

# Proceedings of the Second CONNECT Workshop on Land- scape Ecology, 1993

Principles and Tools for the Study  
of Landscape Ecology - Potentials  
and Limitations

NERI Technical Report no. 131

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September 1995

# Datasheet

Title: Proceedings of the Second CONNECT Workshop on Landscape Ecology, 1993

Subtitle: Principles and Tools for the Study of Landscape Ecology - Potentials and Limitations

Department: Department of Wildlife Ecology

Serial title and no.: NERI Technical Report no. 131

Publisher: Ministry of Environment and Energy  
National Environmental Research Institute©

Year of publication: 1995

Editors: Flemming Skov, Jan Komdeur, Gary Fry, Jette Knudsen  
Technical editor: Jan Bertelsen  
Layout: Marianne Hoffmeister

Please quote: Skov, F., Komdeur, J., Fry, G. & Knudsen, J.: Proceedings of the Second CONNECT Workshop on Landscape Ecology, 1993. Principles and Tools for the Study of Landscape Ecology - Potentials and Limitations. National Environmental Research Institute. 105p. - NERI Technical Report no. 131.

Reproduction permitted only when quoting is evident.

Edition closed: September 1995

ISBN: 87-7772-193-4  
ISSN: 0905-815X  
Paper quality: Cyclus offset, 100% genbrug, 90 g.  
Printed by: GP-Tryk, Grenå  
Circulation: 300  
Number of pages: 105  
Price: DKR 85,00 (incl. 25% VAT, excl. freight)

For sale at:

National Environmental Research Institute Department of Wildlife Ecology Grenåvej 12, Kalø DK-8410 Rønde Denmark Phone: +45 89 20 14 00 Fax: +45 89 20 15 14	Miljøbutikken Information & Bøger Læderstræde 1 DK-1201 København K Denmark Phone: +45 33 92 76 92 (information) +45 33 83 92 92 (books)
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## Preface

This report presents the papers read at the 2nd CONNECT workshop on landscape ecology held at Fuglsøcentret in Denmark, October 1993. The first meeting on landscape ecology within CONNECT took place in The Netherlands in Orvelte in early spring 1992. The purpose of that meeting was partly to exchange ideas and opinions on landscape ecology, partly to create a solid base for future scientific collaboration. An important outcome of the Orvelte workshop was a joint CONNECT proposal that was submitted to the European Union: The LANDECONET proposal, finally endorsed by the Commission in 1994, was officially launched in June 1994.

During the process of acquiring founding for LANDECONET, a number of studies within the agreed framework of LANDECONET were initiated or continued. There was clearly a need for a follow-up meeting to maintain the contacts established in Orvelte. The main purpose of the 2nd CONNECT workshop was accordingly to make selected research issues and themes within landscape ecology more specific. The contributions

were roughly divided into five main groups that reflect important research issues and examples of the potential use of landscape ecology for the management of natural resources:

- Future directions for landscape ecological research
- Case studies to pattern analysis
- Spatial modelling
- Pattern analysis (GIS & spatial descriptors)
- Applied landscape ecology

It is my hope that the workshop and the present proceedings will contribute to a clarification of what this relatively new branch of ecology contains and to give ideas of the ways in which landscape ecology may be used as a tool for environmental planning.

H. Sandbech  
Director



# Chapter 1: Future directions for landscape ecological research

## 1.1 Current and future needs for landscape ecological expertise

Paul Opdam

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### **Landscape ecology as a problem-oriented science: what are the problems?**

Landscapes are large heterogeneous parts of the earth's surface. The landscape mosaic consists of a particular combination of ecotope types, in a specific spatial arrangement, which is characteristic for a particular landscape type. Each ecotope functions as an ecosystem, but spatial flows of water, nutrients and organisms between the ecotopes link them to become an ecosystem of higher order, the landscape.

In the workshop, much emphasis was placed on the flows of organisms, how these relations are controlled by the spatial arrangement of ecotopes, and how they govern the spatial dynamics of populations. Abiotic flows and their interrelationships with the landscape pattern were not considered, and therefore this paper does not pay attention to this (important) part of landscape ecology.

Landscape ecology plays an important role in solving problems related to the spatial allocation of land use functions, some of which cannot be combined in space and time. The near future will bring major changes in the agricultural landscape in Europe. As a consequence of the economic and environmental constraints of the EU policy, large parts of the arable lands may be taken out of production. Some scenario studies predict figures as high as 25%. These areas could be redeveloped into landscapes where

natural processes dominate. Elsewhere, agro-industrial complexes will be concentrated in high production areas. In the remaining areas a multifunctional landscape will emerge, which combines food production next to housing and recreation functions, drinking water production and nature conservation. Other scenarios predict large areas of sustainable agriculture, like semi-wild cattle breeding for meat in semi-natural landscapes. Almost all studies predict big changes in the landscapes, and landscape ecologists should be ready to guide this transformation process and develop a vision on the future landscape in Europe. The ideas about the development of a European ecological network of nature reserves and connecting areas are already a concrete challenge to landscape ecology. If the predictions about climatic change are right, European nature will need such a network to be able to disperse over the continent to suitable climatic zones.

### **Towards usable results**

My paper focuses on the type of results landscape ecology must produce to meet the current and future needs in spatial planning, nature conservation, and environmental impact assessment. An essential condition for results to be applicable is that they can be expressed in terms of the landscape pattern. The challenge to landscape ecologists is, therefore, to link spatial processes and their

function to the landscape pattern, and vice versa.

Predictions should be made in terms of loss or gain in biodiversity or sustainability, e.g. in terms of changes in the survival chance or probability of occurrence of target species, or in changes in the fluctuations of densities (causing higher extinction changes). These predictions should always be related to spatial characteristics of the landscape, like area of ecotopes or habitat patches, interpatch distance, patch density or permeability of the matrix in-between the patches (corridor density, barrier density and so on). If not, then the results cannot be applied in a spatial planning context. An important thing is that results are also presented in a spatial context: for example, a map of probabilities of occurrence, or a map of bottlenecks in the connectivity, or possible scenarios for the solution of a problem. Such representations appeal more to the imagination of the planner than a regression model or an abstract graph.

### **Three kinds of activities**

Landscape ecological activities can be classified into three types which are all important to be successful in problem solving. These activities are:

- Developing the basic knowledge.
- Developing the instruments to apply the knowledge:  
Regression and simulation models, expert systems for problem assessment and finding solutions, and standards for spatial characteristics of sustainable landscapes or landscapes with a particular biodiversity.
- Contributing to applications by designing spatial scenarios, evaluating them, and carrying out impact studies or problem analyses. By this we can demonstrate how our knowledge and instruments must be handled and interpreted.

### **Two approaches**

From the point of view of organisms, land-

scapes can be regarded as comprised of archipelagos or mosaics. In the case of landscapes dominated by ecotopes which are so intensively used that they do not allow the survival of many species important for nature conservation, the emphasis is placed on the remaining archipelago of (semi-) natural elements. We then study fragmented populations, and can use metapopulation theory as a basis for our approach (which is not to say that we should assume that all fragmented populations fulfill the conditions of the Levins (1970) model).

On the other hand, in landscapes without a dominant land use form, the basic pattern for organisms is a mosaic rather than an archipelago in an unsuitable matrix. For instance, if we are working on the relationship between bird diversity and landscape structure in an agricultural landscape with small woods and hedgerows, we have to combine the two approaches: an archipelago approach for species restricted to the forest, a mosaic approach for species using other parts of the landscape as a habitat (edges, combination of elements). The approaches differ in their underlying theoretical structure, in the sampling strategy and in the set of spatial characteristics which are relevant to measure.

### **Pattern analysis the starting point: problem detection**

A spatial analysis of presence/absence or density distribution patterns will give a quick insight into the spatial conditions and the scale at which species start to have survival problems. To increase the chance of being successful, such an analysis must be founded on theoretical predictions. For instance, a species which appears to be absent in 50 % of the suitable patches in a fragmented system may be regarded as being affected by fragmentation to a serious degree. Such an analysis should be supported by statistical models relating a species parameter to a set of spatial (and habitat) characteristics. From this we get indications of spatial effects on the species distribution, which could be translated into (preliminary)



landscape planning standards. However, a serious cause of misinterpretations one should be aware of in pattern studies is the occurrence of time lags between the change in the landscape and the response in the distribution of the population.

### **Process studies: adding dynamics**

Process studies should be aimed at supporting the results of the pattern study, and make the static pattern approach more dynamic. For instance, a presumed meta-population pattern could be monitored for several years to see whether local extinction and recolonisation occurs, and whether differences in the frequencies of these patterns are related to spatial characteristics of the surrounding landscapes. Also, such parameters can be used to feed meta-population models.

Further steps to add more detail to our knowledge are to study dispersal or local movements and link these to the pattern of landscape elements. We also need to study the dynamics of local populations to understand the factors that govern local extinction. Dispersal studies are at the individual level, but they are indispensable for answering questions about the role of specific landscape elements in the dynamics of fragmented populations: are corridors effective, how wide should they be, do barriers have an adverse effect, are technical devices to mitigate the barrier effect effective?

### **Mathematical models: indispensable tools for application**

Regression models and simulation models are necessary instruments in problem detection, the development of planned standards and the evaluation of planning scenarios. Usually the relationships between species survival, habitat quality factors, and spatial characteristics in a landscape system are so complex, that only with the help of such models we can get insight into the best measures to be taken. General simulation

models can be used to produce planning standards such as the minimal area of patches in a network under particular degrees of connectivity, and the number of patches which must be connected to get a sustainable network.

To construct and validate simulation models is a laborious task, and parameter estimation is often a problem (which questions the degree of reality of the calculations), but the result is a dynamic model which can be used to express survival chances in terms of landscape structure, and which can be used in all kinds of landscapes. Regression models can be constructed rather quickly, are based on real world data, but are static and difficult to extrapolate. So, both models have advantages and should be used in combination.

An often heard criticism of predictions of ecological trends based on models is that models can never predict the future, since they are unrealistic and can never include all the factors influencing a biological system. This is to some extent true, and therefore models should be applied in a comparative sense rather than in an absolute sense. So, instead of predicting the situation in a landscape in the year 2002, one could better compare scenarios and say which one comes closest to the goals we want to reach.

### **The planning cycle**

Spatial planning is often a cyclic process. After problem analysis, goals for the planning procedure can be set, and one or more spatial scenarios can be designed, each representing one strategy to solve the problem, under different assumptions for future conditions. Standards, spatial concepts and rules of thumb can be used to solve particular problems, i.e. minimal area standards. In a further step, scenarios may be evaluated to see to what extent they will achieve the planning goal. Then, the best scenario can be chosen and in the next cycle it can be adapted and improved further. Mathematical models are helpful tools in assessing problems, producing planning standards for the spatial structure of landscapes, and for evaluating the success of planning devices.

## Major challenges

- To integrate knowledge at the species level to the ecosystem level. Our research is often at the species level, since processes are so species-specific. The questions, however, are in terms of ecosystems.
- To link dispersal movements to the pattern of landscape elements.
- To determine the significance of long-distance dispersal (the tail of the dispersal distance distribution) for range extension and recolonisation in the archipelago network.
- To link population dynamics at the landscape scale to the scale of the European ecological network. This is of utmost significance in the context of the expected shifts in species distributional ranges due to climatic change.

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## 1.2 Status of landscape ecological research of mammals

Henrik Andrén

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### Introduction

Habitat fragmentation implies a loss of habitat, reduced patch size and an increasing distance between patches, but also an increase of new habitat. The simplest explanation for describing the effect of habitat fragmentation is that small fragments are random samples from large ones (Connor & McCoy 1979, Haila 1983). If the random sample hypothesis is correct then the population size of single species is only related to the proportion of suitable habitat in the landscape, i.e. a halving of the proportion of suitable habitat in the landscape should result in a halving of the population size.

However, the effect of habitat fragmentation on species richness has usually been studied using the theory of island biogeography (MacArthur & Wilson 1967), whereas in studies of single species living in a landscape with habitat fragments one has usually adopted metapopulation models (Levins 1969). These two theories are related to one another, because they work with the same fundamental population ecology processes; extinction probabilities are related to population size and colonisation probabilities are related to the degree of patch isolation. If these two hypotheses are correct, then the population size in fragmented landscapes should be lower than predicted from the proportion of suitable habitat alone, because some habitat patches are too small or too isolated to be occupied.

### Random sample hypothesis

There is no simple relationship between the

degree of habitat fragmentation, patch size, and isolation; instead rapid changes occur at critical proportions of suitable habitat in the landscape. For randomly dispersed fragments, with a very low proportion of the original habitat, a further reduction in habitat will result in an exponential increase in the distance between patches of this habitat. Therefore, the relative importance of pure habitat loss, patch size and isolation are expected to differ at different degrees of habitat fragmentation. A review of studies of birds and mammals in habitat patches in landscapes with different proportions of suitable habitat suggests that the random sample hypothesis will probably be a good predictor of the effects of habitat fragmentation in landscapes with more than 30% of suitable habitat (Andrén in manus a).

In these landscapes, habitat fragmentation can be described as pure habitat loss. However, it is very important to note that the random sample hypothesis also predicts a decline in number of species and population size with increasing habitat fragmentation. However, in landscapes with highly fragmented habitat, patch size and isolation will strengthen the effect of habitat loss and the loss of species so that the decline in population size will be greater than expected from random sample hypothesis. Predictions from the random sample hypothesis and the theory of island biogeography may be very similar. For example, the random sample hypothesis predicts that, for statistical reasons, the rarest species will be the first species to disappear as the proportion of suitable habitat declines in the landscape. Whereas, the theory of island biogeography predicts that the species with the lowest density will be the most sensitive to habitat

fragmentation due to the assumption that the probability of extinction is related to population size. Therefore, to estimate the statistical power to reject the random sample hypothesis, Andrén (in manuscript) simulated the effect of habitat fragmentation on population size using models based on the random sample hypothesis and models based on the metapopulation concept, i.e. the probability of occupation of a fragment is related to area and isolation of the fragment. The statistical power to reject the random sample hypothesis was low in landscapes with a high proportion of suitable habitat, but increased as the proportion of suitable habitat decreased. Therefore, the results of tests supporting or rejecting the random sample hypothesis might not be due to different underlying population ecological processes. The different outcome of the tests might be due to differences in statistical power, that in turn is related to the proportion of suitable habitat in the landscape. There are several different possibilities to reject the random sample hypothesis, for example by comparing species richness in artificially drawn samples from large areas with species richness in real patches, by comparing patches with similar sized subplots in large areas or by testing for a relationship between population density and patch size.

### **Island biogeography and random sampling hypothesis**

However, a rejection of the random sample hypothesis is not necessarily a support for the theory of island biogeography or metapopulation models. Firstly, it depends on, for example, the scale of habitat fragmentation (Haila 1990). Habitat fragmentation on the scale of individuals means that the individuals breeding in different patches still are parts of the same population. Habitat fragmentation on the scale of population means that the populations in different patches are relatively independent of one another (Haila 1990). Secondly, the random sample hypothesis and the theory of island biogeography give similar prediction about the relationship between population density and patch size.

Random samples from a large area would yield the same density irrespectively of patch size. The survival model in MacArthur and Wilson (1967) states that a population on an island would reach carrying capacity if natality exceeds mortality. Everything else being equal, an island being twice as big as another island should have a population of twice the size, i.e. the population density should be the same. However, a rejection of the random sample hypothesis means that the effect of habitat fragmentation on species richness or population size is larger than expected from pure habitat loss and that configuration of habitat patches influence the species richness or population size. This would apply independent of the scale of habitat fragmentation.

Lande (1987) modified Levins' original metapopulation model. Instead of modelling the dynamics of a set of local populations, he modelled the occupation dynamics of a set of territories, i.e. he modelled the effect of habitat fragmentation on the scale of individuals. He replaced local extinction of a sub-population with the death of an individual occupying a territory and colonisation of an empty patch with dispersal and settlement of an individual in an empty territory. Lande reached similar results, as the original metapopulation model. Therefore, it seems that models based on the metapopulation concept could be used to describe the effects of habitat fragmentation on the scale of individuals, as long as one fulfils the assumption that the occupation of a patch is related to its size and that the probability of reoccupation of an empty patch is related to the distance to occupied patches.

### **Scale of habitat fragmentation**

To understand the effects of habitat fragmentation, it is essential to distinguish the scale of habitat fragmentation. Habitat fragmentation on the individual scale is related to area requirements of individuals, home-range boundaries and movement patterns of individuals (Haila 1990). The individuals living in the patches are a part of the same regional population in the surrounding areas. On the other hand, habitat fragmenta-

tion on the population-scale means isolation of local population, exchange of individuals between generations and the survival probabilities of local populations (Haila 1990). The theory of island biogeography and metapopulation dynamics are relevant on the population scale. Lande (1987) found that the population could not persist below a certain proportion of suitable habitat in the landscape (extinction threshold). Andrén (in manus b) found another threshold in the proportion of suitable habitat in the landscape, i.e. whether the fragment size and isolation of fragments influenced population density more than expected from the random sample hypothesis.

Thus, there seems to be two thresholds in the population responses to habitat fragmentation. The location of these thresholds depend on the ecology of the species, e.g., area requirements, and dispersal distances.

Many studies on the effect of habitat fragmentation on species richness or single species have assumed that population density is related to habitat quality, which is not at all necessary (Horne 1983). The conclusion that small habitat patches are poor areas are often based on the finding that the density is lower in these small patches. Therefore, to really understand the population responses to habitat, one must either show that population density is related to habitat quality or, preferably, study fitness factors, like reproduction or mortality, in relation to the degree of habitat fragmentation. Both the theory of island biogeography and metapopulation dynamics assume that the patches of suitable habitat are isolated from one another by hostile habitat and that each subpopulation only uses one habitat patch, a coarse-grained landscape. Species with large home ranges may use several patches in a fine-grained landscape. For example, the population size of capercaillie was related to both proportion of old forest in the landscape and the grain size of patches of old forest (Rolstad & Wegge 1987).

### The landscape mosaic

Habitat patches are parts of the landscape mosaic, and the presence of a species in a

patch may be a function not only of patch size and isolation, but also of the neighbouring habitat. Many species might view the landscape as a mosaic of habitat patches of different quality, i.e. heterogeneously undivided landscape (Addicott et al. 1987). Habitat generalist may survive in very small patches because they can also use the surroundings (Andrén 1992, in manus a). Source-sink models might be applied to such species (Pulliam 1988). Furthermore, the total species diversity across habitats in a given landscape (beta diversity) will increase when new patches of habitat are created within the continuous habitat, since new species will be found in these new habitats, even if they are man-made habitats (Andrén 1992). Although patterns in alpha diversity, like the species-area relationship, are major themes in ecological studies, far less attention has been paid to beta diversity. However, to understand the effect of habitat fragmentation on biological diversity one will have to measure both alpha and beta diversity in the landscape.

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## 1.3 Plants in landscape ecological research

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### Introduction

Since the first CONNECT meeting on landscape ecology in the Netherlands in 1992, a lot of work has been devoted to the formulation of a common, EU financed research program. This work gave an excellent opportunity to discuss different aspects of the landscape ecological approach for different groups of organisms. In this paper, I summarise the problems associated with applying a landscape perspective to the study of plants and vegetation.

A major concern amongst botanists is the relevance of landscape ecology in vegetation studies. Traditionally, the distribution of plants has been explained in terms of local habitat quality expressed in pure chemical and/or physical properties. In the recent literature of plant ecology, however, there is a growing tendency to include aspects of heterogeneity and landscape structure in plant studies. Habitat quality is a very important factor but it is not possible to predict all observed plant distributional patterns using only chemical and physical properties of a habitat patch. In a dynamic, ever-changing cultural landscape, aspects of local extinctions and colonisations, the function of barriers and corridors - in other words landscape ecology - must be taken into account.

But, to place plant ecology in a landscape ecology perspective means that we want the ability to accurately describe patterns of plant distribution, understand, explain, and model the underlying processes, predict likely consequences of landscape changes, and provide tools for application into landscape planning.

This is, modestly understated, not an easy task. How do we tackle such a problem? It

mainly depends on our research criteria. In my opinion, one criterion for good science is its ability to predict. To make science or, in this case, landscape ecology predictive, we must formulate clear and simple hypotheses, use operational and clearly defined terms, and choose dependent and independent variables with great caution. To be able to predict does not necessarily mean that we also understand the underlying processes. We can, for example, predict with some certainty that total floral biodiversity on a global scale increases with decreasing latitude. This is a valuable scientific result despite the fact that we are unable to understand its causality. The plant project reflects these thoughts: we will try to make simple, predictive rules (and perhaps simple spatial models) using simple and operational dependent and independent variables.

### Landscape ecology and plants

Pattern and process are closely linked concepts in landscape ecology. Patterns are created by various processes, but, on the other hand, processes - especially biological ones, are also influenced by landscape patterns. It is normal practice to initiate a landscape ecological study with a pattern analysis to gain an overview of the field and to get some idea of which processes to study in more detail and how to conduct experiments.

### Pattern studies

There are many ways to study plant distribu-

tions. It is, however, common practice to use a nomenclatural angle of approach and study distribution patterns of species or species assemblages (vegetation types, ecotypes, etc.). These studies can be qualitative, i.e. absence/presence data, or they can be quantitative and make use of some kind of abundance or cover scale.

In a simple pattern analysis one would look for correlations between independent variables such as habitat quality, landscape structure and history and dependent variables like absence or presence of individual species, total number of species, vegetation cover, etc. There are examples of this kind of research from Germany, where Zacharias & Brandes (1990) have shown a relationship between size of forest patches and ground flora composition and total number of species. Dzwonko & Loster (1988) have in a Polish study established simple correlations between different variables of landscape structure and history and floristic richness and composition.

Investigations of this type pose several problems:

- There are many plant species, and they are very different. Some are rare, others almost omnipresent; some are very site specific, others are present in many different habitats. There is absolutely no reason to believe that landscape structures and variables of habitat quality affect different plant species the same way. This means that what is a true correlation for one species might be false for another.
- It is necessary to develop a scale awareness, i.e. to recognise that some patterns of distribution relate to large scale, regional patterns, while others are a result of local, microprocesses.
- And finally some practical considerations: Accurate and reliable information on distributional patterns are of utmost importance, especially when this information is used in a meta-population context. Meta-population theory predicts local extinctions and colonisations and can only be tested against accurate field data. Field experience has shown that it is almost impossible to map floristic diversity for larger areas completely. There is no way

to tell with 100% certainty that a plant really is missing from a habitat patch under survey, moreover many habitats are not easy to delimit. As a result lots of ground must be covered, literally by the square meter, to produce quality floristic surveys.

One suggestion is to abandon the taxonomical species approach and look at the flora from a functional point of view. Functional traits can be generalised from one situation or place to another, independently of the local flora. By testing for predictable relations between functional traits and environmental parameters or landscape patterns, it may be possible to test for general theories about plant distribution in different landscapes. This is not a new idea but it has not yet been used in landscape ecology. This approach requires a number of steps as described by Boutin & Keddy (1993):

- Do a pattern analysis (species in real landscapes)
- Define important functions (reproductive strategy, type of dispersal, habitat preferences, response to landscape structures, etc.)
- Find traits that reflect these functions and scan the flora and construct a trait matrix
- Classify guilds or functional groups of plants
- Relate guilds to landscape patterns

This approach represents a marriage between pure, descriptive pattern studies and process analysis. We would be forced to think in terms of functional ecology and the method could evolve into an iterated process where formulation of hypothesis could lead to tests and experiments.

## Process studies

Pattern analyses will undoubtedly provide us with some new insights and knowledge. It will, however, be necessary to study landscape processes if we want to refine our predictive tools or start modelling. Most studies of biological processes on a landscape level



had a zoological starting point, and there are some basic differences between animals and plants that make studies of plant processes difficult:

- Plants do not move. This means that gene flow (as seeds or pollen) requires some kind of vector or transportation. These can be physical (wind, water) or biological (on or in different species of animals)
- Plants often have a seed bank and can be present in a patch for ages without being (obviously) visible.
- Plants are often long-lived or can persist as clones with vegetative reproduction. The presence of a species does not necessarily reflect the current suitability of the habitat as a regeneration niche; it rather indicates that the habitat used to be a good site.

What does this imply? First of all that many important processes that are vital for plant distributions within a landscape occur over very large areas and on long time scales. It is almost impossible to actually follow the dispersal of individuals in a landscape. We can forget about marking experiments if the important dispersal process takes place once in a century or is a rare long-dispersal event. Many plant species simply do not 'perceive' the landscape at a 'human' scale of time and space as most animals, e.g. the roe deer or the nuthatch might do.

These considerations leave botanists with a serious problem as they like to undertake process studies at a landscape scale but are left without proper means to do it.

One way to avoid troublesome real-world process studies is to turn to pure theoretical modelling studies. It is possible within a computer to create whole landscapes (even in three dimensions) and to simulate changes over centuries. In these artificial scenarios the behaviour of different 'species' could be tested while changing the values of important character traits such as dispersal rate, occurrence of rare long-dispersal events, colonisation success, etc. In spite of the pure theoretical character of such an approach, results can be compared and evaluated with real distribution data.

## Conclusion

Botanists have up to now mainly studied vegetation patterns on a macroscale (global vegetation belts, floristic regions, etc.) or on a microscale (plots, small scale gradient, habitats, etc.). The mesoscale or landscape scale represents a relatively new arena for most students of plants. We find methods used for macroscale studies too coarse; and we run into money and time constraints if we try to apply microscale methods to the landscape level. In this paper I have described (a lot of) problems but have also tried to suggest some solutions: Let us try to reduce the complexities of taxonomic groups to the more manageable entities of functional groups and use them in a pattern analysis; try to find new ways of conducting process studies and experiments; and make better use of modelling approaches.

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## 1.4 Conservation of amphibians: The importance of a landscape approach

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### Introduction

Destruction of essential habitat, such as breeding ponds or terrestrial habitats used during the post-breeding season (e.g. Loman 1981), is undoubtedly a major and deterministic factor in the seemingly world-wide decline of amphibian populations (e.g. Barinaga 1990, Elmberg 1993). Furthermore, pollution and acidification certainly add to this troublesome situation (e.g. Wyman 1990). However, the fact that amphibian disappearances were reported also from relatively remote and pristine habitats prompted many herpetologists to delve into discussions of global atmospheric deterioration, while basic demography of the amphibians was largely neglected (Sjögren 1991a). Data imply that many amphibian populations are highly susceptible to environmental stochasticity (e.g. Corn and Fogleman 1984, Pechmann et al. 1991, Sjögren 1991a,b), mainly because weather conditions have a major impact on the reproductive result of the animals. The resulting fluctuations in population size put such single populations at severe demographic risk (Goodman 1987), and this combined with the indigenously subdivided population structure (Sjögren 1991a) suggests that conservation strategies for temperate zone amphibians should focus on efforts to guarantee regional persistence at the metapopulation level (Sjögren 1991a; cf. Murphy et al. 1990); hence, the importance of a landscape approach.

Here, I will briefly review some recent population studies of temperate zone amphibians to further emphasise this point. I will argue that the landscape approach to ensure amphibian persistence is equally relevant for species which have a significant

period or life away from the breeding pond during the post-breeding season (e.g. Loman 1978, 1981, Hels 1993) as for pond-dwelling taxa which virtually remain in the same habitat throughout the active season (e.g. water frogs, Berger 1977). Finally, some computer software is reviewed in the context of population modelling.

### Isolation effects - statistical evidence

Studies on various organisms have shown that immigration and connectivity may reduce the risk of local extinction significantly (see Sjögren 1991a); at the regional level, this means that the quality of the 'non-habitat' over which the organisms disperse may be important for both local and regional persistence.

Studies on amphibian distribution and extinction patterns have reported that degree of isolation (distance to the nearest occupied pond/site) and elements of pond/site connectivity have a significant impact on amphibian persistence and species diversity. Laan and Verboom (1990) found a major effect of distance to the closest forest habitat in explaining local species diversity at ponds in an agricultural Dutch landscape; for old ponds, pond size also had a significant effect. Since many of the ponds were recently created by man, they interpreted their results as the forest habitat facilitating dispersal from one pond to another, and the pond area effect being similar to that of the common species-area relationship described by island biogeographic theory (e.g. MacArthur & Wilson 1967).

Mann et al. (1991) found clustering of ponds to be a major factor explaining the distribution patterns of various amphibians among fish ponds in Germany. They interpreted this pattern as habitat fragmentation having a positive effect on species abundance, but Edenhamn et al. (1992) corrected this erroneous interpretation by presenting some important demographic aspects of the study results that emphasised the importance of pond proximity and habitat connectivity rather than fragmentation for the demonstrated pattern.

In a single-species analysis, Sjögren (1991a & Sjögren 1994) found that proximity to a neighbouring local population was a major factor preventing local extinction of the pond-dwelling pool frog (*Rana lessonae*) in Sweden. In an isolated situation, local extinction occurred also in high-quality habitats, but habitat quality (i.e. local climate) was not spatially autocorrelated and, thus, could not explain the geographical clustering of persistence sites (but see below). Investigating this pattern further, Sjögren Gulve & Ray (in prep.) found that the occurrence of large-scale forestry (draining) between the ponds had a significant effect on both local extinction ( $P < 0.016$ ) and the colonisation of vacant ponds ( $P = 0.0713$ ; 2nd variable entered after distance to closest neighbouring pool frog pond; stepwise logistic regression). Hence, in areas dominated by large-scale forestry, local extinction probabilities are increased irrespective of other pond parameters for this water frog species, and the probability of recolonisation is reduced, which results in a regionally declining system although the frog ponds per se have not been altered (cf. Petranka et al. 1993).

Similar patterns of habitat occupancy occur in the analyses of distributions of the common frog (*Rana temporaria*) and the common toad (*Bufo bufo*) in Stockholm, Sweden (Sjögren Gulve & Norström, in prep.); both these species have a significant terrestrial life away from the breeding pond during summer. While habitat quality was found to correlate with different pond parameters in these species, the probability that a pond was occupied by either of them declined significantly with distance to the closest occupied pond. Since the pressure of urban develop-

ment has steadily increased in this region, this probably represents a relict pattern with greater persistence among clustered populations rather than a pattern associated with ongoing range expansion.

Finally, additional emphasis on the importance of the habitat(s) between breeding ponds for amphibians with more terrestrial habits is provided by an analysis of the colonisation pattern of European tree frogs (*Hyla arborea*) during 1990-92 on the island Lolland in Denmark (Hels 1993). Of the geometrical factors and habitat parameters examined, proximity to the closest pond with extinction recorded was the prime determinant of the colonisation probability of vacant ponds ( $X^2 = 44.85$ ,  $P < 0.0001$ ). As these data were collected for a time period less than the average life-span of an adult tree frog, this pattern suggests that single males move around between ponds in search for a good or better breeding site. This and the fact that tree frogs spend the post-breeding season in forest or meadow habitats between the ponds emphasise the importance of a landscape approach for the conservation of this threatened species.

### Isolation effects - demographic evidence

Despite the fact that temperate zone amphibians are highly qualified for demographic analyses, see for example Sjögren (1991a) and Berven (1990), not much has been done pertaining to population growth rate and the risk of extinction. One recent analysis based on a capture-mark-recapture study of more than 2,400 pool frogs (Sjögren Gulve, in prep.) showed that local frog populations which exchange migrants (so that immigration balances emigration) increase by about 10% per year; whereas population growth rate ( $r$ ) was negative if the emigrants were lost from the system and not compensated for locally by immigration. This analysis, and the fact that similar results have been obtained for birds (Stacey & Taper 1992) and mammals (Fahrig & Merriam 1985), suggest that dispersal and emigrant survival are important factors to consider in

conservation strategies for subdivided populations in general.

## Computer modelling and the development of conservation strategies

Once the necessary data have been gathered, computer simulations are useful for sensitivity analyses etc. in the development of conservation strategies. However, data collecting takes time, and one should not underestimate the intuition following from extensive knowledge of a system or a species. Regarding computer modelling of amphibian systems, the software that I know of applies to single populations or single-species situations (metapopulations). At this point, one can choose between modelling of metapopulation dynamics on the basis of patch parameters/characteristics (e.g. METAPOPOP II; Ray & Sjögren 1992) and demographic modelling of meta- or local populations based on age- or stage-specific life-history parameters (e.g. VORTEX: Lacy & Kreeger (1992), RAMAS/age: Ferson & Akcakaya (1991) or RAMAS/stage: Ferson (1991)).

METAPOPOP II models turnover of local populations in a metapopulation system using patch parameters and geometric factors known to influence the probabilities of colonisation and extinction, respectively. Using the software, one needs data from repeated censuses of a system where extinction and colonisation have occurred, preferably analysed using logistic regression which helps to develop specific models for these processes. METAPOPOP II uses the Monte Carlo technique and patch/pond specific colonisation and extinction probabilities (per time step) based on functions designed by the user or derived from logistic regression analyses. Contact us, or see Ray & Sjögren (1992) for more details.

Both RAMAS/age and RAMAS/stage use projection matrices to model one single population; they are user-friendly and the age- or stage-specific parameters are easily entered and edited, R/age even more so than R/stage. Immigration and emigration/har-

vest rates can be specified for each age or stage class, and degree of covariation (correlation) between different demographic parameters (e.g. immigration vs. fecundity) can be specified. Demographic stochasticity is simulated using a binomial distribution for sampling annual numbers of surviving individuals in the different age categories and a Poisson distribution for sampling annual age specific fecundity in a similar way. A third program, RAMAS/space which also is user-friendly, is available, but its lack of structured modelling of the local populations, plus an unsatisfactory approach of handling migration (a bug?), limits its present use to educational purposes.

VORTEX is a much better choice for demographic modelling of meta-populations. However, since this software is primarily designed for moderately fecund taxa (e.g. mammals and birds) and does individual-based demographic modelling combined with monitoring of loss of alleles and heterozygosity, simulating highly fecund animals such as amphibians may call for ways of solving the 'too many animals'-problem (e.g. eliminating egg and larval stages) which may arise when using the software. VORTEX assumes totally independent variation of population parameters among the local populations, and correlated events are simulated as 'catastrophes'. The software is less user-friendly than the RAMAS programs, but in addition to the genetic aspects of the program (loss of heterozygosity; simulation of inbreeding depression) it also allows much greater flexibility in modelling demographic stochasticity and investigating combined effects of spatial and demographic structuring of populations, all of which is very useful. For demographic modelling of amphibian populations, I think combined use of these programs (e.g. RAMAS/age and VORTEX) is the best strategy.

In conclusion, the distribution and demographic patterns mentioned in this review seem applicable not only to various amphibians, but to a wide range of taxonomic categories. Therefore, conservation strategies based on studies of amphibians are likely to have positive effects for several other taxa with similar life cycles.

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## 1.5 Urban nature - a resource for biological diversity and environmental education

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### Introduction

A rich flora and fauna is desirable from an ecological point of view. Today, monocultures with poor flora and fauna diversity are characteristic of large parts of the productive land as well as in city environments. In order to encourage diversity, different kinds of biotopes must be maintained and developed. This applies not only to the rural but also to the urban landscape. By intensifying ecological islands and corridors, plants and animals are encouraged to spread into developed sites.

In addition to its ecological functions, urban green space has an important social and educational function. Access to nature near living areas, schools, and places of work gives opportunity for a valuable leisure time, a healthy life, and an increased concern about the environment.

This paper presents three examples where ecological principles have been implemented in landscape planning, design, and management.

- General physical planning on an ecological basis in Lidingö municipality
- How to increase biodiversity through establishment and maintenance of the urban green space.
- Parks and green spaces used as an environmental educational resource.

### Lidingö - planning on an ecological basis

Lidingö is a green island NE of central Stock-

holm. The area comprises 30 square kilometres, a great part of which is agricultural land and forest. The first houses on the island were summer cottages built around 1860. Today, the municipality has more than 40,000 inhabitants of which about one half lives in their own houses and the other half in multi-family houses. In spite of a great demand for housing in the region, politicians agree to preserve and develop its green spaces.

In 1988, the Lidingö municipality approached MOVIMUM, Swedish University of Agricultural Sciences, Alnarp, for assistance to develop an ecological basis for the general plan of the municipality. The project was carried out as a research and development project parallel to other programmes in the municipality.

A biotope map provided the background for the ecological analysis. Fourteen different kinds of biotopes were identified: four forest, three open land, three water and meadow, and four urban biotopes.

The biotope list was used as the basis of two analyses: (a) an analysis of areas which are ecologically sensitive, and (b) an analysis of areas which have high recreational values. An example of a biotope which is ecologically sensitive is old pine forest on rocky ground with a thin layer of soil. It has slow regeneration capacity, high risk of erosion and a low buffering capacity against acid rain. Every biotope type was described in a way which explained the ecological consequences if houses or roads were built on them or if they were used frequently for recreational purposes.

It is worth noting that the project exclusively used existing and available material.

This material was provided from the local administration and people who use and know the nature in Lidingö well. The ecological influence on the final plan can be summarised in two points:

- Future land use. In the general plan, which shows projected land use in the municipality in 1990-2005, several plans for areas intended for housing estates were changed or excluded as a result of the ecological evaluation.
- Recommendations of planning and housing estate. For future detailed building plans Environmental Impact Studies are required. The conditions for ecological planning are unusually favourable in Lidingö. This is partly because of the administration's good intentions and partly because of the availability of comprehensive information including nature studies, forestry plans, environmental measurements, etc. The most important contribution of the developing project described above was to collate the scientific material in a systematic way which made it possible to integrate it in the planning process and make it accessible for the non-specialist reader.

### **Increased biodiversity through establishment and protection of the urban recreational areas**

Urban areas are usually considered as poor areas from an ecological point of view. This is only partially true. Even in urban areas unique and rare biotopes are found. Unique biotopes can come into existence at waste disposal sites, water treatment plants and in harbours, along railway tracks etc. where vegetation might spread and develop. Urban areas create their own special conditions for flora and fauna. For example, urban areas often have a milder climate than the surrounding landscape, which enables species with a southern distribution to survive there. It is also important to describe the value of special biotopes in the urban environment and take care of them. They are threatened as they often occur in non-developed areas,

which are liable to exploitation in connection with expansion of populated areas. Contrary to Germany and The Netherlands, research on urban flora and fauna in the Scandinavian countries is still in an early stage.

An intensification in agricultural and forestry practices has resulted in a decline in biodiversity. All over the world projects are carried out in order to save endangered species. One of the most important aims of urban and landscape ecology is to contribute to rescuing some of these species. Two possibilities are illustrated in the following. One possibility is to use subsidy schemes within the EU which subsidise farmers who transform some of their farm land to non-production land-use. There are, however, no demands to coordinate these actions with environmental issues. Another possibility is to exploit the increased interest in environment and urban ecology which is found among urban planners and park managers. It is generally believed that nature-like parks and green spaces are cheaper to maintain than the traditional garden-like ones. No matter how it is done, knowledge is required in order to reach the desired results. In The Netherlands, England, and Sweden, knowledge and experience of how to establish semi-natural biotopes in cities has been collected. It is acknowledged that the established biotopes should be as authentic as possible. Examples of initiatives which might contribute to this are:

- Use of local material when establishing new vegetation. Topsoil as well as vegetative small plants and seeds collected from plants in the surroundings might be used here.
- Use of a plant material (primarily among trees and shrubs) of the right provenance as regards the conditions on the growth site and the geography.
- Through studies of changes in genetic variation of plant species when they are used for seed production. At the Danish Forest and Landscape Research Institute such a research project (a study of some common herbs used for seed production) is ongoing.

Protection of established biotopes is always



important. In meadows with poor soil, grass must be removed after seed throw, otherwise it supplies nourishment to the soil encouraging vigorous grass species at the expense of flowering herbs. In forest biotopes, it is important that land clearing, thinning, and felling is carried out in a way which results in great variation in age, density, and species composition of trees. An extensive urban concentration might result in the partition of existing green spaces. This might disrupt dispersal corridors for plants and wildlife.

### **Parks and green spaces as an environmental educational resource**

Finally, a variety of biotopes in a city is an important factor in the personal development of many people, especially children. The general understanding of nature and the ecological consciousness which is obvious to Scandinavians is rather unusual in an international perspective. It has grown through access to and close contact with nature, including frequent visits to forests and agricultural lands through generations.

As more and more people grow up in densely populated areas where the only contact with nature is acquired during short vacations, this natural knowledge of nature is decreasing. As a result, the strong support for nature preservation and ecological principles is decreasing. This effect is intensified by the fact that the Scandinavian countries are becoming plural societies. Large groups of immigrants are arriving from parts of the world where the environment is ecologically exhausted and where attitudes to the environment and nature are fundamentally different.

Bearing this in mind, it is important that everybody, especially children, have access to a variety of biotopes close to their homes. In the following, examples of schools that have used their neighbourhood as an educational resource to improve the children's understanding and care of the environment are presented.

- Children who grow up in urban sur-

roundings may believe that food is produced in factories or directly in the shops. In order to obtain a fundamental knowledge of the environment, the children must be familiar with the development from seed to plant and from grain to dinner table. Many nursery teachers say that the best way to teach children basic knowledge of the environment is to let them plant seeds and teach them to take care of them while they watch them grow. The idea of nature cycles should be established early, preferably in nursery schools. Learning can be tangible and practical by illustrating the chain: growing - cooking - composting. The Rambodal school in Norrköping in Sweden carries out these ideas in practice.

- If children are to understand biological diversity, they must have access to various types of biotopes. In cities, there are often no suitable study objects. Instead, they are forced to go to outlying recreational areas. An alternative would be to create common biotopes in a school yard or a park area close to the school. A Danish school in Tvis near Holstebro decided to establish a school botanical garden in a closed yard. In an area of about 1,100 m<sup>2</sup>, they have succeeded in establishing a small aboretum with trees and shrubs from all over the world as well as a biotope collection. In the biotope collection, the following biotopes have been established: inland dune, rocky heath, moor, heath, alder marsh, foliage meadow, and oak forest.
- People's attitude to nature always influences nature somehow. This influence occurs continuously and is the result of people's decisions and behaviour. A way to help children understand the dynamic of the landscape is to study an area and see how it has changed in the course of time. At the Haslaröd school in Osby in the north of Skåne, the history of the local environment has been studied. Pupils have studied the changes in a local forest from the end of the sixteenth century. The involvement of the children in this project has taught them that human behaviour forms the landscape. In

the light of the historical development and the forestry planning of today, the future landscape development is discussed. What will the forest look like in 100 years? Here the pupils are stimulated to describe their own ideas of how the forest will develop.

## **Do managers need landscape ecology**

At the UN-conference in Rio de Janeiro 1992, world politicians demonstrated that environment is a decisive factor for the survival of the human race. The above review shows that landscape ecology plays an important part in this connection. Landscape ecology provides knowledge which makes it possible to plan a sustainable city and landscape development, a new kind of park and landscape management and an increased concern for the environment among children and adults. However, the distance between research and practice is still huge. Therefore, a lot of work has to be put into research and into developing projects within the area of landscape ecology.

## 1.6 The use of insects in landscape ecological studies

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### Defining what landscape ecologists need

A large number of concepts in landscape ecology are based on theory and intuition whereas empirical evidence and especially experimental investigations are few and often weak because of design or logistic constraints. To investigate many of the themes in landscape ecology including meta-population dynamics, source-sink relationships, connectivity, barriers and corridors demands large-scale experiments in both time and space. The limited data available to us, is mostly in the form of a description of patterns of species occurrence which are correlated to the spatial pattern of habitats. If we are to understand the causal relationships between species abundance and survival and the spatial arrangement of landscape elements we will eventually need more rigorously controlled experimental approaches.

The landscape ecology literature provides us with some evidence of the groups of organisms of value for these studies. Not surprisingly, it has been organisms that have the ability to respond rapidly to landscape change and configuration that dominate published papers. Birds, mammals and insects are among the most worked groups. These groups represent wide ranges of dispersal ability, niche breadth and reproductive capacity but most importantly they can be studied at several levels. Pattern studies, population modelling and experimental approaches are all possible. In contrast investigations of the landscape ecology of long-lived, k-strategists such as large mammals (game species, whales, elephants etc.) and perennial plants (perennial herbs, trees) are limited to pattern studies.

Species suitable for landscape studies need display measurable changes in behaviour, population processes or distribution within a short (3-5 year) experimental programme. Rare species are almost impossible to work with since they are few in number and experimental manipulation always carries with it a finite risk of making matters worse. Species suitable for investigation must be amenable to study. This sounds rather obvious but there are many landscape questions which are very difficult to investigate and also species which are difficult to work with. We require species that:

- have quick responses to landscape change
- restricted dispersal for habitat isolation to be a problem
- occur in large numbers to allow individual variation to be studied
- large numbers are required also for statistical analysis
- cover a wide range of ecological types and life history traits

### The use of insects in landscape ecological research

Some of the earliest studies of landscape effects used insects as study organisms. The pioneer work of den Boer and his students at Wageningen provided the basis of much of modern landscape ecological theory long before the term landscape ecology was coined. Similarly, a wide spectrum of basic research into insect population dynamics focused attention on spatially structured populations in the 1960s. Later, the work on fragmented butterfly populations in the USA

(Harrison 1991), Finland & England (Thomas 1991; Thomas & Harrison, 1992; Thomas et al. 1993) and carabid beetles in hedgerows in France (Baudry 1988; Burel 1989; Burel & Baudry 1990) contributed significantly to the development of many landscape ecological principles.

Insects fulfill most of the requirements for landscape ecological studies, specifically of their responses to landscape patterns and change. They have the advantage that large data sets with replicate treatments and controls can be collected.

### Advantages of insects

Within the insects there exists an extremely large range of ecological types making the group suitable for the study of many aspects of population and habitat biology including the effects of the spatial arrangement of resources. Insects offer the following as study objects for landscape ecology:

- Well-documented taxonomy and ecology for some groups
- A wide range of mobility, habitat specialisation, etc. can be found
- Many insect species are quick to react to landscape change
- Large numbers and widespread distribution allow variation to be studied
- They present a spectrum of social organisation and parental care
- Population processes are well studied for some insect groups including empirical and modelling work on;
  - predation and parasitism
  - food/prey selection and foraging behaviour
  - space use and competition for space
  - selection of breeding sites
  - phenology
  - summer/winter habitat choice
  - dispersal and migration

Insect studies have played a major role in the development of theory in population biol-

ogy. More specifically, in landscape ecology insects have provided insights into the effects of a number of spatial phenomena on insect movement and survival. Some of these are:

- Landscape structure
  - field size
  - boundary structure and network
  - spatial arrangement of habitat/resource patches
  - patch quality
  - landscape permeability
  - corridor use
- Random influences and large scale processes
  - catastrophic events such as pesticide events
  - ploughing and other forms of cultivation
  - climate change
  - landscape change

### Insect dispersal

Several of the key issues in landscape ecology are linked to the spatial behaviour of organisms. This is clearly the case in metapopulation dynamics where the ability of individuals to move between habitat patches, found new or supplement declining populations are vital to the balance between local colonisation and extinction rates. Here insects offer both many advantages and some problems. Key issues are:

- What affects insect movement
- How do we quantify insect movement
- How do we link spatial behaviour to population processes

Fortunately, there is a long history of entomological studies on insect dispersal, and among insect groups we find species that have long-distance purposeful movement at one end of the scale to others which have only trivial movement patterns and those with very limited movement capacity (Hodgson 1993).

## Applications of insect studies in landscape ecology

Linking spatial behaviour of insects to a landscape patterns is important for a better understanding of the ecological processes involved in many of today's environmental and health problems such as:

- Pest/disease control (Thomas et al. 1991)
- Nature conservation/game management (Samways 1993)
- Pollution effects (Jepson 1989)
- Pesticide impacts (Sherratt & Jepson 1993)
- Farming systems (Paoletti et al. 1992)
- How much habitat and where (planning standards, set-aside)

## Collecting data on insect movement

The disadvantage of working with insects is that they are usually small and delicate creatures. The problems associated with catching, handling, marking, and tracking insect movement have led to a wide range of innovative methods:

- Survey and monitoring using trapping techniques (where most pattern data come from)
- Mark-release-recapture techniques to give dispersal patterns
- Individual marking to provide insights into individual spatial behaviour
- Telemetry (e.g. passive radar methods are getting smaller)
- Video techniques
- Construction of experimental model systems and arenas (mini landscapes)

In recent years, there have been rapid advances in these and other methods of quantifying movement behaviour. Although several obstacles remain, the insects are clearly a group where large data sets amena-

ble to numerical analysis may be collected within realistic time and financial budgets.

## What is missing in traditional agricultural and planning research

The failure of traditional agricultural research and planning-related studies to address landscape-scale processes has been a major problem in both the generalisation of results and in the formulation of policy. Part of the explanation for the poor performance in terms of predictability has been the failure of studies to examine:

- Dispersal when using small replicated plot designs which are rarely mimic field situations as the movement of animals results in severe edge-effects or dispersal between treatments
- Patch dynamics, i.e. metapopulation/source-sink or other spatially explicit population processes
- Landscape-scale models in real landscapes.

These factors pertain to most animal groups whether pests, beneficials or conservation objects. Yet the failure to examine larger-scale ecological processes, even though difficult, has resulted in several unsuccessful management strategies based on traditional site-based approaches.

## Why is it missing

There are many interesting problems in landscape planning which are difficult to research or are currently impossible due to lack of suitable methods or resources. Whether we are considering insects, other animal groups or plants, planning landscape-scale investigations often gives rise to problems associated with:

- Lack of replication and controls
- High cost in manpower
- Involvement of cross-disciplinary teams

## Discussion

We clearly need better biological data to test many of the current landscape theories. Insects because of the wide range of niche, movement ability and ease of recording are making a significant contribution to this process. However, several studies have warned us to beware of generalisations. It will remain difficult to generalise from one study to another and assume that results on landscape effects can be transferred from one situation, country or species to another. Grouping species into broad ecological types may be the best way forward.

We need to think big. In very few studies has the experimental procedure been realistic in terms of the activity range of insects which sometimes may be on the regional level. Small plot or field scale experiments may provide us with misleading results.

Movement is important for understanding many large-scale ecological processes. Insects are a group providing many useful species as study objects. New tools are developing quickly to assist in the difficult task of monitoring the movement of insects in relation to landscape parameters. We need a major shift from purely theoretical studies to ones examining population processes in real landscapes. The EU LANDECONET research programme, organised by the CONNECT groups, uses detailed field investigations of insect behaviour and ecology to provide input parameters for model building and time-series of distribution data (pattern studies) to validate models.

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## Chapter 2: Case studies to pattern analysis

### 2.1 Effects of forest fragmentation on breeding bird populations in Denmark

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#### Introduction

Many studies predict large changes in the landscape (Opdam, this volume), especially an increase in habitat fragmentation, which implies reduced patch size, an increasing distance between patches, and reduced habitat quality. These changes may have profound effects on the biodiversity or sustainability of species occupying these patches. Landscape ecologists should be ready to guide this transformation process and develop a vision of the future landscapes in Europe.

Landscape ecological activities include among others effect studies of size and isolation of habitat patches on the number of species present in these patches. An essential condition for results to be applicable is that they can be expressed in terms of landscape pattern. However, some of these studies have some shortcomings. In the first place, species-specific responses to habitat fragmentation are not quantified; each species has its own response to changes in landscapes. For example, for birds of prey a landscape is a mosaic of more or less suitable habitat elements, whereas for small passerines a landscape consists of suitable habitat patches separated by unsuitable habitat. In the second place, very few studies investigate the detailed effects of confounding

variables, such as quality, diversity and isolation of habitat. For example, an increase in number of species with area does not necessarily indicate an 'area effect' per se; it could be no more than a by-product of a cause-effect relationship of these confounding variables. It is very important to correct for these shortcomings, preferably before starting the research.

Nevertheless, nuthatches and other forest birds in the Netherlands were shown to be affected by distances between small woods and the density of hedgerows (Opdam et al. 1985, Dorp & Opdam 1987, Verboom et al. 1991). These conclusions were based on a study in a small part of Europe, and it is therefore necessary to conduct similar studies in other geographical areas. This is especially important in the light of recent evidence of variation in species performance in different parts of the distribution range, thereby linking the population dynamics at the landscape scale to the scale of the European ecological network. Quantification of the relation between landscape structure and the distribution and survival of fauna groups is an important task for nature conservationists.

In this paper, distribution patterns, local persistence and recolonisation of breeding birds are discussed in relation to size and degree of isolation of beech (*Fagus sylvatica*) woodland plots in Denmark. The study was

designed to answer two questions related to woodlot size and degree of isolation:

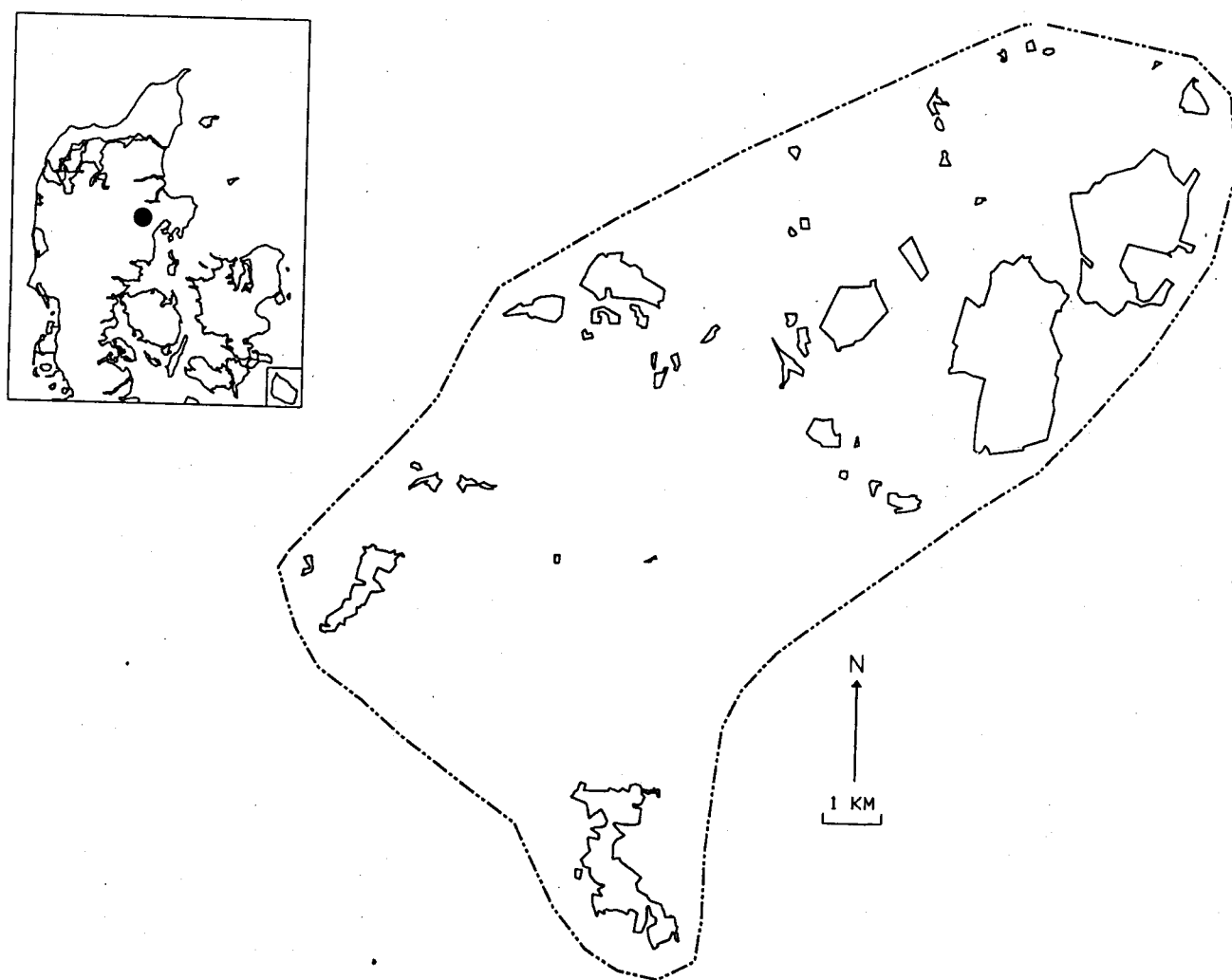
- How does fragmentation affect the total number of breeding bird species present in each wood
- How does this affect local extinction and immigration of bird populations sensitive to habitat fragmentation

## Methods

The area of investigation is situated in East Jutland, 10 km north of Århus, in Denmark (Fig. 1). The approximately 115 km<sup>2</sup> area consists of agricultural land and 49 mature woodlands differing in size and degree of isolation; six large woods (50-454 ha), interspersed with 43 smaller woods (0.2 to

24.8 ha). Some plots are connected with hedgerows. All woodlands are dominated by beech (*Fagus sylvatica*) of the same age, and their edges form sharp boundaries to cultivated fields.

In order to analyse the effect of patch size and isolation, it is important to consider only those species restricted to beech habitat. A selection of 13 breeding bird species restricted to these woodlands was made (Table 1). Other species occurring in the same woodlands, but also in other woodland types (e.g. gardens around farmhouses) and hedgerows within the study area, are not further analysed. For studies on nuthatch, treecreeper and marsh tit, only woodlands larger than 0.5 ha were taken into consideration as suitable habitats, i.e., 43 woodlands, as this was the minimum size in which these species occurred. The presence of nuthatches is not expected to be limited by



• Figure 1. Map of study area, showing distribution of woodlands, and the position in Denmark (inset).



Table 1. Percentage occurrence of birdspecies in 49 mature deciduous woodlands.

Species		% of woodlands occupied
Pied flycatcher	<i>Ficedula hypoleuca</i>	2
Woodwarbler	<i>Phylloscopus sibilatrix</i>	4
Green woodpecker	<i>Picus viridis</i>	6
Hawfinch	<i>Coccothraustes coccothraustes</i>	6
Jay	<i>Garrulus glandarius</i>	10
Spotted flycatcher	<i>Muscicapa striata</i>	14
Marsh tit	<i>Parus palustris</i>	27
Great spotted woodpecker	<i>Dendrocopus major</i>	33
Common treecreeper	<i>Certhia familiaris</i>	33
Nuthatch	<i>Sitta europaea</i>	45
Blue tit	<i>Parus caeruleus</i>	59
Chiffchaff	<i>Phylloscopus collybita</i>	78
Chaffinch	<i>Fringilla coelebs</i>	96

the availability of nest sites, because potential nesting places (old unoccupied woodpecker holes) were present in all small woods.

In 1992 and 1993, all small woods were checked twice between March and the middle of June, for the presence of nuthatches, marsh tits and treecreepers. Three cassette tapes, each containing calls and songs of one species, were used for this purpose. The species are very territorial and respond to recorded song. To attract birds, the recording was played using a portable cassette recorder with an integral speaker. Small woods, less than 7 ha, were scanned for birds responding to the recording during a five-minute period. In the larger woods more time was needed to cross the whole area, at most between 30 and 45 minutes.

In 1993, a list was compiled of the presence of bird species for each woodland in the area. The census was conducted in April and June, in order to include both early and late breeders. In small woods, larger than 7 ha, fixed 250-m transects, chosen at random before the first census, were scoured, stopping for 2-minute periods at points 50 m apart. During each stop, all bird species seen or heard were noted. In order to cover each woodland equally, the average 'transect-density' was 30 m/ha.

In order to analyse area and isolation effects on the distribution, we regarded only those species found in less than 80% of the woodland plots, assuming that these species are affected by fragmentation to a serious degree. However, species occurring in less than 25% of the woodland plots were not

Table 2. Variables for landscape attributes determined for each woodlot.

AREA	Total area of woodland (ha).
AREA (3)	Total area of woodland within a 3 km radius (ha).
SUIT (3)	Number of suitable woodlands within a 3 km radius.
DIST	Shortest distance to nearest suitable woodland (km).
DIST (20)	Shortest distance (km) to nearest suitable woodland > 20 ha.
DIST (100)	Shortest distance to woodland > 100 ha (km).
CONN	Number of woodlots within a 3 km radius from the edge, which are connected by hedgerows and/or other woodlots (e.g. woodlands are connected if distance between corridors and woodlots < 250 m).

included in further analyses, because of small data sets.

#### Nuthatch breeding activity

To record breeding activity, an occupied territory was chosen at random in each woodland with nuthatches present. It was checked for the presence of an occupied nest during nest building in April 1993. The same territories were visited each fortnight to check for the presence of eggs (incubating females), nestlings (feeding parents) and fledglings.

#### Variables pertaining to patch size and isolation

In order to analyse the effects of patch size and isolation on the distribution of the individual species, woodlot size and variables pertaining to isolation were calculated from maps at a scale of 1:25,000 (Table 2). Area of small woods and length of woodland-edges were measured using GIS on digitised maps. The other variables (Table 1) were measured and calculated directly from the maps. Because all small woods consisted of mature beech with the same cover and without a shrub layer, habitat diversity variables were not measured.

#### Statistical procedures

Statistical analysis was conducted using logistic regression. The logistic regression approach is analogous to classic multiple regression, because independent variables can be added to a model sequentially ('orthogonal effects'), allowing a test of the

additional effect of a given predictor variable after correcting for the effects of previously entered variables. For the case of a single independent variable, the logistic regression model can be written as:

$$\text{Probability (event)} = 1/(1+e^{-z})$$

$$z = B_0 + B_1 * X_1 + \dots + B_p * X_p$$

where  $B_0$  to  $B_p$  are regression coefficients calculated from the data with the maximum likelihood method,  $X_1$  to  $X_p$  are the independent variables, and  $e$  is the base of the natural logarithm. The degree to which a given model (e.g. occurrence vs. area) fits a null hypothesis is described by 'scaled deviance' ('D'), a statistic that has a probability density function similar to that of the Chi-square statistic. When not specified in the text, values of statistical tests are reported in the legends of figures or tables.

## Results

### Effects of forest fragmentation on occurrence of woodland birds

The relative abundance of woodland bird species is shown in Table 1. Woodland bird species were distributed very differently within the study area; some being restricted to few woodlands (e.g. pied flycatcher and woodwarbler), others being present in almost all woodlands (e.g. chiffchaff and chaffinch). For further analyses, the follow-

Table 3. Forward logistic regression relating the probability of presence of marsh tit, great spotted woodpecker, common treecreeper, nuthatch, blue tit and chiffchaff (43 woodland plots; 1993) to landscape parameters (see Table 1). Values are (Delta) Deviance, steps are indicated between brackets.

Species	ln(AREA)	DIST (100)	CONN
Marsh tit	17.91 <sup>(1)**</sup>	-	-
Great spotted woodpecker	25.46 <sup>(1)**</sup>	-	0.43 <sup>(2)**</sup>
Common treecreeper	22.39 <sup>(1)**</sup>	-	-
Nuthatch	32.74 <sup>(1)**</sup>	2.85 <sup>(2)**</sup>	-
Blue tit	14.65 <sup>(1)*</sup>	-	-
Chiffchaff	32.91 <sup>(1)**</sup>	-	-

\*\* P<0.005; \* P<0.05; - NS; Not significant: AREA (3), SUIT (3), DIST, DIST (20)

ing six species are included: marsh tit, great spotted woodpecker, common treecreeper, nuthatch, blue tit and chiffchaff.

The results of a stepwise logistic regression show that for these species the area of the woodland plot is of paramount importance for their occurrence (Table 3). The larger the woodland area, the higher the probability that the species are present. However, each species is affected to different degrees; marsh tits require the largest areas followed by treecreepers and nuthatches (Fig. 2). After correcting for area effects, the degree of isolation had only an effect on the presence of nuthatches and great spotted woodpecker; the shorter the distance to the nearest large woodland the higher the probability that nuthatches are present (Table 3).

#### Effects of forest fragmentation on probability of colonisation and extinction

The larger the woodland plot, the higher the probability of local colonisation, i.e. woodland plot changing from empty in 1992 to occupied by nuthatches and treecreepers in 1993, and the lower the local extinction, i.e. woodland plot changing from occupied in 1992 to empty in 1993 for all three species (Table 4). After correcting for size, the degree of isolation of woodland plots only had a significant effect on local colonisation and extinction rates for nuthatches (Table 4). The larger the distance to the nearest large woodland, the lower the probability of colonisation by nuthatches. The more suitable woodlands present within a 3 km radius, the lower the probability of local nuthatch populations becoming extinct.

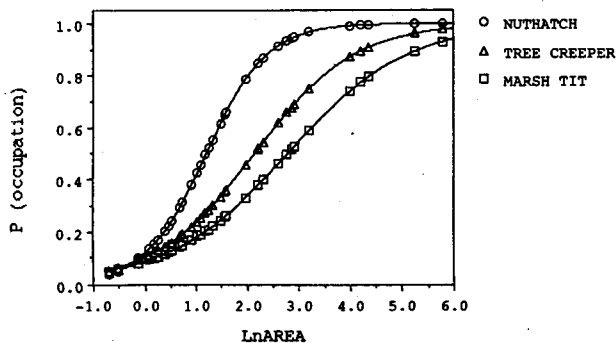


Figure 2. Effect of woodland size on the probability (P) of presence of nuthatch (N), treecreeper (T) and marsh-tit (M), (43 woodlands in 1993). N:  $D=25,09$ ,  $df=1$ ,  $P<0,001$ ;  $P(\text{present}) = 1/(1+e^{-z})$ ;  $z=1,70 (\ln(\text{AREA}))-2,04$ . T:  $D=17,57$ ,  $df=1$ ,  $P<0,001$ ;  $z=1,03 (\ln(\text{AREA}))-2,21$ . M:  $D=14,25$ ,  $df=1$ ,  $P<0,001$ ;  $z=0,86 (\ln(\text{AREA}))-2,40$ .

## Discussion

### Occupation of woodland plots

In the uniform mature beech forest fragments studied, distribution of a restricted set of six bird species not widely spread in the woodland plots, are best predicted from patch size. The larger the woodland plot size the higher the probability of occurrence (Table 3 and Fig. 2). An isolation effect on species' occurrence (corrected for area effects) was only found for the nuthatch (Table 3). This could mean that variation in total species number attributable to isolation is small. In small isolated woodland plots local colonisation and extinction may be important processes influencing species distribution.

### Colonisation and extinction probability

In the three species studied, nuthatch, treecreeper and marsh tit, the local colonisation probability is related to woodland plot size for nuthatch and treecreeper only. An isolation effect, corrected for area effects, on local colonisation and extinction rate was only found for the nuthatch. It seems that local extinctions of nuthatches are not entirely the result of stochastic mortality in local populations, but maybe also a result of local extinctions in nuthatches being masked by immigration from neighbouring patches ('rescue effects'). This result is at variance with Levins metapopulation model (Levins 1970), which assumes that local populations become extinct at random, independent of area and the degree of isolation of patches. Results from the nuthatch study in the

Table 4. Forward logistic regression relating the probability of colonisation and extinction of marsh tit, nuthatch and common treecreeper (43 woodland plots; 1992-1993) to landscape parameters (see Table 1). Values are (Delta) Deviance, steps are indicated between brackets.

	Species	ln(AREA)	DIST	(100)	SUIT (3)
Colonisation	Marsh tit	-	-	-	-
	Nuthatch	6.37 <sup>(1)*</sup>	12.27 <sup>(2)***</sup>	-	-
	Common treecreeper	6.81 <sup>(1)**</sup>	-	-	-
Extinction	Marsh tit	8.99 <sup>(1)***</sup>	-	-	-
	Nuthatch	9.44 <sup>(1)***</sup>	-	-	23.05 <sup>(2)***</sup>
	Common treecreeper	9.19 <sup>(1)***</sup>	-	-	-

\*\*\*P<0.005; \*\*P<0.01; \*P<0.05; - NS; Not significant: AREA (3), DIST, DIST (20), CONN

Netherlands (Verboom et al. 1991) show that extinctions were independent of the degree of isolation.

So far, we do not know much about the processes responsible for the probability of local colonisation and extinction. One may expect that colonisation probability is related to dispersal capacity. The better the ability, the higher the probability that an empty patch will be colonised. On the other hand, species occupying very small patches may become extinct due to reduced fitness (higher mortality and lower reproduction output of individuals) or due to the absence of rescue effects from nearby areas. It is clear that studies are required on dispersal, rescue effects and fitness (mortality and reproduction) in relation to the degree of habitat fragmentation.

The landscape parameters responsible for colonisation and extinction (AREA, DIST (100) and SUIT (3)) had no effect on the probability of presence of nests, eggs, and nestlings in an occupied nuthatch territory. However, the size of a woodland plot had a significant effect on the probability of presence of fledglings in a nuthatch territory (D=5.19, df=1, P=0.023, n=22). Also number of fledglings produced per territory shows a significant increase with the size of a woodland plot (Spearman  $r=0.67$ , df=9, P=0.023).

#### Proposed research

In the coming years, it is important to focus on process studies (e.g. nuthatch and marsh tit), in order to explain the results of our

pattern studies. Process studies will be used in simulation models to investigate the viability of populations in existing landscapes and to predict the effects of changes. For studies on habitat use, foraging, reproduction, mortality and dispersal it is important to colour-ring individual birds, both adults and fledglings. Firstly, it may be an idea to translocate nuthatches or marsh tits to an unoccupied island, for example Samsø (Denmark), with suitable habitats present for both species in order to investigate the effect of complete isolation on the development of a population. Secondly, a decline in the size of a population may have implications for its genetic diversity. Therefore it is necessary to study the effects of landscape fragmentation on genetic variation in subpopulations by DNA-fingerprinting (e.g. birds that colonise small woodlands may have good genes for dispersal, but bad genes for reproduction). In small populations there are a tendency for mating pairs to be related and a relatively high chance of inbreeding, which may effect fitness of these populations.

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## 2.2 Research on birds in small woods within an arable landscape

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### Introduction

This paper presents an outline of the approaches and methods used in a research programme investigating the population dynamics of bird communities of isolated small woods, set in the intensive arable landscape of south-east England.

### Methods

#### Woodland bird census and vegetation mapping

A large part of the first three years of research was spent on an extensive survey of 151 broadleaved woods ranging in size from 0.02 to 30 ha, and of various degrees of isolation. Birds were censused annually (1990 - 1992) using a mapping technique based on four visits a year, evenly spaced between mid March and the end of July. This provided good estimates of breeding species numbers and composition for each wood, and for species with high detectability provided reasonable estimates of numbers of breeding pairs. During census visits, simple statistics describing woodland structure and position in the landscape, such as woodland area, densities of field, shrub and canopy layers, surrounding land-use and the number of connecting elements (hedgerows, ditches etc.) were also collected. Additional landscape variables, including areas of adjacent woodland, lengths of hedgerows and distances to features such as the nearest wood and village, were obtained from maps and aerial photographs. These data have enabled us to look at how breeding species numbers, species composition and turnover rates between breeding seasons vary with

different woodland and landscape characteristics.

#### Marking of breeding birds

Another aspect of our work involved the marking of breeding populations of particular species in 16 small woods of about 0.5 ha. Adult breeders were caught using mist nets and marked using plastic colour-rings. The colour codes denoted the wood where caught and the year of capture. Hence turnover of individuals between seasons could be measured. Any unringed breeders present in a subsequent breeding season would be replacements. Nestlings and 'home-grown' juveniles were also ringed in an attempt to assess the relative contributions of immigrants and home-grown juveniles to the replacement breeding population. These data on colour-ringed birds have not been analysed in detail yet, but certain trends will be presented.

### Results

#### Bird species richness, composition, and turnover

Results from the first three years survey work showed that woodland area was an important factor in bird species richness and composition. Numbers of breeding species present increased with increasing area; approximately 70% of the variation in species numbers being explained by area alone (Fig. 1). Species richness was also related to habitat diversity and some measures of isolation but the relationships were much weaker. There were clear differences between woodland species and edge species. Numbers of woodland species increased with increasing

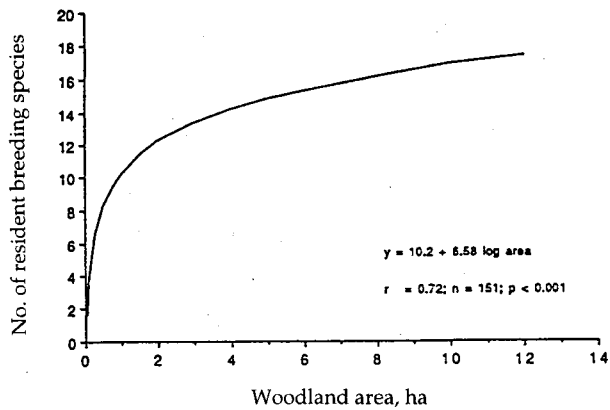


Figure 1. Relationship between the number of resident breeding species and woodland area for 1992.

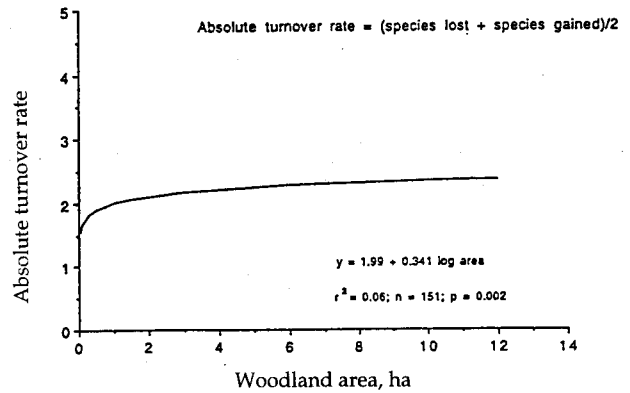


Figure 3. Relationship between absolute turnover and woodland area.

area of woodland, number of habitats and densities of shrub and canopy layers. Numbers of edge species increased with increasing length of perimeter, number of habitats and greater isolation from other woodland. We also found that more species were present in small woods than in equivalent sized areas of large woods; the difference being due to higher numbers of edge species in small woods. As was predictable from the species/area relationship, relative turnover rate (turnover expressed as a proportion of number of species present) decreased with increasing woodland area (Fig. 2). In contrast, absolute turnover rate showed no meaningful relationship with area (Fig. 3) but the species affected by the

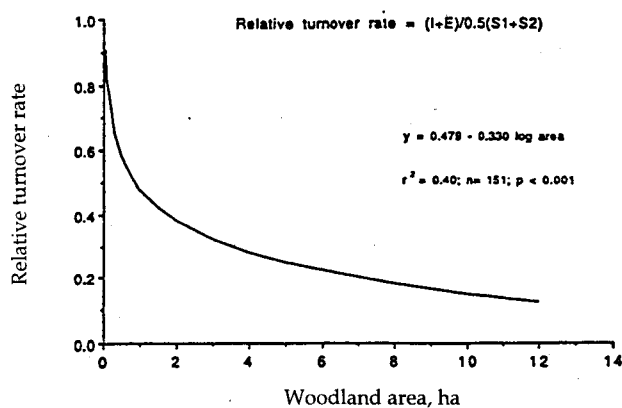


Figure 2. Relationship between relative turnover and woodland areas.

majority of the turnover changed as woodland area increased. The species with the smallest population sizes were those most likely to come and go between breeding seasons.

Between 1990 and 1991, the number of breeding adults replaced between years was very high and the large majority of replacements were immigrants. Only a very small percentage of juveniles were found breeding on their natal sites in the following season. At some sites, certain species were present in both years but all individuals concerned were new birds. Some of our ringing sites comprised groups of small woods, and sightings and recoveries of ringed birds indicated that most immigrants were coming from further away than just adjacent woodland. Although this is as yet a very limited analysis, it does stress the importance of immigration in the maintenance of the bird populations of small woods.

## Future research

Both aspects of the first three years' work are being continued in a modified form. Census work is continuing in about 50 woods to extend the data set in relation to variation in overall population sizes, e.g. to examine the consequences of one, or a run, of severe winters. Our ringing programme has changed direction, with work continuing in

only seven of the original woods. However, results obtained here will be compared with those from ten new ringing plots located within three large woods (71, 130 and 157 ha respectively). This is to investigate whether the high turnover found in small woods differs from that occurring in large, continuous habitat tracts.

We are also using a comparative approach in small and large woods to look at differences in reproductive output of some species in relation to habitat fragment size. We are providing nestboxes for blue tits *Parus caeruleus* and great tits *Parus major* to quantify breeding success in terms of laying date, clutch size, biomass at a given age and fledging success. We are also recording various parameters of nesting success or failure for certain open nesting species, e.g. blackbird *Turdus merula*, song thrush *Turdus philomelos*, and chaffinch *Fringilla coelebs*, some of which may use the landscape surrounding the woods and hence show different relationships with woodland patch area.

Our research effort began with a broad survey approach, producing statistical relationships and general patterns in space and time, between certain aspects of woodland bird communities and their habitat patches and surrounding landscapes. We have now moved to a more species specific approach, concentrating on key features of population dynamics which might be directly affected by habitat area, and contribute to an understanding of the observed patterns. The natural development of this type of study, looking at breeding bird communities of discrete patches in the landscape, is to identify the processes which determine whether a breeding population persists or not. We need to determine to what extent these processes are species specific, to what extent they are common between species (or groups of species) and how they are influenced by the landscape scale at which the problem is addressed.

In many cases, large, continuous habitat tracts offer the best chance of long-term species survival. Unfortunately, the demand for land for other uses makes provision of large undisturbed natural areas increasingly unlikely, and landscape mosaics, involving

compromises and competition between the different land-uses, are often the result. Landscape mosaics can also be approached from the opposite direction by adding semi-natural habitat patches to areas, such as continuous urban or industrial sprawl and intensive arable agriculture, in which much wildlife interest is already extinct. In particular, we are interested in how to determine the best combination of habitat patch sizes and degree of connectivity required to achieve a given aim in a specified landscape. In the case of woodland birds, to have a landscape capable of supporting viable populations of certain species, in addition to accommodating other land-uses, requires a certain mix and spatial arrangement of large and small woods. To produce the right mixture would require knowledge of 'source-sink' and 'mainland-island' relationships, especially with respect to dispersal rates, and estimation of the contribution of small populations (*sensu* a Levins-type metapopulation) to colonisation rates.

Landscape mosaics, through the presence of small patches and connecting elements, will also include a lot of 'edge' habitats. Currently, one area of bird work in landscape ecology which appears to be under represented is the study of edge species. Many studies split bird communities into species entirely dependent on the habitat patch and those which breed there but also use elements of the surrounding landscape. Such species use the landscape as a matrix of different elements, i.e. at a different scale of patchiness to that perceived by a strictly woodland bird. For example, yellowhammers *Emberiza citrinella* may nest at the edge of a wood but feed in the adjacent crop or on weeds in ditches and uncultivated patches some distance away. These species contribute to the wildlife diversity of the landscape but need different conservation measures to those applicable to the 'strict' patch inhabitants. There are well worked examples of game birds which have an economic value to land owners e.g. pheasant (*Phasianus colchicus*). This is essentially a bird of woodland edges, which in winter depends on woodland for food and shelter. In spring, males set up breeding territories along the



woodland edge and most of the first nests are found here. As the adjacent crop grows the pheasants move in to the fields to nest and rear their young, returning to woodland again when the crop has been harvested. The highest densities of pheasants are found in areas where there is 20-40% woodland cover and 60-80% crops (Robertson 1992).

There is also the possibility of an experimental approach; manipulating both patch populations as well as the habitat patches themselves. We have done a small pilot study involving the experimental removal and addition of robins (*Erithacus rubecula*) in a few small woods. We found that the amount of time and resources needed to run, and replicate, such a project was prohibitive when combined with our other work, and would be best pursued as a single project. Habitat manipulation would present similar problems plus that of the need to work over a very long time-scale (e.g. Lovejoy et al. 1984). However, both these approaches could be very valuable.

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## 2.3 Application of landscape ecological data for the evaluation of planning scenarios

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### Introduction

Land developing programmes involve spatial planning on a local scale. Originally these plans mainly focused on improving the landscape for agriculture. In recent years, however, the programmes have evolved to plans where different kinds of land-use are combined in the best possible way. Nature conservation and restoration are some of these land use functions. In agricultural landscapes many species depend on the semi natural elements. Because of the intensification of agriculture many of these species have dramatically declined or have completely disappeared. In a mainly agricultural landscape total separation of land-use functions is not possible. It is possible, however, to develop small nature restoration areas of a few hectares and corridors and to connect these natural areas in a spatial network. To evaluate these planning scenarios quantitative data of the habitat needs of the tree frog (*Hyla arborea*) were used.

The tree frog plays a central role in this evaluation for several reasons:

- It is a red-list species threatened with extinction with high priority in policy making
- It was a common species in the planning area in the recent past
- For amphibians as a species group the spatial configuration of land and water habitat is relatively important because of their seasonal migrations.

In the planning area, Sealand Flanders, the present distribution of the tree frog is highly

fragmented and the population is totally isolated from other populations. The land-use is solely agricultural: extended fields with a variety of crops in which wooded dikes, coastal dunes and meadows with drinking ponds form the natural elements of the landscape. The habitat of the tree frog in this landscape consists of cattle drinking-ponds as reproduction sites and its land habitat consists of natural elements such as shrubs, bushes, especially blackberries, and fringes of high herbs and grassy vegetation.

The aim of this study was to answer the following question: First, does habitat fragmentation play a role in the explanation of the decline of the tree frog? In other words, is there a difference in the spatial configuration of the landscape surrounding occupied and empty ponds?

In a fragmented landscape local populations exist, separated from each other by unsuitable habitat. Extinctions of these local populations are regular events. When habitat patches - or ponds in this particular case - in which the tree frog has become extinct can be recolonised by dispersing animals from surrounding ponds the network of a metapopulation as a whole can persist. The loss of habitat affects this spatial structure of a metapopulation; habitat patches will become smaller and isolation of local populations will increase. When too much habitat disappears the spatial structure will break down and the species will eventually disappear from the area.

Secondly, are there indications that the tree frog occurs as a metapopulation? And does loss of habitat because of agricultural demands explain the recent tree frog decline?

## Methods

To answer these questions, a six-year-data set of presence and absence data of the tree frog was analysed. In 50 out of 500 ponds, tree frogs were found during this period. To get a first impression of whether isolation plays a role in the explanation of this distribution pattern, the distance to the nearest occupied pond was calculated for occupied and unoccupied ponds.

## Results

Only a few ponds were occupied during the whole period. Many ponds remained empty and extinctions (23) and recolonisations (35) were regular events. It turned out, that occupied ponds are indeed closer to other occupied ponds: nearly all occupied ponds have another occupied pond within a radius of 500 m. The many ponds that remain empty, the frequent extinctions and recolonisations and the fact that occupied ponds are near to other occupied ponds, all indicate that the tree frog indeed functions as a meta-population and that the configuration of habitat explains the present distribution of the tree frog.

Because ponds form only part of the habitat, all potential land and water habitat in the study area were surveyed and were put into a geographic information system (Arc/Info). Isolation parameters were calculated with Arc/Info in circles ranging from 100 up to 2,000 m around each potential water habitat.

With logistic regression analysis, habitat quality and isolation parameters of occupied and empty ponds were compared. In this type of regression, the model predicts the chance of a pond being occupied given the values of the response parameters.

In the first steps of the regression analysis (Table 1), only habitat quality factors were tested. A low water conductivity and a high coverage of water plant vegetation explained the presence of tree frogs. In the next steps it was tested if isolation parameters could be added to the model. It turned out that the landscape surrounding an occupied pond differs significantly from that surrounding an empty pond in regard to three isolation parameters. The pond density is higher in the surroundings of an occupied pond. Also the two components of the terrestrial habitat of the tree frog differ significantly around occupied ponds. Both high perennial herbs and grasses like shrubs and bushes are more frequent around occupied ponds. Using the statistical model for each pond, the occupation chance can be predicted based on the amount of land and water habitat in the surroundings.

## Evaluation of planning scenarios

Knowledge of habitat configuration of the tree frog can be used on a landscape level to evaluate different land developing programmes. For this purpose a translation step was made from the occupation chance of individual ponds to the occupation chance per grid cell of 500 x 500 m. The advantage of

Table 1. Regression model (level of significance: \*\* P = 0,01; \*\*\* P = 0,001).

Stepwise Logistic Regression		Deviance
Habitat quality parameters	Vegetation cover pond	***
	Water conductivity pond	**
Isolation parameters	Number of ponds 0-750 m	***
	Area high herbs/grasses 0-1,000 m	***
	Area shrubs/bushes 0-1,000 m	***

this method is that the problem of overlapping circles does not exist.

One of the scenarios of the Land Developing Agency was digitised and the parameters of the new situation were calculated with Arc/Info.

In the scenario, a few nature restoration areas and corridors for tree frogs are planned. In nature restoration areas, meadows or arable land will be transformed into fields of high grasses and herbs and spontaneous growth of shrubs such as blackberry. Also new ponds and marshes are designed. Corridors are linear landscape elements such as dykes or meadows along creeks where ponds, shrubs and high herb vegetation will be developed.

To evaluate the effect of the scenario it was compared with the present situation. For both the present situation (Fig. 1, left side) as well as for the scenario (Fig. 1, right side) the occupation chances for each grid cell were calculated, based on the isolation parameters. To interpret these pictures, it is of course important to take the present distribution of the tree frog into account. Improvements of the landscape must be preferably in the immediate surroundings of occupied ponds (Fig. 1, the black stars) so that the present populations have a chance to increase and become a source of dispersing

animals. Secondly the network has to be improved by connecting the local populations by corridors. When this scenario is evaluated by these criteria it is not yet optimal. For instance the situation is not improved for all tree frog locations and not all tree frog areas are connected.

## Discussion

Isolation does play a role in explaining the present distribution of the tree frog in Seal and Flanders. The landscape surrounding occupied ponds is relatively rich in both land and water habitat. By the described method different landscape planning scenarios can be compared at their potential benefit for the tree frog. Also, guidelines can be given on which locations habitat increase will probably be most effective. Therefore, it is possible to give a quantitative indication of the area demands which will be needed to preserve natural values in combination with other land use types.

Several questions remain unanswered. For instance, statistical models give no answer to what number of (occupied) ponds is needed to have a reasonable chance of a persistent metapopulation. How large does the net-

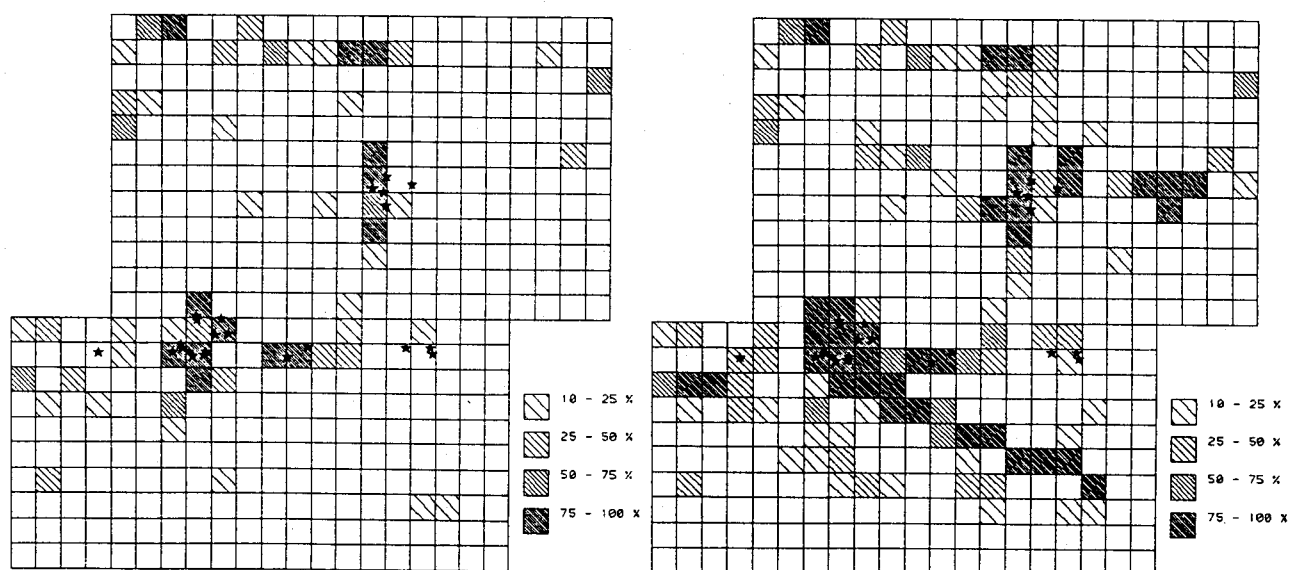


Figure 1. Occupation chance of the planning area per grid cell of 500 x 500 meter of the present situation (left) and of the scenario (right) (\* = occupied ponds; see legend for occupation chances).

work have to be, for the recolonisations to compensate for the extinctions? To get more insight into this question, a simulation model is needed.

The results give no insight into the optimal configuration of habitats. Will connectivity between populations be optimal if ponds are actually connected by corridors of terrestrial habitat? Or will dispersal be more successful by stepping stones of terrestrial habitat, which function as regular shelter areas in the agricultural landscape. To answer these questions, more has to be learned about the actual movements of animals in non-habitat.

Finally, there is a limitation in this kind of studies, that only one species at a time can be taken into account. It would be nice, however, to have information about the natural system as a whole. Of course, it is not possible to repeat this study for all species separately, but a selection of key species could be a solution; for instance is this study also being carried out for marshland birds.

## 2.4 A study of population dynamics and habitat choice in a (meta)population of tree frogs (*Hyla arborea*) in Denmark

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### Introduction

The European tree frog (*Hyla arborea*) in Denmark is - as many other amphibians all over the world - an endangered species. Earlier, it was far more common in Denmark than today. At present, one re-introduced and six natural populations persist in the south and eastern parts of the country, making up a total of approximately 3,600 calling males in about 300 ponds.

The aim of this research is to gain a better understanding of demographic and environmental factors that are important for persistence and expansion of the population of tree frogs on the island of Lolland in Denmark. In 1991, a project was set up in order to improve conditions for the tree frogs. This project includes dredging of ponds to improve the water quality, cutting down trees and bushes around the ponds to ensure a higher degree of exposure to the sun, and digging of new ponds to connect breeding localities and thus improve the stability of the population by creating a meta-population.

### Methods

The study area covered approximately 600 km<sup>2</sup> on the island of Lolland, situated in the southeastern part of Denmark. A total number of 215 ponds were surveyed encompassing all present, former, and potential populations of tree frogs known in the area. The area was an intensively cultivated farmland, and most of the ponds were relatively deep marl pits.

Demographic data (numbers of calling males and breeding success) from former surveys in 1981, 1982 and 1991 were supplemented by this survey in 1992. Data on environmental parameters were collected in 1992 and included among others: area of the ponds, degree of exposure to sun and wind, amount of vegetation cover around the ponds for the frogs to sit in while not in the water, and water quality as estimated by a new water quality-scale with 8 levels based mainly on presence and amount of certain aquatic plants (*Ranunculus aquatilis*, *Lemna* spp. and *Chara* spp.). Data on all demographic and environmental variables were not available for each of the 215 ponds.

Finally, the spatial distribution of the population was viewed in a metapopulation context based on analyses of population dynamics and computer simulations. The computer package, Metapop2, (Ray & Sjögren, 1992) is designed for modelling turnover events in a metapopulation living in a heterogeneous environment. It simulates the heterogeneous environment, whereas within-patch dynamics is not included in the model. To simulate within-patch dynamics a new model was sketched. This model is constructed for simulation of population dynamics within a meta-population (*sensu lato*) of amphibians. It follows the fate of five age-groups, and turnover is based on within-patch dynamics (as determined by mortality and fertility rates) as well as migration between patches. Thus, colonisation probability of a patch is a sum function of all potential colonisations within the area in question. The probability of a patch being a donor-patch in colonisation is a function partly of migration rates of newly metamorphosed and juvenile frogs,

assuming that only these two age-groups migrate, and partly of the distance between patches. Extinction probabilities of a patch is an inverse function of the number of calling males in a given time step. The model is planned to be implemented into a computer program in the winter of 93/94.

## Results

Statistical analyses showed that the water quality was highly important for the number of adult frogs as well as for the number of larvae. Besides, there was a significant positive correlation between the number of calling males in a pond and the amount of vegetation cover around it, and between the number of calling males and the area of a pond. This is much in accordance with the results of other European investigations, except for the apparently significant effect of area.

The population showed a drastic decline from 1981 to 1991 (from 558 to 258 calling males), whereas it stabilised in numbers from 1991 to 1992 with 323 calling males recorded in 1992. The reason for the decline was most probably low breeding success caused by poor water quality due to eutrophication from agricultural fertilising followed by stochastic extinctions of subpopulations. High mortality rate in the terrestrial habitat might also play a role.

The population was separated into four areas that most probably were isolated from each other, since they were separated by at least 5 km.

Analyses of the spatial and demographic data revealed the population to be organised in a traditional source-sink structure.

## Discussion

The pond restoring project had one short-term positive effect on the population: the breeding success was greater in dredged ponds than in undredged ones. This was most probably due to improvement of water quality, but dredging might also have dimin-

ished the amount of parasites and predators. This, however, was not assessed in this work.

Dredged ponds and newly dug ponds did not have significantly more calling males than the rest, and in fact only one out of eight new ponds was colonised in 1992. This does not, though, indicate that the project of restoring ponds is unsuccessful. The increased population of larvae needs two years to mature, which means that they will only manifest themselves as adults from 1993 and onwards. Since the colonising stage of the tree frog seems to be the juvenile one, 1993 is also the year when colonisations of new ponds can occur from source ponds. A classic metapopulation structure is less likely, since extinctions of subpopulations were not balanced by be expected to be revealed by the calling activity of the 1991 brood.

It will be of great importance to continue the survey in the coming years to check which colonisations actually take place. Moreover, it is necessary to continue to dredge ponds in order to raise the number of larvae (and thereby the colonisation potential). If this is combined with digging of new ponds, the distribution area of the tree frog can probably expand to cover the whole study area making up a classical 'metapopulation, which will then be stable and have a high probability of survival. If not, the mortality rate in the terrestrial habitat must also be lowered, for example by extensifying the agricultural use in the near surroundings of the breeding ponds.

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## 2.5 The Green Hairstreak in a fragmented landscape

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### Introduction

This study investigates whether fragmentation of habitat poses a problem for the persistence of populations of the butterfly Green Hairstreak (*Callophrys rubi*) in the Netherlands. Basis for this study is the metapopulation theory with colonisation and extinction as the two important processes (Levins 1970). These processes can lead to a turnover of local populations.

### Methods

To assess the effect of fragmentation on the Green Hairstreak in a fragmented heathland, the following research questions are posed:

- Does patch size affect the distribution of the Green Hairstreak?
- Does patch isolation affect the distribution of the Green Hairstreak?
- Do local populations show a turnover?

### Results

Distribution pattern analysis was conducted in 57 and 55 heathland patches situated in the north of the Netherlands in 1991 and 1992, respectively. Presence or absence was determined during two visits. The Green Hairstreak was found as often in small patches as in large patches. In a multiple logit-regression model, constructed with habitat quality variables, patch size did not significantly add to the explanation of the distribution pattern in either year (Fig. 1). In

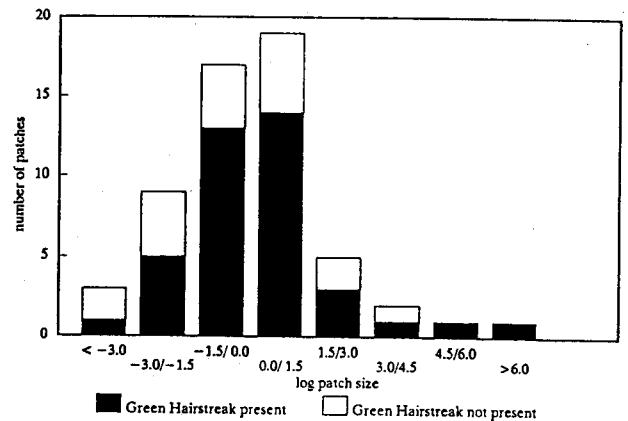


Figure 1. The size of habitat patches and the presence of the Green Hairstreak in 1991. Patch size was transformed by taking the logarithm.

a multiple logit-regression model, constructed with nine habitat quality variables, all patch isolation variables except distance to the largest patch added significantly to the explanation of the distribution pattern in 1991. In 1992, none of the patch isolation variables contributed significantly to the explanation of the pattern. In 22% of the patches extinction or colonisation was found (Fig. 2).

### Conclusion

- The distribution of the Green Hairstreak is not affected by patch size.
- The distribution of the Green Hairstreak is affected by the spatial configuration of habitat patches.

A turnover of local populations supports the view that the fragmented heathland functions as a network of patches for the Green Hairstreak. The largest patch did not seem to play any special role in the network as a source of colonists.



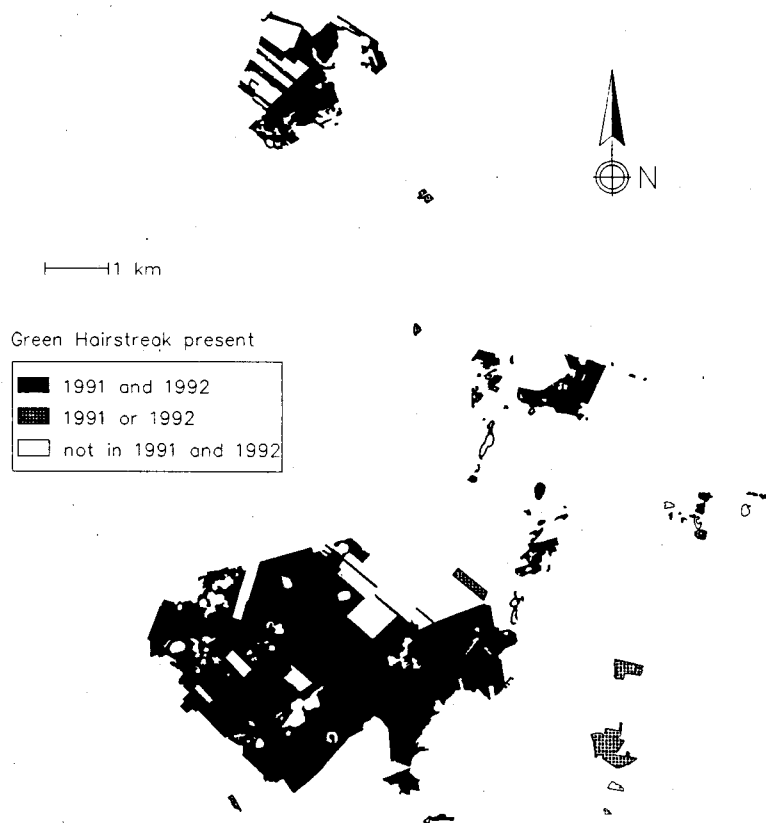


Figure 2. The presence of the Green Hairstreak in 1991 and 1992 in the habitat patches, situated in the north of the Netherlands.

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## 2.6 Spatial distribution patterns of *Laemostenus terricola* (Carabidae) in an agricultural landscape; correlations with habitat and landscape features

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### Introduction

There are several reasons to study *Laemostenus terricola* (HERBST) in a landscape ecological context.

- this carabid species only occurs in uncultivated habitats in the agricultural landscape.
- *L. terricola* does not possess high powers of dispersal; it is not able to fly and doesn't walk long distances outside its preferred habitat (Gruttke, in press). Thus it needs adequate corridor habitats for dispersal.
- *L. terricola* belongs to an ecological guild which is mostly neglected: the cavernicolous fauna of animal burrows.
- Numbers of *L. terricola* are decreasing in many countries (Desender & Turin 1989) and it is considered to be endangered (Blab et al. 1984, Barndt et al. 1991).

In a previous study (Gruttke, in press), it has been shown that the occurrence of *L. terricola* at a local habitat scale is closely correlated with the distribution of rabbit burrows.

The importance of the factors 'soil type' and 'cover of trees/bushes' could not be checked completely. Both were correlated with catch numbers of the beetle and numbers of rabbit burrows as well. Special questions of the present study are:

- which habitat and landscape features correlate best with the occurrence of a *L. terricola* at landscape level?
- does *L. terricola* also colonise newly created habitats inhabited by rabbits?

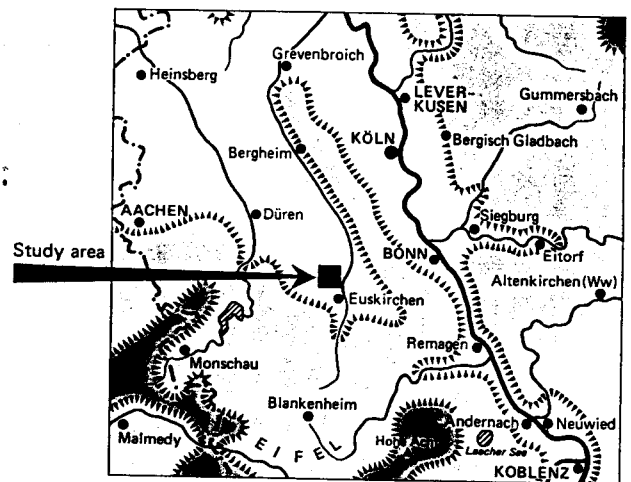


Figure 1. Geographical location of the study area in the so-called 'Zülpicher Börde'.

- are historical landscape patterns important for interpreting today's distribution of this species?
- could *L. terricola* be a model or keystone species for assessing habitat connectivity and functioning of new corridors in agricultural landscapes?

### Methods

The study area is an intensely cultivated countryside (Zülpicher Börde) about 30 km west of Bonn, Germany (Fig. 1). Within this area, a number of 18 semi-natural/ uncultivated habitats with rabbit burrows was selected for detailed investigation (Table 1):

- 5 old forest fragments > 2 hectares

Table 1. Habitats studied and catch numbers (per 5 traps) of *Laemostenus terricola* 1992 (\* = data from 1990, age classes: y = young < 20 years old, o = old, > 20 years of age.)

Site	Habitat type	Age class	Numbers of <i>Laemostenus terricola</i>
Aa	Wooded bank (road)	y	-
Ab	Wooded bank (road)	y	-
Fu	Wooded bank (road)	y	-
Ra	Wooded bank	o	7
Rb	Wooded bank (road)	o	92
Rc	Wooded bank	o	96
Rd	Wooded bank (road)	o	-
Re	Wooded bank (river)	o	-
Nb	Wooded bank	o	1
Ah*	Wooded bank	o	775*
Gi	Woodlot/shrubs	o	26
Ki	Woodlot/shrubs	o	32
W*	Woodlot	o	17*
Bb	Forest fragment	o	4
Wa	Forest fragment	o	-
Wb	Forest fragment	o	-
Wc	Forest	o	-
Wd	Forest fragment	o	-

- 10 old small woods and wooded banks (amount of woods varying)
- 3 young wooded banks (road embankments, less than 20 years old).

The distribution of *L. terricola* was investigated by setting pitfall traps (five per site, upper diameter 4.5 cm, filled with ethylene glycol) during 16 weeks between mid-May and mid-October 1992. Two sites (Ah, W) were sampled at comparable periods in 1990. In addition, locations of rabbit burrows, vegetation cover and soil parameters were registered in the field. Analysis of aerial photographs (scale: 1: 5,000) and of modern (1989) as well as

historical (1893) maps (scale: 1: 25,000) were used to quantify spatial land-scape features (Table 2). Statistics used: Spearman rank-correlation and Mann-Whitney two-sample U-test.

## Results

### Changes in landscape structure

The comparison of historical and actual landscape structures reveals the major changes during the last 100-150 years: size-reduction and fragmentation of forests, enlargement of human settlements, construction of new roads and a new motorway (15 years old), some mostly minor changes in amount and location of old embankments, but many new banks along the motorway.

### Spatial distribution of *L. terricola*

Within the investigation programme 1,050 specimens of *L. terricola* were captured at 9 different sites (Table 1). None of the three young road banks studied (Aa, Ab, Fu) was colonised by the species. Catch numbers from sites on sandy soils were significantly higher than those from sites on loamy soils (U-test:  $P < 0.005$ ). For the parameter 'average number of rabbit burrows' no significant difference between the two soil types could be established (U-test:  $P = 0.93$ ).

Among all habitat and landscape parameters considered, 'length of sandy parts within complexes of embankments in 1893' (BCS18) is correlating best with catch numbers of *L. terricola* (Table 2A). Size and connectedness of sandy banks 100 years ago - last mentioned parameter is roughly assessable as difference between BS18 and BCS18 - is more important for explaining today's spatial distribution of *L. terricola* than the respective actual values (BS19 and BCS19).

This is confirmed by the high partial correlation between numbers of *L. terricola* and BCS18 controlled for the influence of BCS19 (Table 2B). The habitat parameters 'cover of tree-layer', 'cover of herb-layer' and 'number of rabbit holes' are of no detectable significance for *L. terricola* at landscape level (Table 2).

Table 2. Spearman rank-correlation matrix of catch numbers of *Laemosternus terricola* and habitat as well as spatial landscape parameters (A), and partial rank-correlations (B) of catch numbers controlled for the influences of BCS18 and BCS19 (n = 18, significance levels: P = 0.01: 0.5480; P = 0.005: 0.5975; P = 0.001: 0.6904).

Abbreviations:		BCS18:		BCS19:		BCS18		BCS19		BCS18		BCS19	
Laem:	Catch numbers of <i>Laemosternus terricola</i>	Length of complexes of connected embankments (max. gap 50 m) in 1893		Length of sandy parts within complexes of embankments 1893		As B18-BCS18, but for 1989		Overall size of wooded area (complex) at the study sites, (max. gap to closer study sites 50 m)		Area of old woods at the study sites			
CoTr:	Cover of tree-layer	B19, BS19, BC19, BCS19:		WAr:		WCAr:							
CoHe:	Cover of herb-layer	Average number of rabbit holes within a radius of 3 m around the traps		Length of embankments of 1893		Length of embankments on sandy soils in 1893							
RabU:													
B18:													
BS18:													

A) Rank-correlations matrix														
	Laem	CoTr	CoHe	RabU	B18	BS18	BC18	BCS18	B19	BS19	BC19	BCS19	WAr	WCAr
CoTr	-0.003	-0.493	-0.246	0.302	0.623	0.831	0.943	0.269	0.293	0.321	0.346	-0.353	0.878	0.510
CoHe	0.073	-0.375	0.191	0.302	0.623	0.831	0.943	0.269	0.293	0.321	0.346	-0.353	0.878	0.510
RabU	0.180	-0.316	0.191	0.302	0.623	0.831	0.943	0.269	0.293	0.321	0.346	-0.353	0.878	0.510
B18	0.687	-0.046	-0.002	0.161	0.623	0.831	0.943	0.269	0.293	0.321	0.346	-0.353	0.878	0.510
BS18	0.894	-0.046	-0.002	0.161	0.623	0.831	0.943	0.269	0.293	0.321	0.346	-0.353	0.878	0.510
BC18	0.869	-0.151	0.131	0.200	0.876	0.894	0.943	0.269	0.293	0.321	0.346	-0.353	0.878	0.510
BCS18	0.935	-0.070	0.049	0.175	0.726	0.894	0.943	0.269	0.293	0.321	0.346	-0.353	0.878	0.510
B19	0.177	-0.011	-0.149	0.102	0.501	0.185	0.390	0.772	0.970	0.973	0.346	-0.379	0.878	0.510
BS19	0.726	-0.223	0.060	0.208	0.498	0.848	0.772	0.772	0.970	0.973	0.346	-0.379	0.878	0.510
BC19	0.211	0.110	-0.189	0.006	0.484	0.232	0.443	0.320	0.970	0.973	0.346	-0.379	0.878	0.510
BCS19	0.742	-0.116	0.034	0.120	0.490	0.842	0.766	0.814	0.268	0.973	0.346	-0.379	0.878	0.510
WAr	-0.319	0.141	0.140	-0.441	-0.425	-0.318	-0.372	-0.371	-0.397	-0.361	-0.379	-0.353	0.878	0.510
WCAr	-0.308	0.205	-0.094	-0.307	-0.464	-0.358	-0.383	-0.330	-0.173	-0.318	-0.159	-0.302	0.878	0.510
WoAr	-0.032	0.026	0.017	-0.034	-0.103	-0.185	-0.088	-0.092	-0.590	-0.229	-0.546	-0.166	0.527	0.510

B) Partial rank-correlations														
	Controlled for: BCS18			Controlled for: BCS19			Controlled for: BCS18			Controlled for: BCS19				
	Laem	CoTr	CoHe	Laem	CoTr	CoHe	Laem	CoTr	CoHe	Laem	CoTr	CoHe	Laem	CoTr
CoTr	0.175	0.124	0.124	0.175	0.124	0.124	0.175	0.124	0.124	0.175	0.124	0.124	0.175	0.124
CoHe	0.077	0.072	0.072	0.077	0.072	0.072	0.077	0.072	0.072	0.077	0.072	0.072	0.077	0.072
RabU	0.048	0.137	0.137	0.048	0.137	0.137	0.048	0.137	0.137	0.048	0.137	0.137	0.048	0.137
B18	0.033	0.553	0.553	0.033	0.553	0.553	0.033	0.553	0.553	0.033	0.553	0.553	0.033	0.553
BS18	0.366	0.745	0.745	0.366	0.745	0.745	0.366	0.745	0.745	0.366	0.745	0.745	0.366	0.745
BC18	-0.107	0.697	0.697	-0.107	0.697	0.697	-0.107	0.697	0.697	-0.107	0.697	0.697	-0.107	0.697
BCS18	0.000	0.880	0.880	0.000	0.880	0.880	0.000	0.880	0.880	0.000	0.880	0.880	0.000	0.880

## Discussion and Conclusions

The results presented have shown that old uncultivated/seminatural sandy banks are the preferred habitat of *Laemostenus terricola* in the agricultural landscape studied. But also a few habitats on loamy soils are inhabited by this species. Turin et al. (1991) classifies *L. terricola* as a species of sandy arable land and conifer plantations, which is confirmed in this study of *L. terricola* as reported by Lindroth (1945) or Klausnitzer (1987) were not subject of the present study.

In a previous investigation (Gruttke, in press), it was shown that number and vicinity of rabbit burrows best explains the spatial distribution of *L. terricola* at habitat scale. At landscape scale, the situation is different. Although the existence of rabbit burrows or other adequate hollows is an essential precondition for the occurrence of *L. terricola*, it is not sufficient. Historically connected old sandy embankments are of paramount importance for the distribution pattern of the species at landscape level. From this finding, two conclusions may be drawn. Firstly, today's *L. terricola* populations are only remnants of one or a few large historical populations. Secondly, *L. terricola* is a poor disperser and seems to require specific corridor conditions for spreading, otherwise its actual distribution range must have been larger. The young (15 years old) road banks studied were not colonised by *L. terricola* probably because they were too isolated from populations on old embankments. Thus, it may be concluded that *L. terricola* is well qualified as model or keystone species to assess the effectivity of new corridors for epigeic arthropods with low dispersal power.

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## 2.7 Pollination ecology and endangered plant species

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### Introduction

In the Westeuropean flora, about 80 % of the species are insect pollinated. The other 20 % are mainly pollinated by wind, and only a small fraction by water. Bees, flies, butterflies, beetles, and thrips are the main groups of flower visitors (Proctor & Yeo 1973), and bees are considered most important (Corbet et al. 1991). Both plants and insects generally benefit from flower visits. Flowers become pollinated and for insects the collection of food, e.g. pollen and nectar, is the most important reason to visit flowers. If the number of flowers is low, then the number of insects is likely to be affected. Monolectic (and oligolectic) insect species, which are unable to switch to other food plant species, are especially sensitive to the numbers of flowers of particular plant species. These insects will disappear when their favoured food plants are no longer available. The reverse, the disappearance of plant species visited by monolectic insects, is less probable when other insect visitors are also present. If numbers of insects are low, the pollination of flowers are likely to be affected. Generally a plant species is pollinated by several taxa of insects, which may or may not belong to the same genus. A one to one relationship (in which a plant species is pollinated by only a single pollinator species) is rare.

In a pollination relationship, the plant depends on insect visitation not only quantitatively for seed set but also for the exchange of genes. Moreover, other organisms such as fruit and seed eating insects, birds and small mammals depend on the foraging activities of flower visiting insects.

Currently, plant populations are declining in numbers, sizes and densities due to a

variety of causes, often the result of human activities. Small populations are also more sensitive to edge effects. In an agricultural landscape, the number and size of natural habitats is reduced leaving isolated patches of habitats in a 'desert' with few or no food plants for flower visiting insects except for a few cases of insect pollinated crops. Each of the remnant natural habitats can sustain only a small plant population. If this is too small to support resident pollinators completely, other food sources are needed. Other flowering species, providing nectar and pollen, may become important not only as food sources but also to enhance the chance of a small population being discovered by insects. If the total floral rewards of a single habitat fragment are inadequate for flower visiting insects, corridors may promote foraging flights between habitat fragments, thus augmenting the food sources for insects.

Visitation rate is sensitive not only to flower population size but also to flower density within populations, as expected from the perspective of the foraging strategies of various visitors. Changes in visitation rate, pollination and seed set, and the resulting increase in inbreeding (with increased levels of homozygosity which may cause inbreeding depression) may influence the future fate of plant species in small remnants.

Population genetic theory predicts that, as a consequence of genetic drift and inbreeding, small populations will have decreased levels of genetic variation. Even favourable alleles may be lost, diminishing the potential to adapt to a changing environment. This genetic erosion may lead to the reduced fitness of individuals in a population and will ultimately increase the chance of extinction of populations and of species. However, the

deleterious effects of genetic erosion in populations, can be counteracted by gene flow. Pollen flow, in particular, contributes to renewal of the genetic variation.

The hypothesis that corridors may be important for exchange between animal populations and for the recolonisation process is generally accepted although evidence is scarce (Hobbs 1992, Opdam et al. 1993). In the case of pollination the movements of insects will also have an impact on the gene flow and seed set of plants. If patches are within the radius of activity of pollinators, the possibility exists that some individuals will specialise on the particular plant species. The presence of flowering plants of the same or other species between patches may serve as a bridge or corridor for insects; pollinators may visit these intermediate plants on their way from one patch to another.

Three hypotheses may be possible concerning the amount of pollen exchange between two patches connected via a corridor:

- Although the patches may be within the radius of activity of the pollinators, each patch has its own pollinator guild and pollen exchange is zero
- Pollen exchange occurs if visitors cross the distance between two patches without visiting the intermediate plants of the same or other species, so no loss of pollen occurs

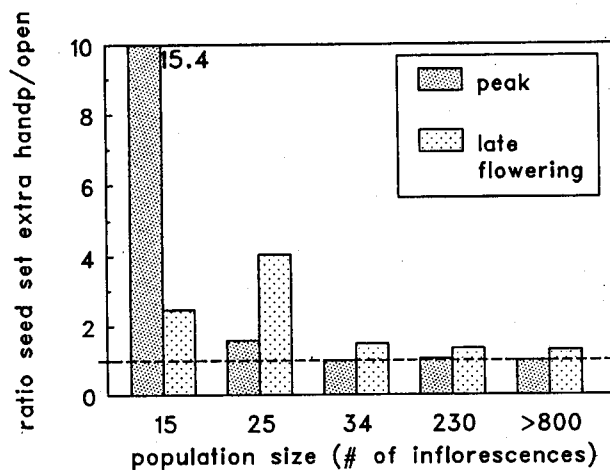


Figure 1. The ratio of seed set of flowers receiving supplementary handpollination to seed set in open visited flowers of *Phyteuma nigrum* in 1993 during peak and late flowering of the populations. Populations are arranged according to total inflorescence production. Dotted line on the ratio 1 level indicates that there is no difference between the seed sets.

- Pollen exchange occurs but the exchange between patches is dependent on the amount of switching of insects between the patches and the loss rate of pollen in the corridor.

In our project, on the minimal requirements for survival of locally rare species, pollination ecology is included. To ensure the survival and long term persistence of populations of outbreeding species there must be

Table 1. Five plant species and some characteristics related to pollination ecology; visitors in bold are considered to be the most important pollinators.

Species	Flower season (month)	Visitors	Remarks
<i>Primula vulgaris</i> ( <i>Primulaceae</i> )	3-5	bees, flies, butterflies	pollen dimorphy very attractive
<i>Phyteuma nigrum</i> ( <i>Campanulaceae</i> )	5(6)	<b>bumblebees</b> , flies, (butterflies)	one pollinator group
<i>Salvia pratensis</i> ( <i>Labiatae</i> )	6	<b>bumblebees</b>	large pollen grains, various insect groups
<i>Scabiosa columbaria</i> ( <i>Dipsacaceae</i> )	7-8	flies, <b>bumblebees</b> , butterflies	large pollen grains, various insect groups
<i>Succisa pratensis</i> ( <i>Dipsacaceae</i> )	8-10	flies, <b>bumblebees</b> , butterflies	large pollen grains, various insect groups

a certain amount of recruitment of seedlings, which must reach the reproductive stage. There are few data available on the effects of fragmentation on attraction, visitation, pollen flow, and seed set of plant populations (Jennersten 1988, Jennersten et al. 1992). Population size is one of the variables that influences these processes. For instance, in small populations of *Phyteuma nigrum* seed set is low but can be increased if hand pollination is applied to open visited flowers (Fig. 1).

A problem in studies on small populations is that sample sizes are often too small for statistical analysis. Every interference or experimental study in a small population has a greater impact than it would have on a large population.

## Methods

We have studied several aspects of the pollination ecology of five species, which nearly all are on the red list of the Dutch flora. The species are outbreeding and visited by a variety of insects. Some are visited mainly by a single group, others by several insect groups (Table 1). The latter allow comparisons in the behaviour of insect groups, e.g. the response to population size and population density and the use of corridors. Data were collected in natural and experimental situations. In addition computer simulations were made, based on field data. *Phyteuma nigrum* was most intensively studied during 1989-1993. *Primula vulgaris* offers the opportunity to use pollen dimorphism as a natural marker to measure pollen flow, although the visitation rate is very low and the flower life time is long. Both *Scabiosa columbaria* and *Succisa pratensis* have very large pollen grains which are easy to count in the field, offering research opportunities without flower destruction.

The impacts of population size and density on insect attraction and visitation and resulting seed set were studied in both natural and experimental situations. The effects of the distance between patches and the importance of flowers in between were studied both in the field and in experimental situations.

## Results and discussion

If patch size (total number of flowers in the patch) increases, the number of insect visits does not increase at the same rate. The result is a higher visitation rate per flower in small than in large patches. The same applies for flower patch density (number of flowers per area in a patch); small patches or low densities often receive numerous visits but the resulting seed set is not always higher than that in large patches or high densities. This may be due to the quality of the pollination: the frequency of heterospecific pollen deposition may be high and/or the frequency of conspecific pollen deposition may be low. For outbreeding species the amount of nonrelated conspecific pollen is important. An extra hand pollination applied to flowers in small populations often increases seed set (*Phyteuma nigrum*, 1993). A population may contain few flowers due to the small population size or due to the fact that it is at the start or at the end of its flowering period. A low density of flowers results in short foraging bouts on one plant species, increasing the possibility of heterospecific pollen deposition.

Pollen flow has been measured, using various methods in several species. Each method has its own advantages, none being completely ideal.

Corridors have an important effect on the exchange of pollen between patches. The quality (in terms of plant species present) and the length of the corridor are important for the exchange rate and the amount of pollen lost in the corridor. Various insect groups may respond differently to the presence of a corridor. Even if flowers in a corridor are not visited, they may have a function for the orientation and guidance of insects during their foraging trips.

## Research perspectives

Small populations of two species (*Scabiosa columbaria* and *Salvia pratensis*) show a reduced level of genetic variation. Future research will concern the effects of population geometry (size, density, shape, sepa-



ration of patches) on insect attraction, visitation rate, pollination, and seed set in relation to realised genetic variation. The ultimate aim is to integrate the data on genetic variation, genetic structure and fitness with the data on gene flow mediated by insects. Insights will be obtained into the role of plant-pollinator interactions for the persistence of both the insect and the plant species.

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## 2.8 Woodland species diversity in relation to forest fragmentation, reclamation and re-afforestation

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### Introduction

This paper presents some results from a ten-year interdisciplinary, historical and ecological study of woodlands, where 'woodlands' includes heathland areas and other 'open' landscapes connected to woodlands. Our research focused on two spatial levels:

- A landscape study of some 650 sites in a historically more or less homogeneous area in the former county of Flanders and some neighbouring areas in Brabant and Henegouwen.
- A case study of one woodland in particular, situated in the centre of the study area, the forest of Ename.

The main themes were: to elucidate the evolution of woodland area from the Ice Age onwards in relation to demographic, social, and economical activities; to evaluate the usage of woodlands for wood extraction, grazing, hunting, other natural resources, by forest people, and other activities; and to evaluate what we can learn about woodland vegetation from archives, herbaria, and publications and how the present day flora is connected to the past in terms of management, land use, landscape structure, etc.

### Results from the study of the forest of Ename

I will try to link some plant distribution patterns to temporal and spatial changes in past landscape structures, and discuss some of the problems associated with this kind of

historical ecological comparative research. It is a popular belief that forest area decreased more or less continuously from the neolithic time onwards. However, this was not the case: the forest area around 1300 was about 8%; around 1760 about 15%, and at present less than ca. 6% of the region. It is suggested that fluctuations are the results of demographic and economic developments during the period. In Roman times, total forest cover was already highly fragmented. The forest was coppiced and probably relatively open and used for grazing. From the 8th Century onwards, reclamation was continued and the forest area was divided into larger complexes more or less connected by smaller woodlands and linear elements. Abbeys played a considerable role in the fragmentation process. The forest of Ename was mentioned for the first time in the 9th century, but it has only been possible to re-construct detailed land use from about 1200 onwards (after it was bought by an abbey in 1063). Between 1200 and 1775, particularly the central part of the forest was highly degraded by grazing, cutting and other agricultural uses.

However, the largest reclamation first started in 1851 driven by demography coupled with famine (potato disease). Soil texture analyses have shown that the length of the reclamation period was clearly linked with the silt fraction indicating that agriculture mainly depended on the natural soil fertility. This was also supported by historical data, which indicated that the use of land for agricultural purposes stopped by the end of the 19th century because of soil degradation.

This dramatic reclamation event still has its effect on the physiognomy of the Forest of Ename. A large number of small, mostly

linear landscape elements often with trees and/or scrubs survived along the arable parcels. An ecological infrastructure remained and probably influenced light and microclimate, in the sense that the woodland climate was not totally destroyed. This infrastructure acted as a refuge for woodland plants. For example, the present day distribution of hazel (*Corylus avellana*), shows the connection with the former landscape structure. If we take the slopes into account, we observe that *Corylus* colonised more quickly down-slope than upwards or horizontally. The pattern shown by bluebell (*Hyacinthoides non-scripta*) is a different one. Bluebell occurs at some parcels used for arable land for more than 25 years suggesting that survival of bluebell in arable land may have occurred.

In terms of number of woodland species there is a marked negative correlation with the length of the arable land use, and also with the length of the non-reclaimed fringes of woodland along the parcels. Thus, it seems as if the diversity of woodland species is strongly linked with the areas of woodland present in the Middle Ages, which coincides with one of the lowest points in afforestation.

## Conclusions

Apart from detailed species lists per parcel, there are about 80 other ecological factors available per parcel in the forest of Ename. As many ecological factors are dependent, this causes severe problems in terms of statistics and data treatment in general. A last but universal problem is that field conditions like those produced by atmospheric and hydrological conditions nowadays are very different from past conditions. Therefore one should be cautious about lessons for future landscape planning and nature development.

In relation to planning forest expansion it is important to: a) preserve existing old forests and woodlands; b) detect 'ancient woodland plants' in and outside forests; and c) use these two parameters in combination as a starting point for forest expansion.

However, taking into account all problems, I am convinced that historical ecological research is essential for a good understanding of woodlands and woodland devel-

opment. Dispersal is only one of the bottlenecks for ancient woodland species colonising or re-colonising new forests. Once arrived, they have to be able to germinate, grow up and reproduce or there will be no further dispersal by diaspores.

## 2.9 Conservation of hay meadow vegetation: A challenge for landscape ecologists

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### Introduction

The biodiversity characterising the traditional Nordic hay meadows depends on their history and the continuity of land-use (Ihse & Norderhaug 1994). Since creation of new meadows is difficult, conservation efforts should concentrate on saving the existing remnants.

Traditional land-use of old hay meadows is expensive and only a small selection of sites can accordingly be saved. To determine the minimum requirements for maintaining the biological diversity of hay meadows, we must consider how many areas should be maintained; how large they should be and what the optimal distances between patches are? These are questions to which the meta-population theory can be applied in plant population studies (Ouborg 1993). However, such analysis may involve certain problems since remnants of hay meadow vegetation are rare and difficult to locate and delimit.

Knowledge of genetics and demography is important for long-term management of any species, but surprisingly little is known about the biology of most wild plant species, including hay meadow species of which many are long-lived perennials (Ekstam et al. 1988). Minimum Viable Population analysis involving both demography and genetics becomes very time consuming and the meadows may be lost before we are able to decide how to manage them (Fig. 1). Accordingly, the challenge to landscape ecologists must be to identify a few key studies which can be used to make rapid, preliminary predictions of fragmentation effects for representative meadow species.

Experimental studies of mating systems may give such key knowledge by indicating

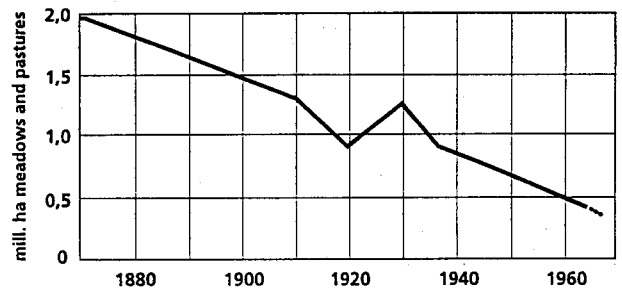


Figure 1. Changes in the area of natural grazing land and traditional hay meadows in Sweden 1870-1966, (based on data from Brinck 1974).

whether plants are autofertile or depend on insect visitors for seed-production, and accordingly if plant-pollinator interactions must be taken into account when evaluating fragmentation problems. Mating systems may also to some extent give indirect information about the genetic diversity within and among populations which is useful when preservation of the genetic diversity is planned.

### Mating systems and life strategy of three meadow plant species

The mating systems of *Dactylorhiza sambucina* (Orchidaceae), *Hypochoeris maculata* (Asteraceae) and *Polygala vulgaris* (Polygalaceae) were studied as part of a research programme on hay meadow ecology in the county of Telemark (S. Norway) during 1990-1993.

All three species turned out to be self-compatible. However, there may be subtle differences in the degree of selfcompatibility and sensitivity to inbreeding depression,

especially polyploid species may be less sensitive to inbreeding depression (Richards 1986, but see Brochmann 1993). Thus of the three species, *D. sambucina* (diploid) is likely to be most and *P. vulgaris* (tetraploid) least sensitive to inbreeding.

### Genetic diversity within and among populations and implications for survival in fragmented habitats

Reviews of plant allozyme literature state that breeding systems have significant effects on the genetic diversity within and among populations (Loveless & Hamrick 1984, Hamrick et al. 1991). Hamrick & Godt (1989) showed that within populations selfing and animal-pollinated species with mixed mating systems have similar levels of genetic diversity; while the level in wind and outcrossing animal-pollinated species is almost twice as high. Among populations, selfing species have fivefold more diversity than wind-pollinated, outcrossed species, while animal-pollinated had intermediate values.

In Telemark, *P. vulgaris* showed low variance in seed set within the population indicating low genetic variability while in *Hypochoeris maculata* with a mixed mating system, the genetic variability within populations was relatively low.

In spite of self-compatibility, fruit set was enhanced by cross-pollinations in *D. sambucina*. The inflorescence offers no reward and pollination is by deceit which has been suggested to enhance outcrossing (Nilsson 1980, Richards 1986). The species is thus predominantly outcrossed. In Telemark, *D. sambucina* showed large differences in seed set among individuals within the populations indicating a higher genetic variability within an.

### Implications for survival in fragmented habitats

*P. vulgaris* is likely to adapt in the best way to the isolation process since this species is a

good selfer and can manage without pollinators. The polyploidy and autogamy probably implies that it tolerates of inbreeding (Lande & Schemske 1985, Nordal 1989). However, loss of genetic variation due to self-pollination may make the populations more vulnerable to environmental changes and affect their short-term survival (Charlesworth & Charlesworth 1987, Ouborg 1993). On the other hand some pollinators show large phenotypic plasticity (Richards 1986) and polyploid species can maintain genetic variation in spite of high levels of inbreeding (Brochmann 1993). The results of the Telemark study, however, does not indicate high levels of genetic variation within the populations of *P. vulgaris*.

The Norwegian populations of *D. sambucina* are at the species' northwestern-most border of distribution, and it consists only of the yellow colour-variety. It is therefore possible that it has gone through bottlenecks. Populations existing at the outer range of distribution may be adapted to high degrees of inbreeding (Menges 1991). On the other hand, according to this and previous studies *D. sambucina* is probably predominantly outcrossed and diploid. It would therefore be expected to be more sensitive to inbreeding than the two other species in this study. Small, isolated populations of *D. sambucina* may thus suffer from inbreeding depression.

Pollinator species are affected differently by degree of isolation, population size, and density of their food plants. Decreased pollinator visitation resulting in lower seed production has been documented in small fragmented habitats (Jennersten et al. 1992, Fiedler 1993). A negative fragmentation effect on seed set due to one vector can perhaps be buffered by another pollinator that is less affected. *H. maculata* and *D. sambucina* depend on pollinators for seed set, but a polyphilic species like *H. maculata* may be less sensitive to changes in behaviour of one pollinator than a specialist like *D. sambucina* (Wells 1976, Nilsson 1980, Richards 1986, Norderhaug unpubl. data).

A fragmentation process may result in isolation at different distances for the three species. The autogamous and antdispersed *P. vulgaris* will probably be isolated at much shorter distances than *H. maculata* and *D.*

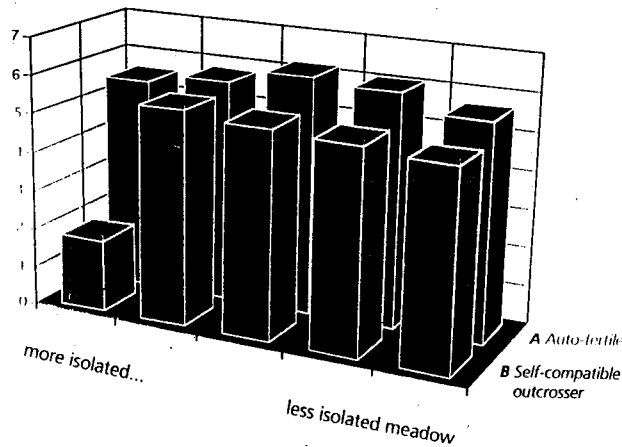


Figure 2. Empirical example: observed seed set of two meadow plant species in relatively isolated habitats are in accordance with predictions made after studies of their mating systems. A) autofertile species, no obvious effects of isolation. B) self-compatible outcrosser, the most isolated small population effected.

*sambucina* which have wind-dispersed seeds and higher outcrossing rates. *H. maculata* and *D. sambucina* populations in such areas may, however, function as metapopulations in which recolonisation can occur when (sub)populations become extinct and a restricted pollen flow between (sub)populations may be maintained. A metapopulation structure may accordingly give subpopulations possibilities of maintaining higher genetic diversity and to be more sustainable in the long term.

## Conclusion

The comparison of mating systems in *D. sambucina*, *H. maculata* and *P. vulgaris* and their implications for survival in fragmented meadow habitats indicates that *D. sambucina* will suffer the most and *P. vulgaris* the least. It is not possible to make accurate predictions about the viability of the populations on basis of mating systems alone, but it is, an initial step to a better understanding of the structure and cohesiveness of fragmented populations. Preliminary results of a seed set study in more or less isolated habitats of the three species (Norderhaug in prep.) are in accordance with the conclusions from the study of their mating systems (Fig. 2), and in combination, the knowledge may be used to

develop a practical hay meadow conservation strategy. However, knowledge of seed dispersal and seed banks is crucial for the judgment of the ability of plant populations to recover after an environmental disaster and hence their long term survival.

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## Chapter 3: Spatial modelling

### 3.1 A spatial model for forest plants

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#### Introduction

Studies on the effects of fragmentation and isolation on forest plants have been conducted in the Netherlands since 1991. Primary forest habitats have disappeared completely in the Netherlands. Earlier forest habitats have been reduced to small woodland plots and wooded banks, mainly because of intensified agricultural activities. However, some relics still contain obligate forest species such as honeysuckle (*Lonicera periclymenum*) and holly (*Ilex aquifolium*).

In more recent landdevelopment programs, new small woods and banks have been planted which potentially could be colonised by forest plant species. There are two possible causes of failing colonisation. Firstly, habitat quality is important for establishment; many small woods have been planted on former nutrient rich agricultural soils. It will take time before these soils become impoverished enough to be suitable for many forest species. Secondly, dispersal could be insufficient in fragmented and isolated landscapes. Forest species, adapted to stable habitats, are often poor dispersers. Their dispersal strategy may not be optimal in fragmented landscapes.

The Ministry of Agriculture, Nature Management and Fisheries (1990) has developed a possible solution to the fragmentation and isolation problem, i.e. the Framework Approach, which deals with the dilemma of the

conflict between agriculture and nature. In this framework, core areas are planned to support the smaller woods, and linear elements will be planted to enhance dispersal between core areas and small woods. Core areas, small woods and linear elements together form a framework. This planning means that, even though isolation is decreased, most elements of the existing structure will disappear and will be replaced by new ones! The question is now whether it is meaningful to create such a dispersal network for forest plants.

In this paper, I try to answer the following questions:

- If there is a problem of isolation and fragmentation, which forest plants are then affected? This will be studied by relating distribution patterns of plants to the spatial arrangement of forest habitat (pattern analysis)
- What are the dispersal capacities and dispersal distances of different forest species? This requires insights in processes of plant dispersal in time and space (process research)
- A simulation model will be developed to be used in future land development programs to predict the effects of framework planning on the preservation of several forest plants (model research).

The pattern analysis has been completed,



while process and model research are being carried out at the moment.

## Methods

### Pattern studies

Using regression techniques and geographical information systems (GIS) presence/ absence of forest species have been related to the spatial arrangement of small woods. The small woods date from the beginning of this century and are all found on sandy soils in the province of Drenthe (northeastern part of the Netherlands). The degree of isolation is calculated as the number of small woods or wooded banks present within a range of 1 km from each surveyed woodlot.

### Process studies

Due to the time limit of the project, long-lived forest plants have to be evaluated in a second pattern study. In the surroundings of Orvelte (Drenthe), a land development project was carried out 20 years ago, which included the planting of many new small woods. I have determined which forest species have colonised these small woods. When a species occurs in older small woods in the area, I tried to find out what distances must have been covered to colonise new small woods, and whether plants could have used corridors for dispersal.

## Results

### Results of pattern analysis

The presence of a species is mainly influenced by habitat factors. The area of the survey woodlot (after correction for sample-effect) is most important for interior species like *Maianthemum bifolium*, *Lonicera periclymenum* and most fern species. A possible explanation is that when a forest has been fragmented, interior habitats disappear; and forest species will eventually become extinct. Some species showed an effect of isolation, and most of them were either interior and/or animaldispersed. The main conclusions are:

- Habitat factors are most important in determining vegetation distribution.
- Species react very differently to isolation within groups showing that it will be difficult in landscape planning to develop adjustments for whole groups of species.
- Especially interior and animaldispersed species seem more sensitive to isolation.

As isolation seems to be an important factor for some forest species, a process study of dispersal will be interesting.

### Results of process studies

As it seems now, only edge species like Common Elder (*Sambucus nigra*) and Rum Cherry (*Prunus serotina*) have colonised the new small woods. They are not very selective in habitat choice and are good dispersers. Apart from *Lonicera periclymenum*, other interior species like may lily (*Maianthemum bifolium*), common solomon's seal (*Polygonatum multiflorum*), and lily-of-the-valley (*Convallaria majalis*) have not colonised yet. They are more strict in habitat selection and are poor dispersers. Thus, complementary data are needed to get information on colonisation of these interior species.

## Future plan - developing a simulation model

The information gained so far will be used to develop a simulation model to evaluate the framework-approach in landscape design. This model will be developed for the bird dispersed fleshy-fruited plants. Within this group, species differ considerably in dispersal capacity, which makes it possible to compare 'mobile' species with 'immobile' ones. Landscapes 'before' and 'after' conversion from a fragmented landscape into a framework-landscape will be compared, considering connectivity (corridors), distances between woody elements as well as area and age of small woods.

Unlike animal species, plants have to rely on a vector (wind, animals, water) to have their seeds dispersed, e.g., most fleshy fruited plants are dispersed by birds. Therefore, a dispersal model of fleshy fruited

plants should consider flying behaviour of forest birds. In this study, no field observations will be carried out on birds. Instead, a theory of Dick van Dorp (1988) will be used. Roughly, there are two kinds of forest birds: Interior plants are dispersed mostly by birds which depend on wooded structures for their movements and have small home ranges. This type of dispersal is called longitudinal. Edge plants are dispersed mostly by birds which are not depending on wooded structures (starling, fieldfare, redwing, mistle thrush) and have bigger home ranges. This is called transversal dispersal. The longitudinal dispersal of interior species is thought to be described as a linear dispersal through a network, with small steps. It depends on distance as well as on connectivity. The transversal dispersal of edge species can be described as a diffusion process and depends mainly on distance.

The input to the dispersal model will be the amount of seed available in each patch per year. This number will be provided by a model describing the population dynamics within each patch concerning processes like germination, establishment, and reproduction. Each year dispersal takes place according to the two dispersal mechanisms above. Using information on area and isolation defined by Arc/Info, it will be possible to estimate whether newly arrived seeds will develop into a reproductive population.

After completing the model it will have to be verified against field observations. Eventually, evaluation of framework plans can be carried out.

## Conclusions

Although modelling is still at an early stage, I will use existing results to discuss the implications of framework planning on dispersal and survival of forest species. In the case of isolation, the development of a network connecting small woods using wooded banks could facilitate the dispersal and thus survival of these plants. However, the habitat quality determines to a large degree the possible presence of forest plants, as such it

will take several to many years before newly created habitats on former agricultural soil are suitable habitats. Furthermore, the linear elements introduced in framework planning may function as corridors for birds, but for forest plants to gain advantage, they have to have a suitable quality. Finally, I want to stress that it will be important to preserve, within the framework, old small woods as they will be the only dispersal sources for a considerable time. Framework planning can therefore only be effective for obligate forest plants if the structure of the developed framework can be safeguarded for long periods of time. Concluding, I will stress that the policy of framework planning should be evaluated carefully.

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## 3.2 Simulation of Carabid beetle movements

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### Introduction

Poor sandy or heathland road verges may contribute to the survival of carabid beetles that are stenotopic for these habitats (Vermeulen 1993a). A simulation program was developed that accumulates individual reactions of organisms to landscape structures (Vermeulen & Opsteeg 1993). By extra-polation of those reactions, it is possible to estimate the distribution of organisms in a certain landscape. For three ground beetle species, *Pterostichus lepidus*, *Cymindis macularis*, and *Harpalus servus*, we calculated movement parameters from field data (Vermeulen 1993b) and tried to predict whether or not certain corridor conditions such as found in road verges may affect dispersal of these animals. Although the data used so far only concern carabid beetles on road verges, the program can be used to simulate the movements of other organisms as well.

### The simulation program

To start, the user draws a landscape on the screen, defines different kinds of habitat and determines the simulation period. A number of animals (beetles) is released at specified or random points in the artificial landscape. Movement rate and preferred direction of the animals depend on the type of habitat. Borders between different habitats may function as barriers for the movements. The animals can reproduce and/or die during their walk. This enables the program to predict the distribution of organisms in a landscape after a set time period. Values for the parameters must be obtained from field studies.

The program simulates the movement of

each beetle individually. When a cycle is completed, the program checks for reproduction and repeats the whole procedure for all new beetles. When the simulation is finished, all end positions of the beetles in the landscape are determined, and the minimum, mean and maximum distances

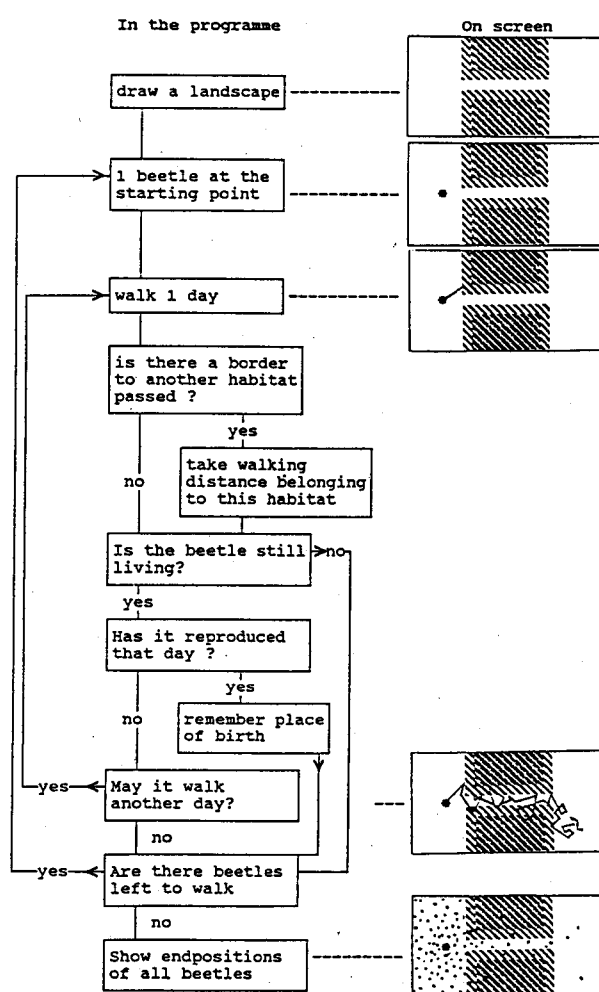


Figure 1. A simple flow chart of the simulation program for the dispersal of organisms in landscapes with different kinds of habitat. It shows the decisions a simulated beetle has to make in the program. To the right the output on screen for a corridor through a piece of forest is given.

covered by beetles during the simulation are calculated. Effects of seasonal changes on dispersal can also be incorporated into the program. A simplified flow chart of steps in the movement algorithm for simulated beetles is shown in Fig. 1. The simulation program is written in Pascal, and all results and graphs produced can be exported as an ASCII-file and be used in other programs. The program is owned by the Ministry of Transport, Public Works and Water Management of The Netherlands, but for non-commercial use, a copy can be supplied by the first author.

### Simulations in corridor structures

On a road-side verge of the A1 highway in The Netherlands connected to a former drift sand area, Caitwickerzand, the distribution

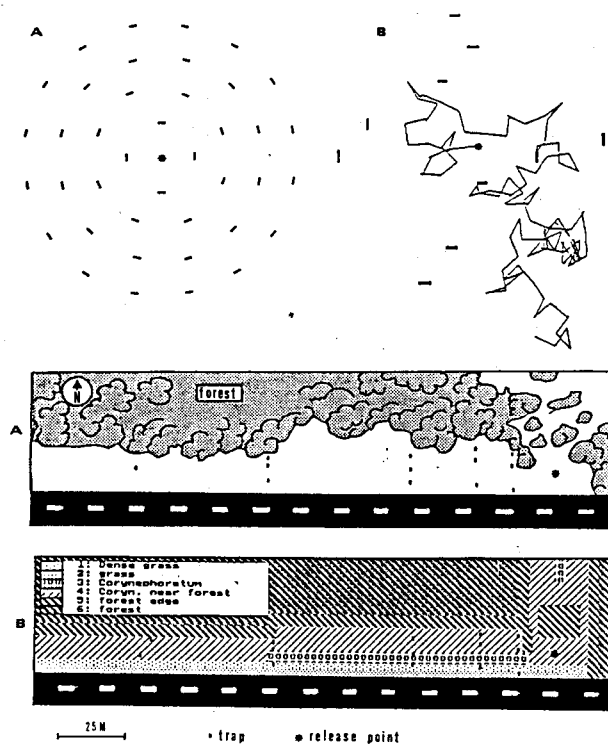


Figure 2. Traps placed in two field situations in and nearby the Caitwickerzand, The Netherlands (A). Marked beetles were released at the points indicated by an asterisk. For three carabid species, the same experiments were repeated in the simulation program (B) 50 times for an open field situation and a road verge. Only in one case, a significant difference was found (chi square test) in the distribution of recaptures between the simulations. B also shows the walking pattern of one beetle in the program.

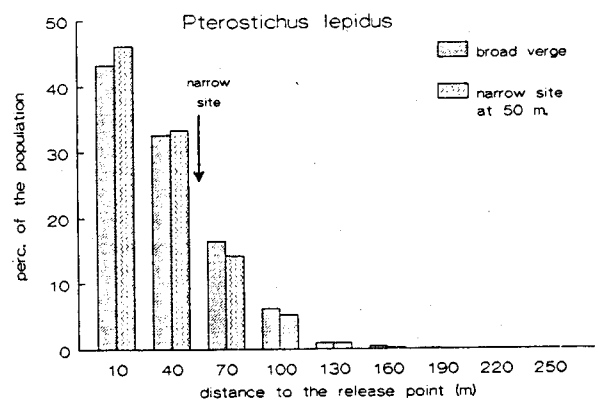
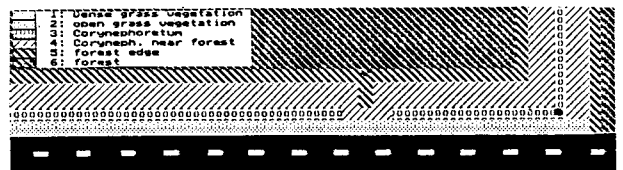


Figure 3. An example of the effect of a narrow site in a road verge. Above, a map of the situation with a narrow site as shown by the program. Below the distribution of a population of 10,000 individuals of *Pterostichus lepidus* along the road verge in situation without and with a narrow site in the road-side verge. The release point is marked by a star.

of carabid species in poor sandy and open areas was studied by mark and recapture experiments. Both Caitwickerzand and the road-side verge had a *Corynephoratum*-vegetation. The same kind of experiments (Fig. 2) were simulated by the program and run 50 times. A Chi-square test comparing the simulation results with those obtained in the field only once showed a significant difference between the two. Furthermore, we tested different kinds of corridors (road verges). Fig. 3 presents an example of the effect of a narrow site in a road verge. From the distribution of beetles along the verge it can be seen that more beetles stay nearby the release point in verges with narrow sites than in verges without them. To summarise, the three species tested so far show that; 1) the species have longer dispersal distances in broad corridors than in narrow ones; 2) their chance for long range dispersal movements along a corridor is higher when the corridor is connected to an area with a high density of individuals; 3) narrow sites in corridors de-

crease the chance of long range dispersal movements; 4) less beetles are lost to adjacent areas in broad corridors than in narrow ones; and 5) corridors allowing a high reproduction show longer dispersal distances after some generations.

## Discussion

In western Europe, man has had a dramatic impact on the landscape. This inevitably leads to conflicts between economic use of the landscape and nature conservation. Only relatively small patches are left for the development of natural or semi-natural vegetation. In these small patches, the risk of extinction for animals restricted to such areas is very high. Governmental institutions in the Netherlands dealing with development of landscape structures try to utilise all kinds of landscape elements to stimulate the survival of plants and animals. However, we know little about how populations react to different landscape structures.

The simulation program presented here tries to simulate the consequences of landscape changes for small, ground-dwelling organisms such as carabid beetles. It does not claim to be perfect, as all factors involving dispersal and survival of populations are not yet known.

With this program, it is possible to test whether different kinds of corridor structures will lead beetles to the wrong kind of habitats (Mader 1984; Mader et al. 1990) or will have a sink effect (Pulliam 1988). It is also possible to test where in a corridor a suitable site for reproduction and survival is necessary; e.g. the cross-sections in a network of hedgerows (Burel 1989).

The results obtained with three carabid species show that certain structures in road verges affect the movements of the beetles. Such results can be used to design road verges, that are more favourable for carabid beetles.

Decisions based on this program may not always be correct, but they are an improvement on decisions made without such models based on empirical evidence.

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### 3.3 Modelling reaction-diffusion processes with system dynamics at the landscape scale

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#### Abstract

A brief introduction to System Dynamics as a language for implementing dynamic models is given. Duplicating models into each cell of a grid is a way of introducing spatial structure into models and enables modelling populations as individuals. A number of examples are given for illustration and inspiration.

#### Introduction

In the past, the task of putting a model into a computer, getting the computer to simulate the model, and dealing with the substantial output of data, has undoubtedly been a major undertaking and one that has usually demanded a good deal of knowledge in the fields of both computing and mathematics. In recent years, however, the task has been simplified considerably with programs like STELLA™ for the Macintosh™ by way of a very easy to use graphical interface and a simple, but powerful concept of modelling using System Dynamics, credited to Professor Jay Forrester (Forrester, 1968).

In System dynamics the model consists of stocks (represented by boxes) that are depleted or incremented via pipes at given rates (valves) from sources that are either infinite sinks (clouds) or other stocks. When two stocks are connected together, stock is transferred conservatively from one to the other. Interdependencies in the model are indicated by arrows. The diagram of a model drawn using these components describes a system whose behaviour is dynamic i.e. changes in time (see Fig. 1). The model may also be categorised as a reaction model,

because stocks can be considered to react with one another or with the outside world. The simulation is carried out by topping up or depleting the stocks by increments specified by the rates and the time step. The result of the simulation is a foot-print of the dynamics of the system and is presented in the form of graphs or tables (See Fig. 2).

#### Example 1

Population dynamics of the Adelie Penguin rookery at Cape Royds, 1955-1990 (Blackburn et al. 1991)

This is an example of a population whose breeding capacity is influenced by the extent of the sea ice during the beginning of the breeding season. The population is divided into different age groups, as can be seen on the diagram (Fig. 1). Field data of the breeding success and the mortality of the different age groups controls the rates. A factor was added to ensure that ageing occurred in the correct order. This type of control is often taken care of by the simulator itself by choosing certain options. Data of the extent of sea ice at breeding time was fed into the model as a table. This is an example of how a System Dynamics model can be partly data driven. An event, interpreted by the authors as global warming, led to an increase in productivity and a decrease in mortality in the early 1980's. The output from the model (Fig. 2) is shown in comparison with the field data gathered on the population size. The model is listed in appendix A. Unfortunately, it is not sufficient to be able to describe systems as reaction models alone. Many systems are also governed by the transport of

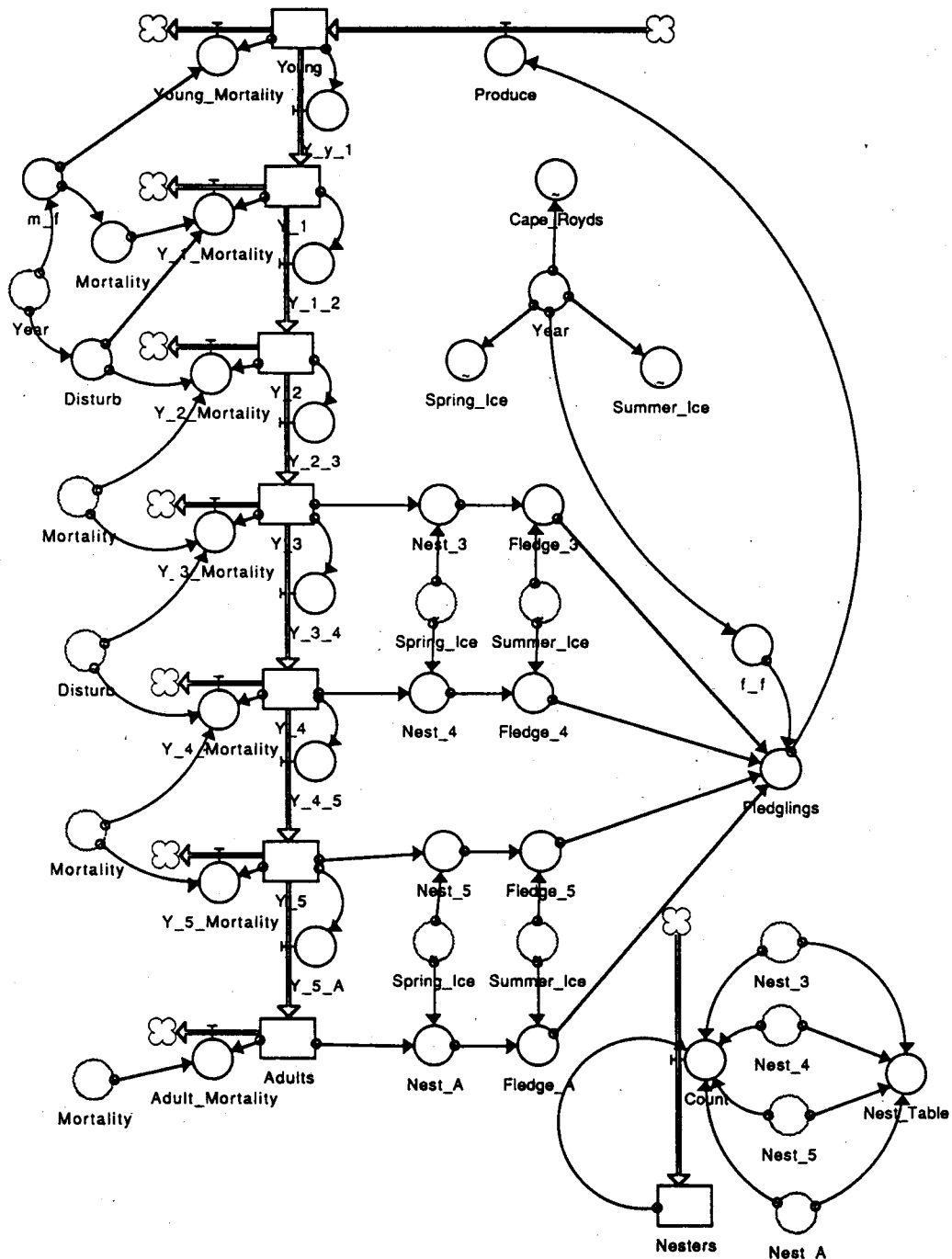


Figure 1. Model of the Adelie penguin rookery at Cape Royds. The stocks represent 7 age groups. The nester stock at the bottom right of the diagram is only used for output. Young, 1 year-olds and 2 year-olds do not breed.

matter in space or are influenced by the spatial structure of their environment. The way to support this in System Dynamics is to have duplicates of interconnected reaction models, each representing a different location in space. However, programs like STELLA are obviously not suited for this purpose, when dealing with complex reaction models in large numbers of locations. This limitation

gave rise to the idea of implementing a program named Cellmatic which would simulate a System Dynamics model on a two dimensional grid of cells, each cell containing its own reaction environment. Mechanisms for conservative flow between neighbouring cells, and flow in or out of the model (to or from a cloud) are the means of "communication" between the stocks in any given cell

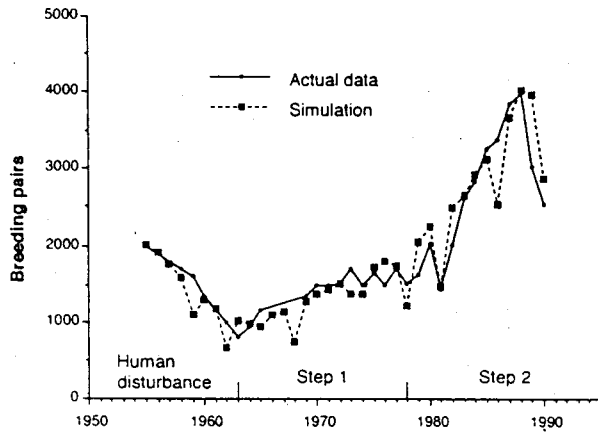


Figure 2. The simulated number of breeding pairs of Adelie penguins at Cape Royds (1955-1990) compared to the number counted, taking into account the effects of: sea ice on chick production, a natural decline and human disturbance during the late 1950s and early 1960s, and events leading to increased chick productivity and decreased mortality in the late 1960s through the 1980s.

and their environment. A model in Cellmatic may be called a reaction-diffusion model; the diffusion concept covering the mechanism of movement in space. The diffusion mechanism inspired changing the metaphor of a stock to that of an agent. The following examples are all models implemented in Cellmatic.

## Implementation of Cellmatic

Cellmatic handles the editing of models, input and output of two dimensional data in a variety of ways both during and after a simulation, sensitivity analysis, and sophisticated logging facilities for saving and retrieving models and previous simulations. Cellmatic simulates parallel execution of models within each cell i.e. the grid is not updated until an entire iteration of the grid has been completed. The original interface was implemented in Hypercard on a Macintosh computer. Newer versions are implemented in LabView (National Instruments) which can be potentially ported from the Macintosh to both IBM and SUN computers. The LabView interface offers very powerful data visualisation facilities and the ability to quickly and easily tailor the system if need be.

## Building the model

The steps in a straightforward method of building a System Dynamics model are as follows:

1. Identify all variables in the model and create stocks for them.
2. Create flows from clouds to or from the stocks which receive stock from outside the model or which lose stock from the model.
3. Create any conservative flows between stocks.
4. Initialise the stocks as a grid configuration.

The behaviour, governed by the rates of flow, applies to all agents in every cell. Specialised behaviour in specific cells may be introduced by specifying flow as a function of cell coordinates. It is simple to do this to model biased movement towards or away from areas of the grid specified by another data layer. Similarly high diffusion rates associated with certain landscape elements could mimic movement corridors.

## Example 2

Pingao versus Marram on the Sand Dunes of Kaitorete Spit, New Zealand.

Both pingao and marram are plants which grow on dunes. Pingao is the indigenous species and marram is an invader. A third species, scabweed, is also included but has little effect on the outcome of the model. This model was constructed to analyse the effect of pre-planting pingao for conservation purposes. The result was found to be negative i.e. the only way to allow Pingao to thrive is to physically remove Marram. The model simulates growth by seed and by spreading. Each cell of the grid can contain at most one individual of each species. When they come into contact, they compete and the strongest, depending on size and aggressiveness, will win and take over the plot. The resource needed for growth is sand which contains nutrients and is needed for supporting the root system. The sand in this model re-



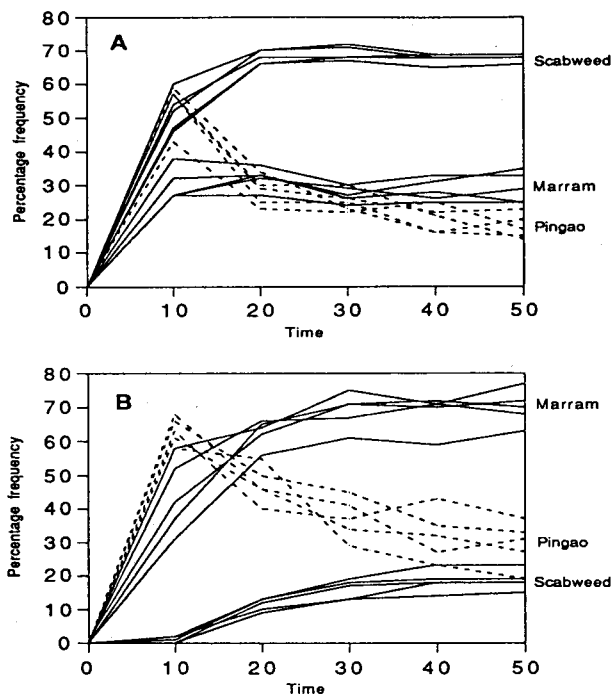


Figure 3. Changes in percentage frequency with time of marram, pingao, and scabweed, at two initial sand depths (A = 1.5 cm, B = 4 cm), as predicted by the model. The results of 5 simulations are shown.

presents a resource which changes in space and time. It diffuses and is trapped to varying degrees depending on which plant is present in which plot. The limited availability of sand is what stabilises the model and allows the less aggressive pingao to co-exist with marram. Pre-planting pingao was done by free-hand painting of the initial configuration of pingao onto the grid. The model is non-deterministic i.e. is controlled by random events. Time series of runs with initial populations of 0 and 2 different initial, evenly distributed depths of sand are shown in Figure 3. The model is listed in appendix B.

### The grid; an analogical representation

Explicitly representing an instance of all variables in each cell of a grid is the key to the ability of solving complex problems involving space dependency. The grid becomes a "playing field" on which reactions between model agents occur. Most models

would have some interpretation of what dimensions each cell of the grid represents. For example, the Sandbinder model (example 3) considers a cell to be a plot big enough to contain a small population of one species (about 1 m<sup>2</sup>). When the grid is used in this way, it is an analogical representation of the system to be modelled. The representation becomes more obviously analogical when the geometry is more complex. Geographical Information Systems (GIS) are ideal for acquiring such configurations for simulations.

### Example 3

#### Foraging strategies for Bumble Bees

This is a hypothetical example of behaviour which might correspond to the behaviour of bumble bees. Actual field data is being collected to parameterise the rates for the model, but this simulated situation suffices for the purpose of demonstration. The example compares two foraging strategies a) random flying until a flower is encountered and b) random flying for a period followed by direct homing in on the nearest flower. The example is to show how behaviour of this type can be implemented in Cellmatic.

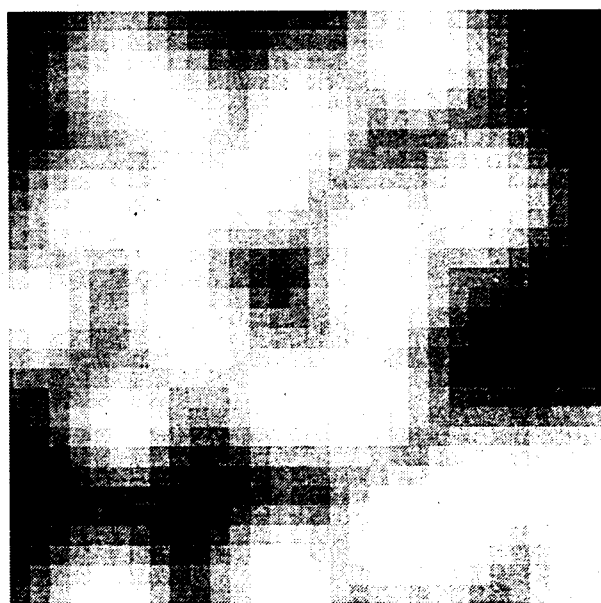


Figure 4. An intensity field calculated by diffusing an agent initially positioned at the same locations as the flowers. The direction of the steepest gradient at any point is the direction to the nearest flower.

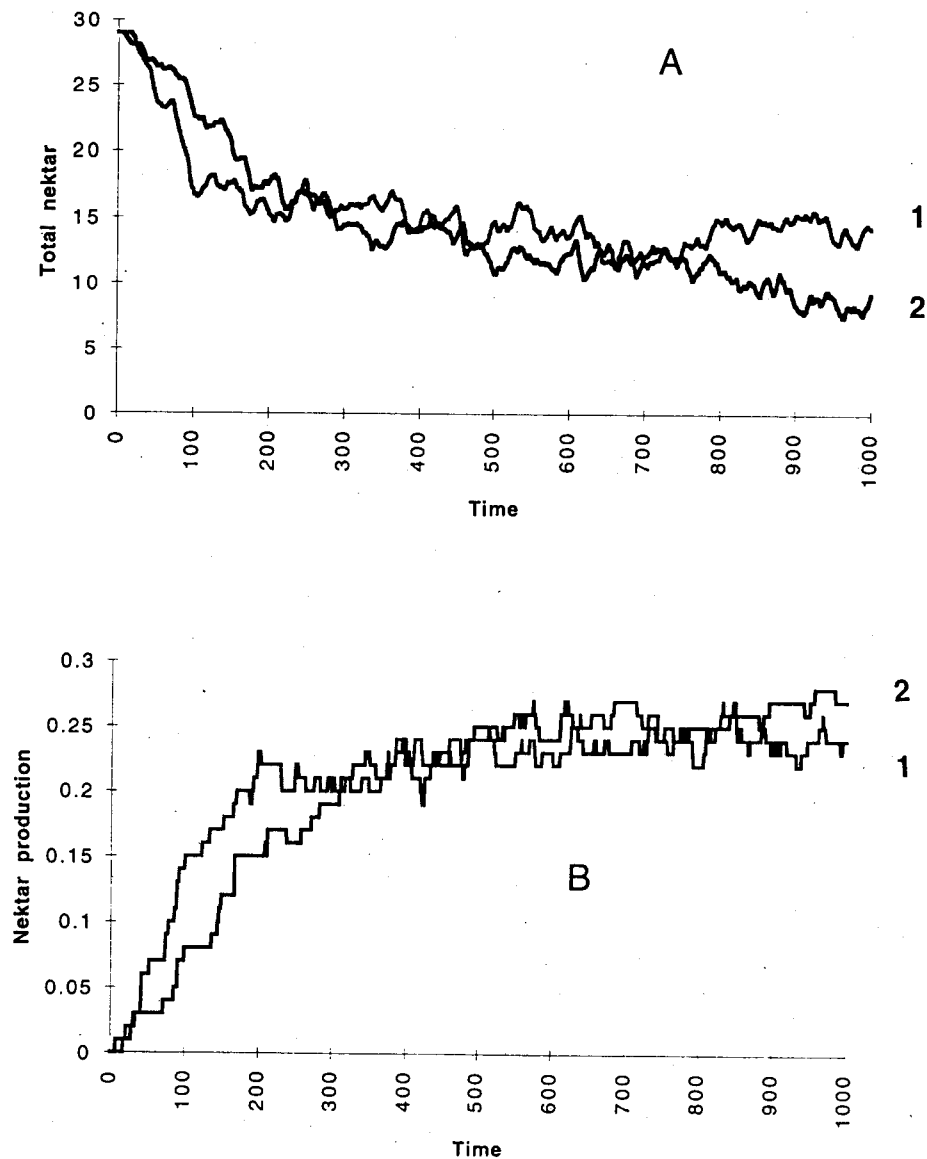


Figure 5. Results from simulations of two different foraging strategies for a flying insect in search of nectar. Grey lines (1) are random searching, black lines (2) are random flying followed by direct homing in on the nearest flower. A) The total amount of nectar available. B) The total nectar production.

The resources (flowers and nectar) are static in space but change in quality with time as bees land and empty flowers of nectar, after which the flowers take time to replenish. Flowers were placed randomly on the grid. An intensity field called "intens" (Fig. 4) was precalculated in a simple diffusion model to create gradients along which bees can follow to the source (i.e. a flower) for implementing the second strategy. The calculation of the field was achieved by allowing an agent to diffuse out from the position of each flower for a number of iterations. The automatic result is a field in which the gradient i.e. the

difference in intensity between the current cell and any neighbouring cell, is strongest in the direction of the nearest flower. Figure 5 shows the results of simulating the two strategies in the form of the total amount of nectar available given a constant potential nectar production (arbitrarily set at 0.01ul for each of the 29 flowers). Both are a measure of how efficient the bees are at finding flowers. For these models, the simulator was run in a mode where a single neighbouring cell only is chosen at random to simulate bee movement. The models are listed in appendix C.

## Concluding remarks

The integration of reaction-diffusion models with system dynamics and GIS databases provide a new tool for investigating the dynamic interactions between several spatially-explicit data layers. It would appear especially applicable to landscape ecological problems where both spatial and temporal dynamics are very important.

Any data layer may itself possess its own system dynamics with the advantage that model animals and plants may have all the standard demographic parameters. Individuals may be born, disperse and die according to defined rates and degrees of stochasticity. These processes are well modelled by Cellmatic but have more recently been incorporated into large GIS systems such as the USA military GIS GRASS™ which both has the most comprehensive battery of landscape metrics and the ability to treat each cell as a STELLA™ model with inputs and outputs determined by surrounding grid cells. Additionally one can find new GIS modelling environments specifically designed to analyse population ecological situations such as the new metapopulation modelling programmes produced by Applied Biomathematics in the USA.

The use of System Dynamics combined with the explicit geometry of the grid is a powerful tool for formalising and implementing conceptual models. In the case of landscape ecology, it can combine data from static geographical information systems with dynamic processes in a simple and elegant way. When discussing models amongst colleagues, it is a major advantage to have a common language in which to formalise models and implement details.

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## Appendices

Appendix A is a listing from STELLA. Appendix B to E are from Cellmatic. The out prefix is to (positive rate) or from (negative rate) a cloud. The toNbr prefix is the rate of flow to neighbouring cells. Conditional expressions such as (bee > 0) evaluate to 1 if true and 0 if false. The nbr(<exp>) function calculates the value of its argument <exp> in the environment of the current neighbouring cell.

### Appendix A

#### Dynamics of the Adelie Penguin rookery at Cape Royds.

```
INIT(Adults) = 2089
INIT(Nesters) = 0
INIT(Young) = 0
INIT(Y_1) = 515
INIT(Y_2) = 275
INIT(Y_3) = 269
INIT(Y_4) = 248
INIT(Y_5) = 231
Adult_Mortality = Mortality*Adults
Count = if mod(time,8) = 0 then -Nesters+Nest_3+Nest_4+Nest_5+Nest_A else 0
Disturb = if year <= 1961 then 1.8 else 1
Fledge_3 = Nest_3*( -(1-0.5)*Summer_Ice/40 + 1)
Fledge_4 = Nest_4*( -(1-0.5)*Summer_Ice/40 + 1)
Fledge_5 = Nest_5*( -(1-0.5)*Summer_Ice/40 + 1)
Fledge_A = Nest_A*( (1-0.7)*Summer_Ice/40 + 1)
Fledglings = (Fledge_3 + Fledge_4 + Fledge_5 + Fledge_A)*f_f*0.6
f_f = if Year < 1962 then 1 else if (Year >= 1962) and (Year <= 1978) then 1.1 else 1.2
Mortality = if mod(time,8) = 1 then 0.11*m_f else 0
m_f = if Year < 1962 then 1 else if (Year >= 1962) and (Year <= 1978) then 0.8 else 0.63
Nest_3 = Y_3*( (0.02-0.09)*Spring_Ice/40 + 0.09)
Nest_4 = Y_4*( (0.15-0.3)*Spring_Ice/40 + 0.3)
Nest_5 = Y_5*( (0.35-0.52)*Spring_Ice/40 + 0.52)
Nest_A = Adults*( (0.6-0.85)*Spring_Ice/40 + 0.85)
Nest_Table = if mod(time,8) = 0 then Nest_3+Nest_4+Nest_5+Nest_A else 0
Produce = if mod(time,8) = 0 then Fledglings else 0
Year = 1955 + int(time/8)
Young_Mortality = if mod(time,8) = 1 then Young*0.49*m_f else 0
Y_1_2 = if mod(time,8) = 6 then Y_1 else 0
Y_1_Mortality = if mod(time,8) = 1 then Y_1*0.49*m_f*Disturb else 0
Y_2_3 = if mod(time,8) = 5 then Y_2 else 0
Y_2_Mortality = Mortality*Y_2*Disturb
Y_3_4 = if mod(time,8) = 4 then Y_3 else 0
Y_3_Mortality = Mortality*Y_3*Disturb
Y_4_5 = if mod(time,8) = 3 then Y_4 else 0
Y_4_Mortality = Mortality*Y_4*Disturb
Y_5_A = if mod(time,8) = 2 then Y_5 else 0
Y_5_Mortality = Mortality*Y_5
Y_y_1 = if mod(time,8) = 7 then Young else 0
```

## Appendix B

### Sandbinders on the dunes of Kaitorete Spit, New Zealand.

```
age_Marram = -(Marram > 0)
age_Pingao = -(Pingao > 0)
age_Scab = -(Scab > 0)
bury_Scab = sand _ 3
die_Marram = (Marram > 8) and (Sand < 2)
die_Pingao = (Pingao > 8) and (Sand < 2)
est_Marram = -((Sand > 1) and (rand 25 = 0))
est_Pingao = -((sand > 1) and (rand 10 = 0))
est_Scab = -((sand < 2) and (rand 10 = 0))
graze = 0*(Pingao > 0)*(Pingao _ 7)*(rand 4 = 0)
sand_diff_Clear = if Sand > 1 then 0.125 else Sand/8
sand_diff_Marram = if Sand > 0.2 then 0.025 else Sand/8
sand_diff_Pingao = if Sand > 0.25 then 0.03125 else Sand/8
sand_diff_Scab = if Sand > 0.5 then 0.0625 else Sand/8
spread_Marram = ((nbr Sand > 1) and (Marram _ 3) and (rand 16 = 0))*0.01
spread_Pingao = ((nbr Sand > 1) and (Pingao _ 3) and (rand 16 = 0))*0.01
spread_Scab = ((nbr Sand < 2) and (Scab _ 3) and (rand 80 = 0))*0.01
win_Marram = (Pingao _ 3) and (Marram _ 3) and (rand (Marram*2 + Pingao) > Pingao)
win_Pingao = (Pingao _ 3) and (Marram _ 3) and (rand (Marram*2 + Pingao) > Marram*2)

out.Marram = if die_Marram or win_Pingao then Marram else est_Marram+age_Marram
toNbr.Marram = spread_Marram
out.Pingao = if die_Pingao or win_Marram then Pingao else est_Pingao+age_Pingao+graze
toNbr.Pingao = spread_Pingao
toNbr.Sand = if Pingao _ 3 then sand_diff_Pingao else if Marram _ 3 then sand_diff_Marram
else if Scab _ 3 then sand_diff_Scab else sand_diff_Clear
out.Scab = if bury_Scab or (sand < 0) then Scab else est_Scab+age_Scab
toNbr.Scab = spread_Scab
```

## Appendix C

### Flying insects and nectar

Strategy 1. Find flowers at random

```
consumption = (bee _ 1)*(nectar > 0.1)*0.1;
production = flower*(nectar < 1)*0.01;
out.nektar = consumption - production;
toNbr.bee = (bee _ 1)*(nectar < 0.1)*(nbr bee = 0);
```

Strategy 2. Fly around at random and then home in on the nearest flower.

```
consumption = (bee _ 1)*(nectar > 0.1)*0.1;
production = flower*(nectar < 1)*0.01;
out.nektar = consumption - production;
toNbr.bee = (bee _ 1)*(nbr intens > intens); { follow gradient to source }
toNbr.w_bee = (w_bee _ 1)*(nbr bee = 0)*(reaction.w_bee,bee = 0);
reaction.bee,w_bee = (bee _ 1)*flower*(nektar < 0.1); { wander if out of nektar }
reaction.w_bee,bee = (w_bee _ 1)*(rand 10 = 0); { stop wandering after 10 }
```

## Chapter 4: Pattern analysis (GIS and spatial descriptors)

### 4.1 Geographical Information Systems: A beginners guide for landscape ecologists

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#### Introduction

The increasing pressure to adopt geographical information systems (GIS) is often matched by lack of understanding as to what these systems are and what they can and cannot do. Given this lack of knowledge, it is very easy to become frustrated by GIS and to make costly and time consuming mistakes, which may ultimately lead to the discarding of what can be a very useful tool.

In simple terms, geographical information systems may be considered to be a suitable tool for landscape ecology because they are designed to handle spatial data and landscape ecology is concerned with the analysis of spatial phenomena. GIS provide an environment in which data from many sources and spatial resolutions may be integrated using a common spatial reference system, from simple (x,y) coordinates to a variety of map projections. These datasets can be overlaid to answer simple questions about spatial coincidence, for example regional coincidence of roads and sensitive habitats (Trewick & Veitch in press).

GIS can be used to calculate the number and size distribution of habitat patches in a region, the area and perimeter of the individual patches and indices of shape and habitat fragmentation (Lyon 1983). GIS can also be used to measure linear features and perform network analysis (Goosens et al. 1991), or to study temporal change in

landscape structure (Kienast 1993). Habitat suitability maps and ecological land classifications can be created and analysed (Palmeirim 1988, Hodgeson et al. 1988, Davis & Dozier 1990, Breininger et al. 1991). More sophisticated spatial models may draw data from the GIS and feed the results of the model back into the GIS for analysis and display, for example inductive modelling using Bayes theorem to predict red deer distribution (Aspinall 1992) and to map habitat suitability for curlew (Aspinall and Veitch 1993) and logistic modelling of red squirrel habitat (Pereira & Itami 1991).

The above examples are intended to give a flavour of the range of applications of GIS in landscape ecological research (see also Johnson 1990, Stow 1993). This paper is intended to be a brief introduction to GIS, highlighting some basic technical points that novice users should be aware of. It is not intended to be a detailed description of the principles of GIS, these may be found in a number of useful publications that are included in the bibliography.

#### What is GIS?

Geographical information systems are computerised systems for the management of spatial data. They consist of software for the capture, storage, manipulation, analysis, dis-

play and output of spatially referenced data (e.g. Arc/Info is a GIS). The term may also be used in the wider sense to describe the database (e.g., an ecological GIS) and the acronym itself has become a loose term to describe the practice of using geographical information systems (e. g. perform a GIS analysis).

Geographical information systems are often perceived as expensive tools for storing and making maps. Geographical information systems do not store maps as such, rather they store the data that allow maps to be produced according to a particular application or analysis. There are two types of data that are held within a GIS, geographical data describing the location and shape of a map feature and attribute data that describe what the feature is. Whilst the ability to produce high quality visual displays is an important aspect of GIS, their great strength lies in the ability to analyse and manipulate spatial data.

## Data Formats and Systems

Geographical information systems can handle three types of geographical data, points, lines and areas. The attribute data relating to these geographic features may take any form, but will always be referenced to one of these geographic features. These geographical data can be stored in two data formats, vector and raster.

### Vector

Vector format seeks to describe the world as precisely as possible. A feature may be a point, a line (or arc) joining points or an area enclosed by lines. Areas are also known as regions or polygons. All may have attributes which are stored in a database. Vector format can accurately depict exact boundaries and linear features and is ideally suited to network analysis and high quality map production. Due to the complexity of the data structure, vector systems may require considerable computing power to perform spatial analyses.

Vector systems are typically mainframe or workstation based, they are often large (i.e. the software takes up megabytes of disk storage) and may be complicated to learn. The installation and maintenance of such systems is likely to require the technical support of a computing specialist. The training courses provide by the vendors of these systems may be essential before any use can be made of the system and the additional cost of such training courses should be taken into account when purchasing a system. Typical vector systems are ARC/INFO, INTERGRAPH and LASERSCAN, though, there are many others on the market. A characteristic of such vector systems is that it may be possible to customise the system to the users' own requirements. Workstation and mainframe systems have the advantage over pc-based systems in their speed of operation and the volume of data that can be stored.

### Raster

The raster data structure consists of an array of grid cells, each cell having a value for the attribute being mapped. Raster datasets are usually referred to as images, and the individual cells are called pixels (picture elements). Data stored in this way can only have one attribute, therefore different attributes relating to the same location must be stored as separate layers or images in the database. Raster format is suitable for heterogeneous surfaces where boundaries are inexact. Map overlay and spatial analysis are straightforward and raster format is ideal for spatial modelling.

Raster systems may be based on a pc, workstation or mainframe. Raster systems, particularly those for use on pc's, are often less complicated and therefore easier to learn than vector systems. However they suffer from a less efficient storage format which may be a problem for pc-based systems with restricted storage space, also pc systems may well be slower in processing the data than workstations or mainframes. A number of raster systems have been developed for GIS education and research and are straightforward to learn. Electronic bulletin boards

often contain public domain software for these systems that a user can download and include in their own system (see Baker & Cai 1992). The ultimate in low-cost GIS is GRASS (which uses a UNIX operating system), which was developed by the United States military and is available free from an ftp (file transfer protocol) site in the USA. Other raster GIS include ILWIS, SPANS, MapBox and image analysis systems such as ERDAS and PCI EASI/PACE also include raster GIS functionality.

Raster systems are considered more suitable for modelling than vector systems, and most systems contain a modelling language. Most raster systems can also easily accommodate user-written modules (written in Fortran, C, Pascal etc), which may allow a researchers existing model to become part of the GIS.

It is very important to match the system to the format of the data. Vector systems may have restricted raster handling functionality, whilst raster systems may not be able to carry out some functions that are straightforward with a vector GIS. If the majority of the datasets are raster then it is more appropriate to use a raster GIS and similarly for vector data. Whilst it is possible to convert between data types, and most systems contain vector-to-raster or raster-to-vector conversions, the conversion process (particularly vector to raster) may introduce unpredictable errors into your data.

## Data Sources

### Map data

Maps, of what ever sort, are a fundamental part of a GIS as they describe the geographical features to which the attribute data relates. There are two methods of capturing map data: manual digitising or scanning. Manual digitising involves following the lines of a map using a puck that contains an induction coil. The map is mounted on a tablet containing a fine wire grid. Each time the digitising button is pressed, the coordinate is entered into the system and in this way the line is digitised. It is advisable that a researcher does at least some of their own digi-

tising to understand the potential for introducing error into the dataset.

For example this will demonstrate how easily a curve may be changed into a straight line and also how tedious digitising can be. Most, if not all GIS have digitising functionality, though some are more user friendly than others. Digitising tablets come in a variety of sizes from A4 upwards, though a tablet of around 1.5m x 1m will be the most convenient and comfortable to use. It is advisable to ensure that the GIS will support the make of tablet that is to be bought! Alternatively, a bureau service may be used for digitising, though the quality of their work may be directly related to their cost.

An alternative to manual digitising is scanning. Scanners convert paper maps into raster images from which vector data can be generated using line-following software. Scanning is often perceived as a way to capture data automatically. In reality most systems require an operator to supervise the vector conversion process. Not all GIS contain line-following software. Scanners are expensive, and come in a variety of sizes and resolutions, though 500-600 dpi (dots per inch) is probably the minimum requirement.

### Remotely sensed data

Two sources of remotely sensed data are suitable for landscape ecology, satellite imagery and aerial photography. Probably the most appropriate satellite data for use in landscape ecology comes from the Landsat Thematic Mapper.

This instrument provides spectral reflectance data in seven bands covering the blue to middle and thermal infra-red section of the electromagnetic spectrum with a ground resolution of 30m x 30m. Information in the red, near and middle infra-red wavelengths provides the best information for differentiating vegetation types and a combination of such data for summer and winter maximises this discrimination.

The SPOT HRV (high resolution visible) sensor lacks the spectral resolution of TM but has a spatial resolution of 20m x 20m, SPOT panchromatic data has a resolution of 10m x 10m. Radar data is also becoming available from the ERS-1 satellite.

Data from other sensors is available



though they may lack the spatial or spectral resolution required for applications in landscape ecology.

### **Aerial Photography**

The spatial resolution of aerial photography is far higher than that of satellite imagery. However it lacks the spectral resolution available from satellite data. Aerial photography may be converted to digital form using a high resolution scanner, with a minimum resolution of at least 500-600 dpi.

All remotely sensed datasets will require processing to be in a usable form in a GIS. Usually this will involve geometric rectification to remove spatial distortion caused by the curvature of the earth's surface, by the characteristics of the scanner, or distortions caused by aircraft motion. Satellite data is often statistically classified to produce a thematic map, usually representing land cover. Airphotos are less suitable for classification and may be visually interpreted to produce maps. Vector GIS are not designed to carry out this type of processing, so it may be necessary to use specific image processing software. Raster GIS, being closely related to image processing systems can often perform these operations. ERDAS and ARC/INFO have a 'live-link' system that enables the vector GIS to be used closely with the raster image analysis system, though this obviously requires the purchase of two expensive sets of software. If remotely sensed data is to be used as a primary dataset then it may be more appropriate to use a raster GIS, as the conversion of remotely sensed data into vector format, especially if it is classified satellite data, may result in a highly complex dataset, and potentially unmanageable dataset.

### **Tabular data and databases**

Tabular datasets, usually data for points or polygons, are an important aspect of GIS and most systems will have the ability to import data in a variety of formats. For example IDRISI has a link to dBase and ARC/INFO has its own relational database (INFO), though many people prefer to use ARC with a relational database such as ORACLE.

### **Error**

Unfortunately, one of the strengths of GIS is the ability to turn meaningless data into high quality meaningful data. GIS are precise tools but precision should not be confused with accuracy. The result of an analysis is only as accurate as the data that is being analysed.

Error may be introduced in many ways: inaccurate data, poor digitising, misclassifications, etc., and may be compounded by subsequent processing, for example multiple overlay operations. Because of this it is important to know where and what sort of errors occur in the datasets. A GIS is highly unlikely to contain any way of measuring or visualising error.

### **Getting data out**

Output from a geographical information system may be in the form of a complete dataset, for input into another system or into a statistical analysis package, or as a map or picture for illustrative purposes. Most GIS contain conversion and export routines and international standards for data transfer are being set, the most straightforward output format being ASCII.

As map production is an aspect of GIS, all systems have facility to produce annotated hardcopy output. It is also possible to import data into desktop publishing and graphics systems such as COREL. The quality of hardcopy output maps is largely dependant on the amount of money that is spent on the printer or plotter.

Ink jet printers produce reasonable hardcopy at a reasonable cost, but the higher quality hot-wax, electro-static and laser printers are expensive. The costs of these systems are on-going due to the need for consumables (paper and ink/wax/toner).

### **Conclusion**

The range of applications given in the introduction shows how researchers have exploi-

ted the possibilities of GIS for landscape-scale studies. The suitability and detailed application of GIS to a particular landscape ecological problem must be left to the individual researcher to decide.

GIS does not have to be expensive nor does it have to be complicated. For the complete novice, low cost, pc-based raster systems may be the best option, allowing the fundamentals to be learnt at little financial risk. Once the fundamentals have been grasped, the step up to larger vector (or ideally raster-vector systems) should be relatively straightforward.

In simple cost-benefit terms, relatively low-cost GIS potentially offer great benefits. However, as cost increases, the benefits may be relatively low. If increasing cost is due to problems caused by the inability of a system to carry out the required tasks, or through difficulties in learning to use the system, then the benefit can fall off to a point where the GIS can become a liability. The above points are intended to show some aspects of GIS that should be considered and to allow a more informed decision to be made when choosing to adopt GIS as a tool for landscape ecology.

Bear in mind that it may take some time to become familiar with the system and even longer to import data, process it and produce any output. Often GIS are sold as 'THE ANSWER' and are expected to produce result from the moment that the computer is plugged in. This is not possible.

In the short space available it has been very difficult to cover all aspects of geographical information systems and this paper is very much a simplification of the complexities of GIS. The author would like to apologise to more experienced GIS users if an important aspect has been overlooked.

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## 4.2 GIS for Policy and Land-use Planning

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### Introduction

In the UK, the ability to take account of potential new threats to wildlife as a result of new infrastructural development has been strengthened considerably by the introduction of the EU Directive (85/337/EEC) on the 'assessment of the effects of certain public and private projects on the environment'. This was incorporated into existing UK planning legislation through eighteen sets of regulations, and came into effect in 1988. It requires the potential environmental impacts of proposed new developments to be assessed before planning consent can be granted and has created opportunities for the development of formal procedures for ecological assessment which were not previously a feature of the planning process.

However, the current application of the procedures results in highly restricted and subjective assessments which ignore the wider habitat requirements of species and the cumulative effects of development. Such an approach is particularly inappropriate for linear developments such as roads, which often affect many habitat types and have impacts at a range of scales, influencing the functional integrity of habitat types throughout whole regions as well as having direct or localised effects on individual sites.

As well as addressing the direct impacts of land-take, ecological assessments for new road developments should therefore also consider:

- Cumulative loss of habitat
- Habitat fragmentation
- Barrier- and associated isolation-effects
- Effects of road run-off and pollution

- Effects of disturbance due to constructional and operational activities
- Effects on species distributions and status at all relevant scales (not just locally)
- Knock-on effects of associated development (mineral extraction, service areas etc.)

In a study of ecological input to the road assessment process, however, while the majority of statements reviewed (63%) considered direct land-take, only a small proportion mentioned any other category of impact. Those which were mentioned included 'pollution run-off' (31%); 'habitat severance' (16%); 'disturbance' (19%) and 'fragmentation' (0.4%) (Treweek et al. 1993). Furthermore, in only 1% of statements was any attempt made to quantify those impacts which were mentioned, or referred to. This suggested that there may be difficulties in obtaining or handling the spatially referenced data which is required to characterise the environment in such a way that potential ecological impacts can be both identified and quantified at different scales. However, the ability to do this has been considerably enhanced by the development of geographical information systems (GIS), which have been used with much success to assess road schemes and other route corridors in the Netherlands (Appelman & Zeeman 1992).

A study was carried out to investigate techniques for ecological assessment of proposed road developments based on systematic spatial analysis of the relationship between roads and selected categories of land cover derived from satellite imagery (Treweek and Veitch, in press). It was hoped that such techniques might be used in the

design of new roads, allowing full consideration to be given to potential ecological impacts during the selection of preferred route options and at a sufficiently early stage for effective mitigation measures to be incorporated into the planning process.

## The study area

The study area was within the county of Dorset in southern England (Fig. 1). As well as urban areas, a wide range of rural land-uses was represented, including agriculture (both pastoral and arable), forestry and nature conservation. The northern part of the study area was dominated by agricultural grassland, with a band of arable land across its centre and some semi-natural heathland to the south. The south eastern corner included Poole Harbour, and the urban areas of Poole and Bournemouth. Blocks of coniferous plantation forestry occurred largely on soil types which are marginal for agriculture, with broadleaved woodlands scattered throughout the area, usually in relatively small patches. There was an extensive road network consisting of major trunk roads (Fig. 2) and minor link roads (not shown).

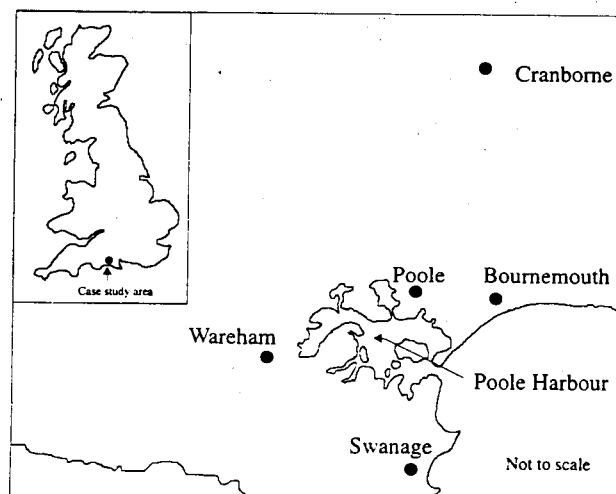


Figure 1. Location of the case study area.

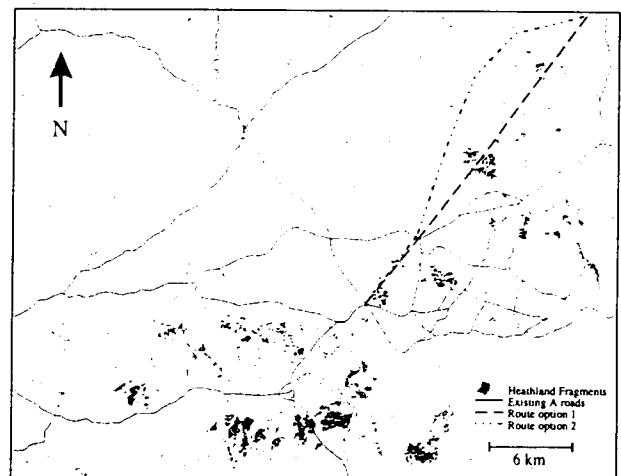
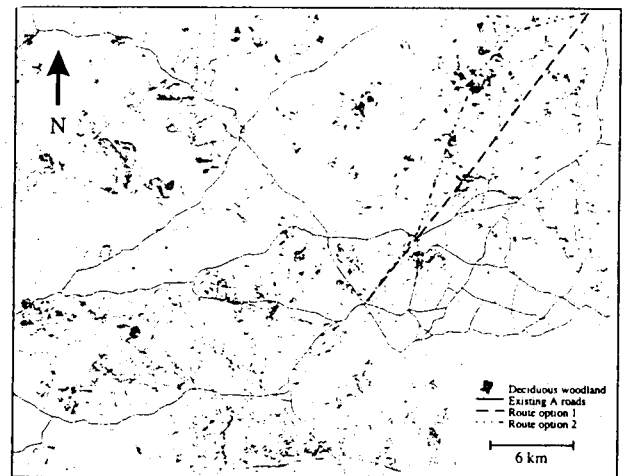


Figure 2. Distribution of deciduous woodland (upper) and heathland (lower) with existing A road network and two hypothetical route options.

## Methodology

All data processing for this study was carried out using IDRISI geographical information system v.4 (1992) on an IBM compatible 486 PC.

### 1. Definition of baseline conditions

The ITE Land Cover Map (Fuller et al. 1993) was used to obtain information on the distributions of six categories of land cover derived from classification of multitemporal Landsat Thematic Mapper data.

### 2. Distribution of land-cover categories in relation to existing major trunk road network

The existing major trunk road network was digitised in vector format and then rasterised

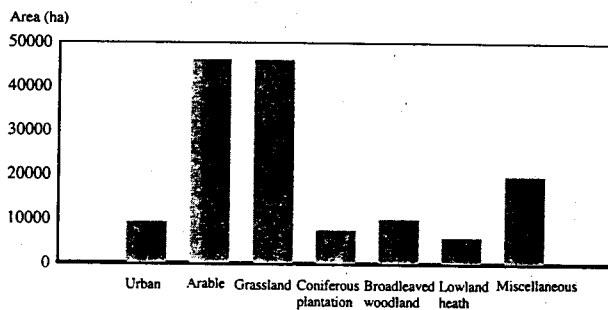


Figure 3. Areas of major land-cover categories in study area.

to produce two datasets, the first with a pixel size of 1 x 1 km and the second with a pixel size of 25 x 25m. The former was overlaid with the Land Cover Map to estimate the baseline relationship between the road network and the distributions of the six land-cover categories. This was done by measuring the area of each category occurring per km square and the number of squares containing each type, both for the study area as a whole, and for those 1km squares in which roads were located. The 25 x 25m dataset was then used to calculate the area of each major land-cover type actually occurring within 1000 m of a road.

### 3. Potential impacts

A hypothetical new route was chosen and two alternative route options digitised. The relative impacts of these route options were assessed in terms of land-take and fragmentation for selected categories of land-cover. Cumulative impacts could be simulated by assessing the impacts of the addition of each of these new routes to baseline conditions.

## Results

### Definition of baseline conditions

Agricultural land dominated the landscape (Fig. 3), covering approximately 64% of the total study area of 1,452,000 ha. Those categories of land-cover considered most important for nature conservation (lowland heathland and broadleaved woodland) were much more restricted in area, covering approximately 4 and 7%, respectively.

Distribution of land-cover categories in relation to existing major trunk road network.

Roads were located in 22% of the 1,452 1 km squares which constituted the study area. Using the 1km square summary data, all the land-cover categories demonstrated a high degree of co-occurrence with roads, arable land occurring in all squares where roads were located, with lowland heathland and broadleaved woodland in approximately 93% and 90% of 'road squares' respectively. In terms of area, 15.8% of the region's total heathland 'resource' occurred in the same 1km squares as a road, and 17% of the region's broadleaved woodland resource (Table 1).

### Potential impacts

As well as causing direct land-take (Table 2), addition of either new route increased the degree to which roads co-occurred with the main land-cover categories on the basis of 1 km squares and also increased the areas of sensitive habitat-types occurring within 1,000

Table 1. Area of land-cover categories occurring in the same 1 km squares as a road.

Land-cover category	Area (ha)	Area (ha) in "road" squares	Percentage of study area	Percentage of total area of category occurring in "road" squares
Urban	9355.38	4889.26	6.44	52.26
Grassland	46117.43	10330.00	31.76	22.40
Arable	46197.69	10869.00	31.82	23.53
Coniferous plantation	7667.44	1530.55	6.95	19.96
Broadleaved woodland	10097.15	1741.94	5.28	17.25
Lowland heathland	5937.31	937.75	4.01	15.79
Miscellaneous	19827.60		13.66	
Total	145200.00		100.00	

Table 2. Length of route and degree of 'contact' with land cover types.

Land-cover category	Route 1 length (km)	Proportion of total length (%)	Direct land-take (ha)	Route 2 length (km)	Proportion of total length (%)	Direct land-take (ha)
Urban	4.075	19.47	20.38	1.975	8.20	9.88
Grassland	4.850	23.18	24.25	8.175	33.95	40.88
Arable	4.425	21.15	22.13	6.500	27.00	32.50
Coniferous plantation	1.574	7.53	7.88	0.575	2.38	2.88
Broadleaved woodland	1.975	19.47	9.88	4.050	16.81	20.25
Lowland heathland	2.825	13.50	14.13	1.050	4.36	5.25
Miscellaneous	1.200	5.73	6.00	1.750	7.30	8.75
Total	20.925	100.00	104.65	24.075	100.00	120.39

m of a road (Table 3). However, the routes had different effects on different land-cover categories, Route 1 having more effect on lowland heathland and Route 2 having a greater impact on broadleaved woodland. The routes also had differential effects in terms of fragmentation and isolation (not considered in depth here).

## Discussion

In the case-study which is presented here, it was assumed that proximity to a road could be used in the regional planning process, to give some indication of the degree of risk that certain adverse ecological impacts might occur. These would include disturbance by noise, the effects of pollution from road run-off or atmospheric deposition and so on. Development of a regional road network to include new routes obviously tends to

increase the average proximity of habitats to a road, and therefore the risk of such impacts occurring. This was measured both on the basis of co-occurrence in the 1 km squares of an artificial grid superimposed on the landscape, or by calculating the areas of the different types occurring within defined distances from a road (in this case 1 km). In the UK, the information which would be required to actually quantify these impacts, however, is not currently available. For example, very few attempts have been made to measure pollution directly, and even fewer to measure the actual impacts on flora and fauna. Similarly, while it proved possible to measure the impacts of road development in terms of changes in the spatial distributions of major land-cover categories, it was difficult to determine the real implications of these changes without recourse to more detailed information on the distributions of species and the dynamics of plant and animal populations. In other

Table 3. Areas of land located within 1 km of a road.

Land-cover category	Regional baseline: Area (ha)	With route 1: Area (ha)	% increase with route 1	With route 1: Area (ha)	% increase with route 2
Urban	6250	6650	6.40	6850	9.60
Grassland	16000	17000	6.25	18000	12.50
Arable	15500	16500	6.45	17000	9.68
Coniferous plantation	2400	2800	16.67	2600	8.33
Broadleaved woodland	2750	3150	14.54	3450	25.45
Lowland heathland	1600	2150	34.38	1800	12.5

words, it was possible to measure the degree of habitat loss, fragmentation and isolation caused by addition of new roads to the regional network, but not to interpret the importance of these effects.

The study suggested that techniques for ecological assessment based on remotely sensed data and GIS would be very useful in the planning process in order to measure landscape-scale effects and to provide a sound and quantitative basis for further studies. The techniques used went some way towards quantifying cumulative and regional effects which are not routinely measured in the UK EIA process, and provided the kind of overview which would be needed to identify areas of 'ecological risk' at an early stage. The inclusion of designated areas, or of the known locations of rare species, for example, would be useful in this context. However, considerably more research is required to characterise the real impacts of the effects measured in terms of the viability of habitats, communities and populations of individual species.

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## 4.3 Spatial indices for landscape ecology - possibilities and limitations

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### Introduction

Complex quantitative descriptors for overall general concepts within landscape ecology such as landscape pattern, diversity, heterogeneity, connectivity etc. are an important challenge for the coming years. Although many basic principles, such as spatial indices based on information theory, have been known for some decades, the practical possibilities of implementing these measures on a broad level has been limited mainly due to missing spatial data and the enormous calculation work necessary.

Integration of remote sensing data with GIS-technology, and the rapid increase in storage and calculation capacity of today's computers has somewhat changed the situation. We just have to look through the last years of *J. Landscape Ecology* and other similar journals to be convinced that quantitative spatial characteristics of landscapes is of growing concern within landscape ecology. However, up to now these indices have often been used on artificial computer generated landscapes. Thus, we are still waiting for empirical data that can give rise to a common understanding of the meaning of these indices in real landscapes.

### Landscape ecology

There are, however, also some major hurdles in this development related to the very nature of landscape ecology as a problem-solving oriented science. Its success will depend on its ability to contribute to the future management of our landscapes, especially our more intensively used and

complex historical-developed cultural landscapes. Landscape ecologists often emphasise the holistic point of view, recognising that a landscape has to be seen as an integrated unit, with a structure and dynamics that cannot be understood fully by the laws and methods of traditional scientific disciplines. They also have ambitions of strengthening an integrated planning of our landscapes. A planning that can recognise both economic, ecological, social and esthetic functions of the landscape and integrate them into plans for a harmonious sustainable land use. As scientists, we can dream about realising these ambitions through the development of not only analytic spatial measures but also synthesising measures that can express our holistic point of view.

### Problems concerning quantitative measures

Quantitative measures within landscape ecology, however, are not always a relevant goal. Used in isolation, they can not only lead down blind alleys, but can also be dangerous by their simplification of complex structures and processes. They deserves to be handled with great caution if not general scepticism. Ernst Neef, the Eastgerman landscape scientist, who was the main speaker at the first worldwide landscape ecological congress (The Netherlands, 1981), gave much attention to these problems, especially in his last years. He showed, how the growing division of labor and the progressive abstraction within science has given rise to fundamental communication

problems - not least within landscape science. This is especially dependent on common mental perceptions of different aspects of the landscape complex, which can be very difficult to obtain. He stressed how the analysis as a simplification of components and factors dissolve the geographical reality as a lucid form, a Gestalt, even in the cases, where the social goal is a better understanding of that reality. So, it is of utmost importance, that the result of the analysis is always placed in a common understanding of the real object being investigated. Neef postulates, that this return of analytical statements to the original frame of reference is often missing. He gives several explanations for it, mostly related to general trends in the social development of science: the fragmentation of science because of specialisation that makes interdisciplinary and synthesis difficult tasks; quantification and mathematisation that have biased science towards elementary and less complex problems; the general low status in the scientific community of popular scientific publications; the devaluation of physionomical descriptions in science and the liquidation of esthetic aspects both having the consequence that the building of hypothesis is often artificially nourished through statistical material rather than basic field studies.

The results are that interpretation is often very difficult and that the translation into normal daily language often shows that the mathematical derived results were already known. And so, probably the most important lesson of this is that the lucid presentation either in plain words or in instructive graphic form are of utmost importance as a control of the growth of knowledge coming out of mathematical methods used in landscape ecology. When it comes to complex landscape indices, the first step to avoid, called 'Der Verlust der Anschaulichkeit' (Neef 1981) is that the scientists understand and get accustomed to the practical functionality of the indices, that is, to develop a set of mental maps, that can link the indices to the perception of different landscape patterns.

## Diversity of indices

To show the principles, the following indices have been used:

- the *landscape diversity* ( $N$ ), measured as the number of either landscape elements (patches or 'objects':  $N_0$ ) or types of landscape element (classes or 'types':  $N_t$ ).
- the *negentropy*<sup>1</sup>:

$$H' = -1 \sum_{i=1}^N p_i \cdot \log_2(p_i)$$

where  $N$  = number of landscape elements or landscape types,  $p_i$  = relative area of the landscape element or landscape types. The negentropy grows with the diversity, but is lowered if the proportion of the areals of the single objects or types is unequal.

- the *maximum negentropy*:

$$H'_{\max} = \log_2(N)$$

which means that it grows with 1 each time the number of landscape elements or landscape types doubles (if  $N = 1, 2, 4, 8, 16 \dots$  the  $H'_{\max}$  will be  $0, 1, 2, 3, 4 \dots$ : this is the advantage of using  $\log_2$ , instead of  $\log_{10}$  or  $\ln$ ). The negentropy will be maximum, when the areas of each patch or type of patch are equal, that is when  $p_i = 1/N$ . Remember, that  $\log_2(N) = -\log_2(1/N)$ .

- the *dominance*:

$$D = \log_2(N) - H'$$

expressing the difference between the maximum negentropy and the negentropy.

A	B	1	Type	Object		
		Diversity:	2	2		
		Negentropy:	1,0	1,0		
		Max. Negentropy:	1,0	1,0		
		Dominance:	0,0	0,0		
		Redundancy:	0,0	0,0		
-----						
A	B	Complexity:	4,0		2	Type
		Max. Complexity:	4,0		Diversity:	2
					Negentropy:	1,0
					Max. Negentropy:	1,0
					Dominance:	0,0
					Redundancy:	0,0
-----						
A	B				Complexity:	8,0
					Max. Complexity:	8,0
-----						
A	B	3	Type	Object		
		Diversity:	2	4		
		Negentropy:	1,0	2,0		
		Max. Negentropy:	1,0	2,0		
		Dominance:	0,0	0,0		
		Redundancy:	0,0	0,0		
-----						
B	A				4	Type
		Complexity:	8,0		Diversity:	4
		Max. Complexity:	8,0		Negentropy:	2,0
					Max. Negentropy:	2,0
					Dominance:	0,0
					Redundancy:	0,0
-----						
A	B				Complexity:	16,0
					Max. Complexity:	16,0
-----						
A	B	5	Type	Object		
		Diversity:	4	7		
		Negentropy:	1,8	2,5		
		Max. Negentropy:	2,0	2,8		
		Dominance:	0,2	0,3		
		Redundancy:	0,1	0,1		
-----						
C	A	B			6	Type
			Complexity:	26,5	Diversity:	4
			Max. Complexity:	28,0	Negentropy:	1,7
					Max. Negentropy:	2,0
					Dominance:	0,3
					Redundancy:	0,2
-----						
A	B				Complexity:	37,0
					Max. Complexity:	40,0
-----						
C	A	B			7	Type
			Diversity:	4	Object	10
			Negentropy:	0,9	2,6	
			Max. Negentropy:	2,0	3,3	
			Dominance:	1,1	0,7	
			Redundancy:	0,6	0,2	
-----						
A	A				8	Type
			Complexity:	35,0	Diversity:	7
			Max. Complexity:	40,0	Negentropy:	1,9
					Max. Negentropy:	2,8
					Dominance:	0,9
					Redundancy:	0,3
-----						
A	B				Complexity:	66,6
					Max. Complexity:	70,0
-----						
C	A	B				

Figure 1. The influence of spatial patterns of types (A-G) and objects (the single areas) on the value of different spatial indices.

- the redundancy:

$$R = 1 - \frac{H'}{H'_{max}}, 0 \leq R \leq 1$$

as a normalised expression for the "unevenness", with 0 for the totally even distribution and moving towards 1 when a few types or object are spatially dominating.

- the *complexity*:

$$C = N_o * N_t - \sum_{i=1}^{N_t} \left| \frac{N_o}{N_t} - F_i \right|$$

where  $N_o$  = the number of occurring landscape objects,  $N_t$  = the number of occurring landscape types,  $F_i$  = the frequency or abundance of landscape element type  $i$ . The complexity combines the diversity measures by objects and types, and can be compared with

- the *maximum complexity*:

$$C_{\max} = N_o * N_t$$

which occurs when the number of objects in each type is equal.

Simple spatial patterns of objects and types influence the value of the different indices (Fig. 1). Note especially, how the change in pattern between map 2 and 3 does not change any of the indices. Other types of indices based on information theory can

Table 1. Indices for five 4 km<sup>2</sup> areas that are a part of 32 test areas for small biotope monitoring in Denmark. The indices are computed by a dedicated vectorbased GIS for small biotope monitoring, described in Brandt et al. (1993). The location of the five areas (2, 9, 10, 12, 13) are indicated on Fig. 2.

		Tågerup (2)	Bøtø (9)	Højreby (10)	Glamsbjerg (12)	Bramsnæs (13)
MATRIX						
Object:	Diversity	120	136	76	165	117
	Negentropy	5.7	6.4	5.5	6.2	5.2
	Max. negentropy	6.9	7.1	7.5	7.4	6.6
	Dominance	1.2	0.6	2.0	1.2	1.3
	Redundancy	0.2	0.1	0.3	0.2	0.2
Type:	Diversity	19	16	7	14	13
	Negentropy	2.1	2.2	1.4	2.5	2.0
	Max. negentropy	4.2	4.0	2.8	3.8	3.7
	Dominance	2.1	1.8	1.4	1.3	1.7
	Redundancy	0.5	0.5	0.5	0.3	0.5
	Complexity	2062	1991	1061	2164	1135
	Max. complexity	2280	2128	1232	2310	1235
PATCHES						
Object:	Diversity	123	72	218	160	152
	Negentropy	5.7	3.8	1.6	6.2	4.1
	Max. negentropy	6.9	6.2	7.8	7.3	7.2
	Dominance	1.2	2.4	6.2	1.1	3.1
	Redundancy	0.2	0.4	0.8	0.1	0.4
Type:	Diversity	10	7	10	12	16
	Negentropy	2.5	1.3	0.3	2.4	2.1
	Max. negentropy	3.3	2.8	3.3	3.6	4.0
	Dominance	0.9	1.5	3.0	1.1	1.9
	Redundancy	0.3	0.5	0.9	0.3	0.5
	Complexity	1157	454	1943	1769	2254
	Max. complexity	1230	504	2180	1884	2384

however be used for that purpose, e.g. contingency (Turner 1990). Note also, how the development towards higher object negentropy in these cases is correlated to the amount of edges, thus indicating an interrelation between this type of indices and landscape indices on (potential) connectivity.

The maximum length of this paper prohibits a further extension of such sketches to principal pattern of more realistic types of landscapes.

The indices for five 4 km<sup>2</sup> areas (Table 1), that are a part of 32 test areas for small biotope monitoring in Denmark are computed by a dedicated vectorbased GIS for small biotope monitoring, described in Brandt et al. 1993. The location of the five areas are indicated in Fig. 2

The indices in Table 1 are based on a detailed classification of land use units ('MATRIX') divided into 44 types (including 2 types of small biotopes: wet and dry patchy biotopes), and of small patch biotopes (uncultivated patchy areas within and between the agricultural fields: 'PATCHES', divided into 19 types. Linear biotopes (hedges, verges, ditches etc.) have not been considered in the computation: There, areas are registered, but how are these objects to be counted? For a further description, see Biotopgruppen et al. 1986 or in condensed form Agger and Brandt 1988.

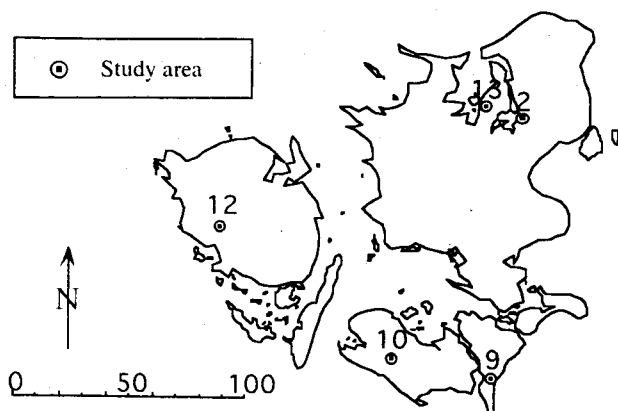


Figure 2. The location of the five study areas on Zealand, Funen, Møn and Falster. The five areas are part of 32 test areas within the Danish monitoring program for small biotopes.

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## Chapter 5: Applied landscape ecology

### 5.1 The value of national land use and wildlife databases for research and decision support systems

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#### Introduction

Landscape ecology is an interdisciplinary science which investigates the spatial and temporal changes in elements in a defined area of land and their relationship with plants and animals. In landscape ecology, landscapes vary in size with the smallest usually being measured in kilometres but more often being defined by political and international borders. Data sets used in the studies therefore, by definition, are often large and spatially referenced and yet may hold information on a wide variety of features ranging from agricultural practices through economics to mosses, mites and zoology. The link through geo-referencing has probably led to the accusation of landscape ecology being 'ecologists discovering geography'!

The management of large datasets is a time consuming and often thankless task. Assessment of data quality is a specialised subject and not always practised as rigorously as it should be. With cartographic data, the tradition of crisp logic and choropleth presentation have tended to lead to expressions of accuracy not being developed. A common approach to assess map quality is to identify a site well known to the assessor (usually his or her home!) and to visually compare the information for that area with personal experience - the rest of the data is assumed to be of the same quality. Where

better techniques are applied, the lack of familiarity has made them difficult to evaluate (Dickinson 1973).

Problems are also caused by different methods of spatially registering data; through differences in projection, scale and style. Different projections have different uses e.g. area estimation, relative position, route planning or measurement of length. No projections are capable of presenting all landscape characteristics correctly and most compromise. Many, if not all, the distortions may vary over a geographical region. Researchers quickly become very aware of the problems and automatically make allowances when trying to interpret disparate datasets.

On the other hand, planners and policy makers may not have the same experience in the field and be naive about the potential differences in quality of the information. A consequence is that the same dataset can mean different things to different people. Therefore it is essential that information qualifying and describing the data set - the meta data - are held and passed with the dataset, along with either the expertise to interpret the meaning or well worded interpretations.

Policy decisions have to be taken; they are drawn up using the best information available often gathered over an extremely limited period of time. Information needs to be presented in a way that can be easily assimilated (e.g. following the type of rules

expressed by Ehrenberg, 1977). Planners and policy makers are keen to assess environmental constraints, but the information must be presented not only in a way that is easy to comprehend, but also in a way that will allow easy integration with other datasets.

One danger in making everything easy to comprehend is the use of everyday terms. The definition of such terms may be vague or multi-faceted and there is a high probability that people will end up talking at cross purposes. Different groups may also collect information broadly about the same feature but define it precisely for their purposes. Using general terms easily understood by layman may mask the detail of the definition being used by specialists. Taking woodlands as an example, the Forestry Commission use the words woodland and forest as broadly synonymous. The areas they define will include areas of felled trees, rides and glades even though no trees may be growing there. Indeed, one dictionary definition (Brown 1993) describes the origins of the word forest as 'outside wood' and includes in the definition areas managed for deer, mixtures of woodland and pasture or even simply a wilderness! Wyatt et al. (1993) have attempted to define the major land cover terms used by different groups surveying Great Britain. Clarifying definitions is the first step in the analysis of the differences between survey estimates.

All these problems need to be taken into account when creating decision support systems. However, the first question before producing a decision support system is 'who are the specific users?'. The questions they will ask, their skills at interpreting information and ability to use a computer should all play an important part in determining the interface between man and machine and the analysis performed.

## **The ITE information system**

The Institute of Terrestrial Ecology (ITE) in conjunction with the Department of the Environment in the United Kingdom (DOE) has been developing a Countryside Information System over the last five years. The

system is now efficient at presenting and extracting information from data sets describing parts or all of the 240,000 kilometre squares in Great Britain (GB).

Whilst some of the data contain information relevant to landscape ecology (either directly or indirectly), it is still well short of presenting the holistic information for the full range of organisms, abiotic factors and their inter-relationships that would be necessary for a fully integrated package. Other types of information and modules would be required to produce such a system.

Much of the existing software would be adequate for the delivery of the information although new programmes would be required for models and visually interactive utilities. The need for such a system particularly for presenting such information to planners and policy makers was discussed at the recent European meeting of the International Association of Landscape Ecologists (IALE) in Rennes.

Many landscape ecologists wish to contribute to rural planning and the transfer of appropriate comprehensible information is essential to this process. However, the experience of ITE and other consultants on DOE projects is that much time is required in liaison so that the correct information is presented in the right format so that it will be interpreted correctly with the right level of confidence.

The origin of the ITE information system was as a joint project with the Highland Region Council who are responsible for 24,000 kilometres square in the north of Scotland (Bunce et al. 1984). Discussions with the potential users of a system identified five main reasons for the production of a Rural Land Use Information System (RLUIS):

- production of basic statistics describing the rural, e.g. boundaries and amenity woodland
- mapping the distribution of those resources around the region
- development of a monitoring programme recording and presenting land use change
- assessment of land use potential
- comparison of the likely effects of different policies

The project built up a dataset around these objectives and set up specific programmes on a PC to present the information. Two principle types of data were incorporated, i) census data available from every kilometre square in the region and, ii) sample data derived from appropriate surveys. The latter data were collected using the ITE Land Classification, described below, as a sampling strategy. This project demonstrated the feasibility of using a selective database which could be mounted on a PC, rather than an all embracing data set on a mainframe which had been tried in other projects.

Other lessons were learnt, for example, the importance of data structure, especially where data is continuously variable. From the point of recording, through most methods of analysis and presentation the tendency is towards the production of discrete units. If the units are not carefully formulated bias can be built into the data structure. Variables can be stored in different styles (nominal, binary, ordinal, interval and rational); the methods of recording and conversion have important consequences on the ability and value of comparison with other data sets.

Data which is sampled may be sampled evenly, randomly or with identifiable biases. However it is collected, it still has value, but the strategy for collection needs to be taken into account when the data is presented. Some groups use volunteers to collect data, and the distribution may then reflect the distribution of surveyors rather than the item surveyed. Other features require heavy equipment to record (e. g. climate or moths) and so may under-sample remote areas with difficult access.

GIS has developed from digital cartography. Cartography in itself is designed to pass information selectively and does it extremely well. Users usually go through a honeymoon period where the ability of the system to present information with authority and clarity impresses. This often gives way to scepticism and disbelief and leads to the garbage in garbage out cliché. Only when the systems abilities and limitations have been used for an extended period and the operator has intimate knowledge of the data, truly valuable interpretations can be made - expert

opinion should not be underestimated.

Although data users are aware of accuracy, there is often confusion with precision. A digital map may be stored on a GIS at metre resolution (i.e. precision), but confidence in the information may be measured in kilometres (i.e. accuracy). Where the data sets describe landscape elements the user has little expert experience of there is danger of mis-interpretation. For example, mechanically it is possible to produce national estimates of areas of different habitats to hectares (or even smaller). The data used to produce may be sampled and extrapolated, or censused from a satellite using a pixel of 25 square.

## The ITE Land Classification

The objective of the classification is to provide a sampling framework within which representative sites can be drawn for detailed survey because it is not possible to carry out a countrywide census for many ecological parameters. Statistically derived estimates can then be made at national and regional levels, as well as predicting their broad distribution. As described (Bunce & Heal 1984, Bunce et al. 1993), the system was designed to give an integrated picture of the countryside enabling progressive layers of information to be built up. The land classification is only the means to an end, which is the production of a coordinated database - the classes are arbitrary points along a continuum of the British environment. Originally only 1200 squares on a regular grid were classified, using multivariate analysis (Indicator Species Analysis), but subsequently every square in GB has been classified into one of the 32 land classes (Bunce et al. 1993).

The ITE Land Classification operates at a resolution of 1 kilometre, and so this is the pixel size for the Countryside Information System (CIS). The CIS holds both sampled and censused data and allows the two to be overlaid. The system also presents error terms which qualify sampled data and textual descriptions of the data which are entered specifically for each data set. The CIS, at present, merely presents snapshots; selective and historical images of features.



Landscapes are dynamic. Whereas some processes, such as nutrient movement may be understood in some environments, there is no widespread or general theorem which allows models to be applied successfully to different landscapes. This is very important when trying to manage wildlife. A species may be well studied, but its position in an ecosystem, its role in different communities and its biotic and abiotic interactions need to be understood. Forman and Godron (1986) breakdown the study of landscape ecology into three groups; structure, function and change. The CIS now handles structure and attempts to present change, to become a full blown landscape ecology tool it needs further development into the dynamic sphere of function.

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## 5.2 Application of knowledge on fragmentation in planning

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### Introduction

Application of landscape ecological knowledge in planning is a process of simplification. We cannot always be as clear and certain as we want, but that should not prevent us from formulating rules and standards. It is obvious that planners often make their plans without a sufficient analysis of the problem. In order to present research results and expert knowledge to planners, it is necessary to make a decision support system that can serve as a guide in the planning process. A methodology for ecological planning should include:

- problem analysis (is there a problem? for what species? and at what scale level?)
- defining priority (what to do first)
- defining the solutions (how to solve the problem)
- working out what exactly should be done

Focusing on the problems of fragmentation and planning at different scales, various kinds of research could be applied to solve different problems:

- pattern analysis, regression/ correlation  
→ chance for presence/absence
- process analysis, simulation/ prediction  
→ chance for survival
- simulation with GIS, landscape structure  
→ chance for dispersal

### Knowledge based approach

In a decision support system, knowledge from research (models) and from experts will

be translated into rules-of-thumb for planning purposes. A knowledge based system for fragmentation needs information on landscape and species characteristics. The approach is species oriented, and when the ecosystem is central the use of indicator species is chosen at different levels. Information on landscape structure should include: lists of ecosystem types that are suitable for the selected species; area of the habitat patches; barriers and corridors; isolation measures derived from research. Information on species should include: relations between species and ecosystem type (number of occupied suitable patches); scale of metapopulation processes; dispersal distances; sensitivity to fragmentation; and minimum area for small local populations.

To derive rules-of-thumb, we concentrate on a metapopulation process (local extinction) for the problem analysis and the estimation of minimum area for local populations as part of the solution. Here, we are concerned mainly with metapopulations in an archipelago structure. For the situation of a core-satellite configuration, other measurements should be used.

To determine if there is a problem of local extinction, the following guidelines are used. When less than 10% of the habitat patches unoccupied there is no problem; when between 10 and 50% of the habitat patches are unoccupied there is an increasing problem; and when more than 50% of the habitat patches are unoccupied there is a chance of extinction of the metapopulation.

When a specific species is in trouble, combinations of the following solutions are possible: improve habitat quality; enlarge habitat patches; increase the number of

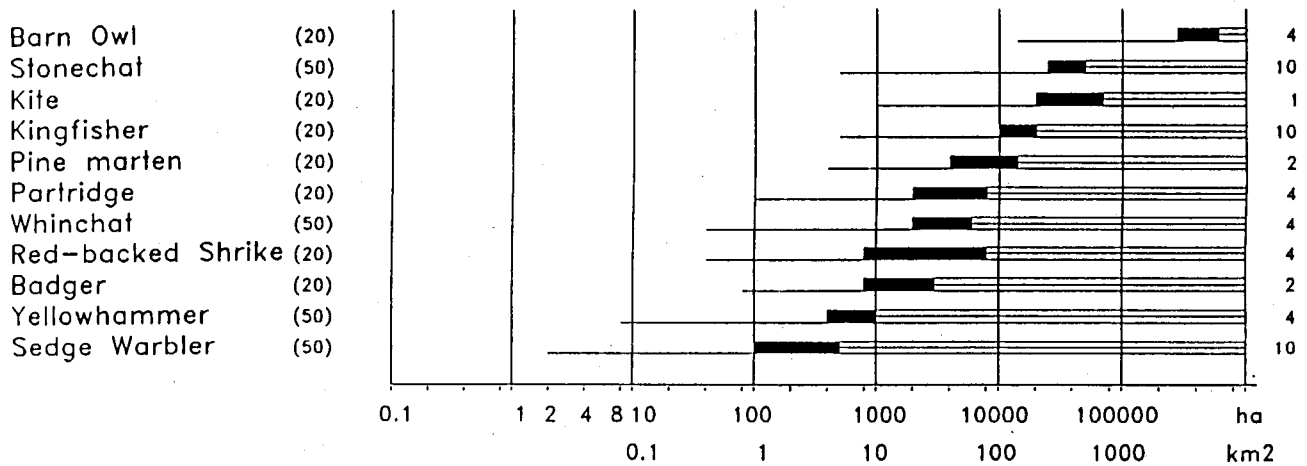


Figure 1. Minimum area for small but stable populations (core populations) of certain animal species of a heterogeneous forested landscape on loamy soils. Small single line: area for one reproductive unit, no core population; solid black line: area for a core population; triple line: area for bigger populations; (20): smallest number of reproductive females building a core population.

patches; connect habitat patches; or increase the permeability of the landscape.

When, for example, 'enlarging habitat patch' is chosen as the best solution, it is essential to know the minimum area and the minimum number of individuals for a local population. Each population is affected by demographic stochasticity. To be certain that a population has a good chance of surviving demographic fluctuations in the long term, the population should consist of at least 20 reproductive females. The impact of environmental stochasticity on animal populations varies according to the size of the animals, i.e., it has a very low impact on populations of large animals, and a high impact on very small animals. Thus, the following minimum population sizes are suggested:

- large and medium sized animals: 20 reproductive individuals
- small sized animals: 50 reproductive individuals
- very small animals: 1,000 to 10,000 individuals

Information about the type of habitat or ecosystem, home range or territory, and the number in the minimum population enables us to calculate the required area for a minimum local population. As an example we

show a figure of area requirements of some reed swamp species (Fig. 1). The other necessary elements for these species are open water, marsh shrub and forest and for some species grassland with ditches (at least in The Netherlands).

If it is not possible to establish areas that are large enough for some species, it is necessary to concentrate on a network of smaller interconnected patches in order to provide sufficient exchange of individuals. If the patches are so small that there is room for only one or two pairs, a network should be established in which at least 20 (or 50) patches on average are occupied.

If the solution is (also) connectivity, there are several possibilities, e.g., diminish the distance between patches, construction of corridors or stepping stones, removal of barriers, or usage of technical structures. Summarised, we distinguish the following steps in solving the problem of fragmentation, for which a decision support system can be helpful: choice of species or ecosystem of interest; description of the planning area; diagnosis of the problem; and defining solutions.

We expect that the system and the planning standards can be used in other countries too, although the problems may occur at another scale. The decision support

system is formulated in an expert system language, but we have to be careful not to make the system too complex, otherwise the overview will be lost. This system is part of a series of tools. Other tools and different models are described in this volume, e.g., a tool for evaluation of scenarios as shown by Claire Vos.

## 5.3 Landscape ecological knowledge for rural planning

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### Introduction

In the past decades, physical planning in Flanders has been restricted to the optimal partition of the area for different kinds of land-use. Meanwhile, little attention was paid to the specific characteristics and the typical dynamics of the different forms of land-use. Today, on the national level, one is working on a new legislation, on new forms of collaboration and on a new type of plan, abandoning the old blueprint plans. On the regional level, a comprehensive planning for the rural areas is the issue. In the new planning, the formulation of an overall vision on the desired structure and organisation of the area is the central theme. During the realisation of the plans, landscape ecological knowledge is used for solving the following problems:

- the formulation of ideas and principles concerning the properties of nature and environment in relation to different forms of land-use
- the use of carrying capacity as a principle for physical planning; the limits for land-use, posed by spatial quality or properties of nature and environment
- the formulation of ecological and spatial preconditions leading to sustainable land-use.

The urgency of the spatial and environmental problems in Flanders and the new political practice of presenting policy plans within very short time, make it difficult to carry out original and specific research. As a result, we have to work with available data that were not intended originally for a particular application.

### Sectorial contribution

In Flanders, the Nature Development Plan and the Ecological Main structure of Flanders, are the official results of that policy. Similar documents are the National Ecological Network of The Netherlands (actually the example for Flanders) and the European Ecological Network EECONET (in preparation).

The Ecological Main Structure of Flanders is accepted as the main policy document for nature conservation and has now to be implemented. Landscape ecology will deal with the following problems:

- determination of the potential development of ecotopes in landscapes with varying types of land-use and different degrees of intensity of that land-use
- determination and quantification of the spatial and environmental requirements of different 'types of nature'
- evaluation of the possibility to combine 'nature' with different types of land-use
- elaboration of workable methods to handle the cited problems, making use of available data and knowledge.

### The Ecological Main Structure of Flanders

A official preliminary version of the Ecological Main Structure of Flanders is now published. It was meant to introduce the idea of region oriented nature conservation and to stimulate the discussion. For the moment, it has the status of the official directive document for nature conservation.

The Ecological Main Structure is defined as 'a coherent and organised structure of sites, in which a more intensive policy in favour of nature is recommended'. Four zones are proposed:

- Core areas: areas with the highest nature conservation values. A minimal surface area is not required; nature has first priority.
- Nature (re)development areas: areas with actually or potentially high, often scattered nature conservation values. A development towards core areas or a co-existence with compatible land-use is the aim.
- Connection or corridor zones. Two categories are distinguished. Firstly, zones between core or development areas that we expect to function as a corridor. Secondly, areas with a dense network of small landscape elements that have a high degree of intern connectivity.
- Buffer zones. Zones that function as a filter for potentially damaging influences from abroad.

The map was prepared, with the use of existing data on the biotic environment: flora distribution maps, waterfowl inventories and the Biological Valuation Map. Three criteria were used: size of individual areas with a nature conservation value; distribution and density of those areas; and degree of human influence due to agriculture, industry and urbanisation.

With these criteria, a first classification of sites in four categories could be derived. In the next step, the regional constituents of these categories were interpreted as the areas and zones mentioned above. Species richness, rarity and diversity were criteria, together with an estimation of the potential of an area to develop towards a more complete natural environment or an area in which natural values could develop together with a less intensive land-use. For this step of the elaboration, the Biological Valuation Map was of great help.

The area of Flanders is about 1.360.000 ha. The Ecological Main Structure foresees: 150.867 ha of core area (11%), 212.286 ha of natural development area (15%), and 171.787

ha of connection or corridor zones (12%). Compared with the 10.000 ha of existing nature reserves (or 0.7% of Flanders), it is clear that the whole project is very ambitious. As an outcome of the consultation round, it was agreed that in a first phase, 133.575 ha of core area and 107.370 ha of nature development area should be realised.

## **Elaboration of the ecological main structure**

When analysing the map and the definition of the categories of the Ecological Main Structure, important conclusions can be made:

- zones are large
- objectives for individual zones are not explicit
- within nature development areas and connection zones,
- land-use must be so that the nature conservation objectives can be reached by the whole area, leaving some flexibility for individual parcels
- the implementation demands for the participation of all involved in the rural environment.

As it is interpreted, now, uniform measures for the whole of a category are of no use for the Ecological Main Structure. Especially for development areas and connection zones, the site specific characteristics, the nature conservation, and other land-use objectives are directive. This involves the responsibility of all. The Ecological Main Structure should be incorporated in their own policy plans. As such this forms one of the basic documents for the preparation of the comprehensive Structure Plan for the new physical planning of Flanders. In this respect, landscape ecology is confronted with the following questions:

- How to convert general nature conservation objectives into site specific measures with preconditions for different land-use
- What kind of information is needed and

how must it be presented to allow nature development projects of lower planning bodies to fit in the overall main structure.

## **A methodology to select nature development sites**

In most of the nature development areas, a selection of the sites, suitable for development projects, must be carried out. Therefore, the ecological objective for the region of which the area is part of, must be made more explicit. The named ecosystems or communities resulting from that, should then be interpreted in terms of abiotic environmental and spatial characteristics. The allocation of suitable sites, having the right combination of environmental and spatial qualities or the potentiality to develop them, is the final step in the spatial analysis. For some applications of the mentioned methodology, elementary GIS techniques can help a lot (see Paelinckx et al. 1991).

## **The Biological Valuation Map of Belgium**

The Biological Valuation Map is based on a standardised, uniform survey and evaluation of the biotic environment of Belgium. The mapping scale is 1:25.000. The field survey was carried out by using a uniform legend for the whole country. This was composed on the basis of existing knowledge of the vegetation types of Belgium and on general landscape ecological characteristics. Legend units largely correspond with formations, as distinguished in phytosociology. The classes grassland, shrub, mixed deciduous woodland and azonal woods were divided in subclasses according to soil conditions and agricultural practice.

Mapping in the field was carried out on a scale of 1:10.000 or 1:25.000. Areas smaller than a quarter of an hectare were not mapped, but were incorporated into a complex with surrounding units. Complexes were also defined if it was impossible to separate individual mapping units or if there was a

more or less regular mixture of them. Small landscape elements were rarely mapped separately. After many years of experience with applications, we can mention a number of limitations:

- heterogeneity in the final maps
- use of complexes is not consistent (due to the lack of guidelines)
- different time bases of the maps
- insufficient legend units concerning pioneer vegetations and
- vegetations of the agricultural areas
- very broad ecological amplitude of many units

Besides an Atlas with flora distribution maps, the Biological Valuation Map is the only data base that gives nation wide information on the state of the biotic environment. Until now, the main application lies in the determination of the nature conservation value of a particular site. As such, the document is used in environmental impact assessment, physical planning, land reallocation, nature conservation policy.

The description in an indirect way of the site conditions of a region using the Biological Valuation Map, poses problems. If it is assumed that legend units give indications of the environmental qualities this still has to be proven. It has to be examined whether the map and the legend units are suitable for e.g. the evaluation of the vulnerability of vegetations and sites to environmental changes (lowering of the ground water table, etc.). However, there are many restrictions.

A number of scientists independently prepared a ranking of the legend units according to their vulnerability for desiccation and eutrofication. The resulting vulnerability maps of a selected region showed very low similarity (only 50%). The vague definition of many of the legend units, leaving a lot to be interpreted, causes this disagreement.

When combining the legend units with phytosociological relevés and using the indicator values of the individual species, a reliable ecological interpretation for about 50% of the legend units could be derived. This approach does not suit for the other half of the units because they could not be interpreted in terms of vegetations or because

their ecological amplitude is too broad (especially grassland in agricultural use and poplar plantations).

Combining the legend units with soil characteristics (using GIS techniques), it could be concluded that there is an overall dependence between legend units and soil types.

From the results mentioned above, it becomes clear that a further combined analysis of the Biological Valuation Map with other data and maps of environmental components, is necessary to make this unique data base more useful for applications in physical planning and environmental management.

### **Landscape ecology for the physical structure plan of Flanders**

The question of the identification and the cartography of the differentiating landscape components and the characteristic landscape ecological processes within and between regions, was approached in two ways. First there is the need for spatial entities. Physical planning formulates general objectives and strategies, applying for a whole region. To put the totality of the landscape, we looked for holistic entities. As their usefulness is often limited when it concerns specific planning problems, we decided to start from the formulation of environmental problems to define the holistic entities.

Following the approach worked out at the Centre of Environmental Science (Leiden University, the Netherlands), we elaborated the ecodistricts of Flanders. Ecodistricts are spatial entities that are homogeneous in the low dynamic abiotic components: geology, lithology, geomorphology, pedology, hydrology. A region-specific flora can be expected. We suppose an ecodistrict to respond in a uniform way to environmental changes, such as acidification, because the ecological processes involved, occur in parameters of the same components as those used for the ecodistrict typification.

Information of the factors determining biodiversity, specific ecosystems, and communities was presented in a map determining elements and processes in Flanders.

With that map we tried to give an overview of the ecological master factors responsible for that biodiversity.

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## National Environmental Research Institute

The National Environmental Research Institute - NERI - is a research institute of the Ministry of Environment and Energy. NERI's tasks are primarily to do research, collect data and give advice on problems related to the environment and Nature.

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