ENGLISH NATURE

The role of corridors, stepping stones and islands for species conservation in a changing climate

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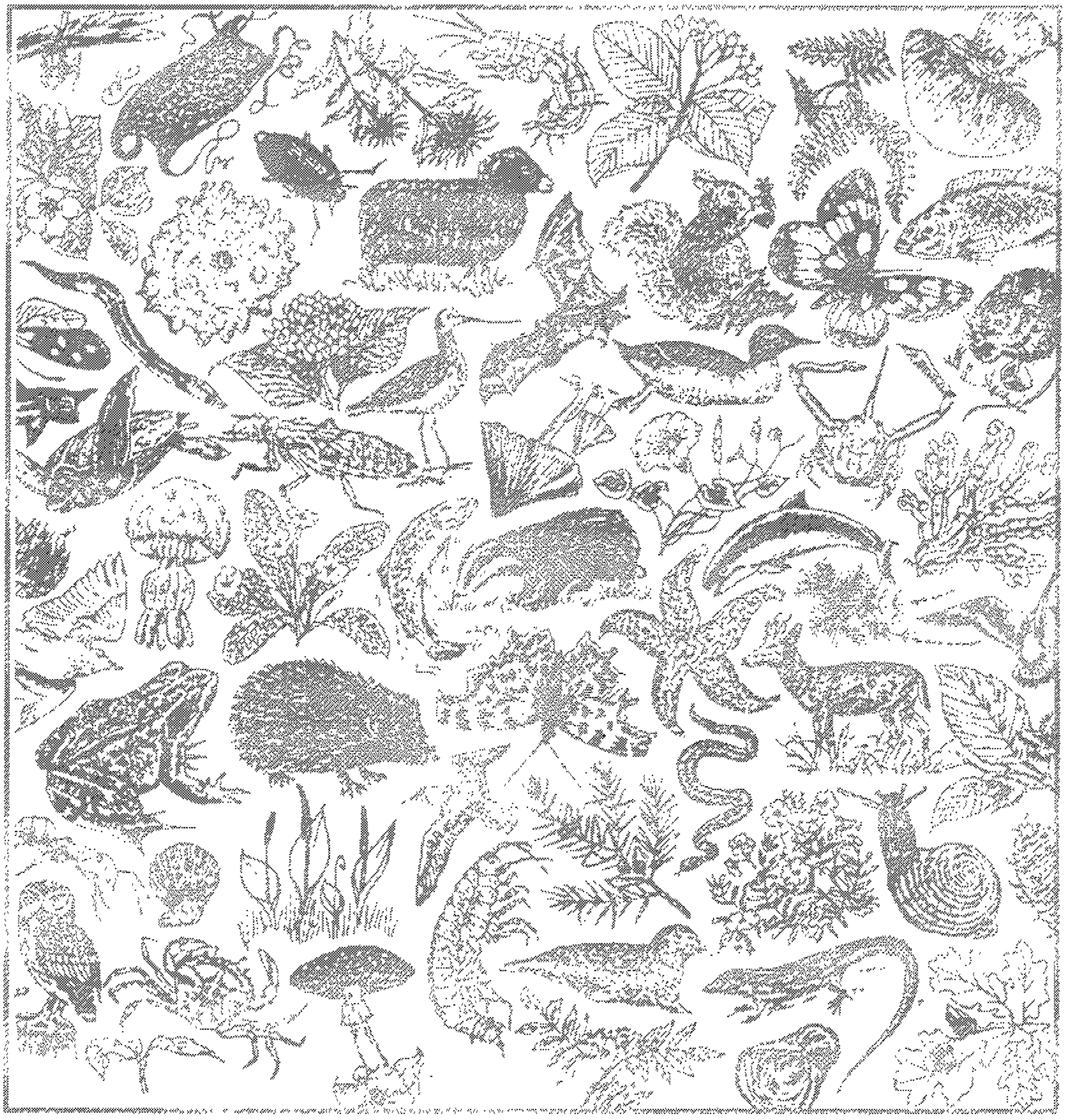

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CONTENTS

SUMMARY

1 The role of corridors in facilitating species movements in the landscape is disputed. In particular the need for a connected network of nature reserves to provide resilience against climate change is often asserted, but the evidence comes mainly from mammals and birds in environments very different from that of Britain.

2 Control of species by macroclimate can be related to three main variables: winter cold, summer warmth and available moisture. Predicted changes in response to CO_2 doubling are an increase of 1.8-2.5°C in winter temperature, an increase of 1.4°C in summer and little net change in precipitation. This would give England a climate similar to that found at the edge of the wine-growing region in northwest France. Scotland would have a climate like that of western England. However, these equilibrium changes are subject to a time-lag, which may be of the order of 50 years, so that they will not be felt fully till about the year 2100.

3.1 The spread of introduced species can give an indication of how native species might spread in a changed environment.

3.2 Spatial models predict that species will expand at a rate dependent on demographic and dispersal parameters. Epidemiologists recognize two types of "diffusion", namely neighbourhood diffusion due to frequent and rather predictable processes and long-distance diffusion whereby distinct new infection centres arise well away from existing areas of infection.

3.3 An invading species must overcome effects of competition from established individuals and from natural enemies. Further barriers to invasion are possible lack of mutualists and difficulties of finding mates in very sparse populations.

3.4 Communities subject to frequent disturbance and with low average levels of plant cover have the largest proportion of alien plants. The rate at which plant communities are invaded depends also upon the area of the target plant community and connectivity with other populated sites.

4 Canals serve as corridors for plants in the sense that they constitute available habitat for a significant number of aquatic plant species. Many aquatic plants are highly mobile; dispersal of vegetative propagules is much more important in the aquatic than in the terrestrial environment. Colonists of canals in Britain have tended to be species with widespread or southerly distributions; 44 out of the 59 submerged and floating species with this type of distribution have colonized the canal network. Coastal and northern species have not established to any significant extent, probably because of trophic requirements rather than climatic ones. Only a small number of species are apparently restricted by dispersal difficulties and might therefore spread more widely if a water grid was established.

5.1 Species live in a patchy landscape. For any species patches vary in suitability and size. Individuals of a species will interact with one another in a population, occasionally with individuals from other populations in a metapopulation and very rarely with individuals outside their metapopulation.

The rate at which species can move across the landscape is dependent on its dispersal capabilities and also the number, size and density of suitable patches in the landscape.

Metapopulation dynamics and the theory of island biogeography can be applied in many cases to studying species in patchy landscapes. Suitable patches act like islands with the population dynamics of islands being affected by individuals moving between them. One scenario is that some populations can act as sources and supply sink populations with new individuals. The sink populations could not maintain themselves without this supply and would go extinct if the source dried up.

5.2 For invertebrates, the distinction between ecosystems, biotopes and habitats must be appreciated. Ecosystem and biotope define the natural world from man's perspective; a biotope is defined by a recognizable combination of physical conditions and plant species. The biotope appropriate to a species may be present without any available habitat.

For those species whose habitat is well known and can be defined and mapped precisely, concepts of island biogeography (eg. stepping stones, patch size, distance) can be applied directly to islands of habitat. Most invertebrates probably exist as local metapopulations. Dispersal distance is crucial. A heathland animal having a large dispersal distance may exist in England as a single large metapopulation. For an animal with poor dispersal, many different metapopultions will exist on islands of heathland biotope. Patchy habitat selects either for dispersal or for sedentary behaviour, together with secondary characteristics associated with the behaviour. As a rule, good dispersers are common (often pest) species that inhabit a wide range of biotopes. Most rare species are intrinsically poor dispersers or, in response to man's activities, have recently undergone selection against dispersal. Climate change resulting in warmer summers might increase insect dispersal because increased ambient temperature is known to stimulate flight and movement.

Many insects are scarcely limited by dispersal, and, moreover, have highly-developed powers of locating their habitat. Some can colonize an island (Britain) from a distance up to 200 km away and a few invading species have occupied most of England in 25-30 years. Rare species, on the other hand, can be remarkably immobile. It is thought that many of them colonized Britain at a time of more suitable climate in the past and have survived only as a result of human modification of the habitat.

Further research is needed on immobile invertebrates in order to evaluate the potential demands for intervention. Dispersal, colonization time and population persistence time may all be related to the spatial perception of individual species. We need to investigate whether ecological theory can be applied at all spatial scales and to quantify and compare the isolation of habitat separated by "seas" of non-habitat of varying threat to an individual trying to cross it. Corridors, however, probably do not exist for most invertebrates.

5.3 Metapopulation theory and metapopulation concepts apply less obviously to plants than to animals. If a plant population exists as a metapopulation, then its survival depends on colonization of new patches. Plants have evolved, mostly in environments very different from those that they now occupy, to have a good, or at least adequate chance of occupying suitable habitat. Their methods of dispersal, although subject to evolutionary pressure, are sufficiently inflexible that, in a rapidly changing world, a species is likely to become extinct before it has altered its dispersal characteristics. However, dispersal can be enhanced either by deliberate introductions or by the construction of corridors.

Few rare plants can use existing corridors, because linear features such as roads, railways and hedges seldom provide good habitat.

In the absence of detailed information, the classification of species into Hanski's categories of core, satellite, rural and urban may help in predicting their metapopulation dynamics. The classification depends on whether the species have large or small local populations and whether a large or small proportion of habitable sites are occupied. It can be used to distinguish plants that may be at risk from fragmentation from those that are not.

6.1 Spatially referenced data on species occurrence can be linked to information on the biotope requirements of species. A system for doing this has been set up by the Biological Records Centre. Threatened or declining species have been assigned to biotope categories of the CORINE system, using information contained in published Red Data Books.

6.2 Proportions of different groups achieving Red Data Book (RDB) status vary widely. Flowering plants have apparently a low proportion of RDB species, but the proportion rises to 15%, similar to that of many other groups if introduced species are excluded. Groups such as reptiles, amphibians and butterflies, many of which are at the northern limit of their range in Britain, have a higher proportion of RDB species (25%). Species can also be categorized according to how much they have declined since records began, using information on the number of occupied 10-km squares.

Vulnerability of species to climate change can be assessed by determining how large a proportion of the present range, expressed as number of inhabited 10-km squares, will remain habitable under appropriate climate-change scenarios. A preliminary sensitivity analysis is given here. The climatic niche of each species has been inferred from its distribution within Britain, and the three major macroclimatic factors of winter cold, summer warmth and available moisture have been varied. In future, the reliability of such sensitivity analyses can be improved substantially, as better baseline climate data become available and the possibility of using European as well as British distributions materializes.

Vulnerability to sea-level rise has been assessed by a similar technique, categorizing 10-km squares as "at risk" when the mean altitude of the square in which they lie is less than 5 m above the present sea-level.

6.3 Species have been classified according to biotope preference and RDB status. Calcareous grassland, fen and reedbed, and broadleaf woodland all have high numbers of RDB species associated with them.

6.4 The position of biotopes can be identified by coincidence mapping. For this report, a biotope is effectively present in a 10-km square if that square contains at least 25% of the maximum number of characteristic species co-occurring in any one square. This method shows some geographical bias.

6.5 Declines in major biotopes can also be recognized in principle, using a combination of coincidence-mapping and the decline methodology developed for species.

6.6 The uplands cover 30% of Britain, but little of this land lies in the montane zone above 600 m. At the time of maximum Postglacial summer warmth, 7000-5000 B.P., forest cover was more extensive than at present; montane biotopes were correspondingly reduced. Although the theoretical lapse rate is 6°C km^{-1}, the high relief of the mountain environment results in wide differences in microclimate.

Much of the present area of mountain in England and Wales is threatened by climate warming, in the sense that it will fall below the future theoretical tree-line. However, other factors such as grazing can maintain montane biotopes at lower altitudes.

Invertebrate populations can often persist long after the climate becomes broadly unsuitable for them. Various boreo-montane species that were much reduced during the warm period ending 5000 B.P. persisted locally for many more centuries. Populations of montane invertebrates still persist at some sites in lowland England. Montane mammals and birds are limited more by habitat than directly by temperature and may be relatively little affected by climate warming.

Survival of mountain plants often depends as much on the existence of special factors such as aspect, calcareous rocks, cliff-faces and freedom from grazing as directly on temperature. Provided they do not have a specific requirement for winter chilling, they also can be expected in many cases to survive for decades or centuries after the climate warms. However, like many declining populations they will no doubt show almost no mobility and will therefore be incapable of benefiting from corridors.

6.7 Two very recent examples of species spread, by the bush-cricket Conocephalus discolor and the wasp Dolichovespula media, suggest rates of dispersal of up to 30 km per year and no dependence on corridors.

7.1 GIS techniques have been used to display the connectivity of the landscape in terms of landcover types. With the full resolution of the ITE landcover map, "unimproved grassland" appears to be scattered across the Cambridgeshire landscape and to be sufficiently connected that few such grasslands are very isolated. However, more than one biotope is included in this landcover type, namely large grazing fields and rough grasses along field margins.

7.2 Information from the landcover map can also be summarized and plotted at the 1-km square scale. Three maps show broadleaf woodland in this way, separating squares with more than 10% cover of broadleaf woodland from those with less. The map suggests that, at the national scale, areas of low woodland density are perhaps more island-like than areas of high density.

7.3 A further application of GIS is in the mapping of heathland fragments, to gauge their viability and suggest positions for possible connecting corridors. Heathland areas can be classified according to size; former heathland can be classified according to its present landcover.

7.4 Where species require more than one biotope for their survival, or where they are affected by distance from another biotope, GIS techniques may be able to display and measure the amount of habitat available.

8.1 More information on dynamics of species spread is required, but there is little evidence that corridors are effective unless they are also an effective habitat.

8.2 Species selected for monitoring studies should be southern or southwestern in British distribution, not specially adapted for long-distance dispersal, should form distinct colonies, and should not be too long-lived or hard to find.

8.3 Montane plants such as <u>Rubus chamaemorus</u>, which are expected to be sensitive to warmer winters, should be kept under observation. However, the main requirement is to get a better understanding of the regeneration dynamics and competitive relations of montane plants. If a single site in England were to be chosen for this purpose, then Upper Teesdale is particularly attractive.

8.4 Sites selected for regular monitoring should not be too numerous, so that a core of sustained sampling can be maintained. Maintenance of high data quality is essential.

8.5 Methods for deriving climate profiles for species should be developed further. Trends in overall species composition may become apparent at a site before individual species show clear effects.

8.6 Because of the long time-scale of climate change, experiments should be designed to test forecasts made by predictive models. Nature conservationists should, at an early stage, formulate questions that they would like predictive models and, later, experiments to answer.

8.7 Field experiments are still a priority, but should be designed to assist in predictive modelling. In particular, experiments using species introductions should be used to examine population dynamics and dispersal of invading species. Observational studies of invading species can also supply useful information. Experiments to establish corridors are unlikely to be fruitful unless designed to test specific hypotheses.

1 INTRODUCTION

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1 INTRODUCTION

1.1 ORIGIN OF THE CONTRACT

In July 1992, the Institute of Terrestrial Ecology (ITE) was invited to tender to English Nature (EN) to make a review of species dispersal along corridors. The tender was successful and the results of the review appear in the report that follows.

1.2 BACKGROUND AND RELEVANCE OF CORRIDORS

Climate change may result in a changed geographical distribution of suitable habitats for species of nature conservation interest. In order to survive and reach their potential, such species will need to move to new locations. It is often asserted that species movement will be assisted by the existence of corridors, ie. by strips of habitat connecting larger habitat patches. An eloquent statement of this view is given by Huntley (1991), who writes: "Reserves must no longer be selected primarily upon the basis of rarity of the organisms currently found within their boundaries; these organisms may in future migrate elsewhere. Instead, we must conserve as large an area and as diverse a range of physical habitats as possible, so as to achieve resiliency in our network of reserves. We must also place greater emphasis upon achieving a connected network that will facilitate migratory movements; so-called 'wildlife corridors' will assume great importance in the future and must become a required part of any structure plan or development plan".

Corridors also have their critics, and a note of caution has been sounded by Hobbs (1992), who has written: "Currently, no one knows whether corridors will be effective in mitigating the impacts of landscape fragmentation. The potential role of corridors in mitigating the effects of rapid climate change (by allowing migration of the biota, including plants) is even less well known." He goes on to observe that the corridor concept has attracted widespread interest in nature conservation circles but that its practical application remains almost totally untested. Indeed, most of the evidence for the use of corridors for movement comes from studies involving relatively few observations on mammals and birds.

Given these differences of opinion, there is a clear need for a review of the potential role of corridors in the British context. In the next century, many southern species will move northwards as the climate warms in response to the enhanced greenhouse effect, but the creation of habitats to facilitate species movement may not be justified.

1.3 OBJECTIVES OF THE STUDY

The objectives of the review are:

1) To review evidence for movement of plant and animal species along corridors and between habitat patches;

2) To identify the practical importance of corridor preservation and creation for conservation;

3) To relate organism attributes to dispersal ability; and

4) To identify possible locations for future experimental or monitoring studies.

1.4 STRUCTURE OF THE REPORT

The report is in 5 main sections. It begins with an introduction to the problem and a statement of likely climate changes over the coming century (Chapters 1 and 2). Then come reviews of species movements along corridors and between habitat patches, including a consideration of biological invasions (Chapters 3 to 5). The question of dispersal ability in relation to organism attributes is also considered in these chapters. A long chapter (Chapter 6) deals with the question of species vulnerability in relation to climate requirements and biotope occupancy, and with the possible effects of climate warming on montane species. Case studies of currently-expanding species are also considered.

The fourth main section (Chapter 7) is exploratory rather than definitive, and examines the ability of raster mapping techniques to display the connectivity of biotopes in the landscape. Finally there are recommendations for monitoring (Chapter 8).

1.5 SUMMARY

The role of corridors in facilitating species movements in the landscape is still poorly understood. This report reviews the migration, dispersal, invasion and vulnerability of organisms in the British context. The applicability of GIS mapping techniques and the need for monitoring are considered.

2 CLIMATE OF BRITAIN AND PREDICTED CHANGES

P D Carey

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2.1 PRESENT CLIMATE OF BRITAIN IN A EUROPEAN CONTEXT

The current climate of Britain is fairly homogeneous when we consider the climate of the whole of Europe. For variables such as monthly mean temperature and precipitation Britain falls into only a few broad categories.

2.1.1 Winter mean temperature

On a scale with 2.5°C bands most of Britain can be categorized with most of France, Spain and the Mediterranean coast. The north of England and inland Scotland are in the same category as eastern France and western Germany and the western coast of Scandinavia. Areas such as the Cairngorms could be in the same category as eastern Germany and the Balkans.

2.1.2 Summer mean temperature

England is very similar to the area on the northern European coast and especially Denmark. Scotland and most of Wales are in a cooler class which is only seen elsewhere in Europe in the Italian Alps and on the Norwegian coast.

2.1.3 Annual precipitation

On a scale with 250mm. bands all of England apart from the western coast is very similar to most of Europe including Scandinavia and Russia. The western coast of England, Wales and western Scotland are similar to most of Ireland, Brittany, the northern coast of Spain, the Alps, the Balkans, and much of the western coast of Norway. The Hebrides and the coast of Scotland inside them are wetter and are similar only to the southwestern coast of Norway and southeastern Iceland.

2.2 CLIMATE CHANGES PREDICTED IN THE NEXT CENTURY

2.2.1 The IPCC future climate scenario

The Intergovernmental Panel on Clmate Change (IPCC) scenario for the climate of Britain after a doubling of pre-industrial CO_2 concentrations in the atmosphere (around the year 2030) was calculated from the results of three separate climate models (Parry *et al.* 1991). Winter (December, January, February) mean temperature will rise by around 1.8°C in England, 2.1°C in much of Scotland and 2.5°C in the far north of Scotland. Summer (June, July, August) mean temperature will rise by 1.4°C over the whole of Britain. Precipitation changes vary greatly from model to model but IPCC suggest that the most likely scenario is a zero change in mean annual precipitation.

This climate scenario is based on an equilibrium model. However, in practice, warming will be much slower, because the ocean takes a long time to heat up. This introduces a lag in climate response, which may be about 50 years, with the result that temperature changes of the magnitude indicated above may not occur until nearer the year 2100 (Hulme *et al.* 1992).

2.2.2 Analagous current European climates

Currently the mean winter temperature of England is at the lower end of a 2.5°C band and by 2030 will be at the top end of the same band. The area in the top end of the current band is the south-west of France. The mean winter temperature of Scotland will become more like those currently experienced in England.

In Summer the mean temperatures will be similar to the current temperatures of France (South of Paris) and the Rhineland of Germany. Scotland and Wales will have a similar summer temperature to those currently experienced in England.

With no change in annual precipitation and the changes in temperature outlined above, England is likely to experince a climate which is similar to that which currently occurs in the wine growing regions of Europe. The climate of Scotland will become more like the current climate of England.

3 SPECIES DISPERSAL AND BIOLOGICAL INVASIONS

P D Carey

3 SPECIES DISPERSAL AND BIOLOGICAL INVASIONS

3.1 INTRODUCTION

As a result of man's activities many species have invaded Britain in the past few centuries. Some of these species have been deliberately introduced to the wild and many others have escaped from captivity or gardens (eg Sika deer *Cervus nippon*, Pheasant *Phasianus colchicus* and Butterfly bush *Buddleia davidii*). Most of these invaders have had little effect on the indigenous species in the communities they have invaded (Simberloff 1981) as opposed to becoming pests (Coypu *Myocastor coypus* and *Rhododendron ponticum*). The probability that an established invader will be a pest in Britain is around 10% (Williamson & Brown 1986).

3.2 INFECTION THEORY

On a 10km scale the Biological Records Centre hold information on how some of the more recent invaders of Britain have spread across the country. Some of this information has been utilized by modellers to investigate particular species eg. the spread of coypu in East Anglia (Usher 1986). Models on a large scale (eg. Kendall 1948; Skellam 1951) indicate that a successful invader will spread at a constant linear speed (Williamson & Brown 1986), assuming a heterogeneous environment. Levins (1970) produced a model (Equation 3.1) which indicates how epidemiological theory can be applied to predicting the range expansion of species (see also Carter & Prince 1981; Hanski 1987).

$$dp/dt = mp(1-p) - ep \quad . . . . 3.1$$

where p is the fraction of habitable sites occupied, e is the extinction rate and m is the colonization rate. In this deterministic model a rare plant or animal may spread into the system of patches if $m/e > 1$. This model (Equation 3.1) has no spatial component, the distance between patches is unimportant which is a major fault. The spread of Muskrat (*Ondatra zibethicus*) in Europe demonstrates how range expansion is determined by the quality of the environment. The pattern of spread in Bavaria was star shaped, mirroring the pattern of river valleys. This model has limited application, as Mollison (1986) points out. A stochastic model is essential when the numbers of invaders are small.

Hengeveld (1989) in a thorough review of models of the spread of species across the landscape, highlighted two particular forms of diffusion, neighbourhood diffusion and hierarchical diffusion, which were first introduced in the study of epidemiology (Pyle 1969; Cliff *et al.* 1981). Neighbourhood diffusion results when a disease progresses from an initial source - patient - to its immediate neighbour - a susceptible. Long-distance diffusion, where the disease leaps great distances avoiding neighbours, often occurs simultaneously with neighbourhood diffusion. New infection centres are created by long-distance diffusion and these will infect neighbouring susceptibles, a process termed hierarchical diffusion.

Different organisms will follow different types of diffusion as they invade a region. There may be a shift from neighbourhood diffusion to hierarchical diffusion as a certain set of conditions are met (Hengeveld 1989). Neighbourhood diffusion is most important if there are a large number of susceptibles in a small area and long-distance diffusion is difficult. This was seen in a cholera epidemic in the United States in the nineteenth century. In a subsequent epidemic, railroads and communications in the United States generally had been improved. This aided long-distance diffusion of the disease and a more hierarchical spread of the disease was noted (Pyle 1969, Cliff *et al.* 1981); with outbreaks following corridors of transportation. A similar pattern is seen with invading animals. The range expansion of the Muskrat is slower in areas with abundant wet regions (a high density of susceptibles) where they build up huge populations at the expense of range expansion (Hengeveld 1989).

3.3 POPULATION DYNAMICS OF INVADING SPECIES

There is, however, little information at a more detailed scale concerning dispersal or population dynamics of invading species. One exception is a study which has monitored the spread of a species, Zander (*Stizostedion lucioperca*), in the lakes,rivers and canals of the south midlands on a detailed scale (Hickley, 1986).

To become a successful invader a species first has to establish itself. Understanding the population dynamics of invading species is vital if we are to predict if these species will establish and how they will spread across the landscape. For any species the population dynamics can be expressed (Crawley 1986) by the equation

$$\frac{dN_i}{dt}=r_iN_i-f_1(\psi,N_i)-f_2\left[\sum_{j=1}^{i-1}N_j,N_i\right]-f_3\left[\sum_{k=1}^{i-1}N_k,N_i,P\right]-f_4(M,N_i)+X \qquad \text{.................... 3.2}$$

where r_i is the intrinsic rate of increase, f_1 is a function describing the effects of exploitation competition, acting through the resource supply rate, ψ; f_2 is a function describing the effects of interference competition acting through the number of individuals of all species (j) that are more 'fierce' than the invading species (the N_j are ranked from the most fierce (1) to the last species (i-1) that is fiercer than the invader; f_3 is a function describing the influence of natural enemies (P) and is related to their preference for alternative prey and to the abundance of prey species prefered to the invader (N_k); f_4 describes the effect of a lack of mutualists (M) on the ability of the invader to increase when rare. X is a measure of the immigration rate to the population. Clearly a population will become established if the intrinsic rate of increase r_i is greater than the cumulative effects of f_{1-4}. A further barrier to animal and some plant species is deleterious low-density effects (Allee effects) operating on the invader (eg. difficulty in finding mates) (Crawley 1987).

3.4 SUSCEPTIBILITY TO INVADERS

Elton (1958) proposed the idea that early successional plant communities, where competition is least, would be more prone to invaders than late successional communities, and this is still the most widely held view (Williamson & Brown 1986, Holten & Carey 1992) and also fits the population dynamics model (Equation 3.2). Crawley (1987) characterized different plant communities found in Britain in terms of their invasibility. He found that communities with low average levels of plant cover and communities subject to frequent disturbance have the largest proportion of aliens. However two of the most invasive species of the British flora at present (Sycamore *Acer pseudoplatanus* and *Rhododendron ponticum*) are both capable of invading late-successional habitats. Rejmánek (1989) suggests that invasibility is also related to a moisture gradient with mesic communities being the most susceptible to invasion. Certain species (eg. *Puccinellia maritima*) are genetically more variable at early successional stages (Gray *et al* 1979, Gray 1987) and could therefore have a higher probability of establishing in these conditions than at later stages of succession when variability is reduced.

Communities close to large sources of potential immigrants have many aliens while isolated areas have few (Crawley 1987 and see section 4 of this report). An example is given by the geographical location of successful and unsuccessful invasion sites for birds in Britain which suggest that locations closest to continental source populations ie. those in south-east England and in Scotland are most successful (O'Connor, 1986).

The rate at which particular plant communities are invaded (given their characteristic levels of ground cover and soil disturbance) clearly depends upon the connectivity of the site with other populated sites, and the area of the target plant community. The time that has elapsed since the last major disturbance (the successional age of the site) will also influence the invasibility of a site.

3.5 CONCLUSIONS

1. Invading species are dependent on the number, size and connectivity of habitable sites; such sites are analogous to susceptible individuals in an epidemic.

2. Invaders tend to be species which can utilise disturbed or open speces.

3. The success of invasions is very dependent on population dynamics.

4 CANALS AS AQUATIC CORRIDORS: A CASE STUDY IN DISPERSAL AND INVASION

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