

Chapter 15

Biogeography and dispersal

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Introduction

This chapter evaluates the role of dispersal in biogeographical processes and their resulting patterns. We consider dispersal as a local process, which comprises the combined movements of individual organisms, but which can dominate processes even at the scale of continents. If this is correct, it is no longer possible to separate local ecological processes from those at broad, geographical scales. However, biogeographical processes differ from those happening in one or a few localities; at the broader scales, there are additional processes occurring which are only evident when examined from this wider perspective.

We integrate biogeography with ecology, explaining broad-scale effects, ranging from processes happening locally as the result of responses of individual organisms to perpetual changes in living conditions in heterogeneous space. The models to be used cannot be those traditional in population dynamics with a dispersal parameter plugged in, but must be spatially explicit. Only a broad-scale perspective of continual redistribution of large groups of individuals or reproductive propagules can give dispersal its biological and biogeographical significance. Our general thesis in this chapter is that adaptation in non-uniform space enables individuals to cope effectively with environmental variation in time.

In our analyses of spatially adaptive processes, we concentrate on principles rather than on details of specific phenomena, such as types of distance distribution. We therefore formulate these principles in terms of simple Poisson processes. In specific cases, these distributions can be replaced by more complex ones which may fit better. Our approach applies both to processes within a range that structure the range, and to external processes that limit it.

This view will be developed in terms of simple stochastic processes in space and time. Eventually, more complicated relations can be formulated to provide greater realism. The present simple approach is intended to set the scene, and assumes, for the time being, biological and spatial independence of individuals and species. Analytical models that would account for various forms of dependence are, for the present, mathematically intractable. In setting up this new framework, we return to data

that in earlier publications (e.g. Hengeveld & Haeck 1981, 1982; Hengeveld 1990) were employed in causal explanations of some biogeographical patterns. Here, we have used them to explain functionally the process of continual spatial adaptation by a species.

To evaluate the possible nature and impact of spatial processes, we start by summarizing ideas on ranges with spatially stationary structure, and then look at insights gained from invasion research. We then concentrate on the spatial dynamics of a range, first in the context of biotope accessibility and waiting times to environmental recovery; after this, we briefly introduce a simple model with spatially stochastic movement. The next section discusses the results of a simulation, which highlights the rapidity of spatial adaptation. The fourth section is concerned with consequences of dispersal in the formation of theory in ecology and biogeography as two distinct disciplines; integration of biogeography with ecology has consequences for the development and evaluation of theory in both disciplines. Finally, we consider speciation, which may be viewed as a side effect of ecological adaptation in space, when conspecific organisms lose contact for a certain period of time; effects that can also be considered in the context of broader-scale spatial adaptation. Overall, we begin to model the dynamics of species' ranges, and their consequent structuring, limitation and fragmentation in simple, general terms.

Structure of species' ranges

Generally, a species reaches its highest abundance at the centre of its range. Its abundance, and the number of biotopes occupied, decline towards the range periphery (see Hengeveld & Haeck 1982; Brown 1984; Hengeveld 1990; Brown *et al.* 1995, 1996). However, although the highest abundance tends to be at the centre, abundances across a range often form a multimodal surface, the structure of which can change from one year to the next. Furthermore, species with larger ranges reach higher abundances at the centre of their range than those with smaller ranges (Hengeveld & Hogeweg 1979; Hengeveld & Haeck 1981). Their choice of biotope also differs across the range (see Walter & Walter 1953; Hengeveld 1990), supporting the possibility that preferred habitat conditions remain the same throughout the range.

This implies that the size and structure of the range of a species express the degree to which the species' physiology and ecology match the living conditions in different parts of this range (Hengeveld & Haeck 1981; Hengeveld 1990). Thus, the species' range represented by an optimum response surface across geographical space (Hengeveld & Haeck 1981; Bartlein *et al.* 1986) is comparable to local optimum curves and surfaces relative to environmental gradients (e.g. Gause 1930, 1932; Whittaker 1967; Kessel 1979; Hengeveld 1990). Ranges are spatially structured, as are ecological processes with respect to local gradients (Jerling 1985, 1988).

How can one understand in simple terms both the general structure of a species' range, and its regional and local dynamics? A dynamic form of gradient analysis, taken from agronomy, is helpful in answering this question.

Parry (1978) expressed the energy required by the oat *Avena sativa* to complete its life cycle by the annual number of growing degree days (GDDs). If it is large enough

to fulfil the plant's minimum requirement, the plants produce viable seeds, whereas at lower GDDs they cannot. Then the population dies out, unless it has a sufficient seed bank. The risk of crop failure at any location can be determined by the percentage of years with an insufficient GDD. The one-dimensional gradient up a mountain slope of the proportion of years falling short in this requirement represents the species' altitudinal risk distribution and the distribution of the probability of failure across the mountain is the species' risk surface. Conversely, the spatial distribution of crop successes represents the temporal dynamics of the physiological optimum surface relative to some environmental gradient. Over time, this surface can shift (Parry & Carter 1985). In their structure and dynamics, such surfaces can determine the species' range in geographical space (e.g. Hengeveld 1990).

Thus, the annual local risks follow a certain probability distribution, which similarly describes the short-term, local dynamics of the species. Its short-term roughness expresses the spatial heterogeneity of the local conditions. Therefore, single measurements at single dates or locations are inadequate to determine how an organism's requirements match with its environment, and should be replaced by the construction of frequency distributions or time series with regard to the requirement concerned. However, over time these local conditions also vary independently, and statistically form more or less continuous gradients with smooth surfaces.

In this way, the location, size, shape, internal structure, bounds and dynamics of a range all reflect the response of the species to particular environmental variables, rather than to local chance distributions of a large number of variables (e.g. Brown *et al.* 1995). Apart from these few, identified variables, one also needs to understand the dispersal dynamics of species at various spatial scales.

Dynamics of species' ranges

Dispersal and accessibility

Locally, and at a certain frequency, populations die out due to unfavourable conditions, after which the localities vacated can be recolonized as soon as conditions improve. For this to happen, the locality must, of course, be accessible to individuals still living in surrounding biotopes. This means that these individuals should be able to traverse intervening unfavourable biotopes in sufficient numbers and at the right time. A recent invasion model describes this process (Hengeveld & Van den Bosch 1997). This model was derived from an earlier one by Van den Bosch *et al.* (1990, 1992), which assumes that the region which individuals can cross successfully is ecologically uniform. The velocity with which invasion progresses was thought to depend both on the rates of dispersal and of net reproduction. The latter, in turn, depends on age-specific rates of mortality and fertility. The parameter values are not constant and specific for a species, but change when environmental variables change. The resulting invasion velocity depends on responses to particular values of relevant environmental factors. Within the model conditions, the rates of population increase and spatial expansion are exponential.

However, this earlier model proved to be too simple. For example, the rate of

progress of the muskrat, *Ondatra zibethicus*, during its invasion across Germany, was greater in areas with many unfavourable biotopes and under unfavourable weather conditions, than where conditions were more suitable (Schröpfer & Engstfeld 1983). Under unfavourable conditions, the dispersing individuals kept moving, thereby increasing the total distance travelled per unit time, and thus increasing the overall invasion velocity. In contrast, individuals tended to stay longer in areas with many favourable biotopes or under favourable conditions, which slowed the progress of the invasion.

This is exactly what the extended version of the model (Hengeveld & Van den Bosch 1997) shows. It takes into account the proportion of unfavourable biotopes within a non-uniform region. The invasion velocity increases with an increasing proportion of unfavourable biotopes. At the same time, though, individuals also suffer a higher mortality in unfavourable biotopes. In fact, with increasing proportions of unsuitable biotopes, the resulting increase in mortality rate eventually overtakes the increase in dispersal rate, implying that at some point the process of invasion will stop. Within this model, these two opposing processes therefore result in a non-linear relationship between the invasion velocity and the amount of favourable biotopes available (Fig. 15.1), irrespective of differences in net reproduction or dispersal risk.

The accessibility of a given biotope from another occupied biotope is given by the rate of movement multiplied by the time available, and divided by the distance separating them. It expresses the ability of individuals to traverse unsuitable biotopes

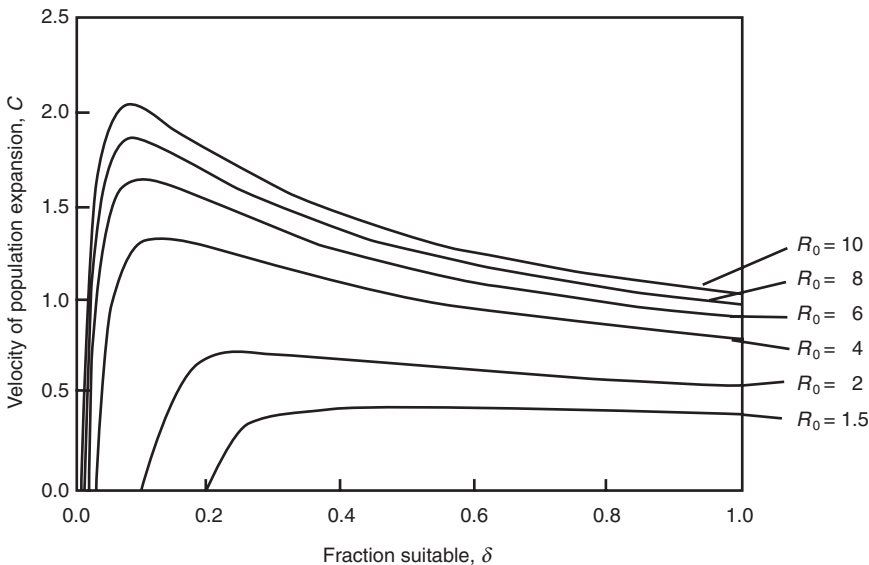


Figure 15.1 Invasion rate C as a function of the fraction of suitable biotope δ in non-uniform conditions for various values of the net reproduction rate R_0 . (Adapted from Hengeveld & Van den Bosch 1997.)

and also the possibility that a vacant locality will be reached. This accessibility, therefore, follows a non-linear function, comparable with that mentioned above.

Biotope accessibility across a species' range

The range centre has not only the highest abundance of individuals, but also, as shown, the highest proportion of different biotopes occupied (Hengeveld & Haeck 1981). Therefore, from the range centre outwards, suitable biotopes become increasingly more fragmented, and the fragments of the species' living space become smaller and more widely dispersed. In fact, the average nearest-neighbour distance between biotopes increases exponentially with a decrease in the number of biotopes (e.g. Harris 1984), thus altering their accessibility. Accordingly, this exponential increase in distances and the exponentially distributed time it takes to recolonize a biotope together have a non-linear effect on biotope accessibility. Regions with fewer suitable biotopes and higher dispersal mortality will be recolonized much more slowly, if at all. Thus, biotope accessibility decreases dramatically towards the margin of the range, at some point limiting the range more or less abruptly (for examples, see Davis 1987). The range becomes sharply truncated as a function of rapidly increasing distances between biotope fragments and severity of the unfavourable conditions in the areas between fragments, causing dispersal mortality.

Waiting times to environmental recovery

The time taken for suitable conditions to return in vacated biotopes also plays a role in determining the structure and limitation of a species' range. This time can be considered a waiting time in the terminology of stochastic processes. The Poisson distribution is the simplest description of the number of realizations of particular events over time, and assumes that individual realizations are mutually independent. Often, as for daily temperature variation, this assumption does not apply; it does, however, apply to temperature changes among years within the scale of a few decades. In consequence, waiting times of a return of suitable conditions are exponentially distributed. By the same reasoning, the durations of favourable times are exponentially distributed; they frequently deteriorate, and only rarely remain favourable for a long time.

The means of the different exponential distributions of waiting times for favourable conditions will increase from the range centre towards the periphery; there, unfavourable conditions will last longer. They also become more frequent, since the duration of favourable conditions will be shorter. Within a particular timespan, suitable biotopes will be accessible for fewer and shorter periods. This expectation defines the time available for recolonizing vacant localities, and further constrains the range limit.

Structure and dynamics of range margins

A combination of several processes leads to well-defined abrupt range margins. Some of these processes involve exponential declines or increases. This means

that margins may expand at an exponential rate when released through environmental improvement. This effect has actually been observed in the silver spotted skipper, *Hesperia comma*, in southeast England (Thomas *et al.* 2001; Wilson & Thomas, this volume). Thus, a margin which has been very well defined for a long time can become much less definite during times of range expansion (see Davis 1987).

It should be noticed that the structure and dynamics of the margin are determined by the very same processes thought to be operating throughout the range; only the parameter values vary. In some cases, only biotope accessibility limits the range, despite the fact that the local net reproduction rates can be greater than one (Carter & Prince 1985), whereas these are always less than one in models invoking demographic sinks (Pulliam 1988).

We now discuss the relevant, spatially stochastic processes in slightly more detail.

Dispersal movements of individuals

Brownian movements

The invasion models discussed above (Van den Bosch *et al.* 1990, 1992; Hengeveld & Van den Bosch 1997) assume that dispersal is Brownian. This is shown to apply to the expansion wave of the collared dove, *Streptopelia decaocto*, in Europe.

For this species, the locations of both birth and first nesting were mapped (Fisher 1953), after which the distances between each pair of locations were measured and depicted as a frequency distribution (Fig. 15.2) (Hengeveld 1993). Logarithmic transformation of the resulting J-shaped frequency curve—assuming an exponential decay rate with distance (Neubert *et al.* 1995; Kot *et al.* 1996)—results in a more linear curve (Fig. 15.2a). This curve only becomes linear when one takes the square root of the logged distances (Fig. 15.2b). This latter transformation suggests that the dispersal underlying the range expansion is Brownian, because in Brownian movement the distance as the crow flies equals the square root of the sum of distances moved.

These curves show that most birds breed near their parents' nest, whereas only a few engage in long-distance dispersal. Thus, they establish beach-heads which subsequently grow exponentially by short-distance movements and quadratically by long-distance behaviour (for examples, see Hengeveld 1989). These two types of dispersal together constitute hierarchical or stratified diffusion (Hengeveld 1989). Shigesada's models (Shigesada & Kawasaki, this volume) show how the initial population grows exponentially, whereas long-distance dispersers originating from them are at first too few to start a new beach-head because of Allee effects. Only after the initial population reaches a certain critical size can the number of long-distance dispersers become effective, thus initiating the high-velocity expansion phase. The same Allee effects can constrain further range extension at the periphery when populations are too small, are too short lived, or produce too few propagules because of reduced net reproduction. This once more truncates the range limit.

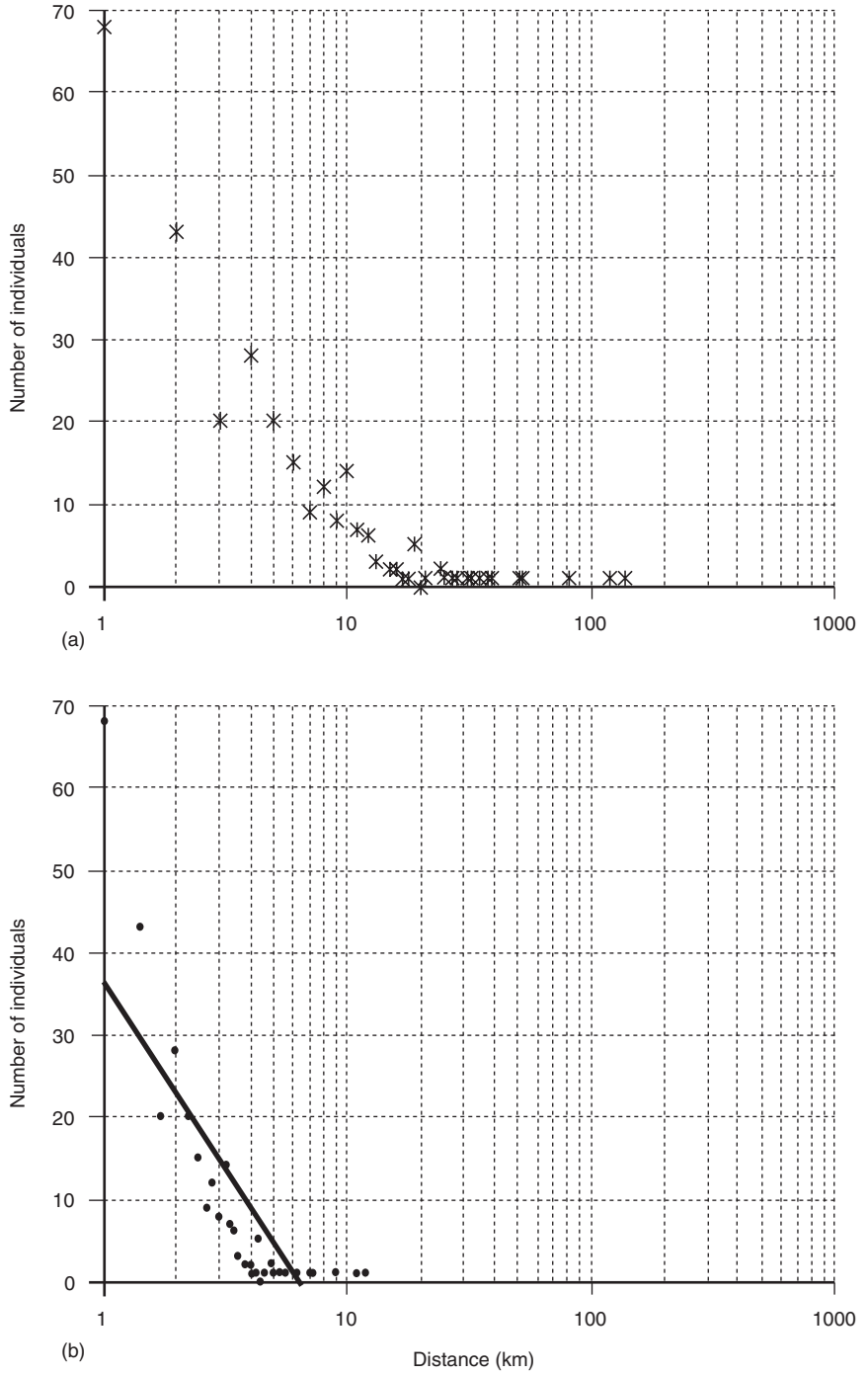


Figure 15.2 Number of breeding birds as a function of the distance from their parent's nest: (a) the logged distances, and (b) the square roots of the logged distances.

Markov chains

Range expansions can be assumed to follow Brownian diffusion, whereas non-expansive spatial movement can be viewed as a Markov process. Such a model describes a dynamic steady state resulting from stochastic movements of individual organisms across a region with ecological conditions that are not uniformly distributed.

For a Markovian process, the region can be represented by a regular lattice, in which each cell is allotted a particular biotope quality with respect to a particular species. Individuals stay longer in a cell of higher biotope quality than in one of poor quality. In the high-quality cells, individuals may still move, but over shorter distances than in cells of unfavourable biotopes (see, for example, Baars 1979). The consequence of the longer residence time in the favourable biotopes is that, according to the Fokker–Planck equation (see Okubo 1980; Kareiva 1982; Turchin 1998), more individuals will be found in these high-quality biotopes. Thus, the size of the congregations of individuals becomes proportional to the local biotope quality.

The resulting distribution of densities remains stationary as long as the configuration of biotope qualities remains the same, despite continual movement of individuals. These continued movements result in a spatially differentiated turnover of individuals across the area as a whole. However, if this spatial configuration changes, the abundances of individuals follow suit, a process known as habitat tracking. Thus, in dynamic environments the spatial distribution of individuals adapts rapidly to the ever-changing living conditions, with more dynamic environments containing more mobile individuals or species (e.g. Lindroth 1949; Southwood 1962). Yet, in contrast to models of (meta)population dynamics based on the logistic equation (e.g. Hanski 1991), the local congregations are open and temporary, and cannot be treated as closed populations with particular properties that have evolved locally. They are open systems, remaining stochastically in a spatially dynamic equilibrium with the ever-changing living conditions.

This spatial view of ecological response also has repercussions for the possibility of species' interactions. In order to have any lasting effect, interactions between species should be in phase, both in time and in space, implying that processes of response to physical factors and to other species should happen at the same scale. For species to remain coherent, this means that mechanisms must operate that tune the individuals to changes in time and space and to each other. An absence of these mechanisms, particularly of spatial tuning in allopatry, is likely to result in speciation. As, in general, no heritable tuning mechanisms exist between individuals of different species, their ecological behaviour becomes individualistic (i.e. species specific and independent).

Simulating range dynamics

Ranges persist under changeable conditions only when favourable and unfavourable biotopes alternate in space. Habitat tracking under such circumstances ideally results when the habitat conditions preferred by individuals remain more or

less constant, the more mobile species having the more sharply delimited habitat association (Mayr 1942).

We simulated the process of establishment of a species range by randomly placing 150 individuals in a grid of 128×128 cells, using a toroidal grid to avoid edge effects. These individuals thus filled *c.* 1% of their world. Each randomly placed individual had the same probability of 0.2 of moving one cell to the left, right, up or down, or of remaining stationary. After 20 steps, each individual produced two offspring when in a favourable biotope, but in unfavourable biotopes the individual died and no offspring was produced. No upper limit was set to the total number of individuals per biotope. The subsequent 15 generations followed the same process. Next, we defined zones of different favourability, expressed by the proportion of favourable biotopes. The biotopes in the zone near the 'equator' of the torus were 100% favourable, whereas 'polar' biotopes were all unfavourable, with a gradient of partially suitable zones in between. For n zones, the $2n$ bands had an approximate width of $128/2n$; the proportion of randomly placed favourable biotopes increasing from pole to equator with step sizes of $100/(n-1)\%$.

How quickly can species with a mean displacement of four grid cells per generation establish in randomly placed favourable biotopes? It appears that the individuals occupy an exponentially increasing proportion of favourable biotopes (Fig. 15.3). Under these non-zonal conditions, the range of a species is established when at least 20% of the biotopes are favourable (Fig. 15.4).

For the zonally arranged biotopes, we simulated 3–6 zones with different proportions of favourable biotope. For six zones, the species' range had built up clearly after

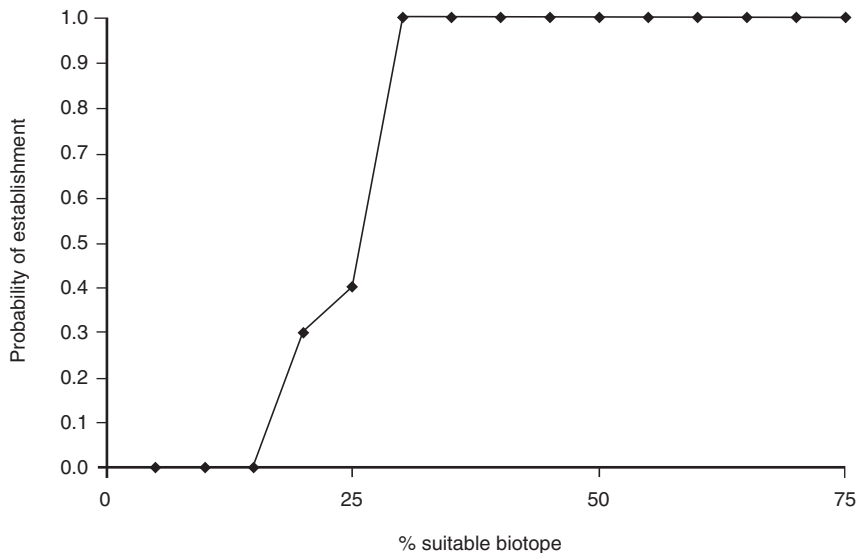


Figure 15.3 Simulated probability of establishment as a function of the percentage of suitable biotope in non-uniform conditions (see text for further details).

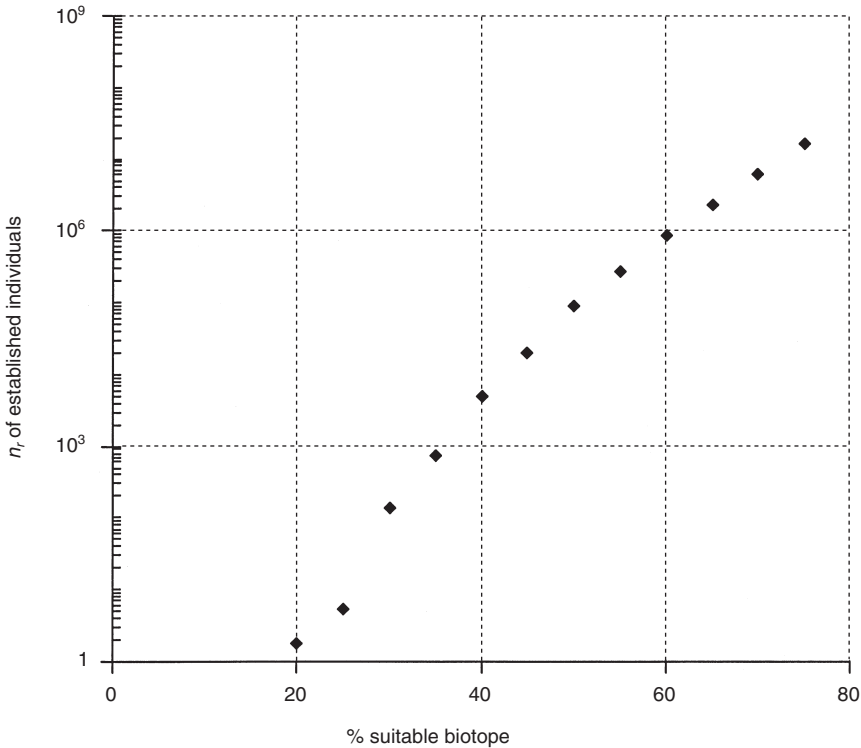


Figure 15.4 Simulated number of established individuals as a percentage of biotope occupied in non-uniform conditions (see text for further details).

as few as 3–6 generations (Fig. 15.5), which also happened in simulations with a smaller number of zones.

So far, we have assumed all animals stay alive during dispersal, an assumption that can be changed in future simulations by incorporating a constant survival probability in each dispersal step. Also, our biotopes were assumed to be constant, which can be relaxed by increasing the turnover of favourable biotopes from the range centre towards the periphery. These assumptions complicate the calculations, although they simplify the spatially adaptive process. However, without these and other complicating assumptions, this simple model serves our purpose by showing the rapidity of spatial adaptation.

Consequences of a spatially dynamic range structure

Surprisingly, for most of their history, both ecology and biogeography have had predominantly spatially static outlooks. In ecology, local populations have mainly been studied as if the processes analysed in one or a few spatially closed (meta)populations or communities were representative of all those found throughout the range of

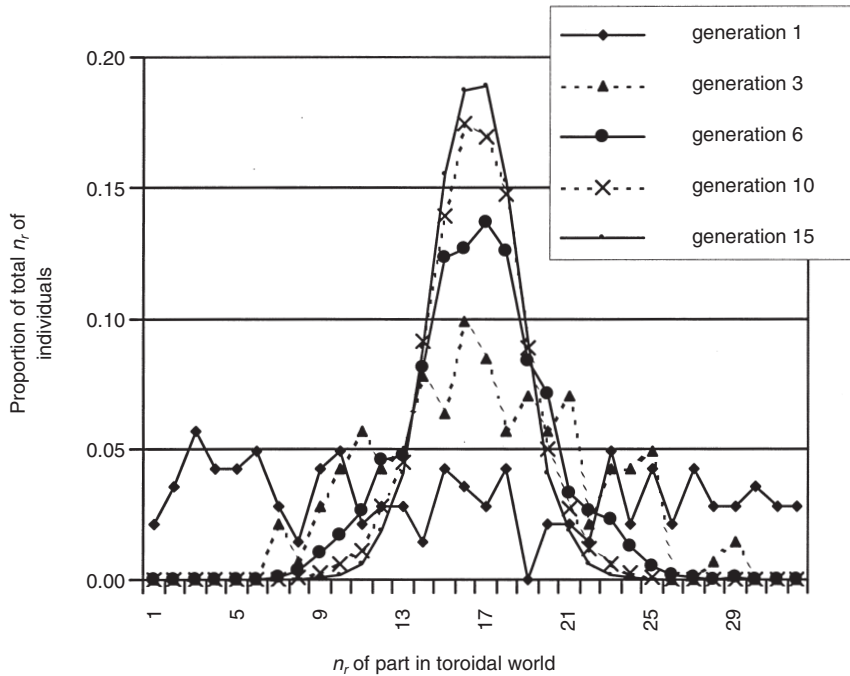


Figure 15.5 Simulated percentage of individuals found across six biotope zones after different numbers of generations (see text for further details).

a species. Similarly, in biogeography, ranges have usually been represented on maps by their outlines only, or as an unstructured shape. According to Ives and Klopfer (1997), this even applies to Brown *et al.* (1995), although they suggested that spatial variation in abundance might require temporal variation, whereas we suggest the opposite direction of dependency. In the next two sections, we look at the impacts the two disciplines have on each other, given the great significance dispersal has for both.

Impact of ecology on biogeography

MacArthur and Wilson's (1967) *The Theory of Island Biogeography* showed that adding dispersal processes permits a more dynamic approach to biogeography. However, vicariance and cladistic biogeography (e.g. Rosen 1978; Nelson & Rosen 1981) still ignore the impact dispersal might have had on the development of geographical patterns, and concentrate on geological (non-biological) explanations (see Nelson 1978).

Five successful approaches

Since MacArthur and Wilson (1967), five developments have taken place: in the anatomy of species ranges, in agronomy, in Quaternary ecology, in research on

climatic change and, finally, in invasion research. The first two have already been described and may be summarized thus: (i) larger ranges have higher abundances at the centre than small ranges; the most likely explanation of this phenomenon is based on a physiological optimum response to broad-scale variation in environmental variables (Hengeveld & Haeck 1981, 1982; Hengeveld 1990; Mac Nally 1995); and (ii) there are risks of failure to reproduce, and therefore of local extinction. As shown, these two points imply that a range can be represented by a dynamic distribution of risk in space, continually changing in structure, shape and location.

The third development is in Quaternary ecology. Since the early 1980s, local pollen diagrams have been integrated into geographical maps (e.g. Davis 1981; Huntley & Birks 1983; Bartlein *et al.* 1986). Although pollen diagrams had previously represented the percentage abundance of all pollen taxa, information now showed the distribution of individual species at certain times. Further, the spatial expansion, contraction, fragmentation or coalescence of their ranges was shown in series of maps for successive periods of, for example, 500 or 1000 years, or from plotting successive range margins on a single map (e.g. Davis 1981). Maps like these showed the behaviour of species in various respects: the refugia from which they spread, and the rate and direction of spread. Individual species differ not only in these respects, but also in temporal variation. These results challenged the spatially static picture in biogeography prevailing up to the 1980s.

Modelling shifts in species' ranges due to climate change (see Watkinson & Gill, this volume) was the fourth development in ecology that affected biogeographical thinking. This development relates to those concerning dynamic optimum surfaces and Quaternary range shifts. In order to predict these shifts, information on the ecological preferences of species was used in models, together with assumed changes in climate (e.g. Sykes & Prentice 1995). Monitoring shows that the ranges of several species are already shifting, and not necessarily in concert (e.g. Parmesan *et al.* 1999; Both & Visser 2001). Also, holes within a range can fill up when climatic conditions improve (Eber & Brandl 1994).

Finally, dispersal is the central issue in invasion research (see Hengeveld 1989; Shigesada & Kawasaki 1997; Shigesada & Kawasaki, this volume), in which models are constructed (Mollison 1977; Okubo 1980; Van den Bosch *et al.* 1990) and tested against observed range expansions (Van den Bosch *et al.* 1992; Lensink 1997, 1998). Here, ability to invade and the rate of spatial spread are assumed explicitly to be completely dependent on the values of ecological parameters (e.g. Hengeveld 1994; Hengeveld & Van den Bosch 1997). Thus, not only does the environment change over geographical space, altering local rates of survival and fertility for different species, but so do dispersal rates.

Impact of biogeography on ecology

Despite the large data bases available on diseases like measles (Infantosi 1986; Cliff *et al.* 1981; Cliff & Hagggett 1988), influenza (Cliff *et al.* 1986; Patterson 1986) and HIV (Gould 1993), as well as in agricultural epidemiology (Campbell & Madden 1990), the impact of processes at a geographical scale on local disease outbreaks has not yet

been fully explored (see, however, Cliff *et al.* 1981). For example, Anderson and May (1992) in their important text, *Infectious Diseases of Humans*, used spatially non-explicit demographic models (for recent spatial models, see Mollison 1995), and hardly discussed spatial processes.

Biotope variation, habitat constancy

A part of metapopulation theory, as derived from MacArthur and Wilson's (1967) biogeographical models, is concerned with the rescue effect (Brown & Kodrick-Brown 1977; Hanski 1982, 1999), rather than with biotope accessibility. The 'rescue effect' assumes that the habitat conditions in all biotope fragments are the same. However, if there are differences in habitat quality, we suggest that an alternative effect, which we dub the 'Santa Claus effect', is more likely to occur. Because individuals congregate in locations with more favourable living conditions, the larger populations become even larger and the smaller, smaller (Verboom 1996). In fact, this effect applies to the Markovian process described above. There have been no empirical studies concerning the construction of distance distributions based on local biotope accessibility, nor concerning changes in accessibility over geographical space towards the margins of species' ranges. In the Netherlands, however, it has been shown that ground beetles occurring in the margins of the species' range are less likely to colonize recently constructed polders than those occurring in the centre (Fig. 15.6).

Gleason (1926), realizing that the locations and shapes of ranges are species specific, long ago introduced the individualistic concept of the ecological behaviour of species (for recent data, see Taper *et al.* 1995). In this, he rejected the idea that species evolve and behave locally as members of a community, to the extent that communities—and, within them, populations as well—might be considered to be evolved entities in their own right (e.g. Emlen 1973; Pianka 1994). In Gleason's formulation, the properties of a species are species-wide, rather than connected with some niche, and locally evolved in the context of a particular community. This formulation is supported, for example, by the facts that a species occupies a different number of biotopes in different parts of its geographical range, and that there is species-wide constancy in habitat preferences (see above).

This habitat constancy implies that dispersal mortality increases towards the range margin, which gives further geographical structure to the demography of a species. Furthermore, there will be mortality due to geographical differences in the recovery time of biotopes, which increases towards the margins, as well as reduced fertility, natality, etc. Local estimates of demographic processes, therefore, lack generality (e.g. Cwynar & MacDonald 1987).

Variable demographic parameters

In fact, even parameters sometimes have to be redefined to include effects of spatially non-uniform living conditions. This applies to the intrinsic rate of natural population growth, r , the value of which varies with the proportion of intervening unfavourable biotopes in an area. Figure 15.7 shows this variation, together with the

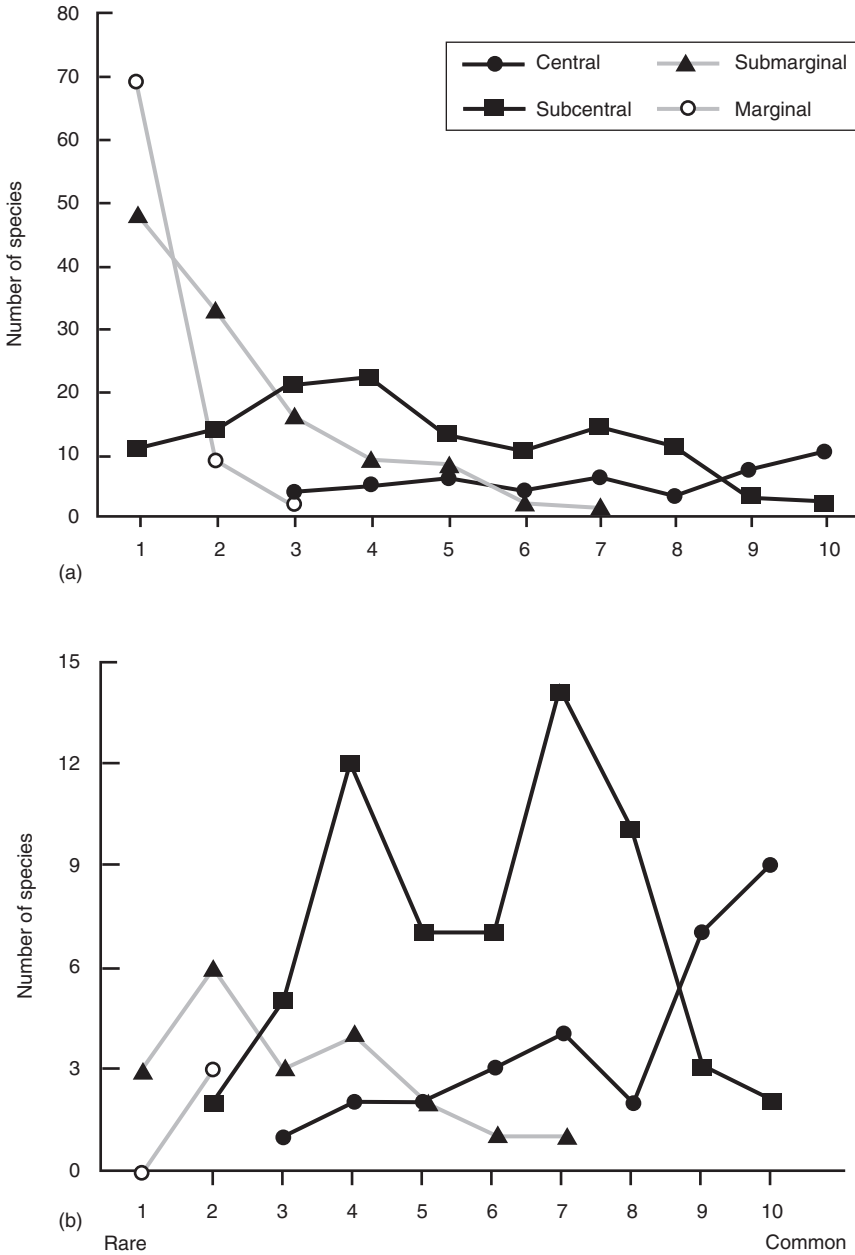


Figure 15.6 The number of ground beetle species of four different range categories in: (a) the Netherlands, and (b) large, newly-reclaimed inland polders within the Netherlands. (From Turin 2000, with permission of the author.)

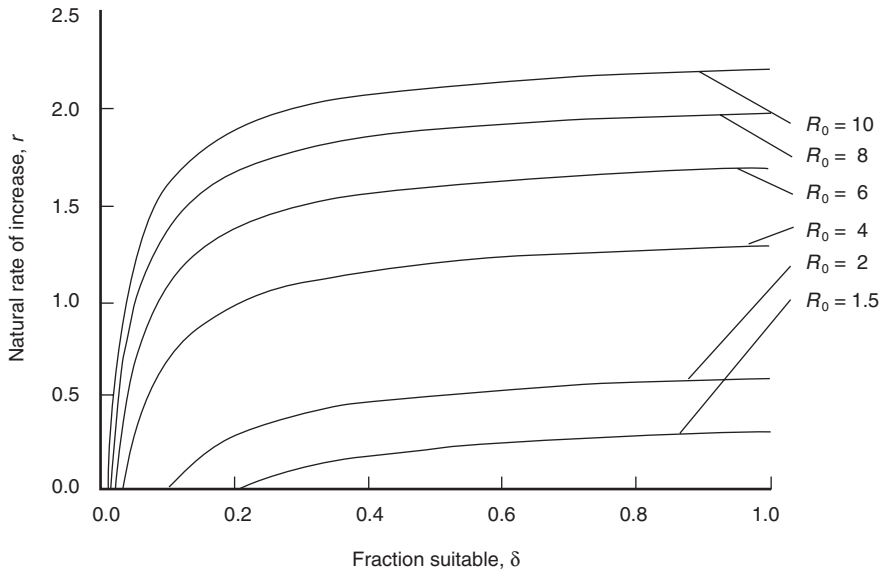


Figure 15.7 Rate of population growth, r , as a function of the fraction of suitable biotope δ in non-uniform conditions for various values of net reproduction rate, R_0 . (Adapted from Hengeveld & Van den Bosch 1997.)

effect differences in risk during dispersal may have. Similar differences in the level of variation are found in net reproductive rate (Hengeveld & Van den Bosch 1997). Therefore, particular values of r have no general relevance, but need to be understood in the context of the spatial heterogeneity of living conditions and of local responses to them. These responses vary with the dynamics and quality of living conditions, which themselves vary in time and across the range of the species.

Geographical differences in abundance across the range cannot easily be interpreted ecologically either, as abundance drives demographic processes among species in communities. Many demographic models assume that processes are density dependent, population numbers being kept within certain specific bounds. These mechanisms become difficult to visualize when the level of numerical fluctuation varies both between different species at the centres of their ranges, as well as across the range of each of them. Therefore, like the number of biotopes occupied in different parts of a range, local estimates of the populations of species cannot be interpreted generally. General models, as well as ecological theory, based on local rather than geographical observations are liable to error.

This has far-reaching theoretical consequences. When a range shifts, for example, one cannot distinguish whether differences observed in local abundance are deviations from the mean, or changes in the mean value itself. This distinction is basic to demographic theory, in which the mean level of fluctuation is assumed to be determined by mechanisms and variables different from those that control the extent of deviations from this mean (Solomon 1949).

Communities as entities

Shifts in the ranges of different species do not take place at equal rates, nor in concert (Davis 1981). Each species responds independently and at its own rate (see Van den Bosch *et al.* 1992) to ecological variation, depending on specific features of its physiology, life history and dispersal rate and direction. The geographical behaviour of a species reflects the ecological responses of individuals to local conditions constituting a Markov chain. Each species thus continually finds itself among other species, all having independent abundances, determined geographically and subject to kaleidoscopic shifts. Therefore, species comprising a community in one locality are replaced by other species at other times and places. Thus, all interactions between species are continually changing, both quantitatively and qualitatively; in consequence, it is not possible for them to coadapt (Davis 1981, 1986; Walter & Paterson 1995).

In fact, because of the individual-based, specific responses of species to continual changes in ecological conditions, communities that may once have seemed well defined gradually change their character, eventually dissolving completely (see Watkinson & Gill, this volume). Huntley (1988) reported that plant communities well established today cannot be found anywhere in the pollen record before *c.* 7000 years ago. This is also seen geographically. Starting from a particular point in space, the vegetation composition gradually changes in all directions (Fig. 15.8); as one species drops out, it is replaced by one or more others (Hengeveld 1997). The temporally non-analogue vegetation types of Huntley and Birks (1983) therefore have their geographical counterpart. Communities are local snapshots of a spatiotemporally fluid system, having no status as distinct biological entities. They are open, dynamic steady-state systems with a certain turnover rate in terms of species, depending on the specific matching of each species individually with the dynamics of its local environment.

Populations as entities

Ecological theory assumes that part of the adaptations of a species to the local environment is demographic, and the remainder is genetic (e.g. Davis & Shaw 2001). Ecological models traditionally exclude spatial adaptation, not recognizing habitat tracking by permanent movement of individuals as an integral part of the response process. However, given the low speed of (population) genetic adaptation relative to the rapid changes in the environment, which are spatially and temporally unpredictable, habitat tracking by random dispersal of individual organisms seems the most likely response to environmental change. This concerns habitat selection by individuals rather than natural selection of individuals. If habitat tracking may take place at a specifically appropriate scale, it is possible for a species to be genetically rigid, with properties static over time (Eldredge and Gould's (1972) periods of stasis) and species-wide in space (Hengeveld 1994). Thus, giving dispersal due weight in the ecological approach, one can envisage a continuous stochastic spatial adaptation to ever-changing conditions.

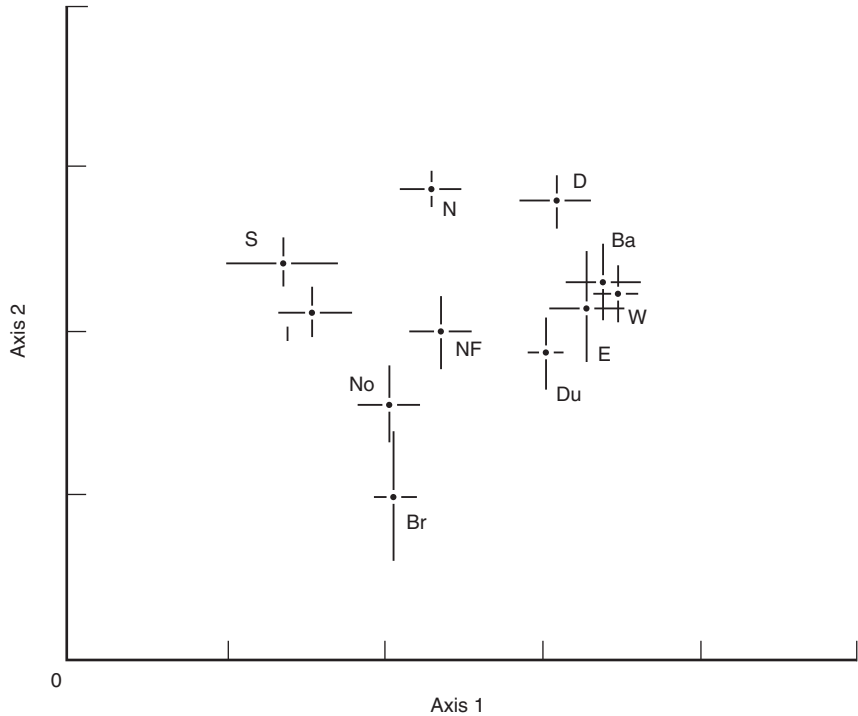


Figure 15.8 Geographical variation in a dune community of dry grasslands throughout northwestern Europe expressed as an ordination of species composition. Ba, Baltic countries; Br, Brittany; D, Denmark; Du, Dune district, western Netherlands; E, England; I, Ireland; N, Normandy; NF, northern France; No, Norway; S, Scotland; W, Wadden district, northern Netherlands. (Adapted from Hengeveld 1994.)

This implies that populations do not exist either, if they are defined as discrete, spatially closed units with a minimum of interchange of individuals, and with specific demographic attributes on which selection can operate. Because of the continual stochastic movements of individuals, congregations of individuals are temporary; but, like communities, they are compositionally steady-state systems with a certain turnover of individuals. The rate of turnover depends on life-history characteristics of individual organisms, such as longevity, fertility and dispersal capacity; and these are influenced or determined by ecological conditions. This turnover rate must match the rate of spatiotemporal change of the environment to prevent the local extinction of the species through spatial rigidity.

In spatially dynamic systems, the individual, rather than the population or the community, is the basic ecological unit. Recognition of this is the direct consequence of extending the spatial and temporal dimensions of observation, and accounting for dispersal at both broad and fine scales of ecological adaptation.

Speciation

How do species persist as identifiable entities with species-wide properties in an extremely loose system of fluid sets of individual organisms, all moving about separately, and mostly unaware of where they are going or of each other's existence? Are they facing the same fate as other supra-individual entities like populations and communities? These questions are particularly acute because the currently accepted model of speciation depends on local partitioning of niches by the erection of various sorts of reproductive barriers against sympatric competitors (Dobzhansky 1937). Accordingly, Mayr (1982) included the occupation of a specific niche as a species characteristic (cf. Hengeveld 1988). As a local phenomenon among individuals and species living sympatrically, though, it would result in allopatry, speciation being an allopatric process (e.g. Mayr 1963). This concept of speciation fits the demographic, non-spatial paradigm of ecology (Hengeveld & Walter 1999; Walter & Hengeveld 2000).

Paterson formulated an alternative model of speciation (e.g. Paterson 1985), which accords with our spatially dynamic approach. Particularly in their reproductive period, the sexes would develop similar habitat preferences, congregating in a specific biotope for mating. Apart from this requirement for reproduction, they also have a fine-tuned life cycle for synchronizing their arrival times at the selected biotope. Finally, the sexes can recognize each other as potential mates with some precision through morphological, behavioural, acoustic, chemical or physiological signals. Because each of these three components results in stabilizing selection, the properties of a species would remain uniform. Habitat tracking by individuals thus leads directly to the stability of species-wide properties and to species identity and rigidity. This, in turn, leads to constraints in variation, and in the structure, limitation and dynamics of species' ranges.

If, however, a number of individuals live for some time under deviating conditions in allopatry—implying that, because they have no genetic interchange, they are lacking the checks of stabilizing selection—they can change and eventually form one or more new species. Thus, species reach and maintain qualitative uniformity and stability, although spatially they are in a dynamic steady state like populations and communities.

This speciation process not only accords with the spatially dynamic view we develop, but it also explains several phenomena of central interest that otherwise remain elusive.

Some new research questions

This approach opens up a vast field of new research. For example, knowledge of risk distributions along transects, or in two-dimensional space at various scales, is badly needed. This may be combined with a study of the local differentiation of ecological processes and its causation. Also, life-history and life-cycle phenomena, together with dynamic biotope association in both their causal and functional aspects, conjoin with other aspects of ecobiogeographical research. Other relevant fields for new

research concern the coupling of internal and external processes at the margins of ranges. Spatial risk, expressed by the variation in biotope accessibility or by ecological barriers and their effects, is important in this. Finally, the resulting species-wide, individualistic species behaviour leads to allopatric speciation. Dispersal is central to all these new research questions.

Conclusions

For a long time, ecology and biogeography have stood apart from each other, and have developed independently. However, neither discipline has explicitly adopted dispersal as a significant process for explaining the observed patterns. This remained so even during the integration of biogeography into ecology following MacArthur and Wilson's (1967) groundbreaking study; at best, dispersal represented an additional parameter in the analysis of causes of the assumed stability of local populations. In this approach, dispersal connects islands or locations, but within these the former models and theories still apply (e.g. MacArthur 1972; Brown 1995). The theoretical basis of ecology in which population dynamics were, in the main, spatially static, was amplified by the addition of dispersal, without it being integrated into a new approach. Part of biogeographical theory, in turn, became more dynamic and causative as ecology expanded into its territory, thereby forming ecological biogeography.

Here, we have integrated these two disciplines on the basis of the dispersal of individual organisms. This leads to hypotheses in the form of simple mathematical models of spatially dynamic responses of individuals to ever-changing environmental conditions. Because of spatial heterogeneity, individuals track their preferred conditions, thus dynamically matching their requirements with these conditions in space. Under spatially uniform conditions, the individuals must adapt either physiologically or genetically, or by developing special protective traits. If individuals do not do this quickly enough, they will die out. Habitat tracking in heterogeneous environments is the only way in which to survive under conditions changing rapidly relative to other forms of biological adaptation.

Integration of these two disciplines has significant consequences for the formation of theory in both, as well as in speciation theory. Their separation arises from the different spatial scales considered. Therefore, in this process of integration, with all its consequences for theories and basic concepts, dispersal plays a pivotal role.

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