a boat travelling to a zebra mussel source; (ii) the probability of the same boat making a subsequent outing to an uncolonised lake; and (iii) the probability of zebra mussels becoming established in the uncolonised lake.



**Figure 6.21** The predictable dispersal of zebra mussels, invading the USA. (a) The predicted distribution (based on 2000 iterations of a stochastic 'gravity' model of dispersal) of inland lakes colonised by zebra mussels in 364 counties in the USA; the large lake in the middle is Lake Michigan, one of the Great Lakes of North America. (b) The actual distribution of colonised lakes as of 1997. (c) The actual distribution as of 1 May 2017. Source: (a, b) After Bossenbroek *et al.* (2001). (c) After United States Geological Survey (2017).

## APPLICATION 6.6 (Continued)

To generate a predicted probabilistic distribution of zebra mussel-colonised lakes, 2000 trials of the model were run for seven years and the number of colonised lakes for each county was estimated by summing the individual colonisation probabilities for each lake in the county. The results, shown in Figure 6.21a, are highly correlated with the pattern of colonisation that actually occurred up to 1997 (Figure 6.21b), giving confidence in

the predictions of the model. However, areas of central Wisconsin and western Michigan were predicted to be colonised, but no colonies had at that point been documented. Bossenbroek *et al.* (2001) suggested that invasion may be imminent in these locations, which should therefore be the focus of biosecurity efforts and education campaigns. Nonetheless, by 2017 the mussel had spread to these areas and way beyond (Figure 6.21c).

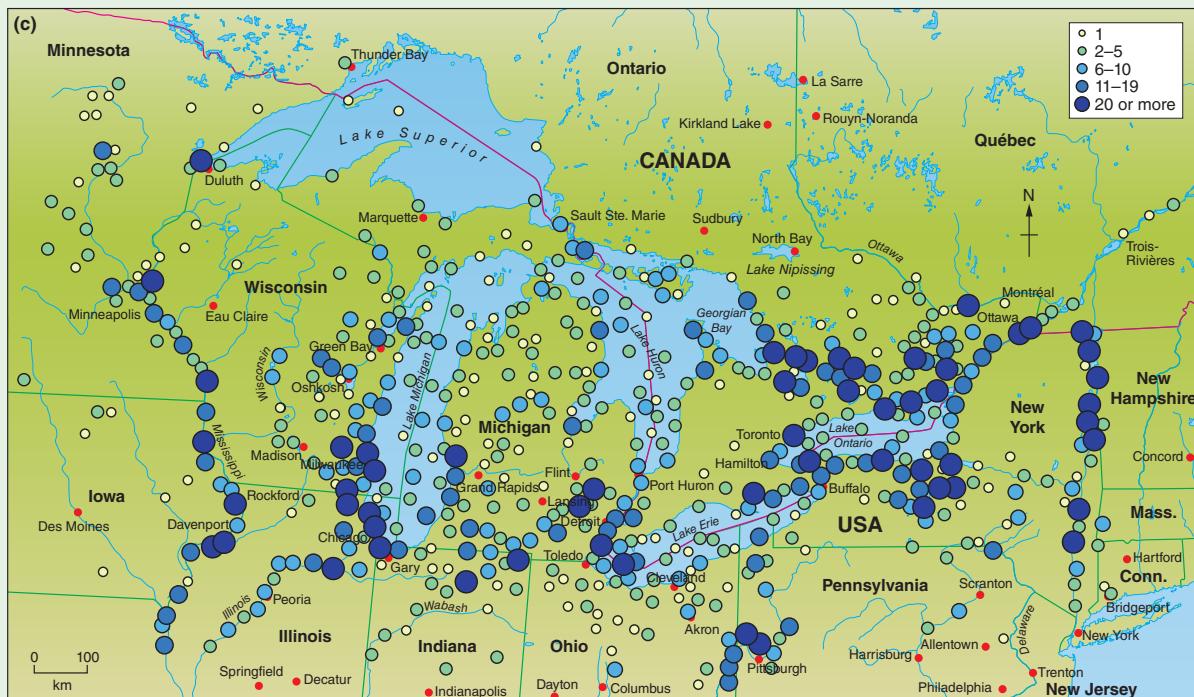
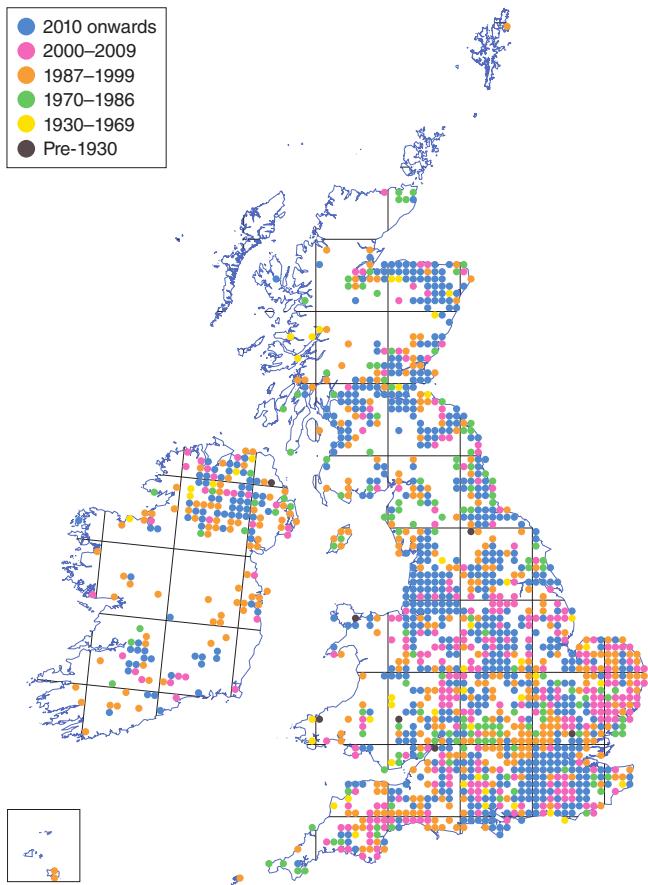


Figure 6.21 (Continued)

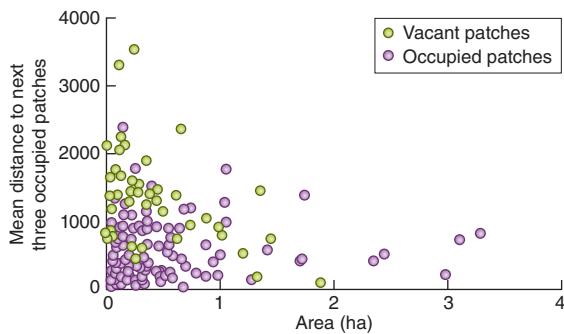
Of course invaders do not all rely on human agency; many disperse by their own devices. We can see the example of the giant hogweed, *Heracleum mantegazzianum*, a noxious weed in the UK and Ireland in Figure 6.22, and we saw something comparable for the western corn rootworm in Figure 6.18.

This dependence of invasion on rare long-distance dispersers means, in turn, that the probability of a species invading a new habitat may have far more to do with the proximity of a source population (and hence the opportunity to invade) than it does on the performance of the species once an initial bridgehead has been established. For example, the violet copper butterfly, *Lycaena helle*, one of the rarest butterfly species in Central Europe, was studied in the Westerwald region in Germany, where it is confined to patches of habitat containing adderwort, *Bistorta*

*officinalis*, its only larval food plant in the area. This was one of several features used to classify habitat patches as 'suitable' for the violet copper, giving 230 patches in total. These were then surveyed to determine whether they were occupied by the butterfly or not, and what features distinguished occupied from vacant patches. Three factors had a significant influence on occupancy. Patches were more likely to be occupied the higher the percentage of the ground covered by adderwort – an indicator of 'patch quality' from the butterflies' point of view. But occupancy was also more likely in larger patches (larger targets for dispersal) and in patches that were less isolated from other occupied sites (Figure 6.23). Abundance was being limited, to a significant degree, not so much by a lack of habitat but by difficulties in reaching it.



**Figure 6.22 Invasion of the giant hogweed.** The changing distribution over time, as of 25 May 2017, of the noxious weed, the giant hogweed, *Heracleum mantegazzianum*, in the UK and Ireland as it has invaded an increasing number of areas. The map is compiled and updated by the Biological Records Centre of the UK, where comparable maps for most other UK plant species can be found at <http://www.brc.ac.uk/plantatlas/plant/species-genus>. Source: Biological Records Centre (2017).



**Figure 6.23 Butterflies tend to occupy the largest, least isolated habitat patches.** The sizes of vacant patches and those occupied by the violet copper butterfly, *Lycaena helle*, in the Westerwald, Germany, and also their level of isolation from other occupied patches. Source: After Bauerfeind *et al.* (2002).

### 6.6.3 Modelling dispersal: the distribution of patches

The nature of the role of dispersal in population dynamics depends on how we think of those populations.

#### metapopulations and subpopulations

The simplest view sees a population as a collection of individuals distributed more or less continuously over a stretch of more or less suitable habitat, such that the population is a single, undivided entity. Dispersal is then a process contributing to either increase (immigration) or decrease (emigration) in the population as a whole, or one that redistributes individuals within the population (see Application 6.7). In many cases, however, we need to remind ourselves of what we noted in Section 6.4.1: the ubiquity of patchiness in ecology and the importance of dispersal in linking patches to one another. From this perspective, many populations are best viewed as *metapopulations*.

A metapopulation is defined as a collection of subpopulations, where a subpopulation occupies a habitable patch in the landscape and corresponds, in isolation, to the simple view of a population described above. However, the dynamics of the metapopulation as a whole is determined, not by dispersal *within* subpopulations, but by the rate of extinction of existing subpopulations and the rate of establishment (colonisation) of new subpopulations by dispersal into habitable but uninhabited patches. Note, however, that just because a species occupies more than one habitable site, each of which supports a population, this does not mean that those populations comprise a metapopulation. As we shall discuss more fully below, ‘classic’ metapopulation status is conferred only when extinction and colonisation play a major role in the overall dynamics.

If we think of dispersal as occurring within a patchy landscape, there are two alternative ways of modelling this (Keeling, 1999). The first is a ‘spatially implicit’ approach (Hanski, 1999), where the key feature is that a proportion of the individuals leave their home patches and enter a pool of dispersers and are then redistributed amongst patches, usually at random. Thus, these models do not place patches at any specific spatial location. All patches may lose or gain individuals through dispersal, but all are, in a sense, equally distant from all other patches. Many metapopulation models (see later), come into this category, and despite their simplicity (real patches do have a location in space) they have provided important insights, in part because their simplicity makes them easier to analyse.

In contrast, ‘spatially explicit models’ acknowledge that the distances between patches vary, as do therefore the chances of them exchanging individuals through dispersal.

## APPLICATION 6.7 Reaction–diffusion modelling of shifting species' distributions under climate change

Variations in the way that we think of dispersal in the dynamics of populations are reflected in alternative approaches to modelling dispersal. If we treat space not as patchy but as continuous and homogeneous, then we can model dispersal as part of a ‘reaction–diffusion’ system. Here, the ‘reaction’ refers to the dynamics at any given location, driven by birth and survival, with dispersal added as a separate ‘diffusion’ term. The approach has arguably been more useful in other areas of biology (e.g. developmental biology) than it has in ecology. Nonetheless, the mathematical understanding of such systems is strong, and they are particularly good at demonstrating how spatial variation (i.e. patchiness) can be generated, internally, within an intrinsically homogeneous system (Keeling, 1999).

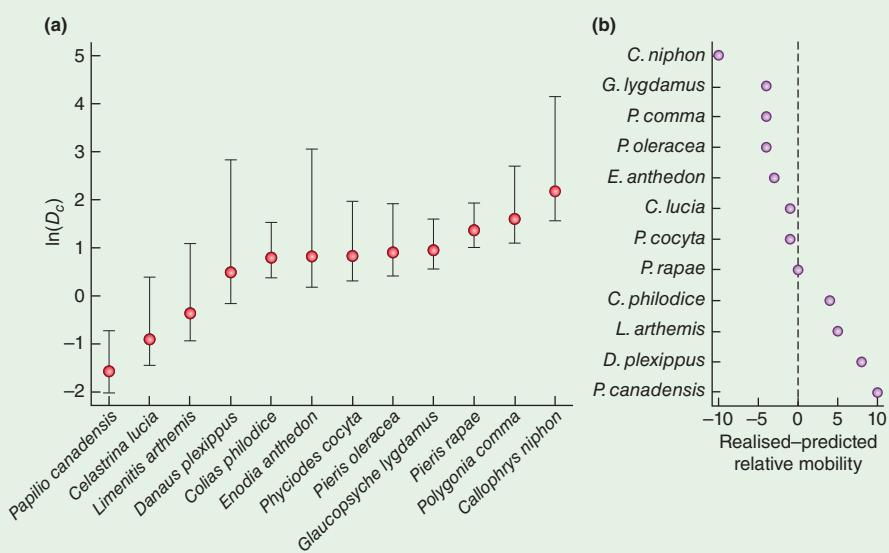
Reaction–diffusion models known as ‘moving habitat models’ (Harsch *et al.*, 2017) can also be valuable in trying to predict how species distributions will respond to climate change. Without going into the details of the models, it is easy to see that as the climate changes, and particularly as

the climate warms, the geographic limits of suitable habitat for many species in temperate regions – their ‘climate envelope’ – will shift polewards. Those species will therefore only survive in the face of global warming if they themselves can shift polewards at a comparable rate, which will require them to be both sufficiently productive at any given location (reflected in the reaction term) and to have sufficient powers of dispersal (the diffusion term). Specifically, a reaction–diffusion model developed by Leroux *et al.* (2013) proposed that a species could only persist if

$$2\sqrt{Dr} > q, \quad (6.1)$$

where  $D$  is the diffusion rate,  $r$  is the per capita rate of increase (Section 4.7.1) and  $q$  is the rate of movement of the climate envelope. This in turn allows us to determine a critical diffusion rate,  $D_c$ , that must be exceeded if the species is to persist, given by

$$D_c = q^2 / 4r. \quad (6.2)$$



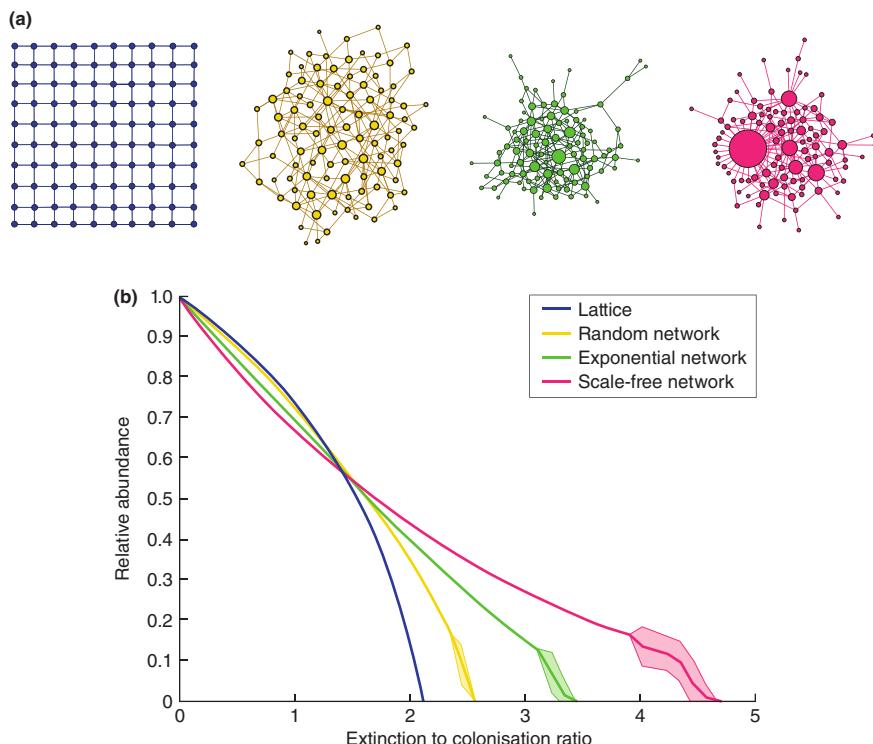
**Figure 6.24 Identifying priority North American butterfly species for conservation by assessing their dispersal ability in the face of climate change.** (a) Log-transformed estimates of the critical diffusion rates,  $D_c$ , of 12 butterfly species in North America that must be exceeded if those species are to persist in the face of predicted climate change and habitat shifting. The bars are the ranges between the estimates of  $D_c$  calculated from the 95% CIs of  $r$ , the per capita rate of increase, used to calculate  $D_c$  (Equation 6.2). (b) The difference, for these 12 species, between the relative rank of  $D_c$  and of estimates of their mobility from consultations with experts. Larger negative differences indicate that species are most at risk of failing to keep pace with climate change, etc. Source: After Leroux *et al.* (2013).

[Continued]

## APPLICATION 6.7 (Continued)

Leroux *et al.* (2013) then used data on  $q$  and  $r$  to calculate values of  $D_c$  for 12 butterfly species in North America (Figure 6.24a), and compared these with mobility scores for the species derived by seeking the expert opinions of 51 North American lepidopterists (Figure 6.24b). Large negative values in the comparison (mobility much less than the estimated critical value) characterise the species most at risk of failing to keep pace with climate change; large

positive values indicate the species least at risk. This ranking of the species is of course not perfect. The methods do not, for example, take account of rare long-distance dispersers. Nonetheless, since conservation ecologists must continuously be setting priorities, and directing their attention to where needs are most urgent or efforts most likely to be rewarded, results from models like these can be a valuable guide.



**Figure 6.25** The spatial structure of a metapopulation affects its overall abundance and persistence. (a) Four spatial networks (metapopulations) of increasing complexity, compared in a simulation study of the effect of spatial structure on overall population persistence. All networks here have 100 subpopulations (nodes) for purposes of illustration, with the size in the figure of each node proportional to its ‘connectivity’ (the number of other nodes to which it is connected). In the simulations, all metapopulations had 1024 nodes and 2048 links between nodes. Hence, they differed only in structure. From left to right: a square lattice with each node connected to its neighbours; a network where nodes are connected together at random, so that long distance movement between nodes is possible; a network where connections follow an exponential distribution, again with long distance movement but with greater variation in connectivity; and a scale-free network where the variation in connectivity is greater still. Each node can either be occupied or unoccupied, and so the abundance of a population is given by the proportion of nodes occupied. (b) The abundance of each type (proportion of nodes occupied) at differing extinction–colonisation ratios. Each line is the average of 10 replicate simulations; the shaded areas represent standard deviations. Source: After Gillaranz & Bascompte (2012).

The earliest such models, developed in population genetics, were linear ‘stepping stone’ models, where dispersal occurred only between adjacent patches in the line. Subsequently, spatially explicit approaches have often involved ‘lattice’ models in which patches are arranged on a (usually) square grid, and patches exchange dispersing individuals with ‘neighbouring’ patches – perhaps the four with which they share a side, or the eight with which they make any contact at all, including the diagonals (Keeling, 1999). Further models can bridge the gap between lattices and spatial arrangements in the real world (Figure 6.25a), but they are all still caricatures of nature. They are nonetheless useful in highlighting new dynamic patterns that appear as soon as space is incorporated explicitly, and depending on how it is incorporated. Of course, spatial models generate spatial patterns (see, for example, Section 10.5), but as we can see in Figure 6.25b, for example, they also typically alter temporal dynamics. In that study, the dynamics of four idealised types of metapopulation were compared that differed only in their spatial structure. That is, they were all the same in terms of their overall size (number of patches), the number of connections between patches, and the extinction–

colonisation dynamics of individual patches. Nonetheless, there were significant differences in the abundance (proportion of patches occupied) and persistence of the metapopulations, especially where extinction tended to dominate colonisation, with the more complex spatial structures promoting greater abundance and persistence.

## 6.7 The dynamics of metapopulations

### 6.7.1 Uninhabited habitable patches

Recognition that many populations are in fact metapopulations was firmly established around 1970, but there was a delay of about 20 years before that recognition was translated into action and an increasing number of studies placed metapopulation dynamics prominently on the ecological stage. Now, the danger is not so much one of neglect, but that all populations are thought of as metapopulations, simply because the world is patchy.

Central to the concept of a metapopulation is the idea, emphasised by Andrewartha and Birch back in 1954, that

## APPLICATION 6.8 Species distribution modelling for (re)introductions and invasions

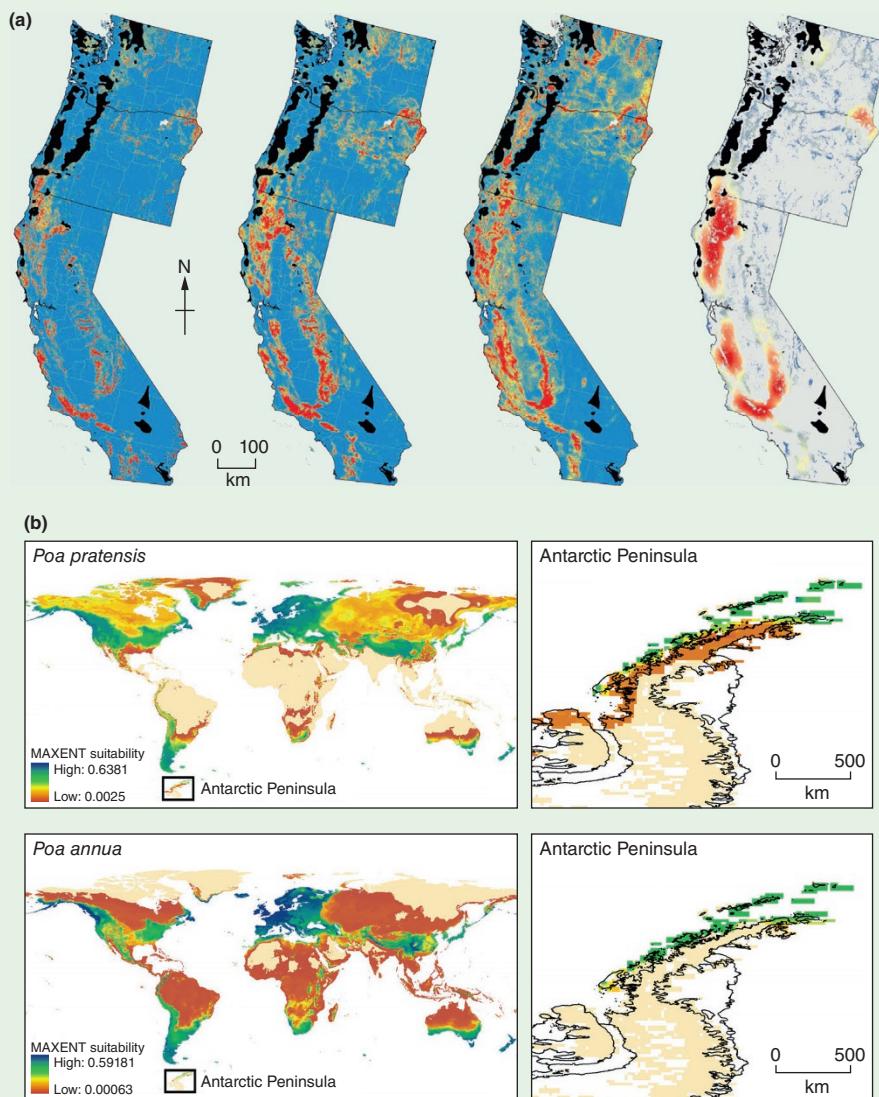
Recently, there have been many attempts to determine where a species would be able to live just as long as it could disperse there. These come under the umbrella term ‘species distribution modelling’ (Elith & Leathwick, 2009), the most influential variant of which has been ‘ecological niche modelling’, which we discussed in Chapter 2. To recapitulate briefly, as much environmental information as possible is taken from all of the locations where a species is currently found and also from a range of locations where the species is *not* currently found, allowing those locations to be identified that meet the species’ requirements even though the species is currently absent. In the present context, the implication is that it may only be the absence of effective dispersal that is currently preventing the species from living in these locations. The approach can be used to plan introductions or reintroductions of species (dispersal augmented by us) so as to maximise chances of success. We see an example of this for Californian condors, *Gymnogyps californianus*, in California, Oregon and Washington States in the USA in Figure 6.26a. Thirteen predictor variables from locations

where they had been observed between 1960 and 2011 were used to ‘train’ the model, which was then applied throughout the region. The results suggest that many parts of the condor’s historical range retain the characteristics that would support it, and they point to sites where reintroductions are most likely to be successful.

It has also been possible to use species distribution modelling to identify locations most at risk from a pest species if it were able to disperse there. We see an example of this for two species of grass in Antarctica (Figure 6.26b). *Poa pratensis* and *P. annua* are the only non-indigenous vascular plants established long term in the Antarctic Peninsula, but have been limited to only one established site for *P. pratensis* and six for *P. annua*. Results from ecological niche modelling, however, using four selected temperature variables – precipitation is of little importance in Antarctic conditions – show that there are a large number of other sites in Antarctica at threat from further invasion. They point in particular to some sites, in the South Shetland Islands, where the need for biosecurity measures is particularly great.

(Continued)

## APPLICATION 6.8 (Continued)



**Figure 6.26 Applications of species distribution modelling.** (a) Ecological niche modelling, using the algorithm MAXENT, for the critically endangered Californian condor, *Gymnogyps californianus*, in the states of California, Oregon and Washington, USA. From left to right, the first three maps show results for nesting, roosting and feeding, with warmer (redder) colours indicating greater suitability. Black areas represent (presumably unsuitable) areas with environmental conditions not encountered during model training. To the far right is a reintroduction suitability map combining the results to the left. (b) Ecological niche modelling, again using MAXENT, for the grasses *Poa pratensis* and *P. annua* globally and in the Antarctic Peninsula. Source: (a) After D'Elia *et al.* (2015). (b) After Perttierra *et al.* (2017).

habitable patches might be uninhabited simply because individuals have failed to disperse into them. To establish that this is so, we need to be able to identify habitable sites that are not inhabited. Early attempts included a survey of water voles (*Arvicola terrestris*) in 39 sections of river bank in North Yorkshire, UK, 10 of which contained breeding colonies of voles (core sites), 15 were only visited, and 14 were apparently neither used nor visited. A 'principle

components' analysis was used to characterise the core sites, and on this basis a further 12 sites were identified that should have been suitable for breeding voles but were uninhabited by voles because they were too isolated to be colonised or in some cases suffered high levels of predation by mink (Lawton & Woodroffe, 1991). In another case, Thomas *et al.* (1992) found that the habitable patches that remained uninhabited of the rare silver-studded blue

butterfly, *Plebejus argus*, in North Wales (those containing the plants its larvae feed on) were small and isolated: the butterfly was able to colonise virtually all habitable sites less than 1 km from existing populations. Crucially, the habitability of some of the isolated (previously uninhabited) sites was confirmed when the butterfly was successfully introduced into them (Thomas & Harrison, 1992).

### 6.7.2 The development of metapopulation theory: islands and metapopulations

MacArthur and Wilson's (1967) classic book, *The Theory of Island Biogeography* was an important catalyst in radically changing ecological thinking in a whole range of areas. The authors developed their ideas in the context of the dynamics of the animals and plants on real (maritime) islands, which they interpreted as reflecting a balance between the opposing forces of extinctions and colonisations. They emphasised that some species (or local populations) spend most of their time either recovering from past crashes or in phases of invasion of new territories (islands), while others spend much of their time at or around their carrying capacity. These two ends of a continuum are the *r* and *K* species we discuss more fully in Section 7.6.1. At one extreme (*r* species), individuals are good colonisers and have characteristics favouring rapid population growth in an empty habitat. At the other end of the continuum (*K* species) individuals are not such good colonisers but have characteristics favouring long-term persistence in a crowded environment. *K* species therefore have relatively low rates of both colonisation and extinction, whereas *r* species have relatively high rates. These ideas are developed further in the discussion of island biogeography in Chapter 19.

At about the same time as MacArthur and Wilson's book was published, a simple model of metapopulation dynamics was proposed by Levins (1969, 1970). Like MacArthur and Wilson, he sought to incorporate into ecological thinking the essential patchiness of the world around us. MacArthur and Wilson were more concerned with whole communities of species, and envisaged a 'mainland' that could provide a regular source of colonists for the islands. Levins focused on populations of a single species and awarded none of his patches special mainland status. Levins introduced the variable  $p(t)$ , the fraction of habitat patches occupied at time  $t$ , reflecting an acceptance that not all habitable patches are always inhabited.

#### Levins' model

The rate of change in the fraction of occupied habitat (patches,  $p$ ) is given in Levins' model as:

$$\frac{dp}{dt} = cp(1 - p) - ep \quad (6.3)$$

in which  $e$  is the rate of local extinction of patches and  $c$  is the rate of recolonisation of empty patches. That is, the rate of recolonisations increases both with the fraction of empty patches prone to recolonisation ( $1 - p$ ) and with the fraction of occupied patches able to provide colonisers,  $p$ , whereas the rate of extinctions increases simply with the fraction of patches prone to extinction,  $p$ . Rewriting this equation, Hanski (1999) showed that it is structurally identical to the logistic equation (see Section 5.7):

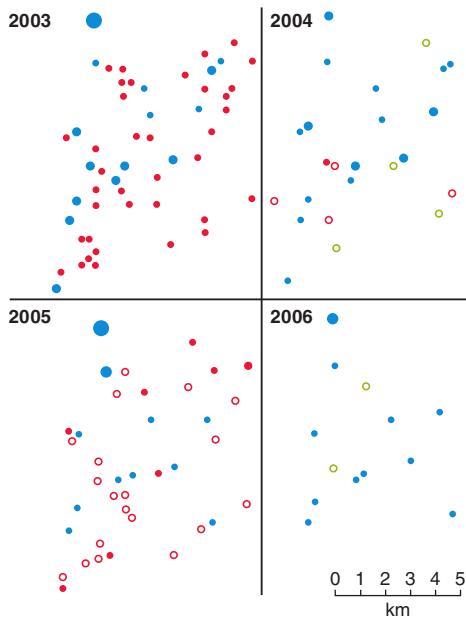
$$\frac{dp}{dt} = (c - e)p \left(1 - \frac{p}{1 - (\frac{e}{c})}\right). \quad (6.4)$$

Hence, as long as the intrinsic rate of recolonisation exceeds the intrinsic rate of extinction ( $c > e$ , or  $e/c < 1$ ), the total metapopulation will reach a stable equilibrium, with a fraction,  $p^* = 1 - (e/c)$ , of the patches occupied (what we would call  $K$  in the logistic equation), or if we refer to  $e/c$  as  $\delta$ , the 'extinction threshold', then

$$p^* = 1 - \delta. \quad (6.5)$$

The most fundamental message from taking a metapopulation perspective, then, which emerges from even the simplest models, is that a metapopulation can persist, stably, as a result of the balance between extinctions and recolonisations even though none of the local populations are stable in their own right. An example of this is shown in Figure 6.27, where a metapopulation of solitary bees, *Andrena hattorfiana*, in southern Sweden was surveyed several times each year from 2003 to 2006. Habitat patches (potential subpopulations) were those containing the bee's main pollen source, *Knautia arvensis*, and it is clear that from one year to the next, the chance of an individual subpopulation going extinct (or a vacant patch being colonised) was extremely high. The metapopulation was stable but the subpopulations were not. Only 16% of the subpopulations remained occupied throughout the study. Those with the smallest bee populations were most likely to go extinct; those covering the largest area were most likely to be colonised. To restate the message another way: if we wish to understand the long-term persistence of a population, or indeed that population's dynamics, then we may need to look beyond the local rates of birth and death (and what determines them), or even the local rates of immigration and emigration. If the population as a whole functions as a metapopulation, then the rates of subpopulation extinction and colonisation may be of at least comparable importance.

extinctions and  
colonisations in  
subpopulations: a  
stable  
metapopulation



**Figure 6.27 Many subpopulations of a bee metapopulation go extinct from year to year but the metapopulation nonetheless persists.** The spatial distribution of subpopulations in a metapopulation of the bee, *Andrena hattorfiana*, in southern Sweden over four years. Filled blue dots represent occupied patches of increasing subpopulation size, in four classes: 1–10, 11–50, 51–100 and >100. Red dots indicate subpopulations that had gone extinct by the subsequent year. Green open dots indicate newly colonised patches. Red open dots indicate either patches that were colonised one year but had gone extinct by the next, or subpopulations that went extinct one year but had been recolonised by the next. *Source:* After Franzen & Nilsson (2010).

### 6.7.3 When is a population a metapopulation?

Two necessary features of a metapopulation have now been established: that individual subpopulations have a realistic chance of experiencing extinction and of recolonisation. To this we should add a third, which has been implicit up to now. The dynamics of the various subpopulations should be largely independent, i.e. not synchronous. There would, after all, be little hope of stability if when one subpopulation went extinct they all did. Rather, asynchrony guarantees that as one goes extinct (or even declines towards extinction), there are likely to be others that are thriving and generating dispersers, promoting a ‘rescue effect’ (Brown & Kodric-Brown, 1977) of the former by the latter.

**sources and sinks:  
mainland-island  
metapopulations**

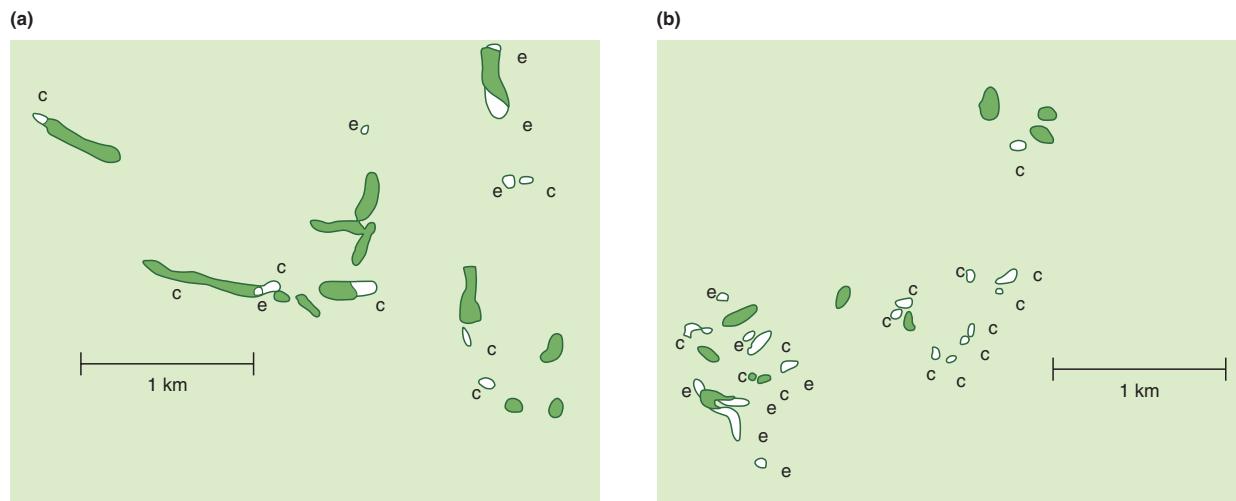
Some metapopulations may conform to the ‘classic’ concept, in which all the subpopulations have a realistic (and roughly equal) chance of extinction. In other cases,

however, there may be significant variation in the quality or especially in the size of individual patches. Thus, patches may be divided into ‘sources’ (donor patches) and ‘sinks’ (receiver patches) (Pulliam, 1988), and metapopulations with marked variations in patch size are often referred to as *mainland-island metapopulations*, acknowledging the gradations between MacArthur and Wilson’s island biogeography (one mainland) and Levins’ classic metapopulation. In source patches at equilibrium, the number of births exceeds the number of deaths, whereas in sink patches the reverse is true. Hence, source populations support one or more sink populations within a metapopulation. The persistence of the metapopulation depends not only on the overall balance between extinction and recolonisation, as in the simple model, but also on the balance between sources and sinks. In practice, of course, 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 6.28 for the silver-studded blue butterfly (*Plebejus argus*) in North Wales. We saw something similar for the violet copper in Figure 6.23. The smaller patches were more likely to be vacant because they were less likely to be colonised (smaller target) and more likely to go extinct (smaller, more vulnerable subpopulation).

Just because a population is patchily distributed, however, this does not necessarily make it a metapopulation (Harrison & Taylor, 1997; Bullock *et al.*, 2002). Firstly, a population may be patchily distributed, but dispersal between the patches may be so great that the dynamics of the individual patches are no longer independent: this is a single population, albeit occupying a heterogeneous habitat. Alternatively, patches may be so isolated from one another that dispersal between them is negligible: a series of effectively separate populations.

**when is a  
metapopulation  
not a metapopulation?**

Finally, and perhaps most commonly, all patches may simply have a negligible chance of extinction, at least on observable timescales. Their dynamics may be influenced by birth, death, immigration and emigration – but not to any significant degree by extinction or recolonisation. This last category comes closer to being a ‘true’ metapopulation, and there can be little doubt that many such patchy populations have been described as metapopulations. Strictly speaking this is wrong, but there can be a danger in being overprotective of the purity of definitions. What harm can there be if, as interest in the metapopulation concept grows, the term itself is extended to a wider variety of ecological scenarios? Perhaps none – and the spread of the term’s usage to populations originally beyond its reach



**Figure 6.28 Mainland-island metapopulations of a butterfly with contrasting proportions of sources and sinks.** Two metapopulations of the silver-studded blue butterfly (*Plebejus argus*) in North Wales: (a) in a limestone habitat in the Dulas Valley, where there was a large number of persistent (often larger) local populations amongst smaller, much more ephemeral local populations; (b) in a heathland habitat at South Stack Cliffs, where the proportion of smaller and ephemeral populations was much greater. Filled outlines, present in both 1983 and 1990; open outlines, not present at both times; e, present only in 1983 (presumed extinction); c, present only in 1990 (presumed colonisation). Source: After Thomas & Harrison (1992).

may, in any case, be unstoppable. But a word, like any other signal, is only effective if the receiver understands what the sender intends. At the very least, care should be taken by users of the term to confirm whether the extinction and recolonisation of patches has been established.

#### metapopulations of plants? remember the seed bank

The problem of identifying metapopulations is especially apparent for plants (Husband & Barrett, 1996; Bullock *et al.*, 2002). There is no doubt that many plants inhabit patchy environments, and apparent extinctions of local populations may be common, but the applicability of the idea of recolonisation following a genuine extinction is nonetheless questionable in any species that has a buried seed bank (see Section 4.4). 'Recolonisations' may often simply be the result of the germination, following habitat restoration, of seeds that are already in place. Recolonisation by dispersal, a prerequisite for a true metapopulation, may be extremely rare. There are, though, at least some examples, one of which looked at an annual plant, the treacle mustard, *Erysimum cheiranthoides*, that occupies sites on stony banks of the River Meuse in Belgium (Figure 6.29a). As an annual, there is clearly no continuity of adults at a site from one year to the next, but individual sites are subject to flooding each winter, which may be powerful enough to also flush away all seeds from a site, leading to extinction of a subpopulation. The river, though, may also bring new seeds (i.e. colonists) to a site. Samples were taken from sites, and DNA extracted and analysed, allowing each site to be genetically characterised and differentiated from other sites. This

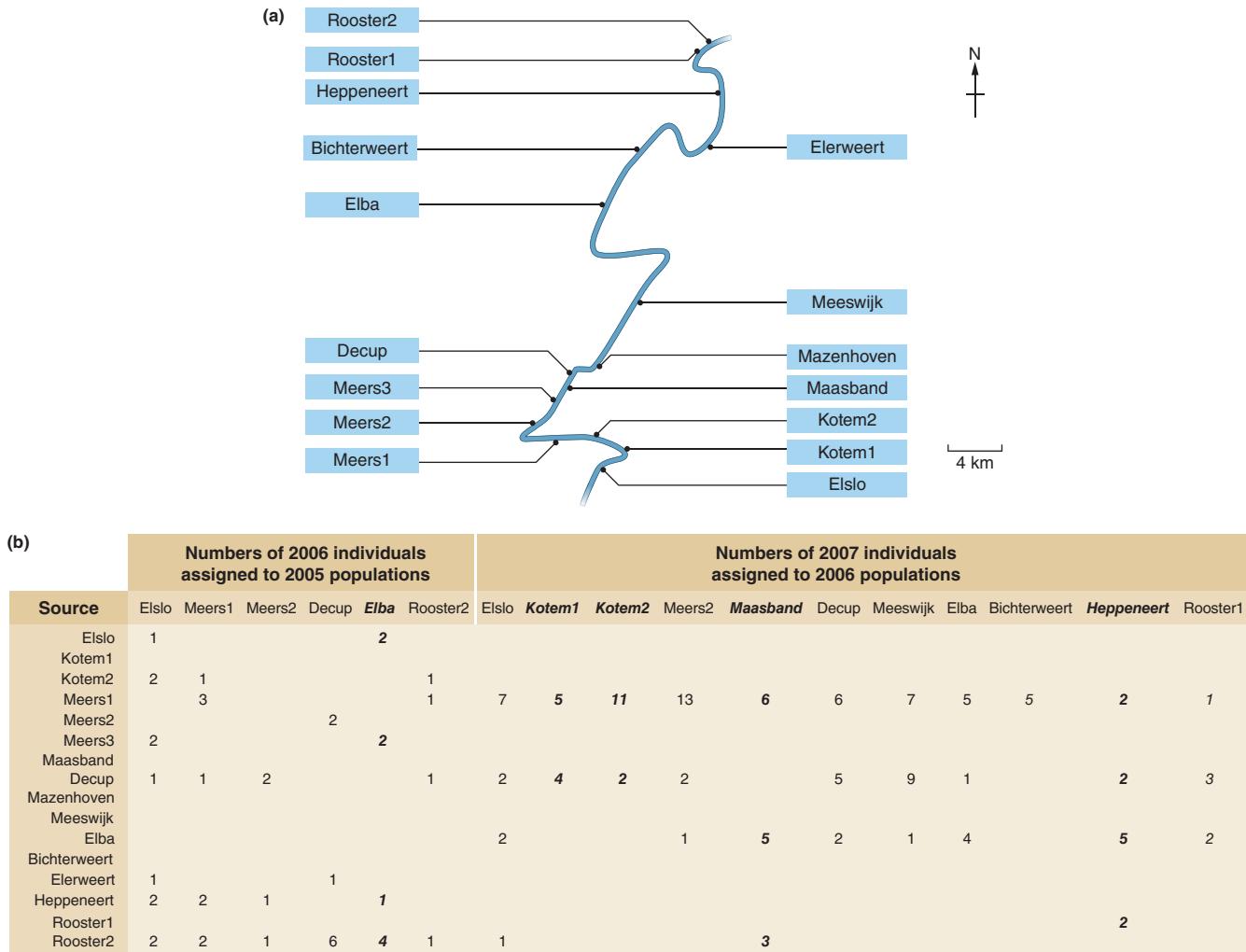
in turn allowed at least a proportion of individuals sampled in 2006 to be assigned to populations from 2005, and likewise for individuals in 2007 assigned to 2006 populations. It was apparent not only that seeds moved between the subpopulations, but also that in some cases they were carried to vacant sites and recolonised them (Figure 6.29b). In this case at least, the plant formed a true metapopulation; its dynamics had at least as much to do with extinction and colonisation as with local birth and death.

Moreover, as Bullock *et al.* (2002) point out, of the plant studies that have documented patch extinctions and colonisations, the vast majority have been in recently emerged patches (the early stages of succession, see Chapter 18). Extinctions mostly occur when the vegetation in a patch develops to a state where it is no longer suitable for the plant species in question, and that patch is therefore also not suitable for recolonisation by the same species. This is 'habitat tracking' (Harrison & Taylor, 1997) rather than the repeated extinction and recolonisation of the same habitat that is central to the concept of a metapopulation.

#### 6.7.4 Metapopulation dynamics

We can understand many aspects of the dynamics of metapopulations by focusing on studies of one key system. As well as playing a central role in the development of

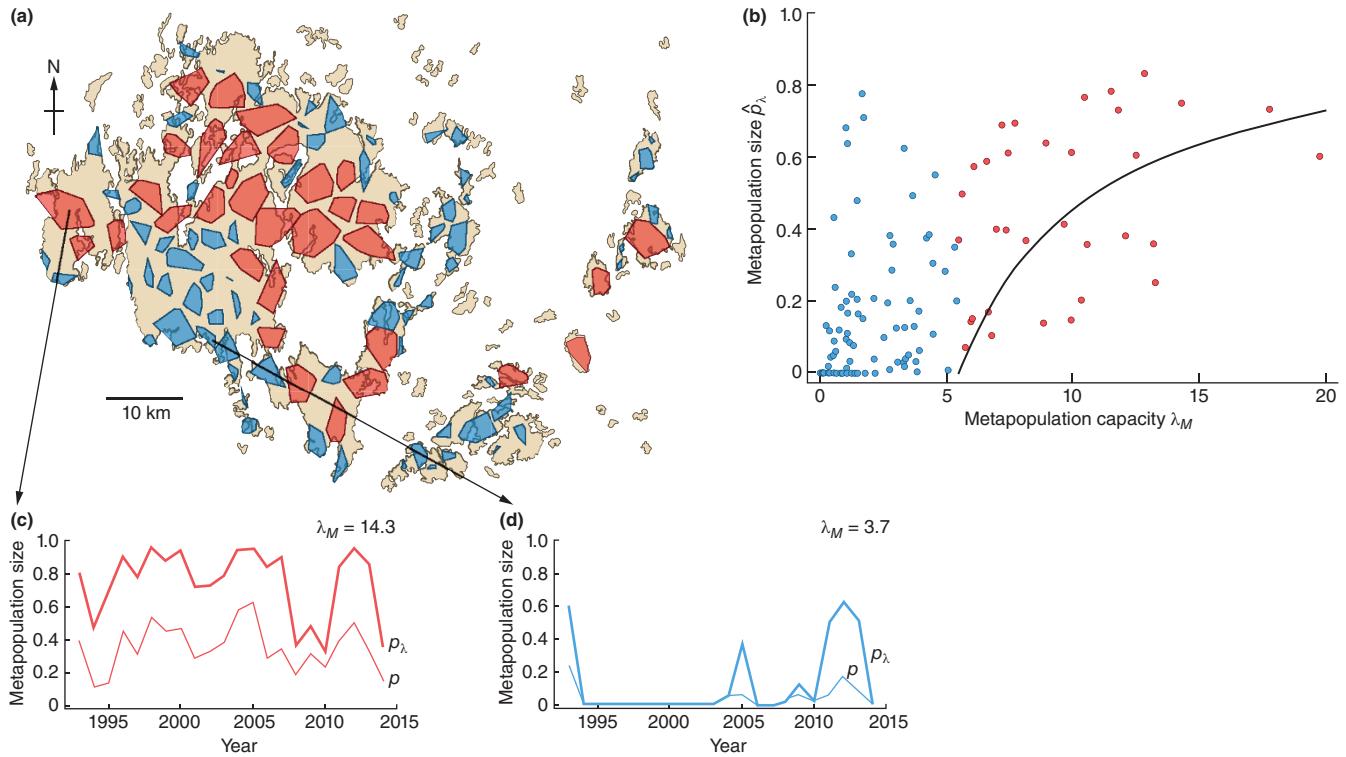
#### a case study: the Glanville fritillary on Finnish islands



**Figure 6.29 A plant metapopulation.** (a) Locations of the subpopulations, on the River Meuse in Belgium, of a metapopulation of the bank-side plant, *Erysimum cheiranthoides*. The river flows from south to north. (b) Table showing the assignment, where possible, of individuals sampled in 2006 and 2007 to populations from 2005 and 2006, respectively. Colonists (individuals reaching a vacant site) and recolonised sites are shown in bold italics. Source: After Honnay *et al.* (2009).

metapopulation theory, Ilkka Hanski initiated in 1993, and then guided, a long-term study of metapopulations of the Glanville fritillary butterfly, *Melitaea cinxia*, on the Åland islands in Finland (Hanski *et al.*, 2017). The butterfly inhabits dry meadows that support at least one of its two larval host plants, the ribwort plantain *Plantago lanceolata* and the spiked speedwell *Veronica spicata*. The whole area, 50 km × 70 km, has been mapped twice, in 1993 and 1998–99, and monitored since, and consists of around 4500 patches (areas containing the host plants). The patches are small. They have a median size of about 0.06 ha and fewer than 1% of them extend to 2 ha. Thus, the distribution of the species is indeed highly fragmented, covering only around 1% of the total area. The team studying them, however, do not consider the butterflies to comprise a single metapopulation. Instead they group them into 125 semi-independent networks of patches (Figure 6.30a) with each network

described as a metapopulation. This itself makes an important point. The clustering is based on the typical lifetime dispersal of the butterflies – mostly limited to 2–3 km. The patches within each cluster, each metapopulation, have a good chance of exchanging individuals within a generation, and hence of providing colonisers that re-establish a subpopulation on a patch, following an earlier extinction there. By contrast, nearby metapopulations exchange individuals only occasionally. The point to understand is that there is no single, objective threshold distance that determines whether two patches are members of the same or different metapopulations. Drawing a line around a metapopulation, like drawing a line around a conventional population, is more often than not a matter of pragmatism. But we cannot, and should not, shy away from judgement calls that apply useful structures to natural patterns filled with shades of grey.



**Figure 6.30** Hanski's metapopulation of the Glanville fritillary. (a) Map of the Åland islands, off the south-west coast of Finland, with locations and extents of the 125 habitat patches where metapopulations of the Glanville fritillary butterfly, *Melitaea cinxia*, have been identified (smallest not visible): red above the extinction threshold (see text), blue below. (b) The relationship between the size and capacity of the metapopulations, along with data for each of the metapopulations, with the same colour-coding as in (a). The line is the best fit from field data of a variant of Equation 6.6. It crosses the horizontal axis at the extinction threshold, 5.47. (c) and (d) show illustrative examples of the variations in size of two of the metapopulations (in terms of both the fraction of patches occupied,  $p$ , and the patch-weighted fraction,  $\hat{p}_\lambda$ ), as indicated, above and below the extinction threshold, respectively. The terms 'extinction threshold' and 'metapopulation capacity' are explained in the main text. Source: After Hanski *et al.* (2017).

**$p_\lambda$ : metapopulation size accounting for patch variation**

The most fundamental aspects of the dynamics of a metapopulation, just like any population, concern its size, variations in its size and its persistence over time. The most obvious measure of the size of a metapopulation, as described above, is  $p$ , the fraction of patches occupied. However, subsequent elaborations of the basic theory have acknowledged, as we did previously, that not all patches are equal – some are bigger than others, some are better connected. A more satisfactory alternative measure of metapopulation size therefore is denoted by  $p_\lambda$ , which assigns different weightings to different patches depending on their contribution to the overall dynamics of the metapopulation (a heavier weighting for bigger, more connected patches, etc.). Without going into mathematical details (see Hanski & Ovaskainen, 2000) the equilibrium value of  $p_\lambda$  may be given by:

$$p_\lambda^* = 1 - \delta / \lambda_M. \quad (6.6)$$

Here,  $\delta$  is the extinction threshold, the ratio of extinction to colonisation rates,  $e/c$ , as previously. This is a property of the particular species concerned, and hence applicable to all

of its metapopulations.  $\lambda_M$  is the so-called *metapopulation capacity*, and it is this that aims to integrate the effects of the areas and spatial locations of patches on the capacity of a particular network to sustain a viable metapopulation, as explained next (Hanski & Ovaskainen, 2000).

The key to the successful application of these ideas is having reliable estimates for the parameters in Equation 6.6. In the case of the Glanville fritillary in the Åland islands, the extinction threshold,  $\delta$ , could be estimated directly from the colonisation and extinction rates,  $c$  and  $e$  (monitored through the massive effort invested in surveying all patches annually) or indirectly from data on individual patches. The two methods produced estimates that were highly correlated (0.97). To estimate the metapopulation capacity, it is necessary to make some assumptions about the dependence of extinction and colonisation rates on patch size and location, and then to carry out some simple mathematical matrix calculations (details unimportant). Here it was assumed, for any patch,  $i$ :

**the metapopulation capacity**

$$\text{Extinction rate}_i = e/A_i \text{ and,} \quad (6.7)$$

$$\text{Colonization rate}_i = c \sum_{j \neq i} \exp(-d_{ij}/\theta) A_j p_j(t). \quad (6.8)$$

That is, the extinction rate of a patch depends on the species-specific constant  $e$ , but also declines with increasing patch area,  $A_i$ . The colonisation rate of a patch from all other patches,  $j$ , depends on the species-specific constant  $c$ , but declines with the distance between patch  $i$  and the other patches,  $d_{ij}$ , relative to the species' average dispersal distance,  $\theta$ , while also increasing with the areas of those other patches,  $A_j$ , and the fraction of them currently occupied,  $p_j(t)$ , since these codetermine the size of the source of new colonisers. These colonisation and extinction rates then contribute to a matrix, the elements of which describe the net effect of each patch on each other patch. As a final step, a particular property of that matrix, the 'leading eigenvalue', is the metapopulation capacity – largest when patches are themselves large and well connected.

#### dynamics of the Glanville fritillary

It is apparent now from Equation 6.6 that for a metapopulation to persist,  $p_\lambda^*$  must be positive, and hence the metapopulation capacity must exceed the species' extinction threshold. Equation 6.6 therefore expresses formally what we would expect: that metapopulations are more likely to persist (and will be larger if they do persist) when colonisation rates are high and extinction rates low, and when individual patches are large and well connected. Crucially, though, in the case of the Glanville fritillary it was also possible to test our understanding of their metapopulation dynamics in a quantitative way. We can see, first, that the estimated extinction threshold (5.47) did a good job in predicting metapopulation viability (Figure 6.30b). All networks with an estimated capacity above the threshold supported a viable metapopulation in the sense that its size, the mean patch occupancy,  $\hat{p}_\lambda$ , was positive. (Note that  $\hat{p}_\lambda$  is based on the observed occupancies of individual patches within a network but applies weightings to those patches when computing a mean occupancy, calculated based on their size and connectivity.) What's more, the most important explanatory variable in accounting for variations in population size overall was the metapopulation capacity (around 40% of the total:  $F_{1,123} = 84.16$ ,  $P < 10^{-14}$ ), and it did particularly well in accounting for variations above the threshold, where the connectivity of patches had negligible effect – these viable metapopulations behaved, effectively, like independent entities.

#### metapopulations of metapopulations

Below the threshold, on the other hand, while simple application of the threshold criterion suggests a non-viable metapopulation,

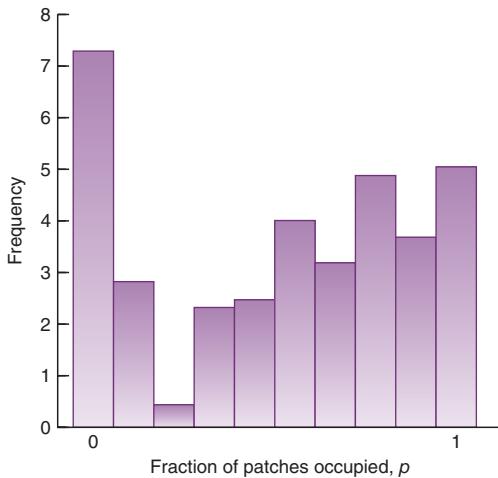
in many cases a positive value for  $\hat{p}_\lambda$  was recorded overall. This, in fact, is not unexpected, since many metapopulations that would not be viable in isolation will be 'rescued' at least temporarily by colonisers from nearby metapopulations. This is emphasised by noting that of the 92 'non-viable' networks, 79 (86%) were extinct for at least five years out of the 22 they were observed, compared with only five (15%) of the 33 viable networks. Furthermore, connectivity to nearby networks was highly influential in accounting for variations in  $\hat{p}_\lambda$  below the threshold ( $t = 3.13$ ,  $P = 0.002$ ). In this very important sense, the Glanville fritillary on the Åland islands exists, as do many populations, as a metapopulation of metapopulations. These contrasts are further illustrated in Figure 6.30c and d, which show time series from a viable and non-viable network, respectively – in the first case, fluctuating but never coming close to extinction, and in the second case, suffering extinction twice, once for an extended period. Of course, most fundamentally of all perhaps, these results demonstrate again how whole metapopulations can be stable when their individual subpopulations are not, and metapopulations of metapopulations more stable still.

The Glanville fritillary study also illustrates a tendency for metapopulations to exhibit alternative stable equilibria. As the fraction of patches occupied by the metapopulation,  $p$ , increases, there should on average be more migrants, more immigration into patches, and hence larger local subpopulations (confirmed for the Glanville fritillary – Hanski *et al.*, 1995). Thus, the extinction rate,  $e$ , of local subpopulations should arguably not be constant as it is in the simplest models, but decline as  $p$  increases. Models incorporating this effect (Hanski, 1991; Hanski & Gyllenberg, 1993) typically give rise to an intermediate unstable threshold value of  $p$ . Above the threshold, the sizes of local populations, and hence the flow of migrants, are sufficiently large for many subpopulations to persist and generate further potential migrants, further sustaining the subpopulations. But below the threshold, the average size of local populations is too low and, with little flow of migrants, their rate of extinction too high. Different metapopulations of the same species might therefore be expected to occupy either a high or a low fraction of their habitable patches (the alternative stable equilibria) but not an intermediate fraction (close to the threshold). Such a bimodal distribution is indeed apparent for the Glanville fritillary (Figure 6.31).

Finally, the Glanville fritillary study illustrates, in the context of metapopulations, a point of much wider significance, namely that evolutionary genetic dynamics can have a significant effect on the ecological dynamics of populations. That is, ecological

#### alternative stable equilibria

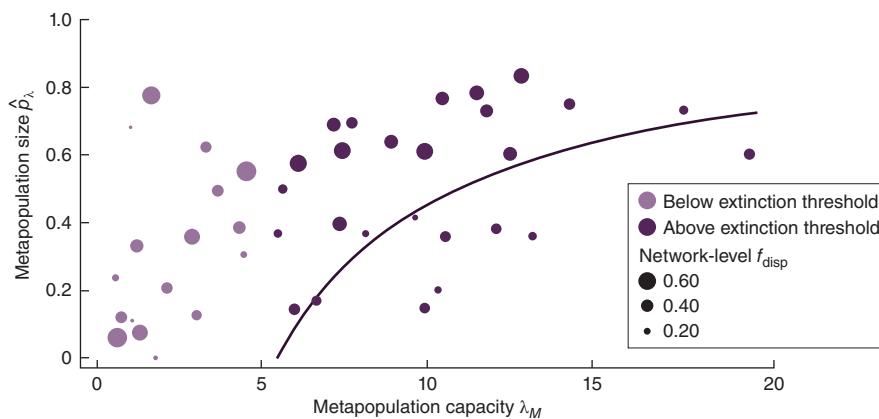
#### important genetic effects on ecological dynamics



**Figure 6.31 Alternative stable states for the Glanville fritillary metapopulation.** The bimodal frequency distribution of patch occupancy (proportion of habitable patches occupied,  $p$ ) amongst different metapopulations of the Glanville fritillary (*Metitaea cinxia*) on the Åland islands in Finland. Source: After Hanski *et al.* (1995).

and evolutionary time scales are not so different as they are often imagined to be (Saccheri & Hanski, 2006). We can see this in the present case by noting that while, above the threshold, the metapopulation capacity accounted for around 15% of the variation in metapopulation size, a genetic effect – the alleles present at a particular gene – accounted for twice that: 30% of the variation. Specifically, individuals with a C substituted for an A in the genetic code

at one particular location in the phosphoglucose isomerase (*Pgi*) gene (whether they are homozygous, CC, or heterozygous, AC) have a higher flight metabolic rate and disperse further than AA homozygotes (though they no doubt pay an energetic cost for this activity). It is the proportion of the population that are either CC or CA that did so well in accounting for variations in metapopulation size. These more dispersive individuals were especially prevalent in newly established subpopulations and in metapopulations with higher turnover rates (many colonisations and extinctions). A very plausible explanation for these patterns, therefore, is that natural selection favours CC/AC over AA in metapopulations with small patches, since these require high rates of colonisation both to persist and to be larger if they do persist. On the other hand, in metapopulations with large patches, the premium on being able to disperse is not so high (less advantage in colonising or preventing extinction through a rescue effect) and the energetic costs of the strategy take on greater importance. Hence, when a given metapopulation capacity is arrived at by having larger numbers of smaller patches, the C-variants are favoured, there are high rates of dispersal and colonisation, and a relatively high metapopulation size. But when that same metapopulation capacity is arrived at by having a smaller number of larger patches, AA homozygotes are favoured, there is less dispersal, and metapopulation sizes are smaller despite individual patches being more stable (Figure 6.32). We see then that when the whole concept of a population is spatially explicit, as it is in a metapopulation, then not only dispersal, but the evolutionary dynamics of dispersal, can play a key role in driving variations in population size.

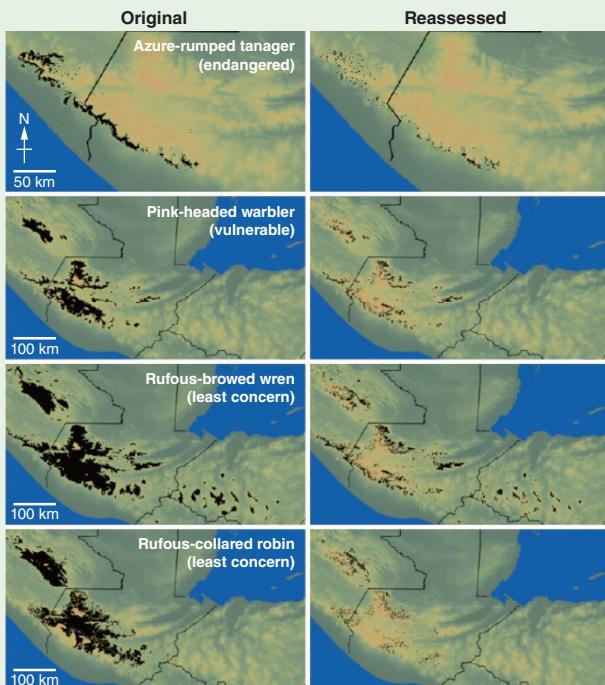


**Figure 6.32 Genetic effects on the dynamics of the Glanville fritillary metapopulation.** The relationship between metapopulation size and capacity for the networks of the Glanville fritillary on the Åland islands where sufficient genetic data were available. The fitted line is the same as in Figure 6.30. Pale and dark purple dots distinguish those below and above the extinction threshold, respectively. Larger dots have a higher proportion ( $f_{\text{disp}}$ ) of the dispersive genotypes at the *Pgi* locus (CC and AC), as indicated. Source: After Hanski *et al.* (2017).

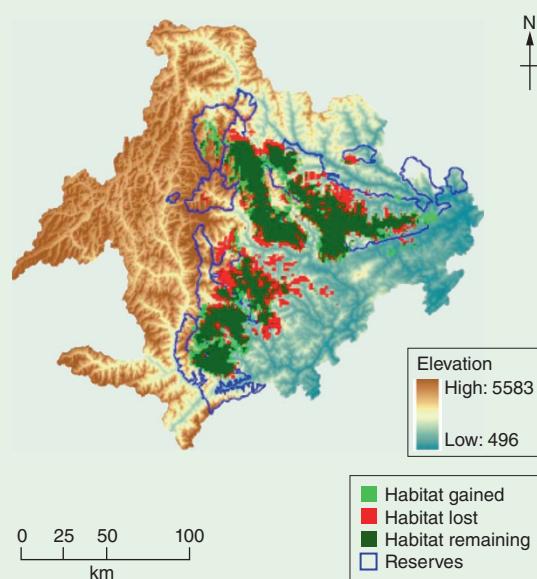
## APPLICATION 6.9 Metapopulation capacities for birds and the giant panda

Recall that the concept of a metapopulation capacity integrates the effects of the areas and spatial locations of patches on the capacity of a network to sustain a viable metapopulation. This has obvious applicability, if, for conservation purposes, we wish to assess the risks of extinction posed to a species in a fragmented landscape. This can be useful both in assessing the current conservation status of a species and in planning future conservation measures. One study, for example, examined recent contractions in the distributions of four species of birds in the central American highlands (Figure 6.33). The species were the azure-rumped tanager (*Tangara cabanisi*), classified as ‘endangered’ on the International Union for Conservation of Nature’s (IUCN) Red List (see Section 15.4.2), the pink-headed warbler (*Ergaticus versicolor*) classified as

‘vulnerable’, and the rufous-browed wren (*Troglodytes rufociliatus*) and rufous-collared robin (*Turdus rufitorques*), both classified as ‘least concern’. The comparisons were between their distributions assessed up to the 1990s in order to determine their conservation status, and a reassessment by Harris and Pimm (2008) based on satellite imagery analysis of the distribution of the forest habitats within their known altitudinal ranges. It is clear from the figure that the reassessment has led to a significant contraction in the areas of their available habitat – down to between 15% and 30% of what they were previously. But when the metapopulation capacity was calculated in each case, the reductions were down to 1% and 6% of the original. Indeed, the robin, officially of least concern, had a metapopulation capacity almost exactly the same as that of the ‘vulnerable’ warbler. Its habitat in the area now consists almost entirely of small fragments. Thus, by taking fragmentation into account in an



**Figure 6.33 Contractions in the ranges of four bird species that have especially profound effects on their metapopulation capacities.** Maps of the distributions of available habitat (marked in black) of four species of birds, as indicated, in the Central American highlands, historically and following a reassessment of available habitat. The border that appears in all maps is between Mexico to the north-west and Guatemala to the south-east. *Source:* After Schnell *et al.* (2013).



**Figure 6.34 The changing distribution of the giant panda in China that will affect their metapopulation capacity.** Projected gains and losses of the giant panda, *Ailuropoda melanoleuca*, habitat in the Minshan Mountains between 2011 and 2100 based on likely climate change scenarios (for location in China, see Figure 6.3). *Source:* After Shen *et al.* (2015).

## APPLICATION 6.9 (Continued)

informed and quantitative way, the metapopulation capacity guards against potential complacency and gives us an arguably more realistic measure of the risks that species face.

A second example has looked to the future in predicting the changing distribution of the giant panda, *Ailuropoda melanoleuca*, in the Minshan Mountains in China between 2011 and 2100, and expressing this, too, in terms of metapopulation capacity. These projections estimate around a 16% loss in habitable area, with around 18% of this occurring in locations currently covered by a network of nature reserves (Figure 6.34). However, these same projections suggest substantial fragmentation of panda habitat, with

mean patch size dropping from 3859 to 1568 ha, and the percentage of patches below the estimated minimum size for panda persistence (400 ha) rising from 3% to more than 11%. Translating these into estimates of metapopulation capacity again paints a bleaker picture than area alone. Currently, the metapopulation capacity of the protected areas is 9% lower than areas outside. But the projections for 2100 suggest that there will be a 35% decline in the capacity of the protected areas, making them 40% lower than areas outside. Given that nature reserves are of the greatest importance, compared with areas outside where panda conservation has to compete with other interests, especially farming, these figures are worrying.

We conclude this chapter, therefore, with confirmation that the movement of individuals often does far more than redistribute them. It may alter local abundances significantly, but when populations are distributed patchily –

and at some scale, all populations are distributed patchily – movement may be the glue that binds the dynamics of subpopulations together and determines the persistence and dynamics of the whole.