DISPERSAL MODELLING: INTEGRATING LANDSCAPE FEATURES, BEHAVIOUR AND METAPOPULATIONS

THÈSE N^{O} 2878 (2003)

PRÉSENTÉE À LA FACULTÉ ENVIRONNEMENT NATUREL, ARCHITECTURAL ET CONSTRUIT

Institut des sciences et technologies de l'environnement

SECTION DES SCIENCES ET INGÉNIERIE DE L'ENVIRONNEMENT

ÉCOLE POLYTECHNIQUE FÉDÉRALE DE LAUSANNE

POUR L'OBTENTION DU GRADE DE DOCTEUR ÈS SCIENCES

PAR

Séverine VUILLEUMIER

ingénieure du génie rural diplômée EPF
de nationalité suisse et originaire de Tramelan (BE)

acceptée sur proposition du jury:

Prof. A. Musy, Prof. N. Perrin, directeurs de thèse
Prof. M.-J. Fortin, rapporteur
Prof. F. Golay, rapporteur
Prof. H. van Lier, rapporteur

Lausanne, EPFL
2003

Remerciements

Tout d’abord je tiens à remercier les personnes sans lesquelles cette aventure n’aurait jamais vu le jour, mes directeurs de thèse, le professeur André Musy et le professeur Nicolas Perrin qui m’ont tous deux accordé une grande confiance et m’ont permis de réaliser cette recherche dans d’excellentes conditions tant scientifiques qu’humaines. Mes remerciements vont également à Roland Prélaz-Droux et à Philippe Gmür qui ont initié et accompagné avec beaucoup d’intérêt cette recherche.

Mes excursions dans divers milieux de la science m’ont permis de rencontrer de nombreuses personnes, je remercie ainsi Nicolas Perrin et son groupe qui m’ont fait bénéficier de leurs connaissances et compétences dans le large domaine de l’écologie. Mes ascensions dans les systèmes d’informations géographiques et dans la programmation Delphi® et MapBasic® n’auraient pas eu lieu sans l’aide de Richard Metzger et de l’équipe des SIRS (actuellement LaSIG). J’ai également bénéficié de nombreux appuis de spécialistes : Pierre Fontanillas en génétique, Anne-Catherine Favre et Gorana Capkun en statistique, Marc Soutter pour les analyses dans S-Plus. Je remercie également Christine Gatabin, Stephane Joost, Abram Pointet, et Cécile Picouet pour leurs commentaires judicieux.

Merci à Ion Iorgulescu qui a bien voulu relire et commenter mon manuscrit, et qui m’a toujours accordé le secours de son expérience. Je tiens à remercier chaleureusement John Beck, pour sa patience et le travail qu’il a fourni lors de la correction de mes textes. Merci également à Michèle, Marie, Alexis et Abdel pour leur efficacité dans leurs taches administratives ou techniques.

Ma gratitude va également aux personnes qui ont accepté la charge d’évaluer ce travail: je remercie les professeurs Marie-Josée Fortin, François Golay et Hubert van Lier.

Cette recherche s'est déroulée dans d'excellentes conditions et ce, en grande partie grâce à l'excellente ambiance et au soutien de l'ensemble de l'équipe de l'Hydram. Ce travail n'aurait pas vu le jour sans le soutien et la bonne humeur de mes compagnons de café, virées, marches, chevauchées et escapades : Flavio, Cécile, Benoît, Fred, Bettina, Colin, Samuel, Henri, Richard, Nicolas, Alex, Christophe et tous les autres…

Je tiens à remercier plus particulièrement Indira, Muriel, Céline et ma sœur Stéphanie, qui ont toujours été là pour me soutenir, tout comme l'équipe « de la ferme » et plus particulièrement Cathy. Je suis très reconnaissante de l'appui de mes parents, ma famille et mes amis.

Enfin, j'aimerais te remercier, Yvan, pour toute l'attention que tu m'as portée pour cette fin de thèse. Merci pour tes encouragements et ta patience.

Cette recherche a été soutenue en partie par l'Office Fédérale de l'Environnement, des Forêts et du Paysage (OFEFP) et par Le Service des Forêts, de la Faune et de la Nature - Centre de Conservation de la faune et de la nature, le Service des Améliorations Foncières et Le Service de l'Agriculture du canton de Vaud, dans le cadre du projet AGICE (Agriculture et Gestion intégrée du Contexte Environnemental). Les données génétiques pour l'application du modèle développé ont été mises à disposition par l'Institut d'Ecologie de l'Université de Lausanne.

Abstract

In human-dominated landscapes, populations and species extinctions are directly related to habitat destruction and fragmentation. To provide genetic diversity as well as population viability, individual exchanges among isolated populations must be maintained. Therefore, animal dispersal processes in fragmented landscape become an important topic for ecologists, and ecological networks planning has become one of the major challenges for landscape planners. Identification of habitat patches as well as assessment of the effect of ecological networks is badly needed. Since little information on the effect of landscape heterogeneities on animal dispersal is available, simulation models are being developed. As dispersal pattern and success strongly depend on the spatial context, species' interactions with landscapes, species behaviour and species ability to disperse, these models must be able to simulate them explicitly.

This research work therefore aims first at developing methods and models that allow realistic animal dispersal simulations in fragmented landscapes. Second it aims at evaluating the effect of landscape heterogeneities and animal behaviour on dispersal and on species persistence. Additionally, the ability of such a model to estimate gene flow is analysed. To carry on this research, the following fields have been explored: landscape ecology, metapopulation dynamic, animal behaviour, genetics, Geographical Information Systems, modelling approaches and programming.

A method, based on properties provided by Geographical Information Systems software, is first proposed to generate ecological networks by simulating animal dispersal according to animal movement constraints induced by human infrastructures. The resulting maps provide a spatial identification of ecological networks, corridors and conflicting areas. This model has proved to be a useful and straightforward tool for landscape planning, even if this model, similar to other present-day models used in dispersal simulations, presents numerous technical and scientific limitations.

To improve models for animal dispersal, a feature-oriented landscape model associated with an expert system has been developed. Its conceptualisation, its formalism, its data structure and its object-oriented design implementation provide a very accurate representation of landscape features and simulation of complex interactions between model entities (individuals and landscape features) based on simple rules. It allows the spatial identification of simulated processes. The ability of this model to incorporate states, relations and transition rules between entities makes it applicable to simulate large ranges of dispersal processes according to specific behaviour and/or landscape uses.

To analyse the influence of landscape heterogeneities and species behaviour on dispersal and their incidence on metapopulation dynamics, the proposed feature-oriented model has been coupled with an animal model. The latter assigns different cognitive and dispersal abilities to individuals. Based on simulations according to three movement strategies (corresponding to the cognitive abilities of the simulated species), two measures evaluate the effect of cognitive abilities on dispersal: the colonisation probability between habitat patches and the ecological distance (due to landscape heterogeneities). These measures give an estimation of metapopulation structures (the habitat patches belonging to the metapopulation) and metapopulation dynamics induced by the landscape heterogeneities (for example, the habitat patches which release individuals). The complexity of dispersal processes, considering species behaviours and dispersal abilities, can therefore be reproduced and analysed at different levels. This application has shown the importance of animal behaviour on metapopulation dynamics and structure.

Since tracking animals and providing sufficient data remain difficult, calibration and validation procedures of dispersal models are difficult to perform. One approach proposed here is to measure one of the consequences of dispersal: genetic differentiation among populations. Geographical distances are in general used to explain a part of the genetic differentiations. But as our fundamental assumption states that landscape heterogeneities and spatial arrangements of landscape features may strongly affect dispersal successes, genetic distance between populations must be better explained by the estimate of a model which considers these factors. We have tested this assumption with the greater white-toothed shrew (*Crocidura russula*). Scenarios considering various behaviours and dispersal abilities of *C. russula* have been performed. Relating measures of genetic, geographical and ecological distances (the latter emerge from scenario simulation results) highlights the model capability to reproduce dispersal of *C. russula* by explaining a greater part of the genetic differentiation than that explained by the geographical distances. This application has not only pointed out the ability of the model to quantify connectivity between habitat patches but also the difficulty to relate gene dispersal and individual dispersal.

Résumé

Dans les paysages anthropiques, l'extinction des espèces et des populations est directement liée à la disparition et à la fragmentation des milieux. Pour assurer la viabilité des populations et la diversité génétique, les échanges d'individus entre les habitats doivent être maintenus. C'est pourquoi la dispersion de la faune dans les paysages fragmentés est devenue un champ d'étude essentiel pour les écologues et la mise en place de réseaux écologiques un des principaux défis pour les aménageurs. L'identification des habitats ainsi que l'estimation de l'effet des réseaux écologiques constituent donc un besoin de plus en plus important. Malheureusement, peu d'informations sur l'effet de l'hétérogénéité du paysage lors de la dispersion de la faune sont actuellement disponibles, c'est pourquoi des modèles de simulation sont développés. Comme le processus de dispersion est largement dépendant du contexte spatial, des interactions entre l'espèce et le paysage ainsi que du comportement et des capacités de dispersion de l'espèce considérée, ces modèles doivent offrir la possibilité de simuler ces facteurs de manière explicite.

Ce travail de recherche a donc pour objectif dans un premier temps le développement de méthodes et de modèles permettant de simuler de manière réaliste la dispersion de la faune dans un paysage fragmenté. Son second objectif est d'évaluer l'effet de l'hétérogénéité du paysage et du comportement animal sur la dispersion et la persistance des espèces. De plus, l'habilité de ce type de modèles à estimer les flux de gènes est analysée. Pour mener à bien cette recherche, les domaines suivants ont été explorés : l'écologie du paysage, la dynamique des métapopulations, le comportement animal, la génétique, les systèmes d'information géographique, la modélisation et la programmation.

Une méthode basée sur les propriétés qu'offrent les logiciels de système d'information géographique a tout d'abord été proposé pour générer un réseau écologique par simulation de la dispersion de la faune. Celle-ci tient compte des contraintes aux déplacements de la faune dues aux infrastructures humaines. Les cartes résultantes permettent une identification spatiale des réseaux écologiques, des corridors et des zones de conflits. Ce modèle s'est révélé être un outil rapide et simple pour la planification, bien qu'il présente, comme les modèles utilisés actuellement pour simuler la dispersion, de nombreuses limitations techniques et scientifiques.

Pour améliorer la modélisation du processus de dispersion, un modèle du paysage « orienté éléments » associé à un système expert a été développé. Sa conceptualisation, son formalisme, sa structuration de données et son implémentation en approche orienté-objet permettent une représentation réaliste des éléments du paysage et la simulation d'interactions complexes entre les entités du modèle (individu et éléments du paysage) sur la base de règles simples. Il permet une identification spatiale des processus simulés. Les aptitudes de ce modèle à incorporer les états, les relations et les règles de transitions entre les entités le rendent applicable pour simuler différents processus de dispersion selon un comportement spécifique et/ou une utilisation du paysage particulière.

Pour analyser l'influence de l'hétérogénéité du paysage et du comportement des espèces sur la dispersion et leurs impacts sur la dynamique des métapopulations, le modèle du paysage « orienté éléments » a été couplé avec un modèle « animal ». Ce dernier attribue différentes capacités cognitives et de dispersion aux individus. Sur la base de simulations selon trois stratégies de mouvement (relatives aux capacités cognitives des espèces simulées), deux mesures permettent d'évaluer l'effet des capacités cognitives sur la dispersion : la probabilité de colonisation entre deux habitats et la distance écologique (due à l'hétérogénéité du paysage). Ces mesures donnent une estimation de la structure de la métapopulation (quel habitat appartient à la métapopulation) et de la dynamique de métapopulation induite par l'hétérogénéité du paysage (par exemple, quels habitats ont tendance à libérer des individus). Le processus de dispersion qui prend en compte le comportement et les capacités de dispersion des espèces peut alors être reproduit et analysé à différents niveaux. Cette application a montré l'importance du comportement des espèces dans la dynamique d'une métapopulation et la structuration de celle-ci.

Au vu des difficultés relatives au suivi de la faune et au nombre de données nécessaires (le processus étudié ici correspond à des évènements rares) pour obtenir des statistiques fiables, les procédures de calibration et de validation des modèles de dispersion sont difficiles à réaliser. Une approche proposée ici est de mesurer une des conséquences de la dispersion : la différentiation génétique entre les populations. Considérant que les connections sont faibles lorsque les habitats sont distants, la distance géographique est généralement utilisée pour expliquer une part de la différentiation génétique entre les populations. Mais comme l'hypothèse de base suppose que l'hétérogénéité du paysage et l'arrangement spatial des éléments du paysage peuvent largement affecter le succès de la dispersion, la distance génétique entre les populations doit donc être mieux expliquée par les estimateurs du modèle qui tiennent compte des ces facteurs. L'hypothèse a été testée avec la musaraigne musette (*Crocidura russula*). Des scénarios considérant différents comportements et distances de dispersion de *C.russula* ont été réalisés. La mise en relation des mesures de distance génétique, géographique et écologique (issues des scénarios simulés) a montré l'aptitude du modèle à reproduire la dispersion de *C. russula.* En effet, le modèle donne une meilleure explication de la différentiation génétique entre les populations. Cette application a démontré l'aptitude du modèle à quantifier la connectivité entre les habitats mais a également montré les difficultés de mise en relation de la dispersion d'individus et celle de gènes.

Zusammenfassung

Die Zerstörung und Fragmentierung von Lebensräumen sind die Hauptgründe für das Aussterben von Arten und Populationen in vom Menschen veränderten Landschaften. Die Erhaltung von Arten und der genetischen Vielfalt hängt von der Vernetzung der Lebensräume ab. Deshalb interessiert sich die ökologische Forschung mehr und mehr für die Verbreitungsmöglichkeiten der Fauna, und für die Raumplanung ist die Erstellung von ökologischen Netzwerken eine neue Herausforderung geworden. Noch bestehende, intakte Lebensräume müssen identifiziert und der Nutzen von ökologischen Netzwerken bewertet werden. Zur Zeit gibt es nur wenig Information über die Auswirkung der landschaftlichen Heterogenität auf die Fauna. Daher werden Simulationsmodelle entwickelt. Die Verbreitungsmöglichkeiten der Fauna hängen von vielen Faktoren ab: z.B. die räumliche Umgebung, die Interaktionen zwischen Tierart und Landschaft oder artspezifisches Verhalten und Dispersionskapazität. Alle diese Faktoren müssen in solchen Modellen ausreichend klar simuliert werden.

Ein erstes Ziel dieser Studie ist das Erarbeiten von Methoden und Modellen für eine realistische Simulation der Ausbreitungsmöglichkeiten der Fauna in einer fragmentierten Landschaft. Als zweites Ziel will sie die Auswirkung von Landschaftsheterogenität und artspezifischem Verhalten auf die Ausbreitung und Überlebenschancen der Arten beurteilen. Ausserdem wird die Eignung solcher Modelle für eine Beurteilung des Genaustauschs geprüft. Folgende Gebiete wurden für diese Studie herangezogen: Landschaftsökologie, Metapopulationsdynamik, Verhaltensbiologie, Genetik, Geographische Informationssysteme, Modellierung und Programmation.

Basierend auf den Möglichkeiten der Geographischen Informationssysteme wurde zuerst eine Methode zur Erstellung eines ökologischen Netzwerkes ausgearbeitet. Die durch menschliche Infrastrukturen bedingten Behinderungen wurden in die Simulation der Ausbreitung der Fauna einbezogen. Auf den resultierenden Karten kann die räumliche Lage der ökologischen Netzwerke, Korridore und Konfliktzonen festgestellt werden. Trotz verschiedener technischer und wissenschaftlicher Einschränkungen, die den heutigen Dispersionsmodellen anhaften, stellte sich diese Methode als einfaches und rasches Planungsmittel heraus.

Um die Modellierung der Ausbreitung zu verbessern, wurde in einem nächsten Schritt ein „merkmalorientiertes“ Landschaftsmodell entwickelt, verbunden mit einem Expertensystem. Dank seines Konzepts, seiner Datenstruktur und objektorientierten Umsetzung, ermöglicht dieses Modell eine realistische Darstellung der Landschaftselemente sowie die Simulation komplexer Interaktionen zwischen den Einheiten (Individuum und Landschaftselement) aufgrund einfacher Regeln. Die räumliche Lage der simulierten Prozesse kann einfach festgestellt werden. Da dieses Modell Zustände, Beziehungen, aber auch Veränderungen zwischen den Einheiten einbezieht, eignet es sich zur Simulation verschiedener Ausbreitungsprozesse gemäss eines artspezifischen Verhaltens und/oder einer bestimmten Landschaftsnutzung.

Um den Einfluss der zahlreichen Formen von Landschaften und artspezifischem Verhalten auf die Ausbreitung und deren Auswirkungen auf die Metapopulationsdynamik zu analysieren, wurde das Landschaftsmodell mit einem „Tiermodell“ gekoppelt. Dieses Tiermodell ordnet den einzelnen Individuen unterschiedliche kognitive Begabungen und Ausbreitungsfähigkeiten zu. Anhand der Simulationen von drei Ausbreitungsstrategien (für unterschiedliche kognitive Fähigkeiten), kann mit Hilfe von zwei Grössen die Auswirkung der kognitiven Fähigkeiten auf die Ausbreitung beurteilt werden: die Wahrscheinlichkeit, dass ein Lebensraum kolonisiert wird und die ökologische Distanz (Resultat der Landschaftsheterogenität). Mit Hilfe dieser zwei Grössen kann die Struktur der Metapopulation (welcher Lebensraum gehört zur Metapopulation) sowie die Dynamik der Metapopulation (z.B. welche Lebensräume haben Individuenüberschüsse) beurteilt werden. Komplizierte Ausbreitungsprozesse werden somit wiederholbar und können in verschiedener Hinsicht analysiert werden. Diese Anwendung zeigte die Bedeutung artspezifischen Verhaltens für die Struktur und Dynamik einer Metapopulation auf.

Die Kalibrierung und Überprüfung von Ausbreitungsmodellen erweist sich als problematisch, einerseits aufgrund der Schwierigkeiten, der Fauna überhaupt zu folgen und andererseits, weil sehr viele Daten nötig sind für zuverlässige Statistiken (der hier studierte Prozess ist ein seltenes Phänomen). Eine Möglichkeit zur Überprüfung der Modelle ist die Messung der genetischen Differenzierung zwischen Populationen, eine Konsequenz der Ausbreitung. Im allgemeinen wird die geografische Distanz benützt, um einen Teil der genetischen Differenzierung zu erklären, da nur schwache Verbindungen zwischen Lebensräumen bestehen, wenn diese weit auseinander liegen. Unsere Ausgangshypothese fordert, dass die Landschaftsvielfalt und räumliche Verteilung der Landschaftselemente den Ausbreitungserfolg weitgehend beeinflussen. Das heisst, dass in unserm Fall die genetische Differenzierung besser durch die Modellvariablen, die diese Aspekte berücksichtigen, als durch die geografische Distanz erklärt werden müsste. Diese Hypothese wurde mit Hilfe der Hausspitzmaus (*Crocidura russula*) getestet. Mehrere Szenarien für unterschiedliche Verhaltensweisen und Ausbreitungsdistanzen der *C. russula* wurden definiert. Der Vergleich zwischen den verschiedenen Grössen, d.h. der genetischen, geografischen und ökologischen Distanz, zeigte, dass das Modell die Ausbreitung von *C. russula* und deren genetische Differenzierung besser zu erklären vermag als die geografische Distanz. Diese Anwendung demonstrierte einerseits die Eignung des Modells zur Quantifizierung der Vernetzung von Lebensräumen, und andererseits die Schwierigkeiten, denen Vergleiche zwischen der Individuen- und Genausbreitung unterworfen sind.

Outline of the thesis

The layout of this manuscript corresponds to the chronological progress of this research. The manuscript starts with two introductory chapters and then follows with chapters dealing with development and studies realized during this research, which have been published or submitted in international relevant journals. Papers are complied in their current state. The manuscript ends with a general synthesis and conclusions.

Chapter 1 introduces the scientific and management challenges as well as the objectives of this thesis.

Chapter 2 provides a scientific overview of the field of animal dispersal processes in a fragmented landscape. It focuses on dispersal modelling approaches at both individual and metapopulation levels. By describing dynamic processes during dispersal and among populations, it introduces concepts, theories and models relevant within the framework of this research. The models underlying assumptions and effectiveness in representing dispersal processes are also exposed. According to today's scientific background, specific relevant points needed in dispersal modelling at the individual and metapopulation levels are presented.

Chapter 3 proposes a new method to identify ecological networks focusing on the impacts of landscape structure, heterogeneities and human infrastructures. This method uses Geographical Information System (GIS) tools provided by the Idrisi® software and integrates movement constraints during animal dispersal. This method aims at identifying ecological networks and corridors at the farmstead as well as the metapopulation scale, at localising areas for renaturation, and at building links between habitat patches. Applications of the proposed method to game species prove its ability to be applied in a human disturbed landscape with a landscape representation at a fine scale and prove that it is easy to apply, easy to understand and capable of analysing scenarios for landscape management schemes within the Swiss context. Thus it provides new instruments for planning ecological networks.

Chapter 4 presents a new model for animal movement and dispersal modelling. The model has been developed in Borland® Delphi™, MapBasic® and MapInfo Professsional® developmental environments. This chapter first discusses the relevance of actual landscape models and, second proposes a new landscape model according to limitations in animal dispersal representation and assessment. Such a model allows different animal movements and landscape uses. It also provides information on landscape entities (shape, topological and typological information) and related interactions between them depending on their properties (neighbouring or distant relation). Thus animals can perceive a landscape entity as an attractor or repulsor.

Chapter 5 considers the question of the influence of landscape heterogeneities while taking into account species cognitive abilities (which induce different movement strategies) on colonization processes and its impact on metapopulation structure and dynamics. This question is a key point for management schemes and, if understood informs us about the planning strategy that should be considered according to species behaviour. In order to answer such a question, a new dispersal model associated with the landscape model presented in chapter 4 is used. The model allows species interactions with landscape features according to various animal dispersal and cognitive abilities. Simulations of individual dispersals in a fragmented landscape in Switzerland have been performed according to various movement strategies. Results, based on the simulation of dispersal processes at local scale (species interaction with landscape features), provide a characterization of the metapopulation structures (habitat patches encompassed) and dynamics (level of participation of a patch). Relevant implications in theoretical ecological fields are drawn up as well as management measures according to species behaviour in fragmented landscapes.

Chapter 6 aims to reproduce dispersal of the greater white-toothed shrew (*Crocidura russula* (Hermann, 1780)) in a highly fragmented landscape and to correlate results form dispersal simulation to genetic population differentiation measures (for genetic measures see *appendix A*). Dispersal simulations are performed with an adapted feature-oriented landscape model (chapter 4) and animal dispersal model (chapter 5). Thus, this chapter provides an application of the developments presented in previous chapters, compares simulated results with collected data and informs us on the ability to reproduce dispersal processes by comparison with genetic data. To capture the essence of *C. russula* dispersal, varying behaviour, dispersal distance and habitat patches are tested. With measures of *C. russula* genetic differentiation, simulations performed are analyzed. Genetic differentiation explanations provided by geographical distances are compared to that obtained by simulations results. Additionally, sensitivity analysis of the model is realized with the simulations performed.

Chapter 7 provides an overview of the research and presents the scientific and management contribution of this thesis and the potential application of the methods and models developed within this research. It finally identifies directions that could be explored in future research.

Appendix A introduces genetic processes among populations and estimations of genetic differentiation between populations, and appendix B summarizes statistics used in chapter 6.

Table of contents

CHAPTER 3: MAP OF ECOLOGICAL NETWORKS FOR LANDSCAPE PLANNING 29

CHAPTER 4: A FEATURE-ORIENTED LANDSCAPE MODEL FOR ANIMAL MOVEMENT AND BEHAVIOUR ASSESSMENT 49

Chapter 1

Introduction

Why do species and populations go extinct?

One of the most serious threats to biological diversity worldwide is the destruction of habitat and fragmentation due to human actions (Saunders et al. 1991, Harrison and Bruna 1999, Britton et al. 2001). Destruction of habitat may be due to the conversion of one habitat type into another (e.g for agriculture) and the modification of conditions within an habitat (e.g managing a natural forest) (Calow et al. 1998). As an example, tropical closed forests have been estimated to disappear at at a rate of 10.7 million ha/year (Houghton 1994), which corresponds to an area greater than Switzerland (Britton et al. 2001). To avoid habitat destruction, land surface has been set as reserves (around 5% of the planet's land surface is in reserves (Pimm and Lawton 1998)) that are protected to one degree or another. The basic role of reserves is to separate elements of biodiversity from processes that threaten their existence in the wild (Margules and Pressey 2000). Consequently, conservation reserves are frequently portrayed as " Islands of natural habitat within a sea of developed land" (Wien 1995). Thus, habitat destruction leaves the remaining habitats scattered through the landscape. This process is "fragmentation", defined as, *"a disintegration into small, spatially disjoint patches, separated by land which is unsuitable"* (Opdam et al. 1993).

Both habitat destruction and fragmentation due to human activities drive populations to extinction at a rate of 100 times greater than the natural rate (Pimm et al. 1995). This deterministic process leads to an overall birth-deficit (Harrison 1991, Verboom et al. 1993), but extinctions may also occur because of stochasticity in demographic, genetic and environmental processes and/or catastrophic events (Shaffer 1981):

- Extinction due to demographic stochasticity concerns the changes in population size caused by randomness in the order of “birth and death” occurrence.

- Genetic stochasticity refers to the loss of genetic diversity. Without the influx of individuals from other populations, a population's genome stagnates and loses the genetic variability to adapt to changing conditions or loses fitness due to inbreeding (see *appendix A*, genetic processes among populations).

- Environmental stochasticity and catastrophes cause temporal variations of the net-growth rate in a population, which enhances extinction risks.

According to general causes of extinction in fragmented habitat, one of the major challenges to avoid extinction is to conserve sufficient habitats (in area and quality) but also to promote exchanges of individuals among these habitats. The latter one is tackled within the framework of this thesis.

Ecological networks

Practically, the negative effects of fragmentation on populations can be reduced by connecting isolated fragments through landscape corridors (Wolff 1999), which form, with habitats, ecological networks. The potential effectiveness of such linkages is still in debate in the scientific community. In a review of advantages and disadvantages of linkages for biodiversity conservation, Bennett (1999) reports the following advantages: (i) an increase in immigration rates to an isolated habitat, which maintain a higher species richness and diversity, (ii) supplemental individuals to declining populations (‘rescue’ effects), (iii) the (re-)establishment of unoccupied habitats and (iv) enhanced genetic variation reducing the risk of inbreeding depression (see *appendix A*), while the disadvantages include (i) spreading of diseases, by unwanted species such as pests, weeds and exotic species, (ii) introduction of new genes which could disrupt local adaptations and co-adapted gene complexes and promote hybridation between previously disjoint taxonomic forms, (iii) exposing animals to competitors, parasites, predators and other sources of mortality (roads), (iv) inducing dynamics acting as “sink habitat” in which mortality exceeds reproduction, and thus functions as a “drain” on the regional population, and (v) spreading of fire or other abiotic disturbances. For fragmented landscapes, connectivity will be considered a priori as an advantage in this thesis.

Other criticisms and scepticisms concern the type of linkage (Bennett 1999), according to the diversity of land used by species. Practical measures to enhance connectivity may concern the whole landscape, habitat corridors (continuous connections) or specific various sizes and spacing habitats/landscape structures (hedges, copses).

Additional difficulties in management and design of ecological networks and corridors is due to the lack of scientific knowledge in the field. Factors like the scale of species movement, their habitat requirements, their tolerance of disturbance processes and factors that constrain or enhance their movement through human-dominated landscape, are not well known (Lima and Zollner 1996, Cabeza and Moilanen 2001).

Conservation plans integrating ecological networks are now under construction. In Europe for example, *the Pan-European Ecological Network* identifies natural areas with nature values of European importance and provides ecological coherence between relevant areas (Council of Europe 1999) and *Natura 2000* (European Commmission 2003) joint-ventured with the *Bern Convention's Emerald Network* (Council of Europe 1997) aims at assuring the long-term survival of Europe's most valuable and threatened species and habitats within the *European Ecological Network*. In a majority of countries around the world one can find national, regional or local projects that aim at connecting habitat patches (e.g. Bennett (1999)). They encompass a large range of spatial scale and level of sophistication, from artificial tunnel and underpasses that assist animal to move across barriers such as roads to corridors between national parks.

Synthesis and general objectives

Habitat fragmentation is one of the main causes of both species and population extinction since it inhibits exchanges of individuals between habitat patches. In a fragmented landscape, connectivity is a key question for conservation and management (Wiens 1995), since it determines the exchanges of individuals among habitats, thus avoiding species and population extinctions. Due to the global significance of species conservation, management schemes are actually applied even though the merit of corridors and ecological networks are still in debate. Guidelines for landscape design and management are today a must due to the lack of information concerning the position and the type of connecting structures that enhance connectivity between habitat patches. Increasing demands concern:

- Identification of the area over which management has to be applied either to increase (conservation) or decrease (pest control) a species of interest (Margules and Pressey 2000, Thomas 2001).
- Assessment of the effect of mitigating measures (e.g restoring linear landscape elements) or measures that add to fragmentation (e.g construction of roads and railways) (Verboom et al. 1993).

In order to reach such objectives, the processes involved between habitats patches must be better understood.

From an ecological point of view, connectivity facilitates exchanges of individuals among populations, which occur when individuals disperse from one habitat patch to another. When dispersal occurs, exchanges will modify dynamics among and within populations and, as a consequence, will modify the genetics within a population (*appendix A*). Resulting metapopulation dynamics and gene flow will then determine species and population viability (see *chapter 2*).

Dispersal is a complex process that differs according to species and landscape structure (Lima and Zollner 1996). Species and individual traits, such as dispersal movement, behaviour and physiological states (see *chapter 2*) define their ability to disperse and colonise new habitat patches. This process occurs, in a heterogeneous environment: the landscape. This is a complex system in which the position, arrangement, shape and properties of landscape entities might affect ecological processes. To handle such complexity, models have been developed aiming at providing a better understanding of the processes concerned and the consequences of dispersal at different levels (see *chapter 2*).

The main objective of this research work is the development of a spatially explicit dispersal model to reproduce dispersal processes in fragmented landscapes. This model has to be efficient in regard to species representation and must simulate species interaction with landscape in a realistic way at individual and metapopulation scales.

Special emphasis will be given to:

Chapter 2: What is the actual general background in dispersal processes and which models capture these processes and their consequences at both individual and metapopulation levels? What are the gaps in the latter field?

Chapter 3: How can current tools in GIS software help in determining ecological networks in a fragmented landscape? Which methods can be developed to consider landscape constraints in dispersal processes and to generate ecological networks representation? What kind of information can be drawn from it?

Chapter 4: What are the current landscape models used in simulation of dispersal processes? What are their limitations? What are the technical developments needed to overcome such limitations? How can landscapes be represented to assess complex dispersal processes in heterogeneous landscapes? What kind of application can be performed with such a model?

Chapter 5: What is the effect of species movement behaviour and dispersal ability at local and metapopulation levels? How can these differences be measured?

Chapter 6: Can spatially explicit dispersal models explain genetic differentiation between populations? Can genetic data be related to individual dispersal? What are the obstacles to such an approach?

Chapter 7: What are the scientific issues for dispersal modelling? What are the quantitative and qualitative values that can be extracted from dispersal modelling? What management recommendations can modelling approaches provide? What do we have to learn for future investigations?

References

Bennett, A. F. 1999. Linkages in the Landscape: The role of corridors and connectivity in wildlife conservation. IUCN, Gland, Switzerland and Cambridge, UK.

Britton, N. F., G. P. Boswell, and N. R. Franks. 2001. Dispersal and conservation in heterogeneous landscapes. Pages 299-320 *in* I. P. Woiwod, D. R. Reynolds, and C. D. Thomas, editors. Insect Movement: Mechanisms and Consequences: proceedings of the Royal Entomological Society's 20th Symposium. CABI Publishing, Oxon.

Cabeza, M., and A. Moilanen. 2001. Design of reserve networks and the persistence of biodiversity. Trends in Ecology and Evolution 16:242-248.

Calow, P. E.-i.-c., E. Board:, D. A. Falk, J. Grace, P. D. Moore, B. Shorrocks, and S. C. Stearns, editors. 1998. The Encyclopedia of Ecology and Environmental Management, Blackwell Science edition.

Council of Europe. 1997. The EMERALD Network - a network of Areas of Special Conservation Interest for Europe. Committee for the Convention on the Conservation of European Wildlife and Natural Habitats, Strasbourg.

Council of Europe. 1999. Nature conservation sites designated in application of international instruments at pan-European level. Council of Europe.

European Commmission. 2003. Commission working document on Natura 2000. European Commmission, DGXI -Environment.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biological Journal of the Linnean Society 42:73-88.

Harrison, S., and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography 22:225-232.

Houghton, R. A. 1994. The worldwide extent of land-use change. BioScience:305-313.

Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution 11:131-135.

Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. Nature 405:243-253.

Opdam, P., R. van Apeldoorn, A. Schotman, and J. Kalkhoven. 1993. Population responses to landscape fragmentation. Pages 147-171 *in* C. C. V. a. P. Opdam, editor. Landscape ecology of a stressed environment. Chapman and Hall, London.

Pimm, S. L., and J. H. Lawton. 1998. Planning for biodiversity. Science 279:2068-2069.

Pimm, S. L., J. L. Russell, J. L. Gittleman, and T. M. Books. 1995. The future of biodiversity. Science:347-350.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5:18-32.

Thomas, C. D. 2001. Scale, dispersal and population structure. Pages 321-336 *in* I. P. Woiwod, D. R. Reynolds, and C. D. Thomas, editors. Insect Movement: Mechanisms and Consequences: proceedings of the Royal Entomological Society's 20th Symposium. CABI Publishing, Oxon.

Verboom, J., J. A. J. Metz, and E. Meelis. 1993. Metapopulation models for impact assessment of fragmentation. *in* C. C. V. a. P. Opdam, editor. Landscape Ecology of a Stressed Environment. Chapman and Hall, London.

Wien, J. A. 1995. Landscape mosaic and ecological theory. Pages 1-26 *in* L. L. Hansson, Fahrig and G. Merriam, editor. Mosaic Landscapes and Ecological Processes. Chapman and Hall, London.

Wolff, J. O. 1999. Behavioral Model Systems. Pages 11-40 *in* G. W. Barrett and J. D. Peles, editors. Landscape Ecology of Small Mammals. Springer-Verlag, New York.

Chapter 2

Background

Animal dispersal processes

Dispersal, definition and terminology

Dispersal links ecology, population genetics, ethology and evolution, within which all investigators do not agree on a terminology (migration, colonisation, dispersal, movement, etc…) (Stenseth and Lidicker 1992). From the ecological point of view, “dispersal” means one-way movements of individuals outside their home ranges (sites) with no return (Jander 1975, Lidicker and Stenseth 1992, Stenseth and Lidicker 1992, Dingle 2001). This definition differs from movements that keep the organisms within their home ranges like foraging and round trips (Dingle, 1996). According to Lidicker and Stenseth (1992), nomadism, exploration, and shifting are excluded from “true” dispersal, which can be divided in three phases: leaving, travelling, and arriving. From a genetic point of view, dispersal or gene flow is considered as a movement of genes, and their subsequent incorporation into a new gene pool (Endler 1977, Gaines and McClenaghan 1980, Barton 1992). It means that dispersers becomes “effective migrants” if they reproduce. In the metapopulation[1] field, dispersal or migration refers to the overall processes while colonisation only indicates a dispersal event between two habitat patches (Hanski 1999).

The boundaries between the underlying processes and the definition of dispersal are not so clear, so, within the framework of this thesis, dispersal refers to the general processes of individuals leaving a habitat patch and travelling in order to join other habitat patches; colonisation processes refer to an individual that leaves a habitat patch, travels and arrives in a new habitat patch area (empty or

---

[1] Metapopulation refers to a population of local populations (Levins 1969, 1970, Hanski 1999)

not); the genetic point of view on dispersal refers to the incorporation in populations of new genes coming from other populations.

Moreover, dispersal may also include the scattering of seeds, pollen, larvae, adults (males, females) and juveniles (Bitton et al. 2001). The character of such dispersers induces variable consequences for population dynamics, settlement and genetic flow as well as interpretation within the effectiveness of dispersal processes.

Why do organisms disperse?

Leaving a habitat can be explained by both ultimate (evolutionary) and proximate (triggering) factors (Lidicker and Stenseth 1992). Ultimate factors are environmental fluctuations, kin competition avoidance and inbreeding avoidance. The proximate factors that are most likely to affect dispersal decisions at the population level can be linked to (Johnson and Gaines 1990, Hanski 1999): (i) population density (crowded conditions or escaping imminent extinction), (ii) scarcity of resources or (iii) parent-offspring conflicts and (iv) conspecific attraction. In some cases proximate mechanisms are closely allied to ultimate factors and the immediate stimulus leading to dispersal may be quite different and functionally disconnected from any evolutionary issue (Hansson 1991, Lidicker and Stenseth 1992).

The reasons and causes of dispersal are many. In this thesis, organisms are assumed to disperse in a metapopulation system in which environmental fluctuations are important. Other causes of dispersal will not be taken into account specifically.

The dispersal abilities

Dispersal abilities determine dispersal successes and vary among and within species although they depend on the following factors (Bell 1991, Lidicker and Stenseth 1992).

First, species internal factors refer to (i) characteristics and abilities for an animal to disperse, this includes its perceptual and locomotory skills and physiological needs (Bell 1991, Lidicker and Stenseth 1992), (ii) behavioural systems (Koenig et al. 1996) and patterns of movements are determined by complex behaviours (Thomas et al. 2000) and (iii) life history (Bell 1991, Koenig et al. 1996, Wolff 1999), meaning that if a species evolves in a stable and continuous habitat (as specialists), it may respond very differently to a fragmented habitat compared to a species that evolves in a patchy or frequently disturbed environment (generalists) (Bell 1991, Lima and Zollner 1996). Generalists use numerous specific habitats, according to different feeding and nesting areas, seasonally available resources, and sex-specific requirements; while, species that are habitat specialists avoid mosaics since they perceive them as a barrier to dispersal (Wolff 1999). Moreover, it is obvious that internal factors are altered by age, reproductive status or external environmental influences (Lidicker and Stenseth 1992).

Second, species external factors concern (i) variability of biotic and abiotic conditions of the dispersal area (Bell 1991), (ii) distribution and risks generated while trying to obtain resources (competition, predators and parasites, abiotic influences) and (iii) sociality (Wolff 1999). Dispersal abilities may be limited due to the social structures of a species (as in most mammalian), as in the situation in which individuals actively defend territories (Wolff 1997, Wolff and Peterson 1998).

According to factors affecting dispersal, Wolff (1999) proposes a classification of characteristics that make species good or poor disperser in a fragmented landscape (see *table 1*). The dominance of one factor over the others depends on the species studied and thus must be carefully analysed for each of them.

Table 1: Summary of the characteristics of species further defined as "good" or "poor" colonizers of fragmented landscapes as measured by their ability to disperse (Wolff 1999).

Life history characteristics	**Dispersal ability**
Mode of life	Aerial > terrestrial > arboreal > fossorials > freshwater
Degree of specialisation	Generalist > specialists
Spacing behaviour	Non territorial > territorial
Body size	Large > small
Trophic level	Carnivores > omnivores > herbivores
Mobility	Migratory > non migratory
Sociality	Asocial > social / Conspecific attraction

Animal orientation during dispersal

According to "active" dispersal processes (species may disperse "passively" with wind, water currents), it is often assumed that animal movement occurs in order to optimise animal chances of locating suitable habitat and to reduce those of revisiting unsuitable one. Theoretically, in unknown places and without environmental cues, only two search strategies are possible:

1. A purely random walk in which each successive step is randomised in a direction (Wu et al. 2000, Dumont and Hill 2001) and/or length (Okubo 1986, Sobol 1994, With et al. 1997, Bergman et al. 2000) according to its previous step (*figure 1*) that allows dispersers to move randomly to any point of the landscape area. However, the disadvantage of a random walk to locate resources is the high probability of crossing the previous track and entering areas already searched, thus restricting the area that is explored. No examples of purely random movements, even in micro-organisms have been found (Bell 1991).

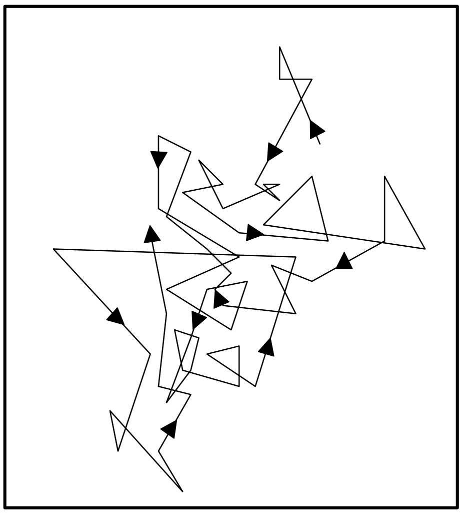


Figure 1: Random walk search strategy when no information is available

2. A correlated random walk implying that the distributions of step lengths and/or turning angles do not change randomly during the course of dispersal (*figure 2*). It is the most efficient strategy, when no information is available about the positions of resources in space (the most likely distribution of resources is patchy) (Jander 1975). Most species supplement straight moves by periodic turns to avoid getting locked into an unprofitable path direction (Bell 1991). For example, birds tend to alternate between left and right turns (i.e thrushes, Smith (1974)). Such a model of searching behaviour has permitted to simulate caribou movements (Bergman et al. 2000). Related movements do concern systematic strategies such as ever-widening spiral, parallel sweeps or looping from a central pivot point.

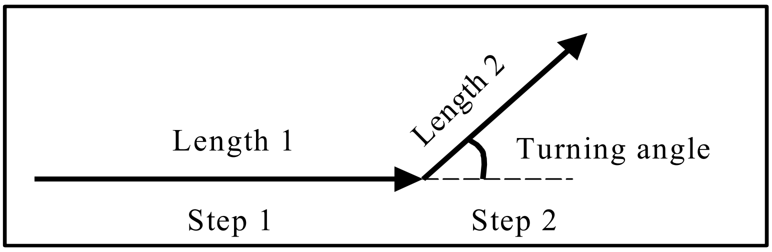


Figure 2: Correlated random walk with changes in turning angles and step lengths

With environmental cues, searching strategies grow more complex. From studies, it seems obvious that most species are incapable of moving very far in a perfectly straight line without some kind of external assistance (topographic or celestial cue). Information about potential distant resource patches can be gained through direct sensory input, for example, through physical contact or even visual, chemical or auditory mechanisms (Bell 1991). One form of directional information for vertebrates is the perceptual range, which concerns the distance from which a particular landscape element (patch) can be perceived by a given animal (Lima and Zollner 1996, Zollner and Lima 1999a, Zollner 2000). Such perceptual abilities are important to consider because they influence an animal's probability to successfully disperse to a new patch in a landscape (avoid high risk of mortality since it would spend less time searching (Lima and Zollner 1996)).

Habitat patch choice

An animal chooses its habitat patch according to the time and energy available for searching, the probability that additional searching will improve the eventual choice, as well as the degree to which continued searching for an even better habitat will change the searcher's fitness (Bell 1991). The way organisms maximize the use of time, matter, and energy can be examined according to the cost and benefits including food, mates, etc. that are incurred by the searching behaviours (Bell 1991, Aborn and Moore 1997) (which is described by the optimal foraging theory (Stephens and Krebs 1986)). The costs include the energy expended on movement, the risk of predation while engaged in searching, but also the time taken away from other activities. In some instances travel costs may be inconsequential while in others they can be considerable. Many animals' dispersal events require considerable investment in terms of time and energy. This process is enhanced by the effect of landscape structures on movement behaviour (Peles et al. 1999).

Wildlife managers dedicated considerable time and research to determine how animals judge the suitability and quality of their habitat (Reed and Dobson 1993). A habitat is partially assessed by the quality of the resources within it. Assessment criteria include: evaluation of the presence of resources and other users or competitors (Bell 1991). The fact that territorial animals are attracted to conspecifics has been largely observed (Stamps 1988). Thus, conspecifics are indicators of habitat quality (Kiester and Slatkim 1974, Reed and Dobson 1993) or may intrinsically affect reproductive success (Reed and Dobson 1993). Understanding the reason ruling animal decision is of interest not only to the theoretical biologist or behavioural ecologist, but is of major importance to site managers, policy makers and conservation biologists specifically in terms of protection and management.

Dispersal environment

The environment in which dispersal occurs affects animal travel paths whatever its dispersal strategies and ability. The area concerned by the dispersal is a heterogeneous environment (Wiens 1995). Thus, resistances to movement vary and lead to an overall directionality in movements (Bennett 1999, Haddad 1999).

In terrestrial dispersal, landscapes constitute the area in which dispersal occurs between two habitat patches, forming a mosaic of patches of different shapes, sizes, arrangement and suitability (Wiens 1995), which affect dispersal by adding attractiveness, repulsiveness or barriers. In dispersal processes detailed analysis of landscape-movement cannot be ignored (Wiens 2001). However, to tackle such processes, landscape heterogeneity has to be explicitly considered.

Conclusion on animal dispersal processes

Dispersal processes in fragmented landscapes constitute one of conservationists' major focuses; this process is complex and thus must be represented with at least a part of its complexity. Among factors involved in dispersal processes, environmental heterogeneities, animal abilities (dispersal distance and cues) and behaviour during dispersal seem to be predominant.

In conservation ecology studies that deal with animal movements in a heterogeneous landscape, dispersal cues are often neglected due to the difficulty to incorporate such abilities in models, and behavioural traits of individual are usually not considered (Sutherland and Gosling 2000) even if they strongly affect dispersal success by either impeding or promoting dispersal.

Understanding how pattern movements are affected by the spatial structure of the environment is a key question for landscape ecologists (Wiens 1995, Diffendorfer et al. 1999). Field experiments may also help in estimating dispersal parameters by capture-recapture, mark-resight data or tracking measures (Bennetts et al. 2001). But, unfortunately, they require large quantities of data, are difficult to obtain, are time consuming and expensive, and lead to further problems of interpretation (Hestbeck 1982, Smith and Peacock 1990, Koenig et al. 1996, Wolff 1999). This is the case often when scientists deal with dispersal processes that imply a movement of an individual from a population to another (rare event) and exclude the home range movements. Under such circumstances, it obviously becomes difficult to distinguish individuals moving within their home range from those dispersing.

To capture such complex systems, simulations by modelling approaches are presented in the next sections.

Methods: Simulation approaches

Introduction

Simulation refers to a set of techniques which lead to the development of models that help one to understand the behaviour of a system, whether real or hypothetical (Bennett 1995). Simulation is used when a system remains globally intractable. By duplicating a system or part of a system and by putting it into mathematical relationships or any other abstract forms, with the assistance of computers it becomes possible to better understand and forecast its behaviour. The form of the model depends on information expected to be obtained by simulation. The information yielded by simulation is different from that obtained from other design tools, because it allows an examination of the dynamic behaviour of system models and enables its application to hypothetical conditions.

In the following sections, two main theoretical models are presented: a metapopulation model and an individual-based model. The first model considers the global aspects of dispersal processes by quantifying the exchange rates of individual among populations (*figure 3*), providing simulation of dispersal processes and estimation of its influence on metapopulations. The second model describes dispersal processes at the local scale encompassing individual interactions with the direct environment (*figure 4*). It therefore allows a detailed description of local individual-landscape interactions.

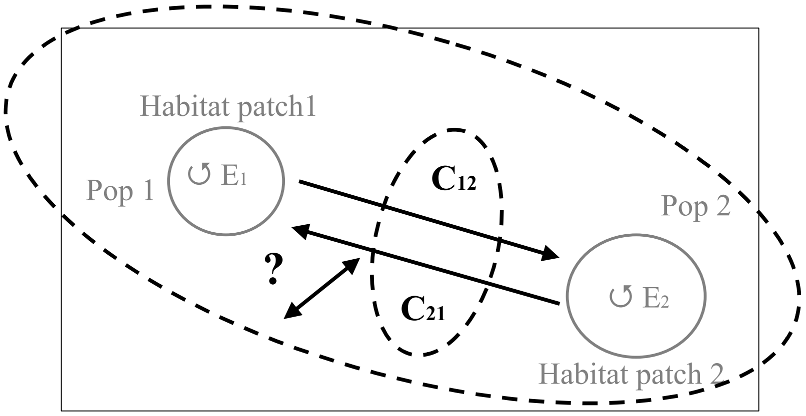


Figure 3: Dispersal processes in a metapopulation composed of two populations and the analysis of its influence on the metapopulation dynamics and structure. In this figure, metapopulation is composed of two populations (Pop 1 and Pop 2) settled in two habitat patches in which extinction processes occur (E_1 and E_2).

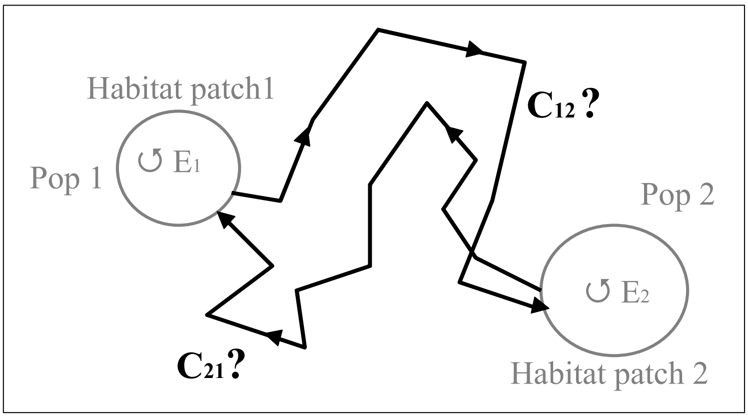


Figure 4: Dispersal processes in a metapopulation composed of two populations according to environmental factors, animal behaviour and landscape use. In this figure, the metapopulation is composed of two populations settled in two habitat patches in which extinction processes occur.

An analytical model at the metapopulation level

Introduction

A metapopulation has been defined by Levins (1969) as "a population of local populations" living in an infinitely large patch network surrounded by uniformly unsuitable habitat. Conservation biologists have developed metapopulation dynamics to predict populations' responses to fragmentation (Hanski and Simberloff 1997, Hanski 1999). The metapopulation concept follows the "*Theory of Island Biogeography*" (MacArthur and Wilson 1967) which focuses on the extinction and colonization processes of oceanic islands and which has quickly been recognized as being equally applicable to terrestrial patchy "islands" of local populations. Levins (1969, 1970) proposed a simple model of metapopulation dynamics based on the idea that the persistence of a metapopulation results from a stochastic balance between local extinction and colonisation related to the dynamics of the populations and the environmental conditions that characterise their habitat.

Levins (1969) modelled the rate of change in metapopulations *p*, measured by the fraction of habitat patches occupied at time *t*. Changes in *p* are then given by:

$$\frac{dp}{dt} = cp(1-p) - ep \qquad \textit{Equation 1}$$

Where *c* is the colonisation rate and *e* the extinction rate.

The equilibrium value of *p* is: $\hat{p} = 1 - \frac{e}{c}$ .The model may have at most one positive equilibrium point, the value of which increases with decreasing *e/c*. When the value of *e/c* is equal to or less than one, the metapopulation goes extinct, *p=0*.

Levins' model (1969) assumes that, on a time-scale of extinction and recolonisation, local dynamics can be ignored and that all local populations within a metapopulation are equally subject to extinction and therefore equally contribute to colonisation. Drechsler and Wissel (1997) show that the local dynamic ignorance assumption can be justified when (i) the immigration rate is sufficiently low in comparison with the intrinsic rate of population increase and (ii) the variance of the growth rate is lower than the average growth rate minus the emigration rate. According to Hanski (1999), there is evidence that metapopulation–level processes matter in population dynamics. For example: colonisation rate, extinction risk and population density are affected by patch area and isolation. It is obvious that due to habitat patch distribution in a landscape, each population is not equally able to give and receive migrants from all other populations. Another implication of Levins' model is that, if all local populations have substantial risks of local extinction, long-term survival is possible only at the metapopulation level, even though there is not many convincing empirical examples (Harrison 1991).

Because of these unrealistic assumptions, Hanski and Gyllenberg (1997) developed a spatially realistic version of Levins' model for a finite number of habitat patches of known areas and spatial locations, which can be constructed by modelling the rate of change in the probability of patch *i* being occupied as:

$$\frac{dp_i(t)}{dt} = \left(\text{Colonisation rate}_i\right)\left[1 - p_i(t)\right] - (\text{Extinction rate}_i)\left[p_i(t)\right] \qquad \textit{Equation 2}$$

$$\text{Extinction rate}_i = \frac{e}{A_i} \qquad \textit{Equation 3}$$

$$\text{Colonisation rate}_i = c\sum_{j \neq i} \exp\left(-\alpha d_{ij}\right) A_j p_j(t) \qquad \textit{Equation 4}$$

With:

A_i : Area of patch i

d_{ij} : Distance between patches i and j

$\frac{1}{\alpha}$: Average migration distance

e et c: Constants

This model introduces two additional variables: the patch area and the distances between patches, which both affect local extinction and colonisation (*figure 5*), but explicitly integrates the metapopulation structure and enables an analysis of the patch occupancy evolution at each habitat patch with respect to time (see for example *figure 6*).

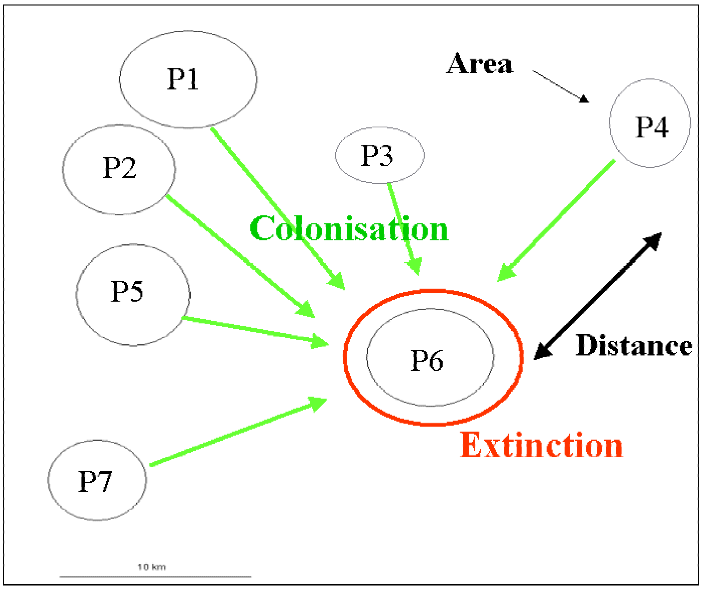


Figure 5: Illustration of the Hanski and Gyllenberg (1997) model. In a metapopulation composed of eight habitat patches, at time t the colonisation rate in the habitat patch 6 depends on its distance to each habitat patch and its area (pool of migrants). The extinction rate depends on the habitat patch area.

In such a metapopulation system, there are four possible scenarios of metapopulation extinction (Hanski 1991): (i) *No positive equilibrium point*. It is the most fundamental cause of metapopulation extinction: the rate of establishment of a new local population (colonisation rate) is lower than the rate of local extinction when p is small (highlighted by Levins's (1969) model (*equation 1*)). Conservation biologists are interested in this result because environmental changes induced by human activities may increase the extinction rate or decrease the colonisation rate in such a way that metapopulation extinction becomes inevitable (Hanski 1991). (ii) *Alternative equilibra*: If there are two stable equilibra, one of them corresponds to metapopulation extinction. It is important to consider when, in a metapopulation, immigration makes a substantial contribution to local population growth and when introducing species (Hanski 1991). If an alternative equilibira exists, the introduction should consist of large enough individuals, located close enough to each other to facilitate dispersal between them as demonstrated by the critically endangered black-footed ferret (*Mustela nigripes*) in North America (Clark et al. 1987). (iii) *Immigration-extinction stochasticity* is a potential cause of metapopulation extinction when the number of local populations is small. (iv) *Regional stochasticity*: The spatial scales over which population dynamics are synchronised by different kinds of regional stochasticity remain largely unexplored.

The metapopulation model provides an estimation of patch-specific colonization and extinction probabilities for a particular network of habitat patches, enabling predictions about patch occupancy, dynamics, and regional population persistence.

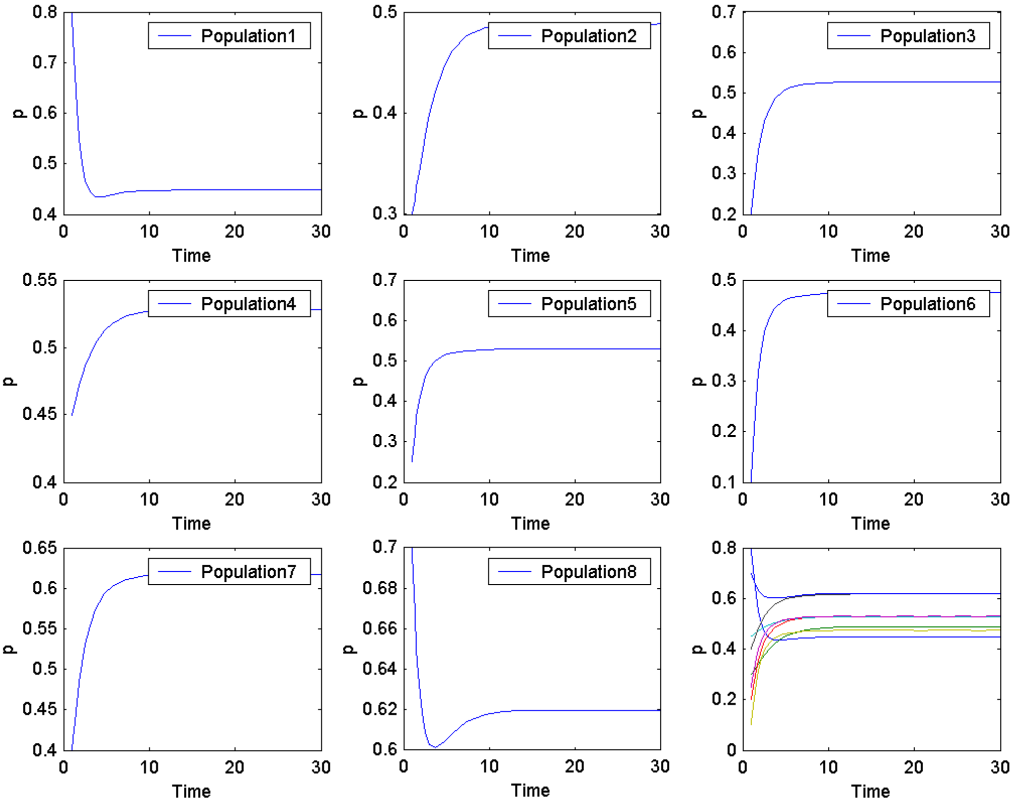


Figure 6: Illustration of the variation of the fraction of habitat patches (p) occupied at time t, in a metapopulation formed by eight habitat patches in a fragmented landscape (c>e). In this case, the spatial structure of the metapopulation leads to a homogenisation of the fraction of habitat patches occupied.

Metapopulation capacity of a fragmented landscape

The long-term and large-scale persistence of species in a fragmented landscape can be quantified by a deterministic threshold condition for metapopulation persistence. Based on Hanski's (1999) spatially-explicit metapopulation model *(equation 2*), Hanski and Ovaskainen (2000) define the *Metapopulation Capacity,* w_k, of a fragmented landscape. According to *equations 2, 3* and *4,* change in the probability of patch *i* being occupied is:

$$\frac{dp_i(t)}{dt} = \left(c\sum_{j\neq i} \exp\left(-\alpha d_{ij}\right) A_j p_j(t) \right)[1-p_i(t)] - \left(\frac{e}{A_i}\right)[p_i(t)] \qquad \textit{Equation 5}$$

and in a matrix form:

$$\mathrm{diag}(A)\overrightarrow{\frac{dp}{dt}} = cK\vec{p} - \mathrm{diag}(\vec{p})cK\vec{p} - e\vec{p} \qquad \textit{Equation 6}$$

with matrix K, so as:

$$K_{ij} \begin{cases} = \exp(-\alpha d_{ij})A_i A_j & \text{for } j \neq i \\ = 0 & \text{for } j = i \end{cases}$$

The *Metapopulation Capacity* w_k of a fragmented landscape corresponds to the leading eigenvalue of the matrix K (landscape matrix, condensing the effects of habitat patch area and connectivity on extinction and colonisation). It can be shown that an equilibrium solution with $p_i^* \succ 0$ for all *i* exists if and only if $w_k \succ \frac{e}{c}$, thus persistence depends on both the structure of the landscape, w_k,and the properties of the species (e/c).

Furthermore, the *Metapopulation Capacity,* w_k, is a good approximation of the sum of contributions from individual habitat patches and thus leads to a quantification of the contribution of different patches (*equation 7*). Additionally, Hanski and Ovaskainen (2000) propose to characterise the increase of the metapopulation capacity by adding a new patch to a specific location (*equation 8*).

$$w_i \equiv x_i^2 w_k \qquad \textit{Equation 7}$$

With w_i : the contribution of fragment *i*

x_i : the *i*th element in the leading eigenvector of matrix K (the value of x_i^2 is scaled to sum up to unity)

$$w_m = \frac{A_m^2}{w_k}\left(\sum_{j \neq m} \exp\left(-\alpha d_{jm}\right) A_j x_j(t)\right)^2 \qquad \textit{Equation 8}$$

With

d_{jm} : distance from the existing patches *j* to the hypothetical patch *m*.

A_m : area of the new patch *m*

The *Metapopulation Capacity* of a fragmented landscape measures the impact of landscape structures on metapopulation persistence. For a spatially extended population, this indicator provides (i) a classification and a comparison of various landscapes according to their capacity of supporting a viable population; (ii) a quantification of the contribution of each patch to the metapopulation capacity; (iii) an analysis of the impact of a landscape modification on the long-term viability of a species and (iv) an evaluation of various scenarios of landscape planning. Unfortunately, this model leads to difficulties in interpretation mainly because of the:

(a) *Temporal scale*. The metapopulation extinction or metapopulation equilibrium is considered with a probability equivalent and independent of time (Harrison 1991). For example, in a landscape, the dispersal abilities, extinction and colonisation rates as well as the spatial arrangement and size of habitat patches of a studied species may lead to a viable metapopulation while the metapopulation equilibrium for this species may not be reached.

(b) *Local population dynamic ignorance*[2]. The metapopulation model neglects the local dynamics (as in Levins' model discussed above) and assumes that the area of habitat patches can represent the population. Therefore, patch areas must be well correlated to the number of individuals within, although this does not seem to be the case due to the variation of the suitability of habitat (Hokit et al. 2001, Thomas et al. 2001). Thus, if colonization and extinction are relatively constant, they lead to an equal probability of patch occupancy. Additionally, habitat quality influences patch choice (Lima and Zollner 1996) and thus affects the colonisation rate.

(c) *Sensitivity of the colonisation rate and extinction rate estimations*. Their under- or over-estimation can lead to a large variability of metapopulation capacity. Ruckelshaus et al. (1997) determined how errors in input parameters disperse into errors in model predictions. They consider misclassification of habitat suitability, incorrect estimation dispersal distance abilities and mortality rate during dispersal. They deduce errors in predicting dispersal successes that result from quite small errors in estimating dispersal mortality rates (90% prediction errors when dispersal mortality is overestimated by 16-24%), while prediction errors in estimating mobility tends to be under 10% and those in classification of habitat quality produced prediction errors rarely exceeding 15%.

(d) *Connectivity quantification*. Connectivity between habitat patches is defined by the geographic distance between habitat patches. This definition does not consider barriers or landscape heterogeneities (With and King 1999b, With and King 1999a, Wiens 2001).

Conclusion on metapopulation models

Spatially realistic metapopulation models offer opportunities for a better understanding and provide predictions on dynamics among spatially structured populations (Hanski 1999). Moreover, they allow the ranking of different landscapes in terms of their capacity to support a viable population (Hanski and Ovaskainen 2000). Thus, major processes involved have been largely analysed: dispersal (Hansson 1991, Doebeli and Ruxton 1998) and local extinction (Harrison 1991, Grasman and HilleRisLambers 1997, Brassil 2001, Fahrig 2002).

Even if, concepts in metapopulation ecology have been recently used for species management and conservation (Drechsler and Wissel 1998), the models presented above are theoretically and analytically useful models in order to gain insight and do sensitivity studies but are not totally reliable for practical use. For example, in dispersal processes, the assumption stating that the distance between

---

[2] Models have been developed that integrate local population dynamics (Hastings 1991, Grimm et al. 1996, Akçakaya 2000).

patches is that of the straight line between them is unrealistic (Harrison 1991, Wiens 2001). Indeed, in a terrestrial system, habitat patches are surrounded by a heterogeneous matrix of varying suitability (Forman 1995) in which the configuration of patches, corridors, ecotones, patch boundaries and links contribute to giving a spatial pattern to ecological landscapes (Wiens 2001). Spatial structures within the matrix may guide or potentially inhibit movement (Kozakiewicz and Szacki 1995, Haddad 1999, Wiens 2001) and therefore may increase dispersal distance or produce an overall directionality movement (Bennett 1999, Haddad 1999). A distant patch, for example, may be colonized more frequently than a nearby patch if a barrier exists in-between.

Within a heterogeneous landscape, how individuals move becomes important, and the movement of individuals through such a complex mosaic is likely to be anything but random (Wiens 2001). Taking into account animal interaction with the landscape during dispersal is unfortunately not simple. Indeed, the spatial occurrence of dispersal processes and implications of the spatial arrangement of landscape features have to be assessed. It implies the need of methods integrating discrete processes (successive interactions of dispersers with each landscape feature) involved in a metapopulation scale (spatial arrangement of habitat patches in a large area). Such complexity may be captured by computer modelling with spatially explicit individual-based modelling approaches (Wiens 2001) presented in the next section.

Individual-based models

Introduction

The individual-based modelling concept was introduced by Huston et al. (1988). This concept was developed to simulate complex interactions in nature. It considers entities that interact with their environment (Huston et al. 1988, DeAngelis and Gross 1992). The entity may represent an individual of a given species, a landscape unit or even an entire community, which varies in both state and behaviour but also interacts with other entities. According to the ecological processes studied, individual-based modelling may be spatially explicit, meaning that the individuals are associated with a location in a geometrical space. During the last ten years, the increase in computer power and in programming concepts has enhanced this development. In ecological modelling, the individual-based modelling starts to predominate (Grimm et al. 1999). Such "expert systems" provide simulation of spatial realistic complex behaviours with relatively simple individual calculations. Several authors have recently used individual-based models to describe ecological systems: spatially realistic population dynamics (Gathmann and Williams 1998), animal foraging (Beecham and Farnsworth 1998, Carter and Finn 1999, Zollner 2000, Dumont and Hill 2001), forest system (He et al. 1999), population dynamics (Turner et al. 1995, Congleton et al. 1997, Ruckelshaus et al. 1997, Gathmann and Williams 1998, Hirzel 2001, Hirzel et al. 2002), community (Ziv 1998, Nally 2001) and dispersal (Dunning et al. 1995, Wennergren et al. 1995, Downing and Reed 1996, Gustafson and Gardner 1996, Schippers et al. 1996, Ruckelshaus et al. 1997, Tischendorf 1997, South 1999, Bian 2000, King and With 2002). In the latter field, individual-based modelling is spatially explicit and relies upon cellular automaton and object-oriented programming implementation techniques, described hereafter.

Implementation of individual-based modelling

In dispersal modelling, cellular automaton is usually a two-dimensional organization of entities, having simple finite states, and whose next state depends on their own actual state and the states of their neighbours. The states are updated according to neighbourhood-controlled transition rules (Hogeweg, 1988; Sipper and Tomassini, 1998) and has been mainly applied when complex non-linear dynamics arise from local interactions of many simple components (Hirzel 2001, Hirzel et al. 2001, Metzger 2002). In ecology, cellular automaton are mainly used for modelling vegetation growing processes (Silvertown et al. 1992, Kleczkowski et al. 1997, Matsinos and Troumbis 2002) because of the proximity of the interactions (neighbouring interaction).

The object-oriented[3] approach is based on the "concept" of an object (Larman 1998). An object has *an identity, a state and a behaviour*. *Identity* is the property that distinguishes an object from all the others. The *state* of an object is its memory. The *behaviour* is the actions of an object based on its own initiative and its reaction to external stimuli, i.e. events, in terms of the changes of state and the output messages. Objects communicate with messages that ask objects to behave in certain way or that change its state. The execution of an object- oriented programme involves receiving, interpreting and responding to messages from other objects. The behaviour of an object usually depends on its history, state or position. Objects may be arranged into classes. A class represents the description of a set of objects that share the same attributes, operations, methods, relationships and semantics (Booch et al. 1997). Each object or class has a “responsibility” in terms of behaviour according to its knowledge and its abilities. To provide such properties, object-orientation is built upon four principles: Abstraction, Encapsulation, Inheritance and Polymorphism (Bouzeghoub et al. 1994).

> *Abstraction* concerns the selection of certain aspects of an object or classes in order to isolate those that are important without including background or unessential details (Rambaugh 1991). Abstraction keeps the interactions among systems as simple as possible by providing the essential details.
>
> *Encapsulation* concerns the way of packaging information by hiding what should be hidden and makes visible what is intended to be visible. Visible properties are a subset of the properties abstracted. Rambaugh (1991) describes encapsulation as the separation of the external aspects which are accessible from the internal implementation of the object hidden from the object (Rambaugh 1991).

---

[3] Object-oriented programming is fundamentally different to traditional functional programming. A central distinction between object-oriented and structures analysis is the division by concepts (objects) rather than division by functions.

Inheritance concerns the relationship between classes where one class is the parent class (base, superclass, ancestor) of another. In implementation, inheritance is a mechanism by which classes share implementation. Therefore, a class may inherit (at run time or not) properties and operations from an ancestor class.

Polymorphism concerns the ability to take many forms. Objects react differently when presented with different information. In object-oriented programming, this refers to the ability of an entity to refer (at run time) to the instances of various classes (Meyer 1988, Booch 1994).

Although the pattern-oriented modelling strategy (Grimm et al. 1996) or component modelling (Bian 2000) is sometimes favoured, object-oriented modelling strategy offers a flexible and efficient tool in ecological modelling (Downing and Reed 1996). Used correctly it can even lead to the development of a very robust, easily expandable and maintainable code.

Dispersal with an individual-based model

Based on the previous discussion, individual-based modelling is well adapted to simulate animal movement in a landscape by providing animal interactions with the landscape. Spatially-explicit, individual-based models, force the development of explicit hypotheses, the organisation of existing knowledge, and the estimations of unknown parameters (Wiens 2001). Hence, to simulate dispersal in a fragmented landscape, the model must contain: (i) a landscape model and (ii) a dispersal model. The landscape model is generally supported by a Geographical Information System (for details see *chapter 3*). Usually, the disperser models integrate movement types, associated or not, with choosing procedures for movement routes according to landscape properties and the disperser abilities and states.

Animal movements are mostly described as random processes (as presented in previous sections), although it is the most extreme of behavioural minimalism in ecological modelling (Lima and Zollner 1996). Other dispersal models consider constraints to movement. The most widely used constraint is “neighbour limitations” (With et al. 1999) (i.e. individuals are constrained to move with equal probability into one of the neighbouring landscape units). Spatial and temporal autocorrelations are then incorporated, producing directionality in dispersal (Schippers et al. 1996, Zollner and Lima 1999b). Other models add anisotropy in the diffusion pattern such as (i) in percolation processes, in which individuals are constrained to move only through suitable neighbouring landscape units (With and King 1999a, King and With 2002), (ii) in correlated random walk (Bovet and Benhamou 1988, Benhamou 1989, Moorcroft et al. 1999) and (iii) in self-avoiding walk, which is based on an a priori probability depending on land cover (Gustafson and Gardner 1996, King and With 2002). Dispersal models may also consider individual choosing procedures based on landscape properties, such as individual habitat affinity (With and Crist 1995, With et al. 1997, With et al. 1999), resources availabilities (Beecham and Farnsworth 1998, Behm and Boumans 2001) and carrying capacity of landscape parts (according to reproduction processes) (Collingham et al. 1996, Hirzel 2001, Hirzel et al. 2002). Moreover, travel paths may be defined with individual or community properties such as physiological state (Blackwell 1997, Rizzotto and Focardi 1997, Wu et al. 2000), metabolic state (Possingham and Houston 1990), behavioural traits (Blackwell 1997, Carter and Finn 1999, Moorcroft et al. 1999, Nally 2001), sociability (Beecham and Farnsworth 1998, Dumont and Hill 2001), competition (Behm and Boumans 2001, Nally 2001) and predation (Bernstein et al. 1988). Finally, developments in dispersal modelling may add memory (Farnsworth and Beecham 1999) or cost-benefit systems as in optimal foraging theories (Possingham and Houston 1990, Rizzotto and Focardi 1997).

Conclusion on individual-based approaches to simulate dispersal

Individual-based modelling implemented in object-oriented approaches is a powerful tool to model complex processes and therefore animal dispersal. They allow connections with explicit representation of the dispersal area (landscape) and thus, provide an explicit simulation of individual movement. Although it has already been largely used, the following chapters will show that more investigations are needed.

References

Aborn, D. A., and F. R. Moore. 1997. Pattern of movement by summer tanagers (Piranga rubra) during migratory stopover: A telemetry study. Behaviour 134:1077-1100.

Akçakaya, H. R. 2000. Viability analyses with habitat-based metapopulation models. Population Ecology 42:45-53.

Barton, N. H. 1992. The genetic consequences of dispersal. Pages 37-59 *in* N. C. Stenseth and W. Z. J. Lidicker, editors. Animal Dispersal: small mammals as a model. Chapman & Hall, London.

Beecham, J. A., and K. D. Farnsworth. 1998. Animal foraging from an individual perspective: an object oriented model. Ecological Modelling 113:141-156.

Behm, P. M., and R. M. J. Boumans. 2001. Modeling herbivorous consumer consumption in the Great Bay Estuary, New Hampshire. Ecological Modelling 143:71-94.

Bell, W. J. 1991. Searching behaviour: the behavioural ecology of finding resources. Chapman and Hall, London.

Benhamou, S. 1989. An Olfactory Orientation Model For Mammals's Movements in Their home ranges. J. theor. Biol. 1989:379-388.

Bennett, A. F. 1999. Linkages in the Landscape: The role of corridors and connectivity in wildlife conservation. IUCN, Gland, Switzerland and Cambridge, UK.

Bennett, B. S. 1995. Simulation Fundamentals. Series in Systems and Control Engineering. Prentice Hall International. London.

Bennetts, R. E., J. D. Nichols, J.-D. Lebreton, R. Pradel, J. E. Hines, and W. M. Kitchens. 2001. Methods for estimating dispersal probabilities and related parameters using marked animals. Pages 3-17 *in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. Dispersal, Oxford.

Bergman, C. M., J. A. Schaefer, and S. N. Luttich. 2000. Caribou movement as a correlated random walk. Oecologia 123:364-374.

Bernstein, C., A. Kacelnik, and J. R. Krebs. 1988. Individual decisions and the distribution of predators in a patchy environment. Journal of Animal Ecology 57:1007-1026.

Bian, L. 2000. Component modeling for the spatial representation of wildlife movements. Journal of Environmental Management 59:235-245.

Bitton, N. F., G. P. Boswell, and N. R. Franks. 2001. Dispersal and Conservation in fragmented landscapes. Pages 299-320 *in* Insect Movement: Mechanisms and Consequences, eds I. Woiwod, C. Thomas and D. Reynolds. CABI Publishing, Wallingford.

Blackwell, P. G. 1997. Random diffusion models for animal movement. Ecological Modelling 100:87-102.

Booch, G. 1994. Object-Oriented Analysis and Design with Applications, 2nd edition. The Benjamin/Cummings Publishing Company, Rewood City, CA, USA.

Booch, G., I. Jacobson, and J. Rumbaugh. 1997. The UML specification documents. See documents at www.rational.com, Santa Clara, CA: Rational Software Corp.

Bouzeghoub, M., G. Gardarin, and P. Valduriez. 1994. Les objets, Eyrolles edition, Paris.

Bovet, P., and S. Benhamou. 1988. Spatial Analysis of Animals' Movement Using Correlated Random Walk Model. J. theor. Biol. 131:419-433.

Brassil, C. E. 2001. Mean time extinction of a metapopulation with an Allee effect. Ecological Modelling 143:9-16.

Carter, J., and J. T. Finn. 1999. MOAB: a spatially explicit, individual-based expert system for creating animal foraging models. Ecological Modelling 119:29-41.

Clark, T. W., J. Grensten, M. Gorges, R. Crete, and J. A. Gill. 1987. Analysis of black-footed ferret translocation sites in Montana. Prairie Naturalist 19:43-45.

Collingham, Y. C., M. O. Hill, and B. Huntley. 1996. The migration of sessile organisms: a simulation model with measurable parameters. Journal of Vegetation Science 7:831-846.

Congleton, W. R., B. R. Pearce, and B. F. Beal. 1997. A C++ implementation of an individual/landscape model. Ecological Modelling 103:1-17.

DeAngelis, D. L., and J. L. Gross. 1992. Individual-based models and approaches in ecology: Populations, Communities and Ecosystems. Chapman & Hall, New York.

Diffendorfer, J. E., M. S. Gaines, and R. D. Holt. 1999. Patterns and impacts of movements at different Scales in Small Mammals. Pages 63-88 *in* G. W. Barrett and J. D. Peles, editors. Landscape Ecology of Small Mammals. Springer-Verlag, New York.

Dingle, H. 2001. The evolution of migratory syndromes in insects. Pages 159-181 *in* I. P. Woiwod, D. R. Reynolds, and C. D. Thomas, editors. Insect Movement: Mechanisms and Consequences: proceedings of the Royal Entomological Society's 20th Symposium. CABI Publishing, Oxon.

Doebeli, M., and G. D. Ruxton. 1998. Stabilization through spatial pattern formation in metapopulations with long-range dispersal. Proc. R. Soc. Lond B 265:1325-1332.

Downing, K., and M. Reed. 1996. Object-oriented migration Modelling for biological impact assessment. Ecological Modelling 93:203-219.

Drechsler, M., and C. Wissel. 1998. Trade-offs between local and regional scale management of metapopulation. Biological Conservation 83:31-41.

Dumont, B., and D. R. C. Hill. 2001. Multi-agent simulation of group foraging in sheep: effects of spatial memory, conspecific attraction and plot size. Ecological Modelling 141:201-215.

Dunning, J. B., D. J. Stewart, and B. J. N. R. Danielson. 1995. Spatially explicit population models: current forms and future uses. Ecological Applications 5:3-11.

Endler, J. A. 1977. Geographic Variation, Speciation, and Clines. Princeton University Press,, Princeton, New Jersey.

Fahrig, L. 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. Ecological Applications 12:346-353.

Farnsworth, K. D., and J. A. Beecham. 1999. How do grazers achieve their distribution? A continuum of models from random diffusion to the ideal free distribution using biased random walks. American Naturalist 153:509-526.

Forman, R. T. T. 1995. Land mosaics: the ecology of landscapes and regions, Cambridge University Press edition, Cambridge, Massachusetts.

Gaines, M. S., and L. R. McClenaghan. 1980. Dispersal in small mammals. Annual Review of Ecology and Systematic:163-196.

Gathmann, F. O., and D. D. Williams. 1998. Inter-site: a new tool for the simulation of spatially realistic population dynamics. Ecological Modelling 113:125-139.

Grasman, J., and R. HilleRisLambers. 1997. On local extinction in a metapopulation. Ecological Modelling 103:71-80.

Grimm, V., K. Frank, F. Jeltsch, R. Brandl, J. Uchmanski, and C. Wissel. 1996. Pattern-oriented Modelling in population ecology. The Science of Total Environment 183:151-166.

Grimm, V., T. Wyszomirski, D. Aikman, and J. Uchmanski. 1999. Individual-based modelling and ecological theory: synthesis of a workshop. Ecological Modelling 115:275-282.

Gustafson, E. J., and R. H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77:94-107.

Haddad, N. M. 1999. Corridor and distance effects on interpatch movements: A landscape experiment with butterflies. Ecological Applications 9:612-622.

Hanski, I. 1991. Single-species metapopulation dynamics: concepts, models and observations. Biological Journal of the Linnean Society 42:17-38.

Hanski, I. 1999. Metapopulation Ecology. Oxford University Press, Oxford.

Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. Nature 404:755-758.

Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain and application to conservation. Pages 5-26 *in* I. A. Hanski and M. E. Gilpin, editors. Metapopulation Biology: Ecology, generics, and evolution. Academic Press, San Diego.

Hansson, L. 1991. Dispersal and connectivity in metapopulations. Biological Journal of the Linnean Society 42:89-103.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biological Journal of the Linnean Society 42:73-88.

Hastings, A. 1991. Structured models of metapopulation dynamics. Biological Journal of the Linnean Society 42:57-71.

He, H. S., D. J. Mladenoff, and J. Boeder. 1999. An object-oriented forest landscape model and its representation of tree species. Ecological Modelling 119:1-19.

Hestbeck, J. B. 1982. Population regulation of cyclic mammals - The social fence hypothesis. Oikos 32:157-163.

Hirzel, A. 2001. When GIS come to life. Linking landscape- and population ecology for large population management modelling: the case of Ibex (Capra Ibex) in Switzerland. Université de Lausanne, Lausanne.

Hirzel, A., J. Hausser, D. Chessel, and N. Perrin. 2002. Ecological-niche factor analysis: How to compute habitat-suitability maps without absence data? Ecology 83:2027-2036.

Hirzel, A. H., V. Helfer, and F. Metral. 2001. Assessing habitat-suitability models with a virtual species. Ecological Modelling 145:111-121.

Hokit, D. G., B. M. Stith, and L. C. Branch. 2001. Comparison of two types of metapopulation models in real and artificial landscapes. Conservation Biology 15:1102-1113.

Huston, M., D. DeAngelis, and W. Post. 1988. New computer models unify ecological therory. BioScience 38:47-68.

Jander, R. 1975. Ecological aspects of spatial orientation. A. Rev. Syst. Ecol. 6:171-188.

Johnson, M. L., and M. Gaines. 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Ann. Rev. Ecol. Syst. 21.

Kiester, P. H., and J. P. Slatkim. 1974. A strategy of movement and resource utilization. Theoretical population biology 6:1-20.

King, A. W., and K. A. With. 2002. Dispersal success on spatially structured landscapes: when do dispersal pattern and dispersal behavior really matter? Ecological Modelling 147:23-39.

Kleczkowski, A., C. A. Gilligan, and D. J. Bailey. 1997. Scaling and spatial dynamics in plant-pathogen systems: From individual to populations. P. Roy. Soc. Lond. B. Biol 264:979-984.

Koenig, W. D., D. Van Vuren, and P. N. Hooge. 1996. Detectability, philoparty, and the distribution of dispersal distances in vertebrates. Trends in Ecology and Evolution 11:514-517.

Kozakiewicz, M., and J. Szacki. 1995. Movements of small mammals in a landscape: patch restriction or nomadism? Pages 78-94 *in* W. Z. Lidicker, editor. Landscape approaches in mammalian ecology and conservation, Minneapolis, Minesota.

Larman, C. 1998. Applying UML and patterns: An introduction to object-oriented analysis and design. Prentice Hall PTR, Upper Saddle River, New Jersey 07458.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity or biological control, Bull. Entomol. Soc. Amer. Bull. Entomol. Soc. Amer.:237-240.

Levins, R. 1970. Extinction, Lect. Notes Math 2. Lect. Notes Math 2:75-107.

Lidicker, W. Z. J., and N. C. Stenseth. 1992. To disperse or not to disperse: who does it and why? Pages 21-36 *in* N. C. Stenseth and W. Z. J. Lidicker, editors. Animal Dispersal: small mammals as a model. Chapman & Hall, London.

Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution 11:131-135.

MacArthur, R. H., and E. D. Wilson. 1967. Theory of Island Biogeography, Princeton.

Matsinos, Y. G., and A. Y. Troumbis. 2002. Modeling competition, dispersal and effect of disturbance in the dynamics of a grassland community using a cellular automaton model. Ecological Modelling 149:71-83.

Metzger, R. 2002. Modélisation des inondations par approches déterministe et stochastique avec prise en compte des incertitudes topographiques dans le cadre de la gestion des risques liés aux crues. Ph.D. Thesis. Ecole Polytechnique Fédérale de Lausanne, Lausanne.

Meyer, B. 1988. Object-Oriented Software Construction, Prentice Hall.

Moorcroft, P. R., M. A. Lewis, and R.-L. Crabtree. 1999. Home range analysis using a mechanistic home range model. Ecology 50:1656-1665.

Nally, R. M. 2001. Interaction strengths and spatial scale in community ecology: simulated quadrat-sampling and confinement experiments involving animals of different mobilities. Ecological Modelling 144:139-152.

Okubo, A. 1986. Dynamical aspects of animal grouping: swarms. schools, flocks, and herds. Adv. Biophys. 22:1-94.

Peles, J. D., D. R. Bowne, and G. W. Barrett. 1999. Influence of Landscape Structure on Movement Patterns of Small Mammals. Pages 41-62 *in* G. W. Barrett and J. D. Peles, editors. Landscape Ecology of Small Mammals. Springer-Verlag, New York.

Possingham, H. P., and A. I. Houston. 1990. Optimal Patch Use a Territorial Forager. J. theor. Biol. 145:343-353.

Rambaugh, J. 1991. Object-Oriented Modelling and Design. Addison-Wesley.

Reed, J. M., and A. P. Dobson. 1993. Behavioral constraints and conservation biology- Conspecific attraction and recruitment. Trends in Ecology and Evolution 8:253-256.

Rizzotto, M., and S. Focardi. 1997. A physiologically-based model of a self-motivated hare in relation to its ecology. Ecological Modelling 95:191-209.

Ruckelshaus, M., C. Hartway, and P. Kareiva. 1997. Assessing the data requirements of spatially explicit dispersal models. Conservation Biology 11:1298-1306.

Schippers, P., J. Verboom, J. P. Knappen, and R. C. van Apeldorn. 1996. Dispersal and habitat connectivity in complex heterogeneous landscapes: an analysis with a GIS-based random walk model. Ecography 19:97-106.

Silvertown, J., S. Holtier, J. Johnson, and e. al. 1992. Cellular automaton models of interspecific competition for space - The effect of pattern on process. J. Ecol. 80:527-534.

Smith, A. T., and M. M. Peacock. 1990. Conspecific attraction and the determination of metapopulation colonization rates. Conservation Biology 4:320-323.

Smith, J. N. M. 1974. The food searching behaviour of two European thrushes I. Description and anlaysis of search paths. Behaviour 48:276-302.

Sobol, I. M. 1994. A primer for the Monte Carlo Method. CRC Press LLC, Boca Raton, Florida.

South, A. 1999. Dispersal in Spatially Explicit Population Models. Conservation Biology 13:1039-1046.

Stamps, J. A. 1988. Conspecific attraction and aggregation in territorial species. The American Naturalist 131.

Stenseth, N. C., and W. Z. J. Lidicker. 1992. The study of dispersal: a conceptual guide. Pages 1-20 *in* N. C. Stenseth and W. Z. J. Lidicker, editors. Animal Dispersal: small mammals as a model. Chapman & Hall, London.

Stephens, D. W., and J. R. Krebs. 1986. Foraging Theory. *in* N. J. Princeton, editor. Princeton University Press.

Sutherland, W. J., and L. M. Gosling. 2000. Advances in the study of behaviour and their role in conservation. Pages 3-9 *in* L. M. Gosling and W. J. Sutherland, editors. Behaviour and Conservation. University of Cambridge, Cambridge.

Thomas, C. D., M. Baguette, and O. T. Lewis. 2000. Butterfly movement and conservation in patchy landscapes. Pages 85-104 *in* L. M. Gosling and W. J. Sutherland, editors. Behaviour and Conservation. University of Cambridge, Cambridge.

Thomas, J. A., N. A. D. Bourn, R. T. Clarke, K. E. Stewart, D. J. Simcox, G. S. Pearman, R. Curtis, and B. Goodger. 2001. The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. The Royal Society 268:1791-1796.

Tischendorf, L. 1997. Modelling individual movements in heterogeneous landscapes: potentials of a new approach. Ecological Modelling 103:33-42.

Turner, M. G., G. J. Arthaud, and R. T. Engstrom. 1995. Usefulness of spatially-explicit population model in land management. Ecological Applications 5:12-16.

Wennergren, U., M. Ruckelshaus, and P. Kareiva. 1995. The promise and limitations of spatial models in conservation biology. Oikos 74:349-356.

Wiens, J. A. 1995. Landscape mosaic and ecological theory. Pages 1-26 *in* L. L. Hansson, Fahrig and G. Merriam, editor. Mosaic Landscapes and Ecological Processes. Chapman and Hall, London.

Wiens, J. A. 2001. The landscape context of dispersal. Pages 96-109 *in* E. D. J. Clobert, A.A. Dhondt, and J.D. Nichols, editor. Dispersal. Oxford University Press, New York.

With, K. A., S. J. Cadaret, and C. Davis. 1999. Movement responses to patch structure in experimental fractal landscapes. Ecology 80:1340-1353.

With, K. A., and T. O. Crist. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76:2446-2459.

With, K. A., R. H. Gardner, and M. G. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. Oikos 78:151-169.

With, K. A., and A. W. King. 1999a. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. Landscape Ecology 14:73-82.

With, K. A., and A. W. King. 1999b. Extinction thresholds for species in fractal landscape. Conservation Biology 13:314-326.

Wolff, J. O. 1997. Population regulation in mammals: An evolutionary perspective. J. Anim. Ecol 66:1-13.

Wolff, J. O. 1999. Behavioral Model Systems. Pages 11-40 *in* G. W. Barrett and J. D. Peles, editors. Landscape Ecology of Small Mammals. Springer-Verlag, New York.

Wolff, J. O., and J. A. Peterson. 1998. An offspring-defense hypothesis for territoriality in female mammals. Ethol. Ecol. Evol.:227-239.

Wu, H., B. Li, T. A. Springer, and W. H. Neill. 2000. Modelling animal movement as a persistent random walk in two dimensions: expected magnetitude of net displacement. Ecological Modelling 132:115-124.

Ziv, Y. 1998. The effect of habitat heterogeneity on species diversity patterns: a community-level approach using an object-oriented landscape simulation model (SHALOM). Ecological Modelling 111:135-170.

Zollner, P. A. 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. Landscape Ecology 15:523-533.

Zollner, P. A., and S. Lima. 1999a. Illumination and the perception of remote habitat patches by white-footed mice. Animal Behaviour 58:489-500.

Zollner, P. A., and S. L. Lima. 1999b. Search strategies for landscape-level interpatch movements. Ecology 80:1019-1030.

Chapter 3

Map of ecological networks for landscape planning[1]

Abstract

This part presents a method based on a geographical information system (GIS) to model ecological networks in a fragmented landscape. The ecological networks are generated with the help of a landscape model (which integrate human activities) and with a dispersal model. The main results are maps, which permit the analysis and the understanding of the impact of human activities on animal dispersal. Three applications in a study area are presented: ecological networks at the landscape scale, conflicting areas at the farmstead scale and ecological distance between biotopes. These applications show the flexibility of the model and its potential to give information on ecological networks at different planning scales.

[1] *Note: This chapter was published in Landscape and Urban Planning 58 (2002) 157-170*
Co-author: Roland Prélaz-Droux

Introduction

During the last decades the rationalisation of agricultural practices reduced the diversity of landscape structures and led to the standardisation of agricultural landscapes. In these landscapes, biotopes have either disappeared or have been isolated (Broggi & Schlegel 1990, Duhme et al. 1997; Broggi & Schlegel 1998). The enticing need for land societal developments, such as the expansion of towns, increasing mobility, and larger recreational areas, create conflicts and pressures on ecosystems. This situation causes a lot of damage to species, if they have not already disappeared (Broggi & Schlegel 1990, 1998; Opdam et al. 1993).

New methods trying to integrate interactions between ecosystems and human activities at the landscape scale are necessary in order to better control land development. New planning tools are needed to maintain and increase biodiversity in fragmented landscape. To reach this goal, the landscape has to be understood not only from an ecological point of view but also from the view of human activities. Humans have to be considered as a part of the system (Burel et al., 1999).

Swiss context

The Swiss landscape has undergone important modifications during the last few decades. Landscape standardisation, isolation and disappearance of biotopes are the results of the rationalisation and intensification of agricultural practice, the human population growth and the increase of road networks. The first policy prohibiting an uncontrolled land use was the Forest Law (1902) that stopped the decline of forested areas. The inventories dedicated to the protection of natural areas appeared during the seventies after the Natural Protection Law (1966) came into effect. A preliminary study on the efficiency and the effects of a Swiss cantonal inventory (Vuilleumier et al., 1999) showed that the results of this form of protection were not sufficient to maintain biodiversity. It is mainly due to local forms of protection that do not take into account the dynamics of ecosystems and impacts to nearby human activities.

Today, the objectives of the Swiss government are to increase the number of biotopes and to develop an ecological network. In the same way, the agricultural purposes have changed. By the way of subsidies, the Swiss Confederation urges farmers to adopt sustainable practices. One of the consequences is the creation of ecological compensation areas (areas dedicated to nature), which represent 7% of the farmer's land. A new Swiss Law is in preparation in order to differentiate the farmers' subsidies in coordination with the quality and the position (in regard to ecological networks) of the ecological compensation areas.

Landscape: a complex fragmented spatial ecological system

Studies, databases and conservation plans usually concern local or global scales. May (1993) showed that a great deal of ecological research focuses on single species or interactions between two species, usually on spatial scales that are often smaller than the characteristic distance over which an individual member of the species moves in its lifetime. According to May (1993), Kareiva et al. (1989) analysed some 97 manipulative field experiments reported in Ecology between January 1980 and August 1986 and they found 43 (44%) of these studies to have a dimension of less than 1 meter and 73 (75%) to be below 10 meters. At the other extreme, databases at large scales are widely available (Swiss land use statistics, GEOSTAT (OFS, 1998), CORINE land cover Project (EC, 1993), and satellite imagery for land cover (Reid et al., 1993)). These data are often used to evaluate and analyse countries in order to develop directives and constraints like inventories and conservation plans based on global analysis (like GAP analysis (Kiester et al. 1996), the TSES concepts (Kubes 1996), or Systematic conservation planning (Margules and Pressey 2000)). These methodologies respond to a serious need of plans for wildlife protection and conservation.

Ecologists, conservationists and land managers refer to habitat loss and isolation as “habitat fragmentation” (Collinge 1996). Ecologists have approached the study of habitat fragmentation for the past 25 years largely within the framework of two key theoretical developments in community and population ecology (Collinge, 1996): the theory of island biogeography (Mac Arthur & Wilson, 1963, 1967) and the metapopulation concept (Levins, 1969). The theory of island biogeography studies the influences of isolation (distance to other islands or continents) and fragment size on species composition considering both colonisation and extinction as fundamental processes. The term, metapopulation, was introduced by Levins (1970) to describe a population composed of many local populations (Hanski, 1999). The metapopulation dynamics concept focuses attention on connectivity and interchange between spatially distributed populations (Hanski, 1999). When modelling metapopulation processes at the landscape scale, different approaches have been used such as structured dynamic models (Hastings 1991, Jorgensen 1999), habitat-based metapopulation models (Akçakaya 2000b) and object-oriented modelling (Grimm et al. 1996, Ziv 1998). Recently, concepts in metapopulation ecology have been used in models for species management and conservation (Simberloff 1997, Drechsler & Wissel 1998, Akçakaya 2000a).

Habitat fragmentation is for many authors one of the most important threats for biodiversity. Those authors have studied and analysed the relationships between the species number and spatial parameters like fragment size, connectivity, shape, context, heterogeneity, and edge phenomenon (Collinge, 1996, 1998; Theobald, 1997; Forman, 1997, Opdam et al, 1993; Vos et al., 1993; Drechsler et al., 1998; Clergeau et al., 1997).

Contributions of landscape ecological studies provide understanding on the implications of particular landscape patches, such as the size and shape on ecological processes (review by Collinge, 1996). Some methodologies are developed for comparative regional scenarios for nature restoration (Harms et al. 1993). Different analytical and design methods for ecological networks are proposed such as the characterisation of core and corridor use for specific species (Shkedy & Saltz 1999), corridor design (Jordan 2000) or reserve networks selection (Polasky et al. 2000). When modelling fragmentation and its effect on dispersal, studies consider different modelling methods like cellular automata (Darwen and Green, 1996), random walks (Johnson et al., 1992a), neutral landscape (With and King, 1997) and GIS based models (reviewed by Johnson et al. (1992b) and Schippers et al. (1996)).

Nowadays, landscape ecology follows research efforts to understand the relationships and the processes between environmental and biological systems. It responds to a serious need for an understanding of the complex processes involved in the landscape. The complexity of the phenomena is directed by the multitude of pressures and constraints acting on the ecosystem as well as the need to maintain and develop the links between the ecosystems. At the landscape scale, patches are spatially structured, and they interact with each other and with their environment. At this scale, conflicts are addressed in various locations. Thus a spatial approach is necessary. In this context:

- Spatial relationships between ecosystems and their environment at the landscape scale have to be analysed and integrated in local (farmstead scale) and landscape planning.
- It is necessary to develop tools based on simple models and available data to understand and analyse factors affecting ecological processes at the landscape scale.
- Planning tools have to be flexible, easy to understand and capable of analysing scenarios.

Purpose

The purpose of this work is to develop a method for assessing an ecological network in a space - landscape - where human activities are involved. The goal is to identify strategic places for the ecological network and the potential area that can accommodate the game species (roe deer, stag, chamois, and boar). This is done in order to help the decision-makers in a planning procedure to identify the most suitable use (renaturation, intensive agriculture) of an area at the local and landscape scale that insure links between ecosystems.

The development aims to propose new instruments for planning, especially for conservation. It has to provide answers to landscape and local planning conflicts between societal development and biodiversity in a human disturbed landscape. The result should contribute to a better understanding of animal dispersal in fragmented landscapes, providing in the end effective tools for conservation planning. To achieve these goals, we propose to develop a new method based on GIS, which integrates mainly human activities data. In our investigation, we propose to model landscape with a resolution that does not exceed five meters in order to produce results that can be integrated into a local planning procedure.

The fragmented landscape is considered like a landscape, in which human activities like agriculture and transportation fragment the habitat. In fragmented landscape, distance between patches is not a strait line between patch centres. Indeed, the distance is largely influenced by topography, landscape structures, land cover and human activities. In fact, at the landscape scale:

- ⇒ human activities interact and add a stress on ecological networks (e.g. through roads, land use),
- ⇒ patches have specific properties as a function of their spatial distribution (habitat, corridors),
- ⇒ patches interact with each other and with their environment (faunal source or sink, edge effect).

For our development we assume that, topography, land use and human activities interact with animal dispersal processes, and the ecological distance between patches is the sum of the real distance (metric) and the distance due to the stress and difficulty to move.

Modelling

To understand and analyse ecological processes involved in landscape, an approach is presented to form ecological networks with two models based on Geographical Information Systems (GIS): a landscape model and dispersal model.

The concept is based on the progression of individuals through the modelled landscape. The model we used is a dispersal from a suitable habitat (sources) throughout a surface of constraints (friction surface). This method is illustrated in *figure 7*. In our case the surface of constraints is the fragmented landscape. The dispersal is simulated to identify the area potentially useable by the simulated species. It attempts to identify the ecological network.

The first step is to identify patches that are suitable for the species (i.e. which can support a local population), and then characterise landscape from the point of view of its limitation to dispersal.

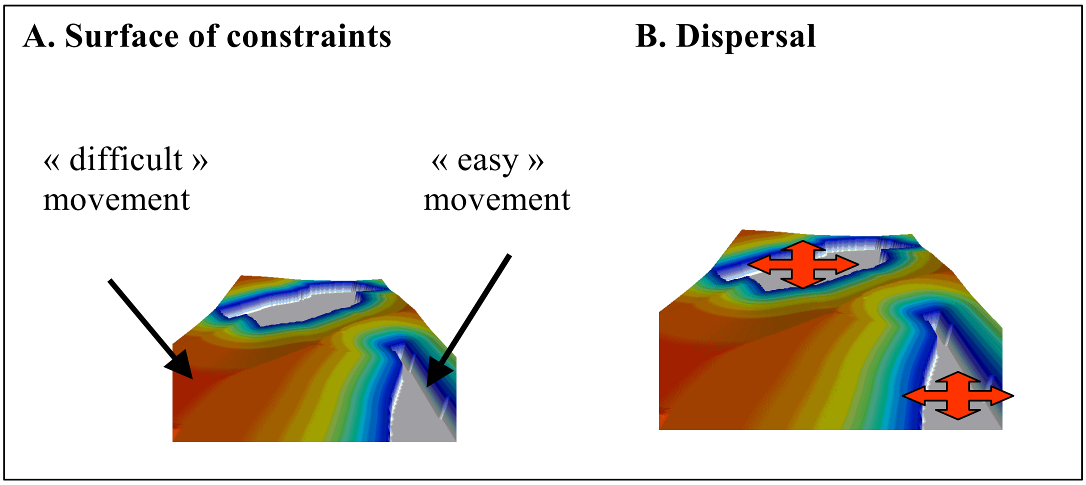


Figure 7: Illustration of the method: A. Development of a surface of constraints considering movement limitation due to human activities. On this surface, values are low where few movement limitations are present and high where movement limitations are important. B. Dispersal simulation from suitable areas on the surface of constraints.

Landscape model

In order to characterise landscape from the point of view of its limitation to dispersal (modelling the landscape in the form of a surface of constraints), three values are associated with every landscape component (e.g. road, building area):

- ⇒ Crossing pressure: difficulty to cross compared to rural area. This value includes difficulty to cross and the repulsive effect of a road or building area. For example if the value of a road is 5, that means that it is 5 times more difficult to cross. The value 1 is assigned to a rural area.
- ⇒ Distance of the influence of the stress induced by landscape components (distance in meters).
- ⇒ Possibility to cross (yes-no).

Each landscape component is represented spatially with its value of crossing pressure. This value is assumed as decreasing linearly to the limit of the distance of influence (see *figure 8*).

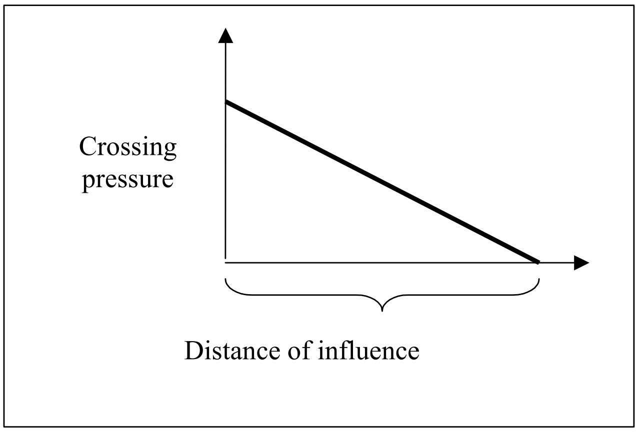


Figure 8: Spatial representation of the crossing pressure; the value is assumed to decrease linearly to the limit of the distance of influence

Dispersal model

The dispersal is simulated with the help of distance operators produced by the IDRISI® software: <u>costgrow</u>. It incorporates a growth algorithm. Distances are measured according to the minimum amount of friction is accumulated during the travel from one cell to the nearest source target. Movements are in 8 directions from any cell, and diagonal movements produce a cost of 1.41 times the friction value. The least cost distance is calculated from a group of targeted pixel, it is a radial distance. The distance operator can integrate frictional effects and barriers (IDRISI® , Clark Labs technical support, 1999).

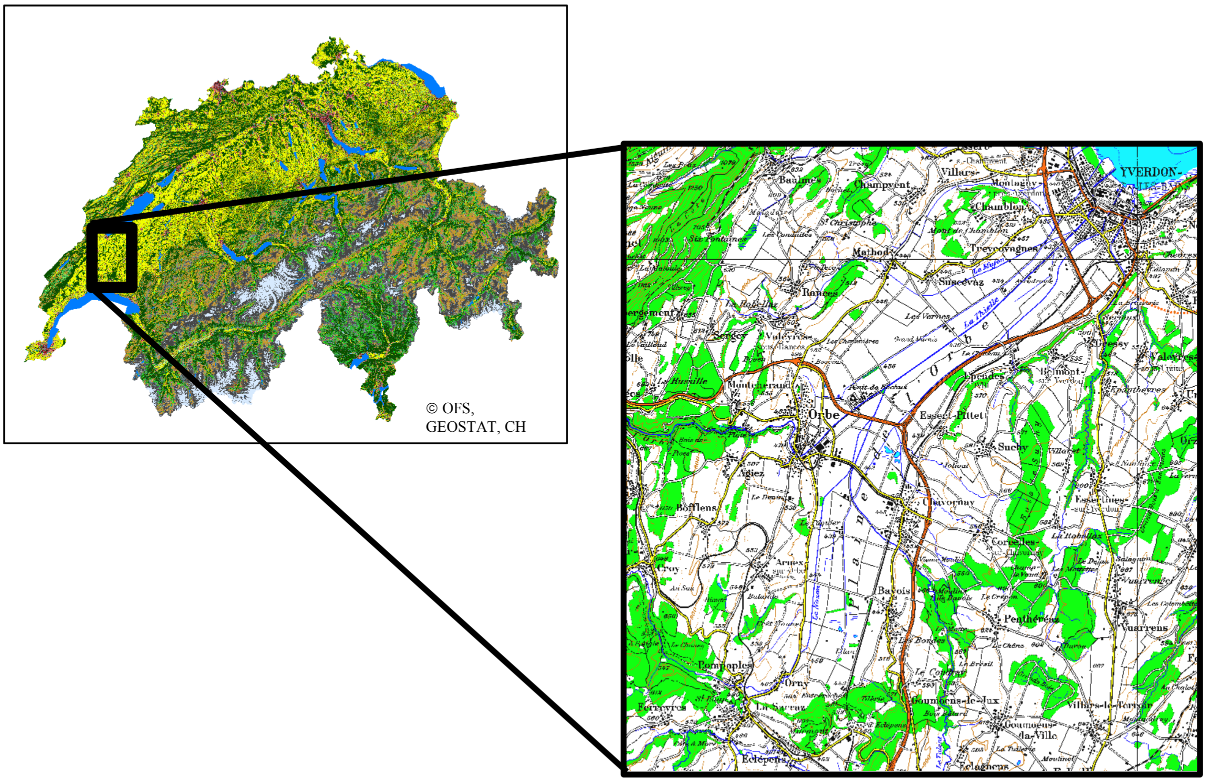
Application

The investigated analysis concerns the assessment of the pressures due to the road networks and human activities in an agricultural plain of Switzerland.

In our study case, the target species consist of "large wildlife" like roe deer, stag, chamois, and boar. We consider that movement limitation is due to physical infrastructure and stress coming from human activities. Two main categories of human activities are considered: road networks and building areas. We assume that constraints due to roads and building areas act simultaneously. In the landscape model they are cumulative.

Study area

The study area “la plaine de l’Orbe” is an agricultural plain of Switzerland (*figure 9*). This perimeter has been chosen because of the great need for regeneration of the biotopes and the need to ensure the faunal transfer between the mountain chain and the major forest area. The study area is about 59 square km. In order to ensure the hedge effect (considering flux and constraints around the study area), the study area has to be extended to 409 square km. Land use involves mainly agricultural practice, and housing zones and road networks.



© OFS, GEOSTAT, CH

Figure 9 : Study area, an agricultural plain of Switzerland

Data

Spatial data collected for the landscape model have a resolution between 1 and 4 meters, they are in a vector form. For the landscape model we transform this vector data to a raster format. The pixel unit is 5 meters to permit a local analysis (farmstead) of a large-scale process.

Data on ecosystems have been collected by the agency for nature and wildlife conservation. The biotopes of the plain have been classified into four major classes: (1) forest, (2) wetland, (3) riverbank vegetation and (4) hedges. These biotopes represent the starting points of dispersal within the model. They are presented in *figure 10*.

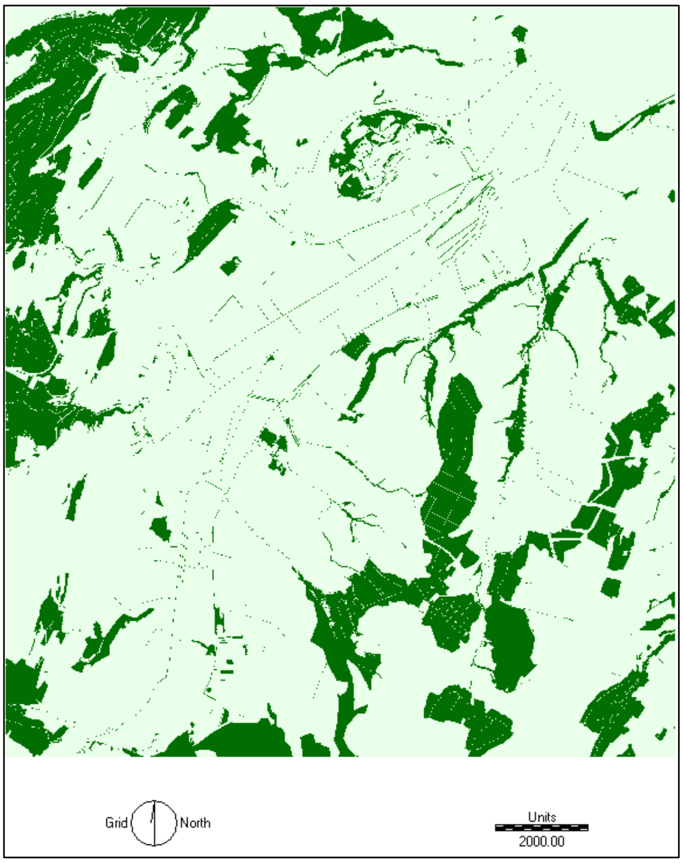


Figure 10 : Biotopes (river, forest, wetland, and hedge) of the study area.

The road networks are classified by their traffic in three categories: highways, main roads and secondary roads. Data on highways and main road networks comes from the digital landscape model of Switzerland, the content and geometry of which is based on the National Map 1:25'000 (http://www.swisstopo.ch). Data on secondary roads and building areas have been digitised from orthophotos (1:20'000 - 1:27'000).

Landscape model

The values assigned to landscape components (crossing pressure, distance of influence and possibility to cross) have been estimated by a study group composed of a group of biologists and wildlife conservation agents concerned with this area. They are presented in *table 2*.

Table 2 : Value of crossing pressure, distance of influence chosen and possibility to cross.

	highway	main road	secondary road	Building area
Crossing pressure	10	5	2	5
Distance of influence (meter)	50	50	10	D = 52 ln (S) – 255 [1]
Possibility to cross	No [2]	yes	yes	no

[1] *S: building surface (m^2), D: Distance of influence (m)*
[2] *Except if bridge or viaduct.*

The distance of influence of the buildings depends on their area (so that the influential distance of a city is lengthier than an isolated farm). This function is presented in *table 2* and in *figure 11*. The crossing pressure is considered to be linearly decreasing from the centre of the road and from the edge of the building to the limit of the influential distance. *Table 2* presents values of distance of influence for roads and buildings and whether or not they are barrier to dispersal (possibility to cross). *Figure 12* presents maps of the highway, main roads, secondary roads and with the distances of influence.

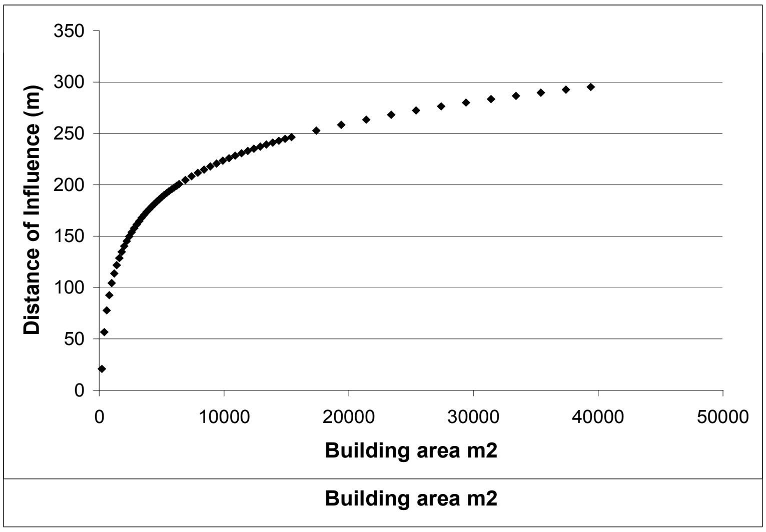
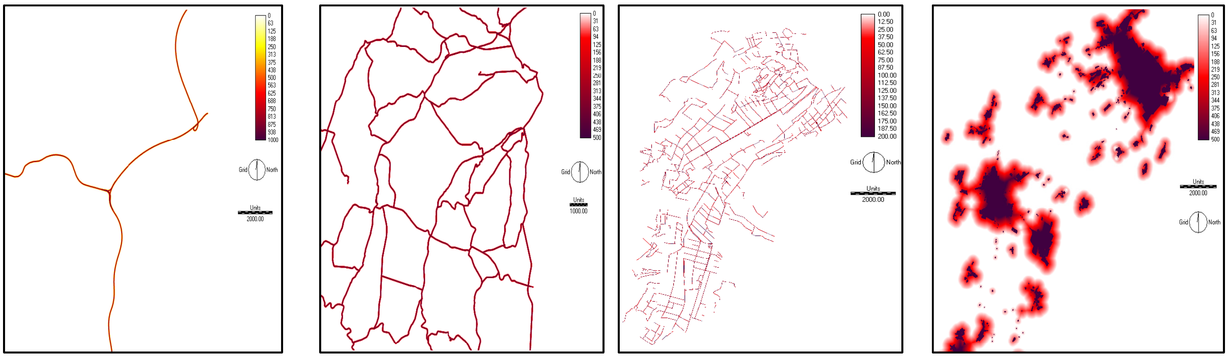


Figure 11: Function of the building influential distance. This function has been built according to expert estimation of influential distances coming from 25 inhabited areas.

All the constraint maps of are overlaid to produce the landscape model (friction surface). The result is presented in *figure 13.*



a b c d

Figure 12 : Maps of the constraints. a, b and c: road networks (a: Highways, b: main roads and c: small roads) and d: Building area with influence distance.

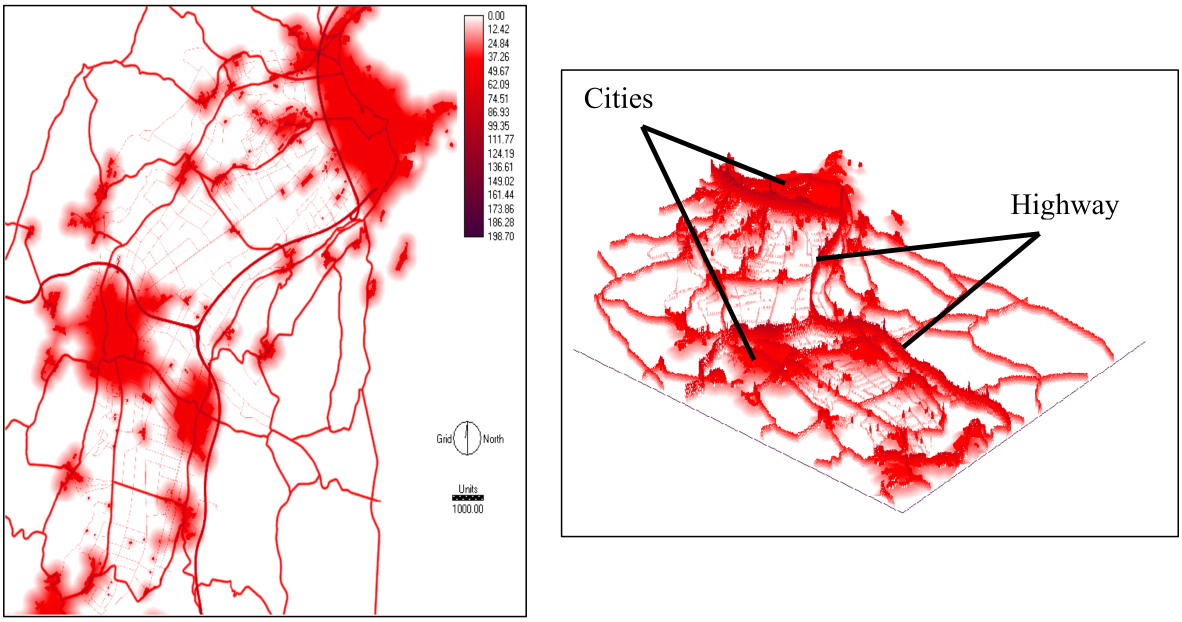


Figure 13 : Landscape model (friction surface): map of limitation to dispersal, considering the sum of constraints for the animal dispersal in the study area; left: representation in two dimensions, and right: representation in three dimensions.

Dispersal simulation

The constraints acting on the target species (in our study case "game wildlife", *figure 13*) are overlaid to generate the landscape model. Considering that the crossing pressure due to landscape component depends on the studied species, it is possible to modify the value of the crossing pressure since components are different for different species. The model offers the possibility to add or subtract landscape components. The starting point of the dispersal can be selected depending on the habitat of the target species. Different scenarios can be analysed (see *figure 14*).

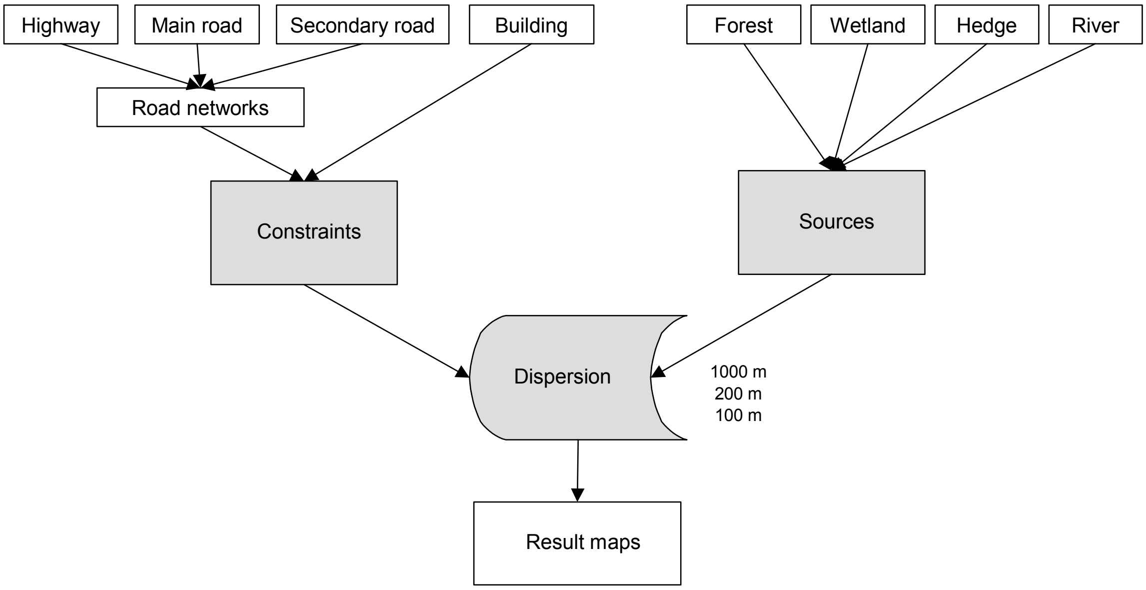


Figure 14 : The landscape model is developed like a database system, constraints and sources can be added or subtracted depending on the target species, and different values can be assigned to them.

Simulation

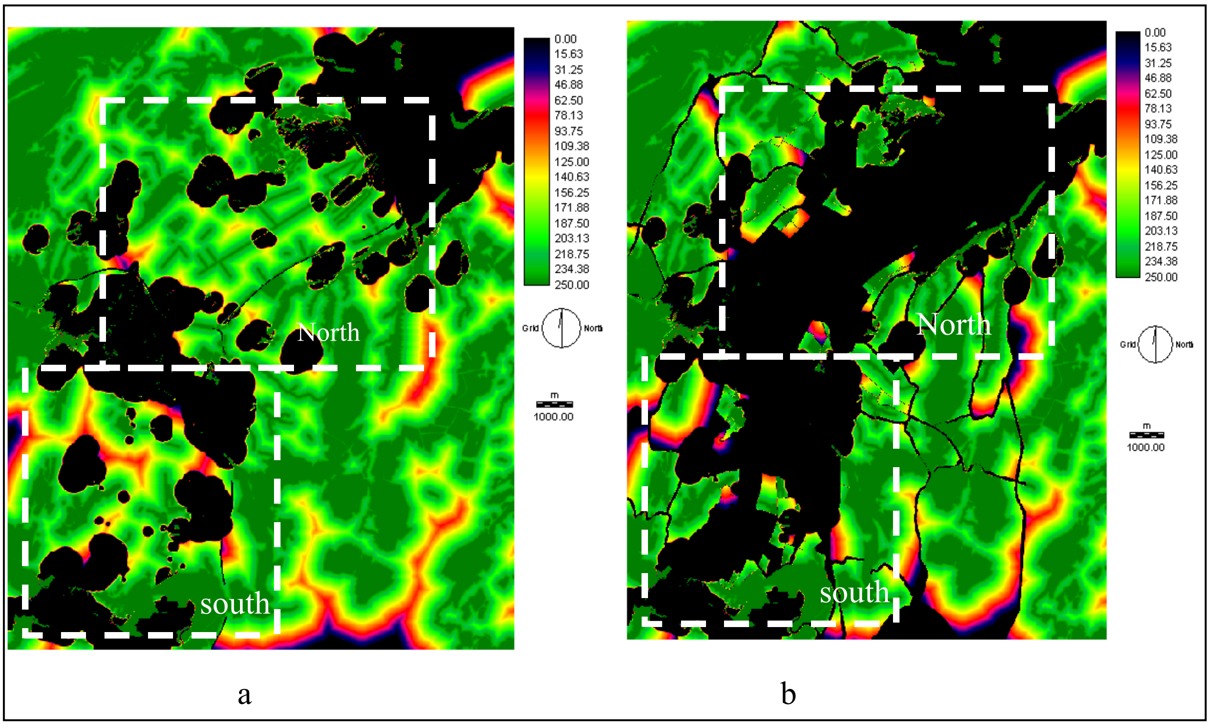
Three major simulations have been generated:

- In the Swiss context, one of the objectives is to find ecological networks which connect all the biotopes. Dispersal from every biotope (forests, wetlands, riverbank vegetation and hedges) has been realised in order to simulate ecological networks. This simulation is compared to a dispersal that considers only forests as the starting points.
- The modification of the farmers' subsidies, considering the position of ecological compensation areas in regard to the ecological network, has an important impact in Switzerland. In this context, we analyse at the farmstead scale the implication of the ecological network for the position of ecological compensation areas.
- In the centre of the plain only two viaducts allow flues of species. The number of individuals crossing under each viaducts have been observed in both directions. This simulation is used to validate the model.

Results and discussion

The maps in *figure 15a* and *15b* present the ecological network generated by a dispersal simulation from every biotope (*figure 15a*) and from forest (*15b*) on the landscape model. The potential of the wildlife presence varies from 0 to 250. The value 0 (black) and 250 (dark green) represent the potential absence and potential maximum presence of the game wildlife respectively.

Comparing simulation results highlights the difficulty to link the eastern and western parts of the plain. The northern part of the plain is mainly composed of small biotopes like hedges and river bank vegetation, which are linking biotopes. The pressures acting on the southern part of the plain are more important than in the northern part (in *figure 15a*). The distances between habitats are more important in the north (in *figure 15b*). In the case of planning ecological compensation areas, these simulations identify the kind of biotopes that have to be developed depending on their spatial position. In our case, these results show the importance of developing linking biotopes in the south and the need of forest restoration in the north. In a renaturation application case, it is possible to evaluate nature restoration scenarios by simulation.



a

b

Figure 15: Expected distribution of wildlife obtained by dispersal analyses: distance is measured as the least cost distance in moving over the friction surface: Areas where no individuals are expected to be are in black, while dark green to dark red represents the maximum to the minimum expected presence. a (left) dispersal from every biotope, b (right) : dispersal from forest.

The high resolution permits a local analysis of a large scale process. *Figure 16* shows the southern part of the plain illustrated in *figure 15a*. The perimeter of the farmstead is represented in white. In this part of the plain, a viaduct permits thegame wildlife to cross the highway. Near the highway pass, pressures due to human activities are important (circled in *figure 16*). It constitutes an area of priority for natural land use planning. This kind of spatial information is very precious to farm advisors in order to plan the position of ecological compensation area (7% of the farmland). Based on such information, a farm plan can be proposed to ensure exchange between both sides of the highway and to increase the connectivity between ecosystems.

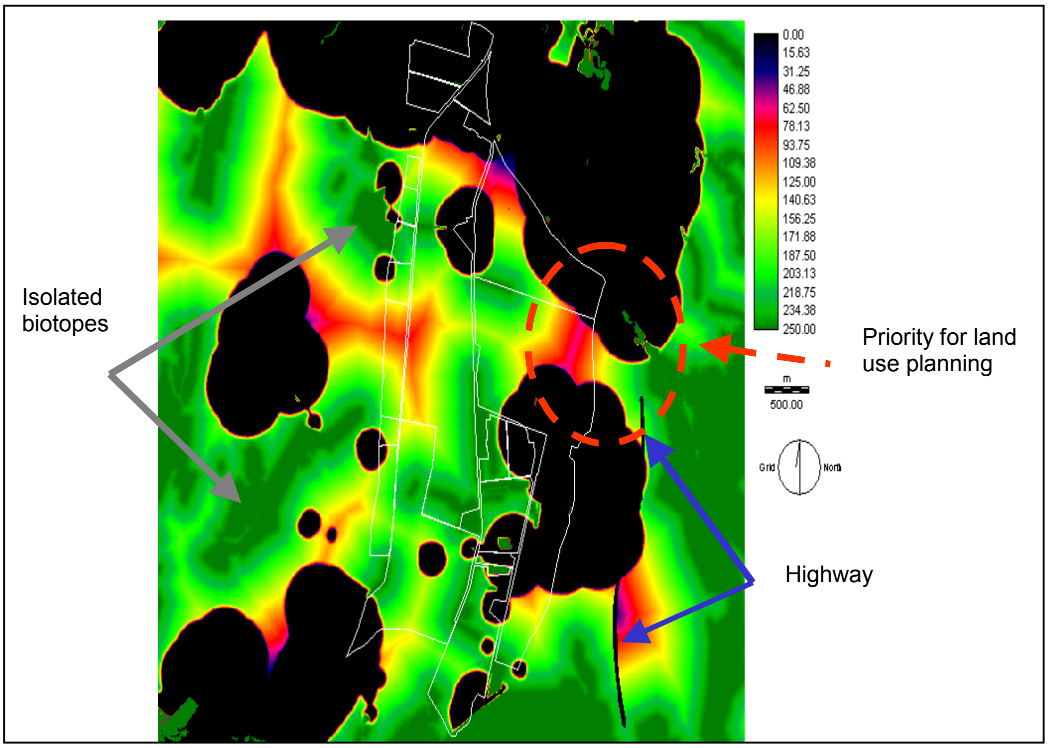


Figure 16: Dispersal analysis result at landscape scale indicating priorities for ecological land use planning at the local scale (in this case the location of ecological compensation areas).

Figure 17 presents the result of a dispersal simulation from two main forests localised in the northwest and southeast of the study area (see small map in *figure 17*). The map presents the cost surface considering ecological distances that represents the sum of the real distance (metric) and the distance due to movement limitations. The highway can not be crossed if no passes (tunnel, viaduct, bridge) are present. The ecological distance varies from 0 (dark green) to 3000 (black). The black area corresponds to an ecological distance greater than 3000 (distance and equivalent distance in meter due to movement limitations (see *table 2*)). *Figure 17* shows clearly the barrier induces by the highway. Only two passes (viaducts) A and B, are possible (see *figure 17*). The results map (in *figure 17*) shows that the shortest ecological distance to get to the pass depends on the direction. From the northwestern forest to the southeastern forest the closest pass is the pass A. In the other direction southeast to northwest, it is easier to reach the pass A. These results have been validated by observations realised by Berthoud (1999). He showed that the flux is not equal in opposite directions on a same pass. Under the pass A (*figure 17*), the number of individual going from northwest to southeast is 50% greater than in the other direction. Under the pass B he showed that in the southeast to northwest direction, there is about 34% more individual than in the opposite direction.

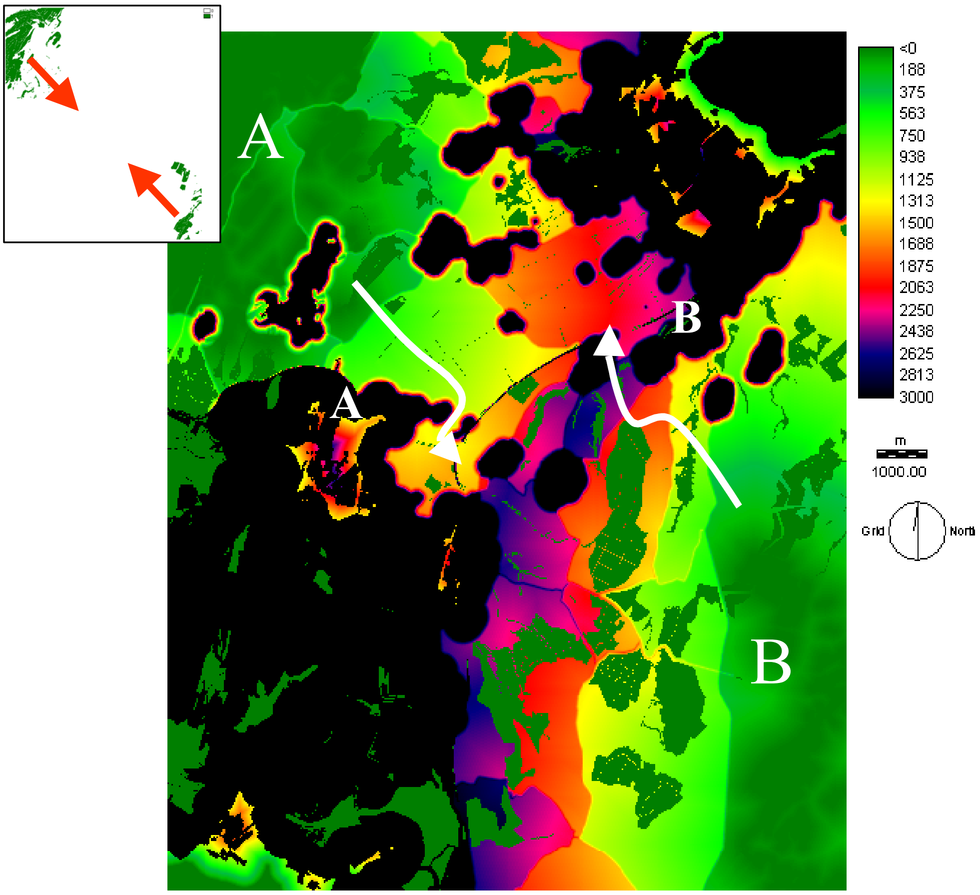


Figure 17: Dispersal analyses: distance is measured as the least cost distance in moving over the landscape model (friction surface) from two main forests located in the NW and in the SE of the plain.

Conclusion

Although our results are based on several assumptions, the method offers a flexible tool to analyse dispersal in landscape. This method provides the possibility to simulate different scenarios of political or managerial decisions.

The application concerning the simulation of animal dispersion on friction surfaces (constraint surfaces) has highlighted the ability of this model to represent ecological networks. Even though this methods does not consider the quality of biotopes and their specific richness, which can be critical for successful species conservation (Cabeza and Moilanen, 2001), simulations can be generated considering different kinds of biotopes, and in this way different kinds of species, depending on available data. The application has shown the applicability of this model to analyse the impact of human infrastructures on animal dispersal, the conflicting areas, the connectivity between biotopes and in a more extensive way the potentialities for ecological networks. In the Swiss context, with the introduction of ecological compensation areas (7% of farm land), case studies have shown the method to provide interesting tools to regulate the position of the ecological compensation.

The result maps have shown several advantages for wildlife conservation and land use planning. These maps are pertinent tools to express, understand, and analyse ecological links between ecosystems. They offer information about conflicting areas (human activities and ecological networks) and highlight regional ecological networks at the local scale. In this way they provide information for the elaboration of land use planning. They provide useful information in order to identify the most suitable use of an area: renaturation, intensive agriculture, etc. Consequently, they help the decision-makers to plan activities at the local and landscape scale that ensure links between ecosystems.

Our model therefore provides an understanding and an analysis of dispersal in fragmented landscape. It can also be a helpful tool in a scenario based analysis. Our development shows great potential for adapting to different landscape. It provides a flexible and useful tool to evaluate the impact of land use scenarios on a landscape.

References

Ahern, J., 1994. Greenways as ecological in rural areas. In: E. A Cook and H. N. Van Lier (Editors). Landscape planning and ecological networks, Elsevier, Amsterdam, pp.159-177.

Akçakaya, H. R., 2000a. Conservation and management for multiple specices: intergrating field research and modeling into management decisions, Environmental Management, 26: S75-S83.

Akçakaya, H. R., 2000b. Viability analyses with habitat-based metapopulation models, Population Ecology, 42: 45-53.

Baschak, L. and Brown, R., 1994. River system and landscape networks. In: E. A Cook and H. N. Van Lier (Editors). Landscape planning and ecological networks, Elsevier, Amsterdam, pp.179-201.

Berthoud, G., 1999. Comportement des mammifères aux abords des passages à faune. Conference Fauna et traffic : Traffic systems and fauna networks : necessity for a new approach, pp. 127-138 Lausanne.

Broggi, M. F. and Schlegel, H., 1990. Minimum requis de surfaces proches de l'état naturel dans le paysage rural, programme national de recherche 22, rapport 31a, utilisation du sol en Suisse, Liebbefeld-Berne.

Broggi, M. F. and Schlegel, H., 1998. Priorité nationales de la compensation écologique dans les zone agricole de plaine, Cahier de l'environnement n°306, Nature et paysage, OFEFP, Berne.

Bruel, F. and Baudry, J., 1999. Ecologie du paysage, Concepts, méthodes et application. Edition Technique et Documentation, Paris

Cabeza, M. and Moilanen, A.; 2001 Design of reserve networks and the persistence of biodiversity,. Trends in Ecology and Evolution, 16 (5): 242-248.

Clergeau, P. and Burel, F., 1997. The role of spatio-temporal patch connectivity at the landscape level : an example in a bird distribution. Landscape and Urban Planning 38: 37-43.

Collinge, S.K., 1996. Ecological consequences of habitat fragmentation : implications for landscape architecture and planing. Landscape and Urban planning 36: 59-77.

Collinge, S.K., 1998. Spatial arrangement of habitat patches and corridors : clues from ecological field experiments. Landscape and Urban Planning 42: 157-168.

Darwen, P.J., et Green, D.G. 1996. Viability of population in a landscape. Ecological Modelling 85 : pp. 165-171.

Drechsler, M. and Wissel, Ch., 1998. Trade-offs between local and regional scale management of metapopulation. Biological Conservation, 83 (1): 31-41.

Duhme, F., Pauleit, S. and Baier, H., 1997. Quantifying targets for nature conservation in future European Landscapes. Landscape and Urban Planning 37: 73-84.

EC, European commission directorate-general environment, 1993. Nuclear safety and civil protection « CORINE Land Cover, Technical Guide » EUR 12585 EN, Office for official publication of the European communities, Luxembourg.

Forman, R.T.T. 1997. Land mosaics : The ecology of landscapes and regions. Cambridge University Press.

Gates, S., Gibbons, D. W., Lack P. C. and Fuller, R. J., 1993. Declining farmland bird species modelling geographical patterns of abundance in Britain, In: P.J. Edwards, R.M. May and N. R. Webb (editors), the 35th symposium of the British ecological society with the society for conservation biology university of Southampton, pp.153-178.

Grimm, V., Frank, k., Jeltsch, F., Brandl, R., Uchmanski, J., Wissel, Ch., 1996. Pattern-oriented modelling in population ecology, The Science of Total Environment, 183: 151-166.

Hanski, I., 1999. Metapopulation Ecology, Oxford Series in Ecology and Evolution, Oxford.

Harms, B., Knaapen ,J. P. and Rademakers, J. G., 1993. Landscape planning for nature restoration: comparing regional scenarios. In C.C Vos and P. Opdam (editors). Landscape ecology of a stressed environment. IALE-studies in Landscape Ecology, Vol.1, Chapman and Hall, London, pp.197-218.

Johnson, A.R., Milne, B.T. and Wiens, J.A., 1992a. Diffusion in fractal landscape - Simulations and experimental studies of tenebrionid beetle movements. Ecology 73 (6): 1968-1983.

Johnson, A.R., Wiens, J.A., Milne, B.T. and Crist T.O. 1992b. Animal movements and population-dynamics in heterogeneous landscapes. Landscape Ecology 7 (1): 63-75.

Jordan, F., 2000, A reliability-theory approach to corridor design Ecological modelling 128: 211-220.

Kareiva, P. and Anderson, M. (1989). Spatial aspects of species interactions: the wedding of models and experiments. In A. Hasting (editors), Community Ecology, pp. 35-50 Springer-Verlag, New York.

Kiester, A.R., Scott, J.M., Csuti, B., Noss, R.F., Butterfield, B., Sahr, K., and While D., 1996. Conservation Priorization using GAP data. Conservation Biology 10 (5): 1332-1342.

Kliskey, A. D., Lofroth, E. C., Thompson, W.A, Brown, S. and Schreier, H., 1999. Simulating and evaluating alternative resource-use strategies using GIS-based habitat suitability indices. Landscape and Urban Planning 45: 163-175.

Kubes, Jan, 1996. Biocentres and corridors in a cultural landscape. A critical assessment of the « territorial system of ecological stability, Landscape and Urban Planning 35: 231-240.

Levins, R., 1970. Extinction, Lect. Notes Math 2, 75-107.

Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity or biological control, Bull. Entomol. Soc. Amer. 15: 237-240.

MacArthur, R.H. and Wilson, E.D., 1967. The Theory of Island Biogeography, Princeton University Press, Princeton.

Margules, C.R. and Pressey, R.L:, 2000. Systematic conservation planning. Nature 405:243-253.

May, R.M., 1993. The effects of spatial scale on ecological questions and answers, in large-scale ecology and conservation biology. In: P.J. Edwards, R.M. May and N. R. Webb (editors), the 35th symposium of the British ecological society with the society for conservation biology university of Southampton, pp. 1-18.

OFS, 1998. Occupation du sol en Suisse et en Europe, Neuchâtel.

Opdam, P., van Apeldoorn, R., Schotman, A. and Kalkhoven, J., 1993. Population responses to landscape fragmentation. In: C.C Vos and P. Opdam (editors), landscape ecology of a stressed environment. IALE-studies in Landscape Ecology, Vol.1, Chapman and Hall, London, pp.147-171.

Polasky, S.; Camm ,J. D., Solow, A. R., Csuti, B., White, D. and Ding, R., 2000. Choosing reserve networks with incomplete species information, Biological Conservation 94: 1-10.

Reid, E., Mortimer, G.N., Lindsay, R. A. and Thompson, D.B.A., 1993. Blanket bogs in great Britain: an assessment of large-scale pattern and distribution using remote sensing and GIS, In: P.J. Edwards, R.M. May and N. R. Webb (editors), the 35th symposium of the British ecological society with the society for conservation biology university of Southampton, pp 223-246.

Schippers, P., Verboom, J., Knaapen, J.P. and van Apeldoorn, R.C., 1996, Dispersal and habitat connectivity in complex heterogeneous landscapes: An analysis with a GIS-based random walk model, Ecography 19 (2): 97-106

Shkedy, Y. and Saltz, D., 1999. Characterizing core and corridor use by Nubian Ibex in the Negev Desert, Israel, Conservation Biology, 14 (1): 200-206

Simberloff, 1997 Flagships, umbrellas, and keystones: is single-species management passé in the landscape era, Biological Conservation 83 (3): 247-257

Starfinger, V. and Sukopp, H., 1994. Assessment of urban biotopes for nature conservation, in Landscape planning and ecological networks, E. A Cook and H.N. Van Lier (Editors).

Theobald M. J. R, Hobbs N. T., 1997. Estimating the cumulative effects of development on wildlife habitat. Landscape and Urban Planning 39: 25-36.

Vos, C. C. and Zonneveld, I. S., 1993. Patterns and processes in a landscape under stress: the study area. In: C.C Vos and P. Opdam (editors), landscape ecology of a stressed environment. IALE-studies in Landscape Ecology, Vol.1, Chapman and Hall, London, pp.1-28.

With, K.A., 1997. The use and misuse of neutral landscape models in ecology. Oikos 79: 219-229.

Yu, K., 1996. Security patterns and surface model in landscape ecological planning, Landscape and Urban Planning 36: 1-17.

Ziv, Y., 1998. The effect of habitat heterogeneity on species diversity patterns: a community-level approach using an object-oriented landscape simulation model (SHALOM), Ecological Modelling 111: 135-170.

Chapter 4

A feature-oriented landscape model for animal movement and behaviour assessment[1]

Abstract

Animal dispersal processes determine metapopulation dynamics and gene flow, which are both fundamental for species and population viability. In heterogeneous and fragmented landscapes, animal dispersal depends on animal interactions with landscape structure and animal use of landscape. Thus, in dispersal modelling, landscape must be represented explicitly and must contain all the information needed to simulate animal movement and behaviour. In this field, there are still limitations due to the landscape models used, which often do not represent in realistic ways landscape features. As an example, structures that can prevent or promote dispersal act or that may be perceived by animals as a benefit or a constraint must be explicitly represented, whatever size and shape they have.

In order to overcome some of the above-mentioned limitations, we present a feature-oriented model developed with a Geographical Information System (GIS). This model allows generating animal dispersal according to specific behavioural traits regarding landscape structure. The model: (i) respects the shape of the landscape features and their related properties, (ii) allows different kinds of landscape use by the animals: entire landscape mosaic, stepping stones, habitat corridors and linear networks (iii) includes close and distant relationships among landscape features, allowing for example animal visual cues in directing animal movement.

Such a model, provided that adequate movement rules are defined, allows to assess the behaviour of a large number of species, and thus to evaluate colonisation processes as well as management schemes (corridors, ecological networks).

[1] *Note: This chapter is submitted to Landscape Ecology*
Co-author: Richard Metzger

Introduction

Animal interactions with landscape

Human activities (habitation, agriculture, infrastructure) as well as the landscape structures and features are spatially localised and can widely modify the ecological processes in a landscape (Turner 1989). They affect the colonisation success between habitat patches (Hanski 1999), the spatial distribution of organisms (Kennedy and Gray 1997) and gene flow (Barton 1992), which are all fundamental for long term species' viability. Additionally, species behaviour in a given landscape determines the patterns of animal spatial use, which has long been recognized important in the field of species conservation (Reed and Dobson 1993; Curio 1996; Lima and Zollner 1996; Ulfstrand 1996; Sutherland 1998; Caro 1999; Reed 1999; Anthony and Blumstein 2000), but seldom considered.

Due to the difficulty to obtain and to interpret experimental results (Koenig et al. 1996; Tischendorf 1997), the modelling of animal behaviour and movement in a fragmented landscape with an explicit realistic landscape model could be very useful in extracting relevant information regarding management and conservation (Kareiva and Wennergren 1995).

From a modelling point of view, integrating the relations between species and landscape implies a realistic representation of the spatial elements that act during dispersal (travelling). It is especially the case when species behaviour is affected by landscape structure. Thus, landscape representations that integrate heterogeneity and fragmentation are needed.

Two main kinds of landscape models, regular grids and patches, are used (Hanski and Simberloff 1997; Bian 2003) to model spatially structured metapopulations. These models correspond to the two main data structures discussed in the following sections: grid-based and vector-based.

Grid-based models

Grid models represent a landscape with a finite number of regular cells covering an area (Burrough and McDonnell 1998). Each cell is characterised by a single value of each of the considered attributes. The cells can be squares, triangles, hexagons or other regular shapes. This simple data structure offers an easy, local-specific, manipulation of an attribute. It allows flexible spatial analysis and mathematical modelling (Burrough and McDonnell 1998) and permits neighbourhood relationships that account for local interactions through state transition rules (Tischendorf 1997) as used in cellular automata (With and King 1997; Thulke et al. 1999; Wissel 2000; Anderson and Neuhauser 2002; Chen et al. 2002). In dispersal modelling, the spatial representation of landscape is commonly based on grid models (With and Crist 1995; With et al. 1997; Beecham and Farnsworth

1998; Tischendorf et al. 1998; Carter and Finn 1999; Thulke et al. 1999; Bergman et al. 2000; Wissel 2000); few other data structures have been investigated.

Data encoding in a grid-cell data structure implies some fundamental considerations that have been emphasized by Laurini and Thompson (1992): (i) the existence of an a priori fixed resolution, (ii) the necessity of aggregative and disaggregative methods when determining an attribute for a cell, (iii) the limitations in representing line features and (iv) the lack of explicit topology (shape and distance relationships). If a high degree of precision is required for capturing linear features like roads or rivers (which can, for example, act as a barrier to dispersal), a very fine resolution may be required, at the expense of needing a large amount of data. Furthermore, this fine resolution may not be required in case of, for example, a large forest and moreover may lead to unrealistic attributes. Conversely, with an increased cell size, linear and point landscape features cannot be represented with sufficient accuracy. The area covered by a large cell might include various landscape features, so that attributes have to be aggregated, implying a loss of information.

Additionally, Tischendorf (1997) listed the limitations of regular grids for animal movement modelling: (i) limitation due to simulation time and memory capacities, (ii) perceptual range that exceeds the resolution (neighbourhood relationships are allowed), and (iii) equal resolution for both landscape features and individual movement. As a consequence of point (i), the sensitivity analysis of a grid-based model is widely limited.

Regarding individual dispersal modelling, which has to integrate behavioural traits, the difficulties in building distant topological relationships impair accounting for factors such as a high perceptual range. Moreover, individuals have to move across adjacent cells in determined directions. For example, modelling the movement of a small individual mammal that uses linear structures (hedges, rivers) to move between patches, as well as stepping stone movement are simply not reasonably feasible.

From the above, it can be concluded that the grid-based approach does not provide an effective framework for animal dispersal modelling.

Vector-based models

Vector data structures represent landscape features according to their shapes and functions (Bian 2003) by three main entities: point, polylines and polygons associated with multiple graphic and non-graphic attributes (Burrough and McDonnell 1998). In vector data structures the topological properties of entities (shapes, neighbours and hierarchy) may be described explicitly in a highly accurate way; these data structures are therefore well suited for network analysis. Furthermore, they offer compact data structures and allow entity interactions as well as a thematic representation of entities (small and large). Even if less used than the grid models, vector models are particularly well adapted to model landscape features and show a high potential that is worthy of serious investigation (Bian 2003).

However, Bian (2003) points out a limitation in vector data structure related to a change in location or the creation of a new landscape feature. For the latter, the attributes and the topological relations of the new element have to be defined and those of the neighbouring objects have to be updated. The internal and spatial homogeneity of object attributes can also limit the ability to represent gradients of spatially continuous variables (as environmental factors) (Tischendorf 1997) and necessitate aggregative methods. Bian (2003) also mentions the cost, the learning curve, the complexity of data handling and the need for sophisticated database management as limitations in the use of vector data structures. These limitations however are overcome with the new available technologies in the GIS fields. Despite these limitations, vector data structures appear to be well suited for modelling the landscape, being able to incorporate the geometry of the patch networks, patch size and spatial relationships between landscape features.

Specific data structure for ecological modelling

Specific landscape representations for modelling environmental or ecological processes are limited by available data structures. Only a few authors have developed specific irregular data structures to allow a more accurate representation of spatial elements. Irregular grids (varying in size but not in shape) may consist of triangulated irregular networks (George and Borouchaki 1997) based on a Delaunay triangulation (Delaunay 1934), surface tessellation using Voronoï polygons (Voronoï 1908) and data structures based on hierarchical data models (Tischendorf 1997). This kind of representation suffers from the complexity of the principles guiding or governing the decomposition process and the type of spatial resolution. Some GIS offer also a square representation that is completed with edges and corners (Kovalevsky 1989), but such developments still have limitations since they do not explicitly address topological spatial properties (Laurini and Thompson 1992).

Spatial database management

In order to improve the simulation of dispersal in a fragmented landscape, the landscape model is usually coupled with an expert model based on an object-oriented approach (Rumbaugh et al. 1991); see for example Downing and Reed (1996), Beecham and Farnsworth (1998) and Lorek and Sonnenschein (1999). This approach considers that objects, in our case the landscape entities and dispersers, have properties and behaviours depending on their attributes and behavioural values which define their spatial, geometric, temporal and thematic dimensions (Worboys 1995). They interact with each other according to information considering their states and properties and communicate with each other by sending messages (which can induce for example changes of state or behaviour). Object-oriented design (OOD), which defines objects and events, includes modularity, abstraction and encapsulation properties (see Rumbaugh et al., 1991). Combining the available general information on and between objects with dispersal movement rules allows creation of chains of spatial entities. These chains are themselves entities and, as such, they can have their own properties. They represent individual travel paths with attributes such as, for example, a limit in distance or in time during dispersal.

The coupling of an object-oriented modelling approach and a landscape model improves animal dispersal simulation by accounting for processes and interactions in a more realistic way. Works in this field have already been reported by several authors, as for example by Carter and Finn (1999) for an animal foraging model, by Beecham and Farnsworth (1998) for a Hierarchical Object Oriented Foraging Simulator (HOOFS) and by Gustafson and Gardner (1996) for the estimation of immigration and emigration rates between habitat islands within heterogeneous landscapes. These studies were based on grid models with the limitations mentioned previously, namely in landscape representation and distant relationships among landscape features.

Outline

This chapter presents a spatially explicit model that includes all landscape features and allows the simulation of individual's interactions within the landscape and the movement of individuals between landscape features. This model is based on the close-coupling of a vector-based landscape model with an object-oriented model covering the specific needs of animal dispersal simulation. The model contains (i) entities that have a representation depending on their properties and (ii) the information required to incorporate behavioural and physiological traits of individuals (dispersal ability). Thus, topology and associated attributes are included, as well as distant relationships between landscape features. Furthermore, the model allows different patterns of landscape uses: the entire landscape mosaic, stepping stones, habitat corridors, linear networks and combinations of them. Finally, simulation time and data volume remain small, so that sensitivity analyses are not limited.

The general conceptualisation framework of this model includes new landscape representation and new topological formalism that will be presented as well as the methods to build and implement the feature-oriented landscape model. Finally applications of this model will be given.

Methods

Conceptual design

Figure 18 shows the conceptual design that was applied to landscape modelling and animal movement and dispersal simulation. To elaborate a landscape representation and model covering the specific needs of animal movement modelling, one has to define in a realistic way: (i) a conceptualisation of the landscape representation that contains objects (landscape features) and theirs properties and (ii) a topological formalism that defines the relations between these objects.

In the present case, the landscape representation is made-up of a mesh of spatial entities (vector based), which are irregular in shape and dimension but internally homogeneous in regard to their properties. Thus, the landscape structure is fully described by three kinds of objects: cells, frontiers and nodes. A cell is a homogeneous area limited by frontiers, which are either linear landscape features (e.g. roads, rivers or hedges) or a linear characteristic of the cell itself, according to the type of landscape feature it represents (e.g. a forest border for example). Thus, cells represent land cover and their related properties, whereas frontiers represent linear features or transitions between land covers (from forest to field, for example). These entities include all the typology- and topology-related information and are never overlaid.

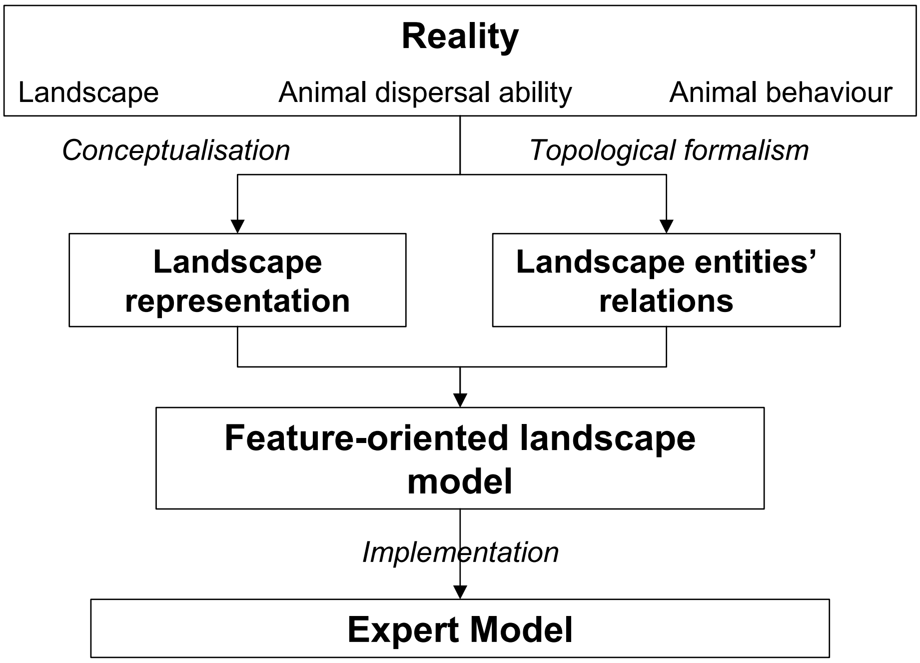


Figure 18: General conceptual framework of the dispersal mode: Reality is decomposed for the needs of landscape representation and the assessment of landscape entities' relations. The feature-oriented landscape model supports both. It incorporates topological formalism. The model is implemented with the help of an expert model.

The topological formalism must account for relations between objects and allow the simulation of different kind of movements and landscape uses. Since animals use linear and areal structures alternatively and/or separately, they must be connected through a coherent topological and hierarchical structure. The proposed topological formalism is as follows: the landscape is composed of cells, frontiers and nodes (*figure 19a*). The cells are connected to each other by their surrounding frontiers while nodes connect the frontiers. Frontiers are modelled using a pair of oriented polylines (unidirectional) so that the 'sister' frontier of a cell's frontier shares the same shape but has the opposite direction. Additionally, frontiers can be crossed or gone along in both directions (see *figure 19b* and *19c*).

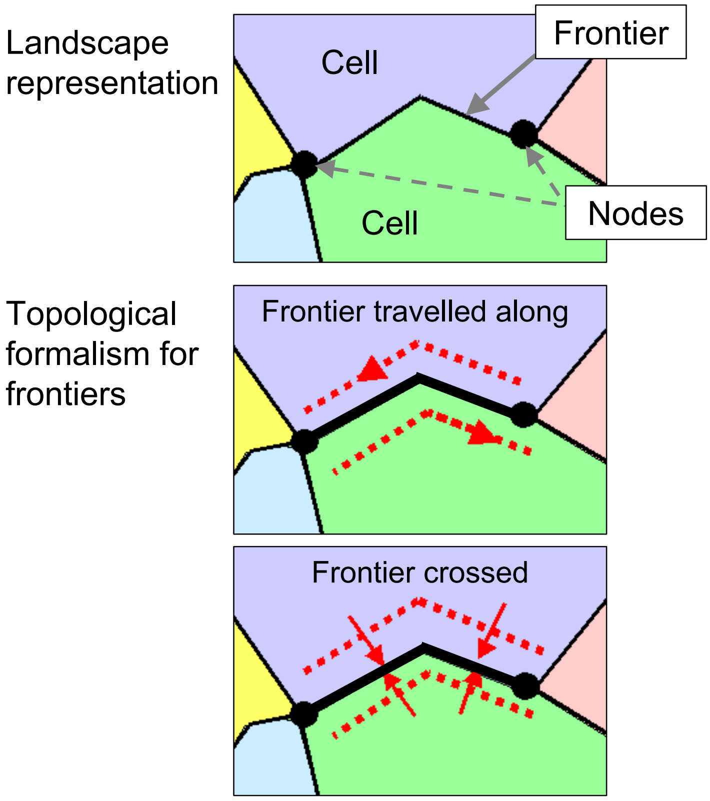


Figure 19 a, b, c: (2a) Landscape representation with three main entities: cells, frontiers and nodes. (2b and 2c) Topological formalism for frontiers: The representation of a frontier can be decomposed in the expert system into two virtual frontiers which allow independent movement in both directions and frontier use

The perceptual range and the dispersal distance, two critical parameters in animal dispersal, which are distance measures, must be defined in the model. The perceptual range is the distance from which a particular landscape element (patch) can be perceived by a given animal (Lima and Zollner 1996; Zollner and Lima 1999; Zollner 2000). In the landscape model, a buffer, in which an animal can perceive the target entity, is defined to represent perceptual range. The dispersal distance depends on the landscape structure (paths used) and the characteristics and abilities of the animal species (Bell 1991). To allow their quantification when simulating animal dispersal, metrics were added as attributes to the spatial entities. In the case of cells, the dispersal distance is defined by the Euclidean distance between the middle point of the frontier that separates the current cell and the previous cell and the one that separates the current cell and the next cell. In the case of frontiers, the distance is the length of the frontier. The crossing of a frontier does not result in an additional distance, but has a cost (see later).

The conceptualisation of the landscape representation and the topological formalism that define relations between landscape entities define the feature-oriented landscape model (*figure 18*). This model is implemented with the help of an expert model, presented in the next section.

Methods to build the landscape model

The procedure described hereafter was used to build the landscape model on the basis of vector data. The study area covers a 260 km^2 highly fragmented landscape in western Switzerland. Basic data are provided by the ‘landscape model’ of the Swiss Federal Office of Topography (*SwissTopo*), which is a vector based model covering Switzerland at the 1:25’000 scale of the national map of Switzerland. The approximately 140 different object types in this model result from the discussions held on the general way to represent landscape features in Switzerland for the national map (Gurtner 1997). Data include: (i) points, such as isolated trees, (ii) polylines such as the road network (by categories), the railway network, the hydrographical network, hedges and (iii) polygons that represent soil coverage. The landscape is thus represented by a complete network of mutually exclusive polygons, overlaid by several networks of polylines.

The transformation of the vector data source entities, i.e. polygons, polylines and points, into cells, frontiers and nodes is achieved with MapBasic® scripts within the MapInfo Professional® environment according to the following steps: (i) data integrity analysis, (ii) cell creation, (iii) frontier creation, and (iv) integration of species’ visual abilities during the search of habitat patches in the form of perceptual distance calculation.

(i) The basic requirement for the cell and frontier creation processes to work properly is to provide them clean data, i.e data without multiple points, overlaps or self-intersections. If the initial data integrity check detects such potential topological problems, the corresponding object is removed.

(ii) The cell creation process starts by superposing all polyline networks. At each intersection point, the related polylines are split and a node is added (see *figure 20*). The resulting elements are gathered in a single layer to form a clean polyline network. A polyline may or may not be hitched on another polyline, which would generally be the case of the starting part of a river for example. If a polyline is not closed, an algorithm joins its end point to the closest point of the nearest neighbouring polyline (see *figure 21*), the join being a line without attributes (a virtual line). Thus a complete network of closed polylines can be obtained. The next step in the cell creation process consists of splitting the polygons of the soil coverage layer according to the new aggregated polyline layer. This process results in a complete irregular network of cells matching the polyline network, the created cells having the same attributes as their parents.

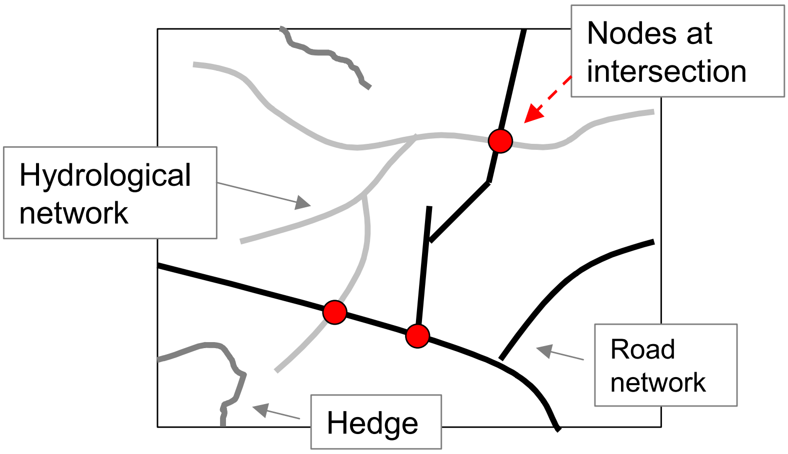


Figure 20: Procedure that connects objects coming from different polyline networks by adding a common node at each intersection

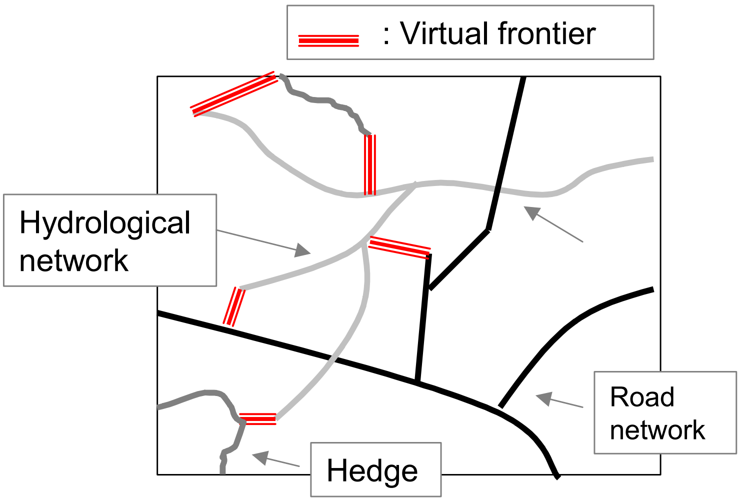


Figure 21: Illustration of the procedure to form closed polylines by adding virtual parts to the frontier networks

(iii) The frontiers are then created by intersecting adjacent cells (*figure 22*). The neighbouring cells are identified using three tests: The first test considers that each neighbouring cell must have a non-null common frontier, the second one verifies that the cell and its neighbour do not share the same attributes (to avoid selection of itself) and the third one checks that the entire frontier entirety belongs to both adjacent cells. An algorithm adds the appropriate landscape feature attributes to the created frontier by comparing its position with the initial polyline networks. Thanks to the initial intersection process (see (ii)), each frontier starts and ends on a node. At this stage the cells, frontiers and nodes are created.

(iv) The perceptual range is a fundamental factor in animal dispersal. It corresponds to a distance from which an individual can perceive a resource (Lima and Zollner 1996; Zollner and Lima 1999; Zollner 2000). In the model, this distance is assessed by a buffer zone from a 'target entity' (see *figure 23*). The target entities correspond to resources that an individual may be able to see. The value of the distance of the buffer zone corresponds to the species perceptual range. This buffer zone intersects frontiers and cells. For each intersected object attributes are added. They are the target entities and the distance from it. This procedure allows the simulation of the perceptual range. Therefore, the perceptual range, depending on the ability of a species to perceive its environment, may direct movements of individuals.

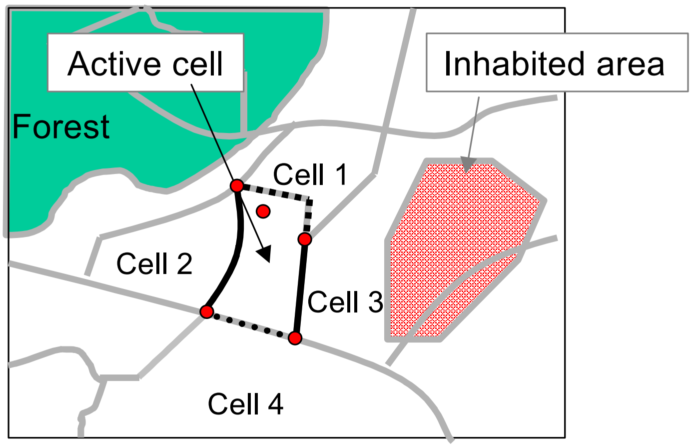


Figure 22: Procedure of frontier creation by intersection between cells

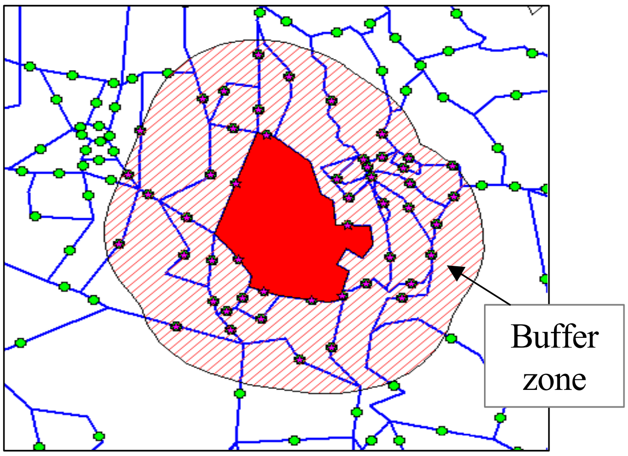


Figure 23: Procedure to represent the perceptual distance between spatial entities; in this figure, the buffer zone represents that range in which the target entity can be perceived.

The expert model

The landscape model and the simulation of individual dispersal are developed in an object-oriented programming (OOP) approach in the Borland® Delphi^{TM} environment with the Object Pascal language. This modelling strategy allows an explicit representation of: (i) individuals (ii) a heterogeneous environment, and (iii) interactions between the individuals and the environment (Downing and Reed 1996; Tischendorf 1997; Ziv 1998; Lomnicki 1999; Bian 2000; Bian 2003).

Each object (individual, landscape entity) is a part of 'linked lists' (i.e. chaining, Sedgewick (1988)), which are themselves objects (e.g. chains of landscape entities). These lists include information about their own properties and relations to other objects (spatial and non-spatial). They provide 'knowledge'. Each object 'knows' other objects by their attributes or through spatial relations. For example, a cell 'knows' the adjacent cells and the frontiers between them, a frontier 'knows' the cells that it separates, a cell 'knows' from which cells and frontiers it can be perceived. Additionally, objects may communicate between each other by 'messages'. They may for instance carry the information requested to update object properties in response to various events.

The simulation of animal dispersal can benefit from these communication skills and be based on movement rules. These rules depend on the simulated species, namely its behavioral traits, its response to landscape features and its ability to perceive its environment. In the movement process, the procedures to choose the spatial entities to be used are thus based on their properties (shape, categories, spatial relation, ability to be crossed and so on) and on species-specific movement rules. As a consequence, individual dispersal fits in the general pattern of the considered species' interaction with the landscape. The sequence of chosen entities during individual movement forms a chain that defines the individual's path. These paths contain all the information, namely attributes, related to the spatial entities they are made of. They additionally have their own properties linked to their spatial and numerical dimensions. The path of an individual that uses only linear landscape features (as small mammals e.g. Peles et al. (1999)) is a succession of frontiers selected according to their attributes and individual preferences. The path of an individual that uses the whole landscape is a succession of cells satisfying the criteria of that individual. The combination of cells, frontiers and nodes allow several kinds of movements.

In the simulation of many individuals, the paths are recorded by the expert system, which manages, updates and links the objects of the landscape model. Therefore, this system allows an analysis of the objects (with their information) composing the paths. The information regarding the frequency of use of the various spatial entities in the paths may be used to represent the pattern of animal spatial use.

Results

Feature-Oriented Landscape Model – FOLM

Figures 24 and *25*, which display the cell network and the frontier network show the Feature-Oriented Landscape Model (FOLM) for the study area. As it can be seen in *figure 24*, the general landscape pattern consists of cells, which are irregular in shape and dimension, including extended homogeneous areas as well as very small ones, thus reflecting the true landscape features. *Figure 25* shows the frontier network. Linear structures, which are too often poorly represented in landscape models, are heavily present in the landscape pattern and well reproduced in the model.

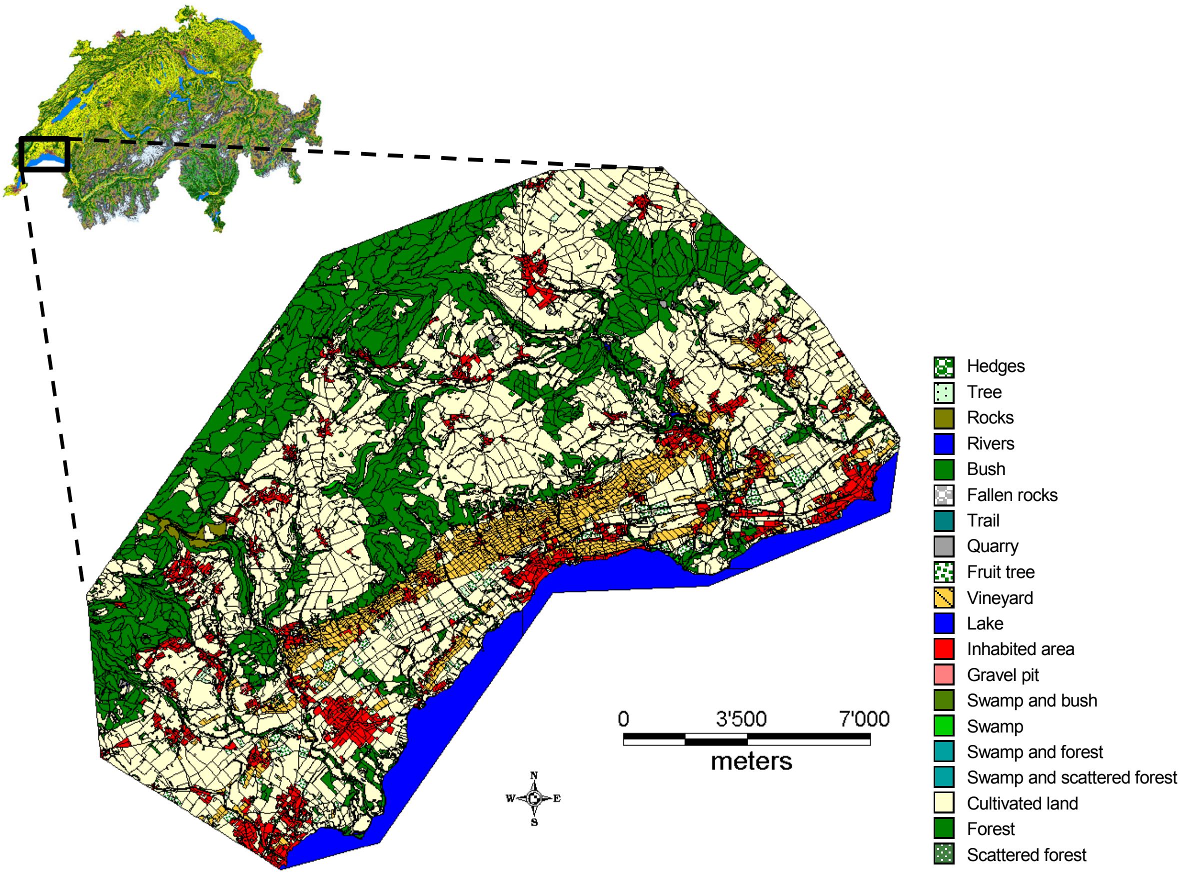


Figure 24: The cell pattern of the feature-oriented landscape model

The comparison of the frontiers (linear features and cell borders) of the landscape model with an aerial photograph (*figure 26)* illustrates the level of detail of the landscape model and emphasizes its accuracy in the positioning and the representation of the landscape elements. The discretisation into cells and frontiers respects the real criss-cross pattern of the landscape. There is no limitation due to the scale in representing landscape elements: small elements like hedges may be included in the model even if a large area is considered. Moreover, each spatial object has the required attributes to supply a representation of its properties (typological and topological), states and behaviour. The spatial accuracy of the landscape element's representation and the possibility to account for all kinds of landscape features at any scale permits a very realistic assessment of the true heterogeneity and fragmentation of the landscape.

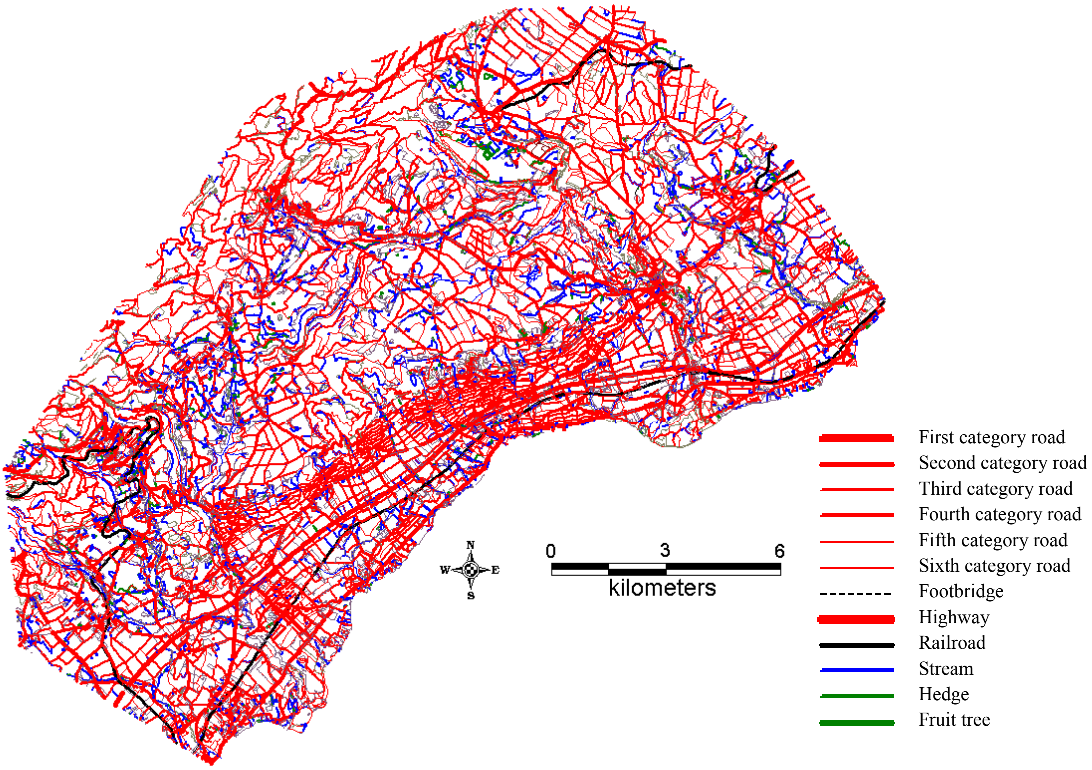


Figure 25: The frontier pattern of the feature-oriented landscape model

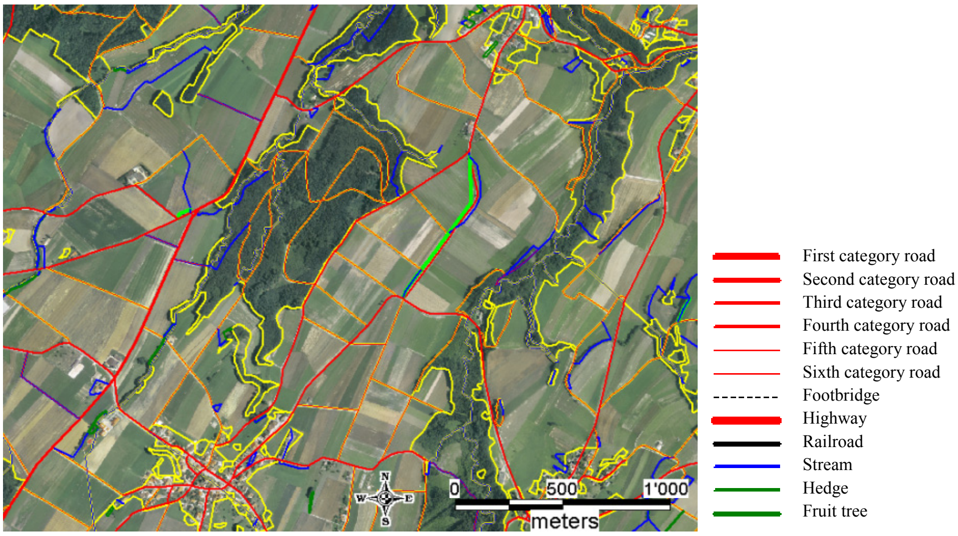


Figure 26: Pattern of the frontiers and cell borders displayed with an aerial photography

Animal dispersal simulations

Figure 27 shows the principles applied to build the sequence of steps forming an individual path. Three inputs are needed: (i) the starting habitat patch, (ii) the Feature Oriented Landscape Model, and (iii) the individual, with its specific behaviour and state. The starting habitat patch, defined by the modeller, initiates the path and becomes the active entity (*figure 27*, part 1).

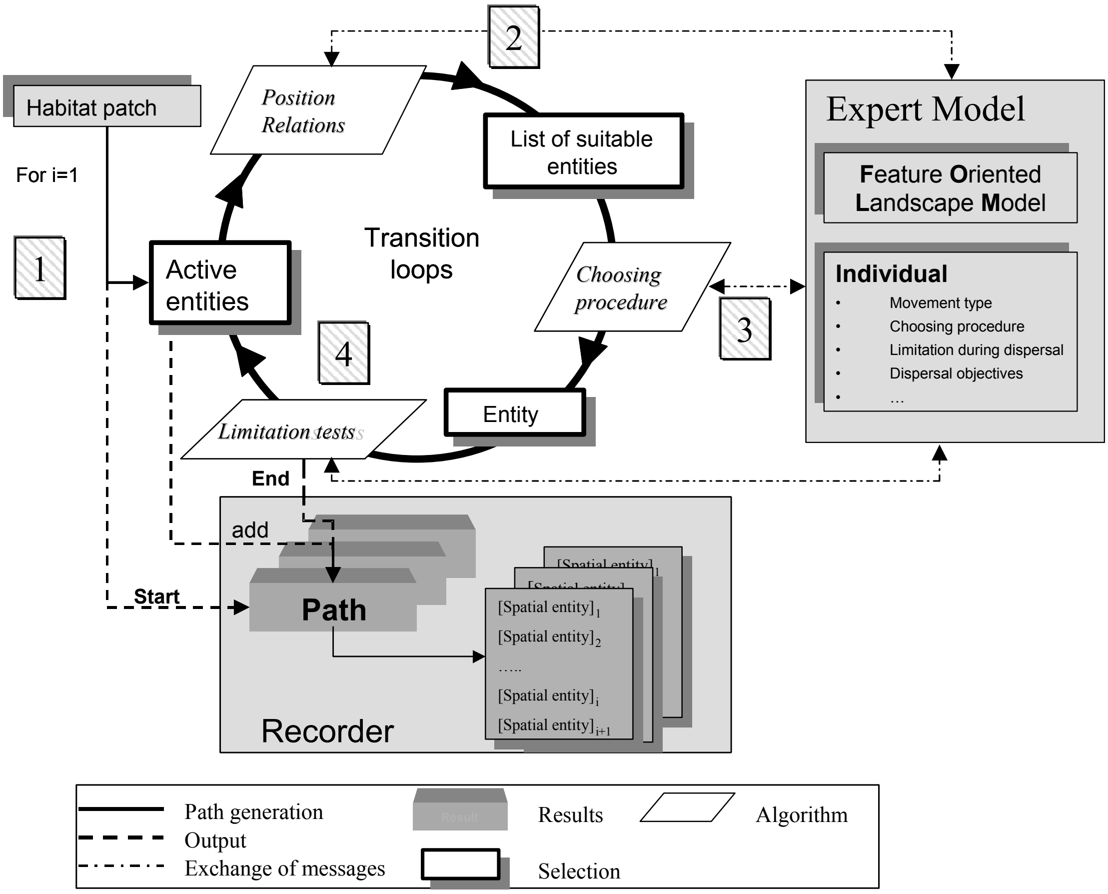


Figure 27: Illustration of a transition loop to generate successive spatial entities that compose a path. The transition is a sequence of four main steps. The first step identifies the active entities (where the individual is located), the second connects information about position and properties of the active entities and defines the related spatial entities, the third selects among the related spatial entities an entity that corresponds to the choosing criteria of the individual and finally the transition of the individuals to the new entities is done and recorded according to limitation during dispersal (e.g. dispersal distance).

Landscape entity attributes and properties are included in the Expert Model as well as the lists of its relations to other entities. According to predefined (animal) movement and behaviour rules, a selection among the entities connected to the active entity is made (*figure 27,* part 2), resulting in a list of suitable entities. A refinement of the selection is then performed according to individual preferences and individual choosing procedures (which is non-deterministic), leading to the determination of the next entity to become the active entity. An example of individual preference could be to select the cell X, if: (1) it is not a barrier, (2) there are no other attractive cells around and (2) it is the closest cell to a forest that an individual can perceive. The process continues recursively (*figure 27,* part 3) until conditions to end the path are met (*figure 27,* part 4). This can be the case either if the maximal value of the dispersal distance has been reached and the disperser failed, or if the selected entity is a target entity (defined by the objectives of the individual) and the individual is successful. Otherwise, the selected entity is added to the path (new element in the chain) and becomes the active entity.

A large variety of rules can be applied in building individual paths (transition rules). Different ways to select entities, according to their shapes and the categories they belong to, express different ways of using landscape features. *Figure 28* and *figure 29* shows illustrative examples of two major kinds of landscape uses: as a mosaic of patches (*figure 28*) and limited to linear features (*figure 29*). Simulating the dispersal of 50’000 individuals has generated both of these maps. Movement rules were based on the attractiveness of the landscape features (defined as their degree of naturalness), with a maximum dispersal distance fixed to 50 km and finding a new habitat patch as the objective of the dispersal. The path followed by each modelled individual is recorded and each time a landscape feature is used, the appropriate attributes are incremented as for example, the number of crossings of a landscape entity. The general patterns of the landscape use illustrated by *figure 28* and *figure 29* are obtained by displaying the number of times the various landscape features have been used by successful individuals.

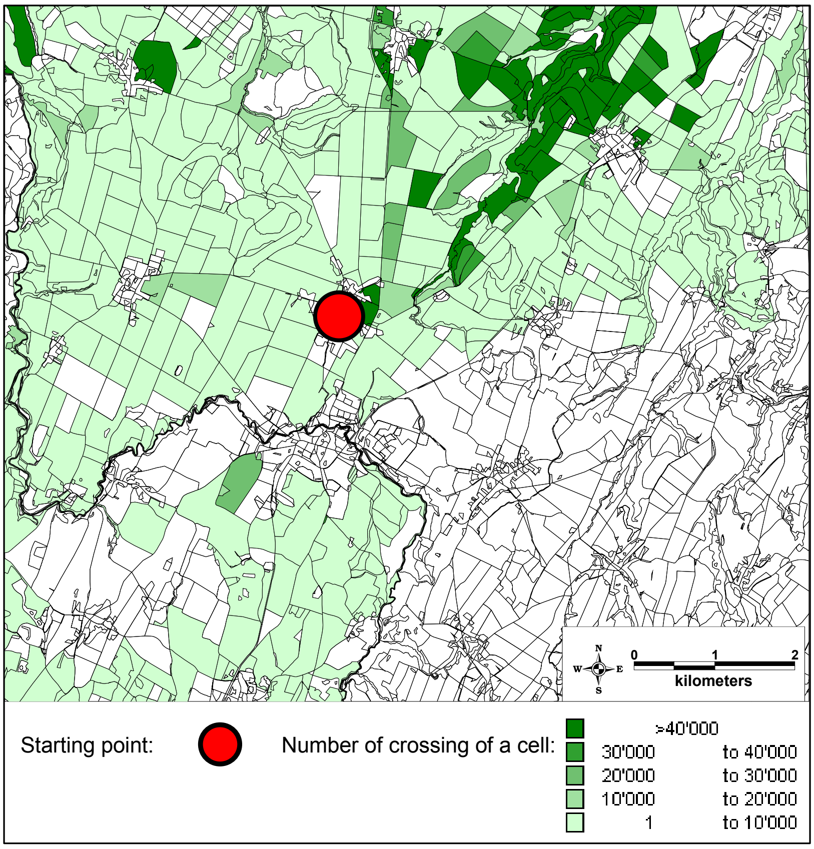


Figure 28: Illustration of landscape use by virtual species that dispersed from a starting habitat patch (the starting point) according to the naturalness of the environment.

This kind of representation is of significant interest in analysing ecological networks and corridors as well as for quantifying the structures and fluxes of individual movements between habitat patches. Such information proves to be highly relevant for landscape planners and conservationists. Moreover, since changing scale is not a problem, animal dispersal analysis is possible both at the metapopulation scale (flux between populations) and at a local scale (corridor planning, local management plan).

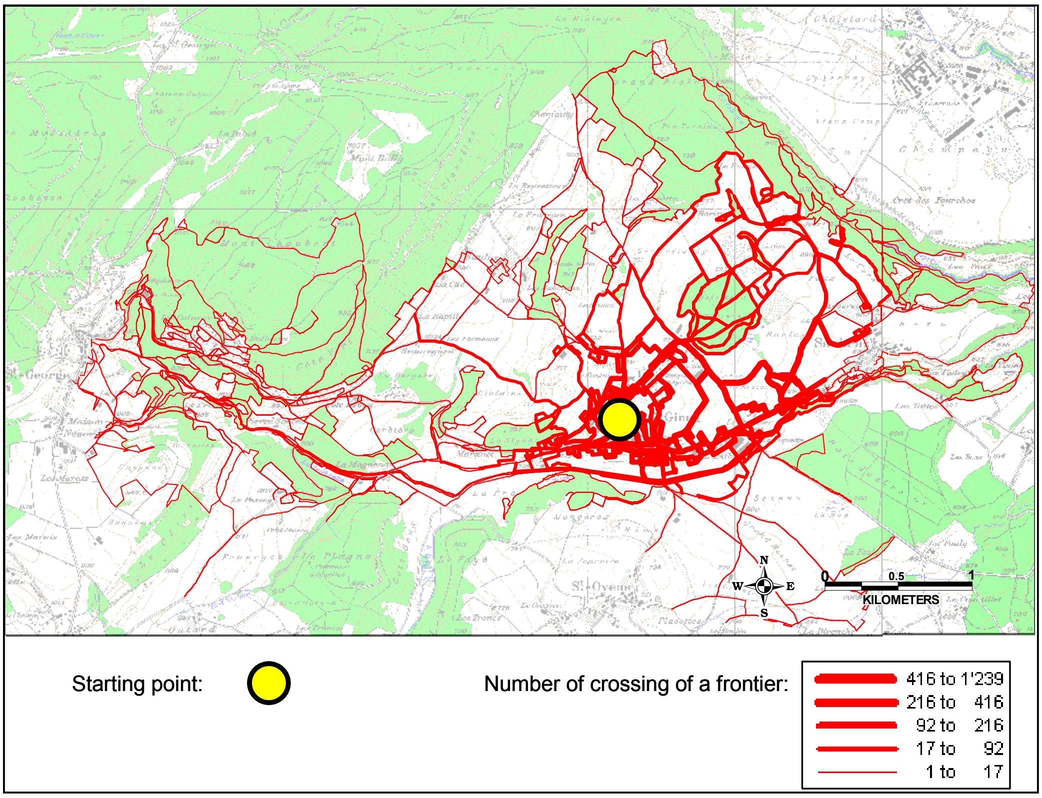


Figure 29: Illustration of landscape use by virtual species that dispersed from a starting habitat patch (the starting point) according to the naturalness of this environment and used the frontier networks to move between habitat patches.

Discussion and conclusion

In recent years, the increase in computer storage and speed performance allowed the development of large-scale animal movement simulation models. Since experimental tracking and analyses of the movement behaviour of individuals remains a time consuming, expensive and difficult challenge (Koenig et al. 1996; Tischendorf 1997), this modelling practice provides an essential bridge between the results of experimental studies and the information needed for critical management decisions even if it increases dramatically the amount of modelling input (Tischendorf et al. 1998).

Virtual (i.e. simulated) ecology might prove to be a very powerful tool (Berger et al. 1999; Hall and Halle 1999), especially in combination with statistics (Grimm et al. 1999). Actually, spatially explicit models have recently been used to explore alternative management schemes for species living in increasingly fragmented habitats (Lindenmayer and Possingham 1996) and to develop management tools for the control of rabies (Thulke et al. 1999). Spatial modelling of animal dispersal may be especially important in evaluating the consequences of changing landscape structures on landscape use by animals, this both from a theoretical and an applied (conservation) point of view (Tischendorf et al. 1998).

This chapter presents a feature-oriented spatially explicit landscape model, which provides a representation of all the landscape features and includes their related information. Based on this landscape model, individual movement between landscape features and thus general animal dispersal can be simulated, accounting namely for species-specific behavioural traits and distant visual abilities. The proposed landscape model is based on a vector landscape representation and is coupled with a topological formalism that allows easy simulation of dispersal processes. Using a vector-based representation reduces the memory needs to include the appropriate landscapes feature information. Moreover, vector data usually result from large investigations regarding object topology and typology. Thus, the model benefits from the efforts already done to classify landscape elements.

In order to allow coherent and optimal relations between spatial entities, a new topological formalism is proposed. It provides a systematic representation of spatial and thematic relations between all spatial entities, making the simulation of movement patterns easier and allowing the simulation of different kind of movements in a landscape.

The implementation of the landscape in an object-oriented programming framework provides flexibility in simulation assumptions and developments. By considering the properties, behaviour and relations of each object, complex interactions can be reproduced. The model offers the possibility to account for behavioural and ecological factors affecting the movements of animals and improves therefore the understanding of the interaction between landscape structures and population ecology (Zollner 2000).

The presented model provides the means of analysing the spatial distribution of animal paths during dispersal and quantifying the colonisation success according to a movement restricted by spatial or thematic constraints. Besides the patterns of landscape use and colonisation probability, the model allows to assess metapopulation structure and dynamics according to individual behaviour on the basis of fluxes of individuals in the landscape. Thanks to its flexibility, the model also accounts for travel costs related to individual behaviour in landscape and thus provides a quantification of dispersal distance in a fragmented landscape.

Two applied studies using the presented model are currently underway. The first one aims at quantifying the influence of behavioural traits on the metapopulation structure and dynamics in a highly fragmented landscape in Switzerland. The second application concerns the simulation of the dispersal of shrews (*Crocidura russula*). This insectivore typically uses linear elements to move in a landscape. The ecological distances and the colonisation success calculated by the model will be compared to genetic data considering effective dispersal rates between populations and genetic distance between habitat patches.

References

Anderson, K. & C. Neuhauser. 2002. Patterns in spatial simulations - are they real? Ecological Modelling 155: 19-30.

Anthony, L.L. & D.T. Blumstein. 2000. Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce N-e. Biological Conservation 95: 303-315.

Barton, N.H. 1992. The genetic consequences of dispersal. pp. 37-59. *In:* N.C. Stenseth & W.Z.J. Lidicker (ed.) Animal Dispersal: small mammals as a model, Chapman & Hall, London.

Beecham, J.A. & K.D. Farnsworth. 1998. Animal foraging from an individual perspective: an object oriented model. Ecological Modelling 113: 141-156.

Bell, W.J. 1991. Searching behaviour: the behavioural ecology of finding resources. Chapman and Hall, London. 358 pp.

Berger, U., G. Wagner & W.F. Wolff. 1999. Virtual biologist observe virtual grasshoppers: an assessment of different mobility parameters for the analysis of movement patterns. Ecological Modelling 115: 119-127.

Bergman, C.M., J.A. Schaefer & S.N. Luttich. 2000. Caribou movement as a correlated random walk. Oecologia 123: 364-374.

Bian, L. 2000. Component modeling for the spatial representation of wildlife movements. Journal of Environmental Management 59: 235-245.

Bian, L. 2003. The representation of the environment in the context of individual-based modeling. Ecological Modelling 159: 279-296.

Burrough, A. & A. McDonnell. 1998. Principles of Geographical Information Systems. Oxford University Press Inc., New York. 333 pp.

Caro, T. 1999. The behaviour-conservation interface. Trends in Ecology and Evolution 14: 366-369.

Carter, J. & J.T. Finn. 1999. MOAB: a spatially explicit, individual-based expert system for creating animal foraging models. Ecological Modelling 119: 29-41.

Chen, Q., A.E. Mynett & A.W. Minns. 2002. Application of cellular automata to modelling competitive growths of two underwater species Chara aspera and Potamogeton pectinatus in Lake Veluwe. Ecological Modelling 147: 253-265.

Curio, E. 1996. Conservation needs ethology. Trends in Ecology and Evolution 11: 260-263.

Delaunay, B. 1934. Sur la sphère vide. Bul. Acad. Sci. URSS, Class. Sci. Nat.: 793-800.

Downing, K. & M. Reed. 1996. Object-oriented migration modelling for biological impact assessment. Ecological Modelling 93: 203-219.

George, P.-L. & H. Borouchaki. 1997. Triangulation de Delaunay et maillage - Applications aux éléments finis. Hermes, Paris.

Grimm, V., T. Wyszomirski, D. Aikman & J. Uchmanski. 1999. Individual-based modelling and ecological theory: synthesis of a workshop. Ecological Modelling 115: 275-282.

Gurtner, M. 1997. Lecture de carte: manuel des cartes nationales. pp. 283. *In:* Club Alpin Suisse & Office fédéral de topographie (ed.), Wabern, Berne.

Gustafson, E.J. & R.H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77: 94-107.

Hall, S. & B. Halle. 1999. Modelling activity synchronization in free-ranging microtine rodent. Ecological Modelling 115: 165-176.

Hanski, I. 1999. Metapopulation Ecology. Oxford University Press, Oxford. 313 pp.

Hanski, I. & D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain and application to conservation. pp. 5-26. *In:* I.A. Hanski & M.E. Gilpin (ed.) Metapopulation biology, Academic Press, San Diego.

Kareiva, P. & U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373: 299-302.

Kennedy, M. & R.D. Gray. 1997. Habitat choice, habitat matching and the effect of travel distance. Behaviour 134: 905-920.

Koenig, W.D., D. Van Vuren & P.N. Hooge. 1996. Detectability, philoparty, and the distribution of dispersal distances in vertebrates. Trends in Ecology and Evolution 11: 514-517.

Kovalevsky, V.A. 1989. Finite topology as applied to image analysis. Computer Vision, Graphics and Image Processing 46: 141-161.

Laurini, R. & D. Thompson. 1992. Fundamentals of Spatial Information Systems. Aademic Press Inc., London. 680 pp.

Lima, S.L. & P.A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution 11: 131-135.

Lindenmayer, D. & H. Possingham. 1996. Ranking conservation and timber management options for Leadbetter's possum in Southeastern Australia using population viability analysis. Conservation Biology 10: 235-251.

Lomnicki, A. 1999. Individual-based models and the individual-based approach to population ecology. Ecological Modelling 115: 191-198.

Lorek, H. & M. Sonnenschein. 1999. Modelling and simulation software to support individual-based ecological modelling. Ecological Modelling 115: 199-216.

Peles, J.D., D.R. Bowne & G.W. Barrett. 1999. Influence of Landscape Structure on Movement Patterns of Small Mammals. pp. 41-62. *In:* G.W. Barrett & J.D. Peles (ed.) Landscape Ecology of Small Mammals, Springer-Verlag, New York.

Reed, J.M. 1999. The role of behavior in recent avian extinctions and endangerments. Conservation Biology 13: 232-241.

Reed, J.M. & A.P. Dobson. 1993. Behavioral constraints and conservation biology- Conspecific attraction and recruitment. Trends in Ecology and Evolution 8: 253-256.

Rumbaugh, J., M. Blaha, M. Premerlani, W. Eddy & W. Lorensen. 1991. Object-orientation modeling and design, New York.

Sedgewick, R. 1988. Algorithms. Addison-Wesley.

Sutherland, W.J. 1998. The importance of behavioural studies in conservation biology. Animal Behaviour 56: 801-809.

Thulke, H.-H., V. Grimm, M.S. Müller, C. Staubach, L. Tischendorf, C. Wissel & F. Jeltsch. 1999. From pattern to practice: a scaling-down strategy for spatially explicit modelling illustrated by the spread and control of rabies. Ecological Modelling 117.

Tischendorf, L. 1997. Modelling individual movements in heterogeneous landscapes: potentials of a new approach. Ecological Modelling 103: 33-42.

Tischendorf, L., U. Irmler & R. Hingst. 1998. A simulation experiment on the potential of hedgerows as movement corridors for forest carabids. Ecological Modelling 106: 107-118.

Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. Annu. Rev. Ecol. Syst. 20: 171-197.

Ulfstrand, S. 1996. Behavioural ecology and conservation biology. Oikos 77: 183.

Voronoï, G. 1908. Nouvelles applications des paramètres continus à la théorie des formes quadratiques. Recherches sur les parallélloèdres primitifs. Journal Reine angrew. Math. 134.

Wissel, C. 2000. Grid-based Models as tools for Ecological Research. pp. 94-115. *In:* U. Dickmann, R. Law & J.A.J. Metz (ed.) The Geometry of Ecological Interactions Simplifying Spatial Complexity, Cambridge University Press, Cambridge.

With, K.A. & T.O. Crist. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76: 2446-2459.

With, K.A., R.H. Gardner & M.G. Turner. 1997. Landscape connectivity and population distributions in heterogeneous environments. Oikos 78: 151-169.

With, K.A. & A.W. King. 1997. The use and misuse of neutral landscape models in ecology. Oikos 79: 219-229.

Worboys, M.F. 1995. GIS- a Computing Perspective.

Ziv, Y. 1998. The effect of habitat heterogeneity on species diversity patterns: a community-level approach using an object-oriented landscape simulation model (SHALOM). Ecological Modelling 111: 135-170.

Zollner, P.A. 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. Landscape Ecology 15: 523-533.

Zollner, P.A. & S. Lima. 1999. Illumination and the perception of remote habitat patches by white-footed mice. Animal Behaviour 58: 489-500.

Chapter 5

Cognitive ability and colonisation success in a real landscape: A modelling approach[1]

Abstract

Animal movements are critical for colonisation success in a metapopulation. There is evidence that animal movement through a landscape depends on cognitive and movement abilities of the animal and that distance covered and patterns of animal spatial use are affected by landscape structures, especially in fragmented landscapes.

In order to assess animal movement in a real fragmented landscape during dispersal between habitat patches, a model is proposed. This spatially explicit model is a combination of an animal model, which provides large perceptual range assessment, and a landscape model based on the representation of landscape features. The purpose of this model is to analyse colonisation success and connectivity by taking into account animal movement strategies and animal interaction with landscape structures.

Results obtained by simulation of animal dispersal in a landscape in Switzerland provide a new measure of landscape connectivity and show that behaviour affect metapopulation structure, dynamic resilience and genetic structure.

Based on this model, conclusions can be drawn on the importance of movement strategies in habitat patch colonisation success, cost due to colonisation, connectivity and metapopulation persistence. Recommendations for landscape management can then be given.

---

[1] *Note: This chapter is submitted to Oikos*
Co-author: Nicolas Perrin

Introduction

In a fragmented landscape, animal behaviour determines travel paths, travel time and travel cost between habitat patches {Turner 1989). Both act on metapopulation dynamics (Hanski 1999) and on gene flow (Barton 1992), which are both fundamental for long-term species viability. Therefore, to understand individual movement and spatial pattern of animal use, it becomes increasingly important to consider animal behaviour (Anthony and Blumstein 2000, Caro 1999, Curio 1996, Lima and Zollner 1996, Reed 1999, Reed and Dobson 1993, Sutherland 1998, Ulfstrand 1996).

Predicting patterns of animal spatial use is limited by a lack of understanding of the behavioural mechanisms involved (Lima and Zollner 1996) and the difficulties in tracking individual organisms, which is time consuming, expensive and difficult to analyse (Koenig et al. 1996, Tischendorf 1997). An alternative way to assess the impacts of landscape pattern is to measure landscape connectivity by dispersal simulation approaches (Backer 1996, Carter and Finn 1999, Lima and Zollner 1996). Landscape connectivity is “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993). High value of connectivity indicates that individuals can move easily between habitat patches. The connectivity has been measured in simulation models by counting the number of successful immigrants into all habitat patches (Delmers et al. 1995, Moilanen and Hanski 2001, Schippers et al. 1996, Schumaker 1996, Tischendorf and Fahrig 2000). Thus, in the ecological modelling field, spatially explicit models become more and more important in order to assess species behaviour in a given landscape. Unfortunately typical modelling approaches assume that animals have no knowledge of the general landscape or of their immediate surrounding (Lima and Zollner 1996). Furthermore, the landscape models used do not represent and contain sufficient information on landscape features to consider their effect on species behaviour. As human activities (habitation, agriculture, road networks) and landscape features are spatially localised and specifically affect animal behaviour, they have to be represented in the landscape model. Even so, models based on behaviour minimalism have been largely used to assess animal movements (Berg 1993, Bergman et al. 2000, Farnsworth and Beecham 1999, Sobol 1994, With et al. 1997).

In order to assess animal movement in a real fragmented landscape during dispersal between habitat patches, a dispersal model, which reproduces animal and landscape interactions, is proposed. This model is the result of a combination of a landscape model and an animal model. The first provides an explicit representation of landscape features. It contains all the information on the landscape properties and the positions of the landscape elements that act as a support for dispersal (an element that an animal uses during dispersal) and/or that direct movement according to animal preferences. The second contains information on physiological and cognitive abilities of animals during dispersal. It allows simple rules of movement as well as complex interaction between individual and landscape features.

With simulations, we attempt to evaluate the influence of cognitive abilities on metapopulation structure and dynamics. In a highly fragmented landscape in Switzerland, we measure the colonization probability and the distribution of ecological cost (cost due to travel path) between habitat patches, considering the animal dispersal and behavioral ability. These values quantify the connectivity induced by the behavioral responses of an individual in a fragmented landscape.

Material and methods

Landscape model

When dealing with animal movement, landscape is usually represented as a grid of regular cells in which an attribute (value) is assigned (Grimm 1999, Gustafson and Gardner 1996, Lindenmayer and Possingham 1996, Thulke et al. 1999, Tischendorf 1997, Wissel 2000). The regular geometry of the grid and its cells implies limitations in the representation of landscape features (Laurini and Thompson 1992). As they can have an important role during dispersal, especially in a fragmented landscape, landscape elements such as rivers or roads have to be represented together with their related information. The grid data structure offers poorly defined topological relations, which provide, when dealing with dispersal simulation, only information between adjacent cells and imply movement in deterministic directions. Additionally, this data structure implies simulation time, memory capacity, and data volumes, which limits simulation extension and inhibits sensitivity analysis (Tischendorf 1997). This landscape representation does not contain sufficient spatial, relational or thematic information to simulate animal interaction with the landscape.

To include the information on landscape features needed to simulate animal movement and behaviour in a landscape, we use the feature-oriented landscape model developed by Vuilleumier and Metzger (2003). This model overcomes the limitations exposed in the previous sections. It represents the landscape with a mesh of spatial entities that are irregular in shape and dimension. Two main spatial entities are used: cell (polygon) and frontier (polyline). Cells are homogenous areas limited by frontiers. The latter represents linear structures such as rivers or roads or the transition between two land covers (for example, a border between a forest and a field). Each entity stores as much information as needed to simulate the interaction between an animal and the landscape features. They conserve their shape and have information on their related entities. These relationships between entities are provided with spatial and non-spatial attributes. It allows interactions among neighbouring and distant entities. Based on this information, simulations of animal dispersal can be performed by rules of movement that consider perceptions and preferences of individuals.

Animal model

Animal behaviour in a landscape is directed by two main factors: the perceptual range and the searching behaviour. The perceptual range is the distance from which a particular landscape element can be perceived by a given animal (Lima and Zollner 1996, Zollner 2000, Zollner and Lima 1999). It allows orientation and recognition of suitable elements during dispersal. Searching behaviour is an active movement by which an animal finds or attempts to find resources (Bell 1991). It depends on the characteristics and abilities of the animal (for example locomotory skills and mobility), on the resources availability and the risks, and on the physiological need and efficiency (Bell 1991). Thus, an individual has a dispersal aim and uses its ability to achieve it. Consequently, we propose an animal model in which: (i) searching behaviour is driven by finding a new habitat patch, (ii) species are moving on the ground and use the whole landscape to disperse, (iii) individuals move across an unfamiliar and hostile landscape, (iv) animals are constrained by time, energy and mobility, and (v) animals visually use the environment to direct their searching and scanning. In the animal model, information on the landscape relies on the perceptual range. Based on this, we define three cognitive abilities:

- no perception of the environment: “**Blind” strategies**
- near perception of the environment that may attract or repulse the individual: “**Near-sighted” strategy**
- distant detection of a target habitat patch (when the habitat patch is in the perceptual range). “**Far-sighted” strategy**

The animal moves between two spatial entities according to its cognitive abilities. We assume that animals gain no information while moving across the landscape. Information provided by the landscape model is included in the animal’s choosing procedure.

Dispersal assessment

To provide interaction between animal and landscape features, entities of landscape are qualified depending on animal perception and animal abilities. In the landscape model, cells and frontiers are characterized by three major attributes: the attractiveness (value between 0-1), the possibility to be crossed (yes-no) and the cost while covered (see *table 3*). The latter characterises the difficulty to move and the distance covered in a spatial meaning. The attractiveness and the possibility to be crossed are related to information on animal preferences. Based on this information, the simulated animal can choose appropriate landscape entities according to its ability to perceive them while moving between habitat patches.

The successive choices of entities form a chain, which defines the path of an individual. Thus, a path is a succession of cells and frontiers (as cells are surrounded by frontiers). The choosing procedure is performed when an individual is in a cell (the first cell corresponds to the starting habitat patch) and decides to move to another cell. To apply the choosing procedure a probability of being selected is attributed to each frontier. This probability depends on cognitive ability as well as the attributes of both the frontier and adjacent cell. For the blind strategy, the probability depends only on frontier length. For the near-sighted strategy, it depends not only on the frontier length, but also on the attractiveness of the neighbor cells and frontiers.

Table 3:Values of attractiveness and cost assigned to landscape spatial entities

Landscape entities categories	*Attractiveness*	*Cost*
Frontiers		
First category road	0.1	6
Second and third category road	0.2	4
Railroad, road bridges, fourth, fifth and sixth category road	0.4	2
Stream	0.4	2
Hedges, fruit trees and rivers	0.6	1
Lake	1	8
Cells		
Rivers	0.4	2
Quarry, fallen rocks, rocks	0.5	1.5
Fruit tree	0.7	0.8
Lake	0	8
Inhabited area	0	8
Cultivated land	0.6	1
Forest, scattered forest, swamp and bush	0.8	0.5

For the far-sighted strategy, it depends on the shortest path (i.e. Euclidian distance) to the nearest habitat patch if the latter can be perceived, or otherwise on the attractiveness of neighboring cells and frontiers. If at least one of them cannot be crossed, the corresponding probability is set to zero. For each transition from a cell to another ($cell_i$ to $cell_j$), the next cell is selected according to its probability of being selected by a pseudorandom number. This procedure permits a stochastic process in path selection. To avoid oscillation the previous cell ($cell_i$) is excluded from the selection.

The simulation of dispersal is performed by the release of thousands of individuals. An individual starts its dispersal in a habitat patch according to the input data and initial conditions ("assigned energy - distance equivalent"). The starting energy corresponds to an arbitrary "distance" unit. A unit corresponds to a meter covered in a homogenous agricultural part of the landscape. As long as the individual has enough energy and has not reached another habitat patch, it goes on and chooses a new cell depending on its cognitive ability. Otherwise, the individual failed and its path is not recorded. During each cell transition, the animal attributes are updated. The distance and cost are computed. The cost is the sum of the frontier cost value and the cell cost value multiplied by the distance covered. When an individual reaches a new habitat patch the path is recorded.

Measure

To characterize the implications of the strategies on metapopulation structure and dynamics, we propose the following measures: (i) the colonisation probability between two habitat patches, from which are defined the overall exchange of individuals between patches, the flow of individuals between patches and the balance of individuals at patches and (ii) the ecological cost to join a patch.

The *colonisation probability* P_{ij} (between patch *i* and patch *j*) is the probability that an individual leaving the patch *i* successfully reaches patch *j*. This value is asymmetric, i.e. P_{ij} may differ from P_{ji}, and gives the intensity of the connection between two habitat patches. The *overall exchanges of individuals* between patch *i* and patch *j* is defined as the sum of two unidirectional probabilities ($P_{ij} + P_{ji}$). Presented in a spatial way, the overall exchanges of individuals reproduce the metapopulation structure. The *flow of individuals* between two patches quantifies the difference between two unidirectional colonisation probabilities ($P_{ij} - P_{ji}$). With this measure, the general flux of individuals in a landscape can be determined. The *balance* of individuals B_j at a given patch is the value obtained by summing the fluxes that reach or leave this patch ($B_j = \sum_{i}^{n} (P_{ij} + P_{ji})$). It gives the contribution of each patch, induced by the landscape, to the metapopulation dynamics. Indeed, with balance, we can examine the tendency of a patch to release or to accumulate individuals, in other words, if the patch behaves as a source or as a sink.

The *ecological cost* measures the effort needed to reach patch *j* from patch *i*. This value is a function of the number of cells and frontiers crossed, weighted by the cost assigned to these spatial entities. Therefore, it is bound to depend on the dispersal strategy. The ecological cost will be described by the median, the minimum and the standard deviation of the number of successful dispersers between two habitat patches. The minimum value shows the smallest cost needed to join a habitat patch. The standard deviation gives the variability of cost for which a probability of success can occur and depends on the number and variety of paths that can join two habitat patches. These descriptors will be compared to the associated success probability. Even though these kinds of descriptors of connectivity suffer from the problem that connectivity is predicted to be zero in a landscape containing just one habitat patch (Tischendorf and Fahrig 2000), this approach can be applied in a metapopulation system.

Simulation

We simulated the dispersal of individuals across a landscape by releasing individuals into an unfamiliar landscape from habitat patches. Simulations of dispersal were run for a highly fragmented countryside landscape in Switzerland. Dispersal was generated from 13 habitat patches. From each patch 50’000 individuals dispersed for each strategy. Each of the 13 patches has been considered successively as the starting patch. The starting ecological energy level assigned is 50’000 arbitrary units. An individual is a successful disperser if it reaches a patch with an ecological cost that does not exceed the ecological energy level assigned to it. The simulations were run with the three movement strategies. For each pair of patches, the cost and the number of successful dispersers were recorded.

Results

Colonisation probability, exchange of individuals and Balance

Among 650’000 dispersed individuals for each strategy, the model generated 241’092 (37.1%) successful dispersals for the Blind strategy, 121’617 (18.7%) for the near-sighted strategy and 247’207 (38%) for the far-sighted strategy. Results of the overall exchange of individuals are represented in *figures 30a* to *c*. These spatial representations of exchanges give the structure of the metapopulation. They point out the connections between patches and the intensity of these connections (see colonization probability matrix for each strategy in *table 4, 5 and 6*). With the blind strategy (*figure 30a*), the metapopulation encompasses all the patches, considering that the total number of potential connections is 156, the blind strategy presents the largest number of connected patches. It allows 89% of the total potential connections compared to 33% and 42% for the near-sighted and far-sighted strategies respectively. The near-sighted strategy (*figure 30b*) divides the metapopulation into 3 groups of patches, connected to each other by low fluxes. Within a cluster, patches have high values of exchanges. The far-sighted strategy (*figure 30c*) seems similar to the near-sighted strategy but leads to a unique metapopulation that contains all patches. This strategy presents two distinct groups of connections: the first characterizes low exchanges between distant patches and the second strong exchange between near patches. The spatial pattern of exchange shows the sensitivity of the near-sighted and far-sighted strategies to connection breaking. In the blind strategy, on average, each patch is connected to 10.6 other patches, compared to 4.1 and 5.0 for the near-sighted and the far-sighted strategies respectively (p-value < 0.05, t-test).

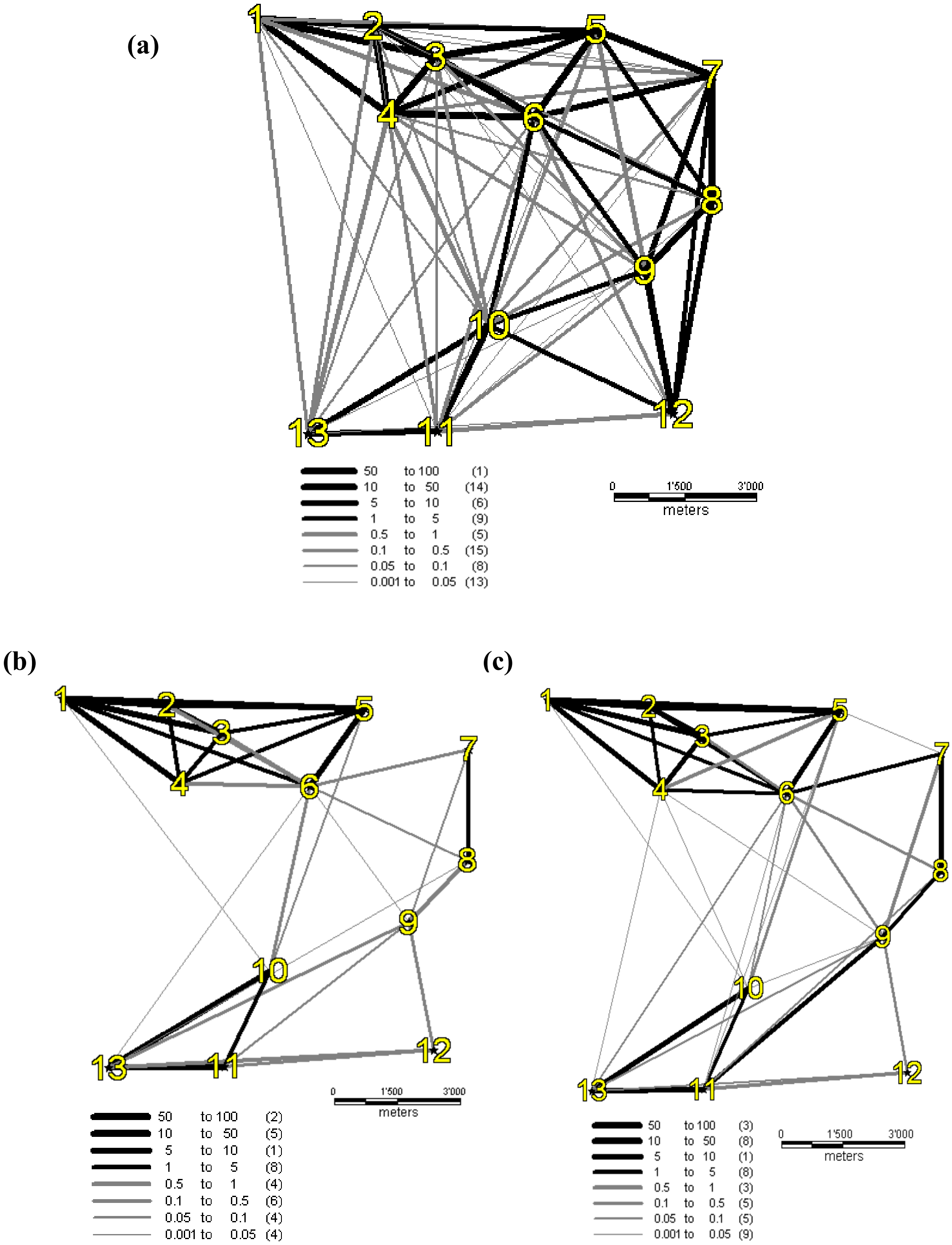


Figure 30a, b and c: Spatial representation of the overall exchange of individuals between patches for the blind strategy (a), near-sighted strategy (b) and far-sighted strategy (c). In gray, values of individual fluxes are between 0% and 1%, and in black, values are larger than 1%.

Table 4: Matrices of colonisation probability between habitat patches (1 to 13) obtained by simulation with the blind strategy

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
1	0	12.48	6.79	14.73	0.29	0.66	0.01	0	0	0.04	0.00	0.00	0.07
2	14.36	0	26.36	21.70	1.35	2.26	0.03	0.01	0.01	0.07	0.01	0.00	0.06
3	3.80	12.95	0	23.92	8.01	10.19	0.26	0.04	0.07	0.21	0.01	0.00	0.03
4	6.72	8.37	18.79	0	2.58	6.09	0.12	0.03	0.05	0.48	0.07	0.00	0.15
5	0.13	0.57	6.76	2.43	0	34.85	8.35	0.52	0.31	0.15	0.01	0.02	0
6	0.26	0.70	7.08	5.59	27.23	0	3.73	0.70	0.98	1.00	0.04	0.09	0.02
7	0.01	0.02	0.21	0.12	9.32	4.36	0	12.25	2.63	0.14	0.00	0.52	0
8	0	0.00	0.04	0.06	1.06	1.47	18.70	0	12.46	0.27	0.02	5.42	0
9	0	0	0.06	0.11	0.59	1.57	3.48	9.74	0	2.19	0.20	11.99	0.01
10	0.01	0.01	0.07	0.36	0.11	0.81	0.09	0.14	1.09	0	10.12	0.57	1.22
11	0.01	0.01	0.05	0.13	0.01	0.09	0.01	0.02	0.28	32.26	0	0.40	3.18
12	0	0	0	0	0.04	0.13	0.61	3.85	10.43	1.07	0.19	0	0
13	0.09	0.05	0.06	0.42	0.01	0.04	0	0	0.01	4.85	4.45	0.01	0

Table 5: Matrices of colonisation probability between habitat patches (1 to 13) obtained by simulation with the near-sighted strategy

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
1	0.00	0.28	0.34	0.06	4.09	0.05	0	0	0	0	0	0	0
2	54.14	0	5.41	1.01	3.87	0.54	0	0	0	0	0	0	0
3	17.01	0.73	0	1.93	2.27	0.36	0	0	0	0	0	0	0
4	11.58	0.52	0.01	0	0.05	0	0	0	0	0	0	0	0
5	24.17	0.08	0.11	1.01	0	0.26	0	0	0	0.07	0	0	0
6	4.64	0	0	0.99	13.46	0	0.17	0.00	0	0.13	0	0	0.01
7	0	0	0	0	0	0.05	0	1.20	0.06	0	0	0	0
8	0	0	0	0	0	0.06	1.21	0	0.42	0	0	0	0.00
9	0	0	0	0	0	0.04	0.01	0.15	0	0	0	0.19	0.44
10	0.00	0	0	0	0	0	0	0	0	0	0	0	36.85
11	0	0	0	0	0	0	0	0	0.06	1.60	0	0.10	50.12
12	0	0	0	0	0	0	0	0	0.04	0	0	0	0.58
13	0	0	0	0	0	0	0	0	0	0.69	0	0	0

Table 6: Matrices of colonisation probability between habitat patches (1 to 13) obtained by simulation with the far-sighted strategy

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
1	0	3.86	0.30	23.06	14.95	0.42	0	0	0	0	0	0	0
2	59.01	0	33.87	1.22	3.64	0.22	0	0	0	0	0	0	0
3	29.24	11.43	0	25.34	2.38	0.42	0	0	0	0	0	0	0
4	71.72	0.15	2.65	0	0.04	0.02	0	0	0	0.02	0	0	0.01
5	17.63	23.23	0.20	0.77	0	1.33	0.02	0	0	0.14	0.00	0	0.02
6	3.03	2.24	0	1.23	23.24	0	2.95	0.21	0	0.06	0.02	0	0.08
7	0	0	0	0	0	0.20	0	14.78	0.12	0	0	0	0
8	0	0	0	0	0	0.05	11.12	0	0.37	0	0.08	0	0
9	0	0	0	0.02	0	0.17	0.82	1.82	0	0.00	5.75	0.03	0.09
10	0.00	0	0	0	0	0	0	0	0	0	0	0	37.23
11	0	0	0	0	0	0	0	0	0	1.46	0	0.01	56.29
12	0	0	0	0	0	0	0	0	0.16	0	0.92	0	0.07
13	0	0	0	0	0	0	0	0	0	0.21	2.28	0	0

Figure 31 presents the balance of individuals at each patch for each strategy. The blind one provides small values of balance. By contrast, the other strategies produce highly variable values, leading to a source-sink behaviour for more than half of the patches. Fluxes have absolute values that are usually much larger and often have opposite signs, as compared to the blind strategy. Thus, metapopulation structures vary drastically depending on the implemented dispersal strategy. This behaviour leads to geographical differentiation. As shown *in figure 31*, the eastern part of the landscape is subject to the smallest fluctuations while the patches in the western part have the higher fluctuations.

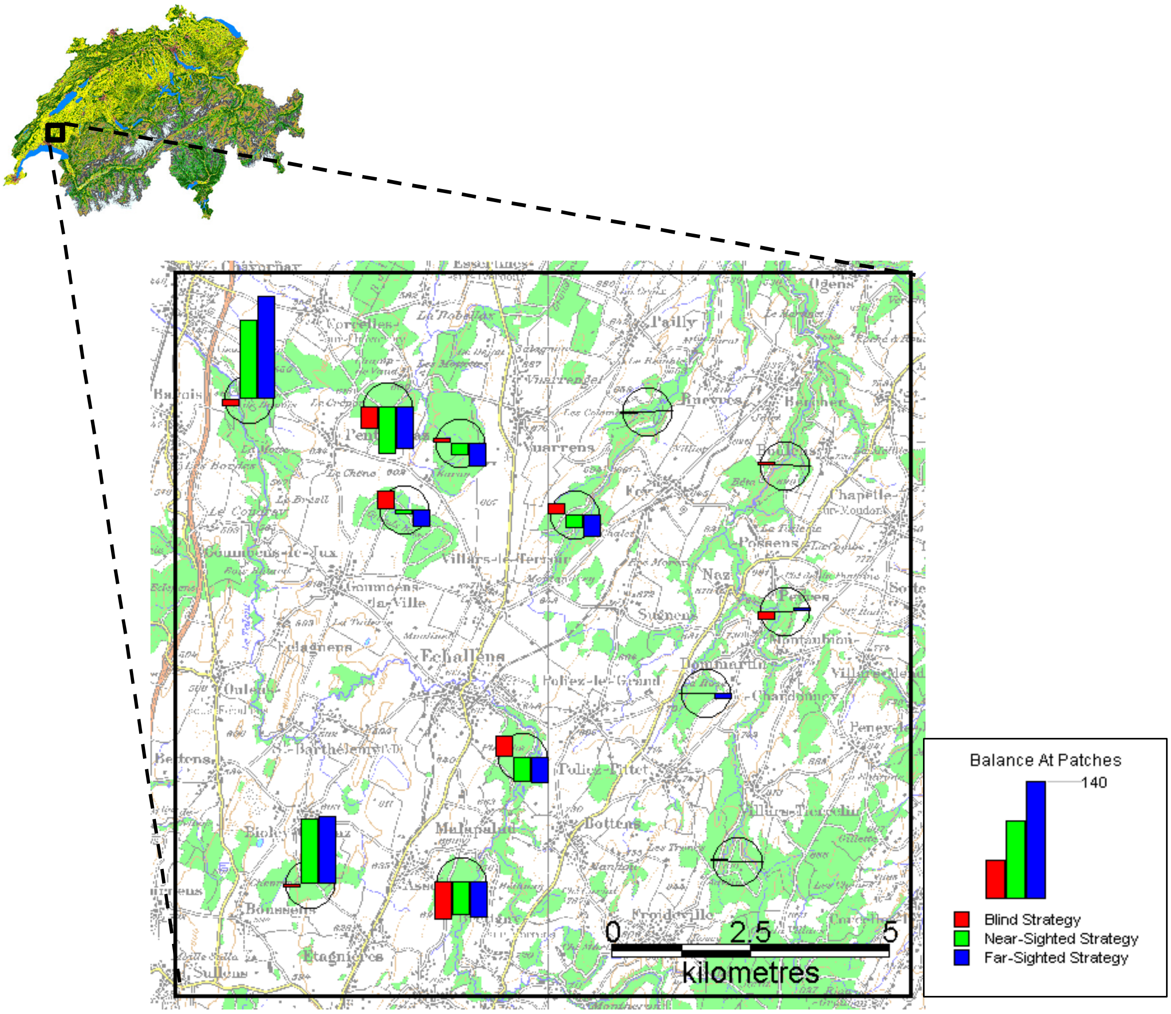


Figure 31: Balance at each patch for the blind, near-sighted and far-sighted strategies

Ecological cost

The density probability of the median value of the cost are presented in *figure 32* for each strategy. The blind strategy presents a steeper distribution with the highest median values of cost (highest probability of occurrence close to 40’000). Conversely, the near-sighted and far-sighted strategies present median values stretched all along the range of ecological cost with a high variability. These strategies provide success at the majority of cost level whereas the blind strategy concentrates its values in a peak, i.e. it is very sensitive to energy reserve and dispersal ability. This peak provides an estimation of the cost that is necessary for an individual to ensure its success in joining habitat patches. These results highlight the importance of the cost and energy reserves for the blind strategy. With this strategy, an individual must be able to cover a large distance to reach a habitat patch successfully.

The analysis of values of colonisation probability corresponding to the ecological cost is presented in *table 7*, in which the Kendall correlations between colonization probability and the median, minimum and standard deviation of the ecological cost distribution are presented. The strongest correlation relationships are found for the blind strategy: the greater the cost, the smaller the success probability; the largest the variance, the largest the success. Relations are much weaker for the near-sighted and far-sighted strategies, highlighting the fact that the probability of success reaches sometimes high values regardless of the ecological cost. Large variance does not induce a high probability of success, meaning that when a patch is well connected, it is usually just by a few paths.

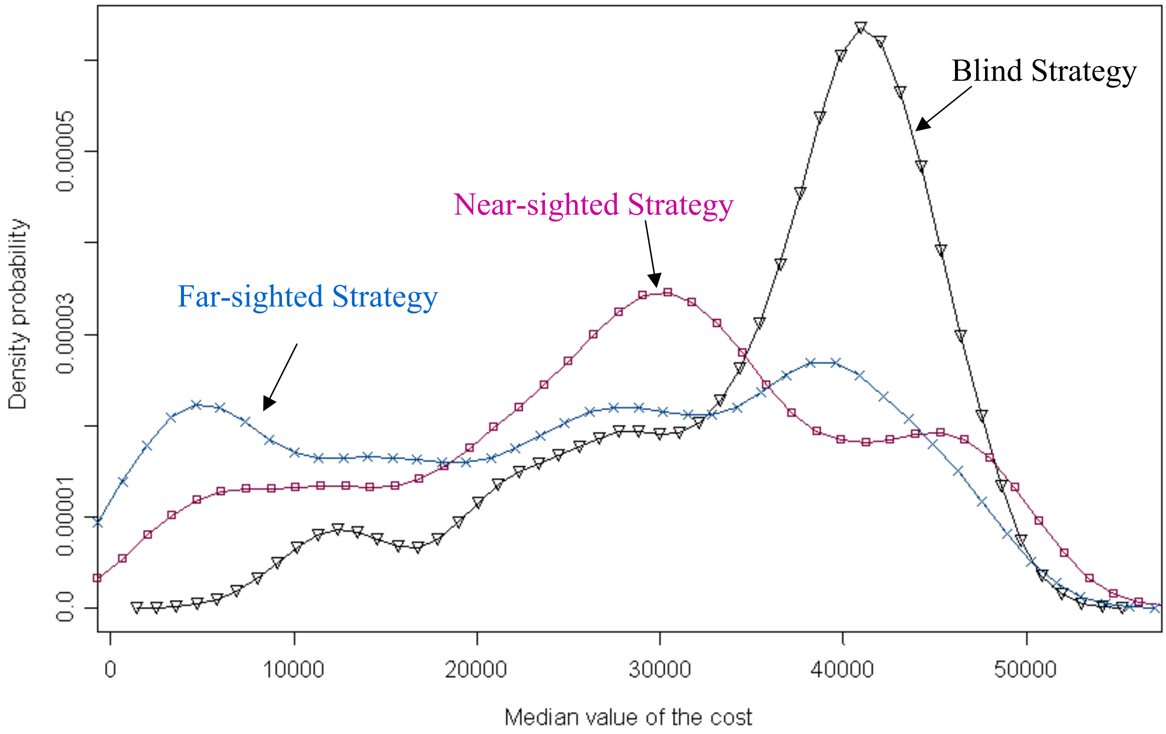


Figure 32: Density probability function for the median values of the ecological cost distribution between two connected patches represented for each strategy

Table 7: Kendall's correlation with the associated P-value between colonization probability and median, minimum and standard deviation

Strategy	Median/Prob		Min/Prob		StDev/Prob	
	Kendall r	P-value	Kendall r	P-value	Kendall r	P-value
Blind	-0.75	0	-0.86	0	0.74	0
Near-sighted	-0.46	0	-0.58	0	0.37	0.0001
Far-sighted	-0.48	0	-0.61	0	0.23	0.0072

Discussion

Due to its importance in the field of conservation biology, landscape ecology, metapopulation ecology and genetics, connectivity has become a major conservation value (Akçakaya 2000, Driscoll 1998, Fahrig and Merriam 1985, Hanski and Ovaskainen 2000, Hansson 1991, Hastings 1991, Henein and Merriam 1990, Taylor et al. 1993) and invoked as a criterion for nature development (Forman and Gordron 1986, Merriam 1984). Indeed, connections between habitat patches avoid loss of species, inbreeding depression and allow rescue effect or recolonisation of empty patches (Couvet 2002, Lande 1998). However, the relationships are not so simple: increasing connectivity can also induce metapopulation extinction (Earn et al. 2000, Johst et al. 2002, Ronce and Kirkpatrick 2001). The connectivity quantifies the ability of a landscape to provide individual exchanges between spatial entities. Results have already shown the importance of the heterogeneity of the landscape, which could affect emigration success (Dunning et al. 1992, Gustafson and Gardner 1996), metapopulation dynamics (Taylor et al. 1993) and gene flow (Couvet 2002). But connectivity is related to a specific landscape and species (Moilanen and Hanski 2001). Thus, in order to measure the potential individual exchange in a landscape, an individual's interaction with the landscape has to be handled. This interaction is the result of landscape properties and individual behaviour and ability. Due to the difficulty to capture with experimental data this complex interaction, simulation approaches are used. Simulations of animal dispersal coupled with habitat affinity (With and Crist 1995, With et al. 1997, With et al. 1999) and with behavioural or physiological states (Blackwell 1997, Wu et al. 2000) emerge from literature and have already provided information for landscape management (Lindenmayer and Possingham 1996) and wildlife management (Thulke et al. 1999). Simulation approaches in ecology have been largely criticized (Grimm et al. 1999, Wyszomirski, Wyszomirska and Jarzyna 1999), due to the complexity of the system, specifically the uncertainty associated with the assumptions (Beven 2000) and the sensitivity of parameters (Ruckelshaus et al. 1997) and the difficulty in interpreting results (Lorek and Sonnenschein 1999). But, due to the difficulty of obtaining information on animal dispersal processes in fragmented landscapes, simulations provide a chance to better understand metapopulation dynamics in a fragmented landscape.

In this study we introduce a new landscape model to represent behavioural aspects of a species during dispersal. We use a landscape model that contains all the information on the shape and properties of landscape features and an animal model that provides different cognitive abilities, in particular, large range perceptual ability.

The measure of colonisation probability between habitat patches in a large area provides a quantification of the number of patches belonging to a metapopulation and the pools of individuals that contribute to metapopulation dynamics (Andersen and Danielson 1997, Couvet 2002). If the number of connections increases, the metapopulation size increases, (Hanski 1999, Henein and Merriam 1990) (although the quality of connections must be considered (Andersen and Danielson 1997)). Due to the large sensitivity of the value of colonisation probability to animal dispersal ability, we add a measure of ecological cost for successful dispersal, which considers costs due to landscape heterogeneity, distance and behaviour.

Simulations show that the blind strategy provides individuals with a diffusive prospecting of the landscape with small colonisation probabilities to join a specific patch and high probability to join any patch. This strategy presents the highest median values of ecological cost. The distribution of the latter presents a distribution with values concentrated in a peak, which leads to a threshold under which success is weak. Even if numerous habitat patches are connected, the chance to join them is small. Thus, individuals who use the blind strategy have to be numerous; otherwise their ability to disperse must be high to increase the rate of colonisation. With the blind strategy, an individual tends to enlarge the metapopulation, indeed, it gives an individual the chance to find a new or empty habitat patch and permits an exploratory behaviour. At the metapopulation level, exchanges of individuals tend to swing around zero (*figure 31*). This strategy provides then, a dynamic that evolves more slowly than the other strategies, implying persistence in metapopulation dynamics. All these conclusions are true if the energy level is sufficient, in the other case the vulnerability to the fragmentation is high. If more energy is available, connections are better and more successes can occur. As high values of success probability are correlated to a high variability of ecological cost to join the habitat patches, this strategy allows numerous paths between them.

Globally the near-sighted strategy provides few chances to colonise patches compared to the other strategies, although this disadvantage decreases with the level of energy (blind strategy becomes less efficient as energy decreases). This strategy presents exactly the reverse advantages compared to the blind strategy, it promotes large flows of individuals between a few habitat patches but does not promote a metapopulation extension. To maintain a metapopulation with individuals that behave according to this strategy, the metapopulation must then have sufficiently connected habitat patches.

The far-sighted strategy is, generally, the best strategy to connect habitat patches and it is weakly sensitive to the level of energy. This strategy presents a large range of colonisation probability, which leads to a large number of poorly connected patches and a small number of strongly connected patches. It implies a possibility to extend metapopulation and promote exchanges between well-linked subpopulations. Nevertheless, this strategy seems to be highly influenced by the landscape heterogeneity, which appears to be favourable for some connections but not for others.

Near-sighted and far-sighted strategies have similar consequences: many small and few important colonisation probabilities, which are not affected by the level of energy. The cost distribution highlights this fact, in that whatever ecological cost you use you can have a high probability of success in reaching a patch. Moreover, these values are associated with any variability of ecological cost. That implies preferential paths in the landscape. Hence, these strategies are weekly dependent on the ecological networks in a landscape.

The high values of individual exchanges occurring at specific patches in both strategies lead to a high resilience in metapopulation dynamics. Moreover, they induce a substructure in metapopulation. According to population genetics theory, this may induce a genetic differentiation between clusters and a genetic homogenisation within a cluster. This process is enhanced by the tendency of these strategies to develop a source-sink metapopulation structure. The near-sighted and far-sighted strategies allow fewer connections compared to the blind strategy. That implies a higher vulnerability to stochastic processes and to small local landscape modifications that can reduce connectivity between habitat patches. On the other hand, this movement strategy does not suffer from sensitivity to the level of energy. It can be noticed that all the strategies behave the same when a habitat patch is close. It is confirmed by the variation of cost: when a close habitat patch is connected with a high probability the cost needed to reach it is spread within a large range of values.

Conclusion

The simulations of dispersal according to animal behavioural abilities demonstrate that they have important influences on metapopulation dynamics and structure. Behaviour influences the number of subpopulations that belong to a metapopulation and the flow of individual between habitat patches, which may lead to different metapopulation dynamics (e.g. source-sink), resilience and genetic structure. Results provide a new measure of landscape connectivity related to behaviour and point out the importance of considering ecological cost between habitat patches so as to avoid the Euclidian distance. Neglecting the effect of landscape fragmentation as well as animal behaviour can lead to incorrect conclusions concerning dispersal. As mentioned by Moilanen and Hanski (2001) connectivity appears to be dependent of both species and landscape type.

These results can be extended (given the residual energy after dispersal) to the study of the ability of the dispersers to settle (fitness, competitors) and gives important information about gene flow. All these aspects are key points in metapopulation viability and species viability. Such simulations experiments may support management decisions, which most likely depend on the concerned animal’s cognitive ability. Finally, we hope that this kind of model will help biologists, ecologists and conservationists in regulating and maintaining populations in fragmented landscapes.

References

Akçakaya, H. R. 2000. Conservation and management for multiple species: Integrating field research and modeling into management decisions. - Environmental Management 26: S75-S83.

Andersen, G. S. and Danielson, B. J. 1997. The effects of landscape composition and physiognomy on metapopulation size: the role of corridors. - Landscape Ecology 12: 261-271.

Anthony, L. L. and Blumstein, D. T. 2000. Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce N-e. - Biological Conservation 95: 303-315.

Backer, B. D. 1996. Landscape pattern, spatial behavior, and a dynamic state variable model. - Ecological Modelling 89: 147-160.

Bell, W. J. 1991. Searching behaviour: the behavioural ecology of finding resources. - Chapman and Hall.

Berg, H. C. 1993. Random walks in biology. - Princeton University Press.

Bergman, C. M., et al. 2000. Caribou movement as a correlated random walk. - Oecologia 123: 364-374.

Beven, K. 2000. On model uncertainty, risk and decision making. - Hydrological Processes 14: 2605-2606.

Blackwell, P. G. 1997. Random diffusion models for animal movement. - Ecological Modelling 100: 87-102.

Caro, T. 1999. The behaviour-conservation interface. - Trends in Ecology and Evolution 14: 366-369.

Carter, J. and Finn, J. T. 1999. MOAB: a spatially explicit, individual-based expert system for creating animal foraging models. - Ecological Modelling 119: 29-41.

Couvet, D. 2002. Deleterious effects of restricted gene flow in fragmented populations. - Conservation Biology 16: 369-376.

Curio, E. 1996. Conservation needs ethology. - Trends in Ecology and Evolution 11: 260-263.

Delmers, M. N., et al. 1995. Fencerows, Edges, and Implications of Changing Connectivity Illustrated by Two Contiguous Ohio Landscapes. - Conservation Biology 9: 1159-1168.

Driscoll, D. A. 1998. Genetic structure, metapopulation processes and evolution influence the conservation strategies for two endangered frog species. - Biological Conservation 83: 43-54.

Dunning, J. B., et al. 1992. Ecological processes that affect populations in complex landscapes. - Oikos 65: 169-175.

Earn, D. J. D., et al. 2000. Coherence and Conservation. - Science 290: 1360-1364.

Fahrig, L. and Merriam, G. 1985. Habitat patch connectivity and population survival. - Ecology 66: 1762-1768.

Farnsworth, K. D. and Beecham, J. A. 1999. How do grazers achieve their distribution? A continuum of models from random diffusion to the ideal free distribution using biased random walks. - American Naturalist 153: 509-526.

Forman, R. T. T. and Gordron, M. 1986. Landscape Ecology. - John Wiley & Sons.

Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? - Ecological Modelling 115: 129-148.

Grimm, V., et al. 1999. Individual-based modelling and ecological theory: synthesis of a workshop. - Ecological Modelling 115: 275-282.

Gustafson, E. J. and Gardner, R. H. 1996. The effect of landscape heterogeneity on the probability of patch colonization. - Ecology 77: 94-107.

Hanski, I. 1999. Metapopulation Ecology. - Oxford University Press.

Hanski, I. and Ovaskainen, O. 2000. The metapopulation capacity of a fragmented landscape. - Nature 404: 755-758.

Hansson, L. 1991. Dispersal and connectivity in metapopulations. - Biological Journal of the Linnean Society 42: 89-103.

Hastings, A. 1991. Structured models of metapopulation dynamics. - Biological Journal of the Linnean Society 42: 57-71.

Henein, K. and Merriam, G. 1990. The element of connectivity where corridor quality is variable. - Landscape Ecology 4: 157-170.

Johst, K., et al. 2002. Metapopulation persistence in dynamic landscapes: the role of dispersal distance. - Oikos 98: 263-270.

Koenig, W. D., et al. 1996. Detectability, philoparty, and the distribution of dispersal distances in vertebrates. - Trends in Ecology and Evolution 11: 514-517.

Lande, R. 1998. Anthropogenic, ecological and genetic factors in extinction and conservation. - Researches on Population Ecology 40: 259-269.

Laurini, R. and Thompson, D. 1992. Fundamentals of Spatial Information Systems. - Aademic Press Inc.

Lima, S. L. and Zollner, P. A. 1996. Towards a behavioral ecology of ecological landscapes. - Trends in Ecology and Evolution 11: 131-135.

Lindenmayer, D. and Possingham, H. 1996. Ranking conservation and timber management options for Leadbetter's possum in Southeastern Australia using population viability analysis. - Conservation Biology 10: 235-251.

Lorek, H. and Sonnenschein, M. 1999. Modelling and simulation software to support individual-based ecological modelling. - Ecological Modelling 115: 199-216.

Merriam, G. 1984. Connectivity: a fundamental ecological characteristic of landscape pattern. - In: Brandt, J. and Agger, P. (eds.), Methodology in Landscape Ecological Research and Planning. Proceedings of the 1st International Seminar of the International Association for Landscape Ecology, 15-19 October 1984. Roskilde Universitätsforlag Georuc, pp. 5-15.

Moilanen, A. and Hanski, I. 2001. On the use of connectivity measures in spatial ecology. - Oikos 95: 147-151.

Reed, J. M. 1999. The role of behavior in recent avian extinctions and endangerments. - Conservation Biology 13: 232-241.

Reed, J. M. and Dobson, A. P. 1993. Behavioral constraints and conservation biology- Conspecific attraction and recruitment. - Trends in Ecology and Evolution 8: 253-256.

Ronce, O. and Kirkpatrick, M. 2001. When sources become sinks: migrational meltdown in heterogeneous habitats. - Evolution 55: 1520-1531.

Ruckelshaus, M., et al. 1997. Assessing the data requirements of spatially explicit dispersal models. - Conservation Biology 11: 1298-1306.

Schippers, P., et al. 1996. Dispersal and habitat connectivity in complex heterogeneous landscapes: an analysis with a GIS-based random walk model. - Ecography 19: 97-106.

Schumaker, N. H. 1996. Using landscape indices to predict habitat connectivity. - Ecology 77: 1210-1225.

Sobol, I. M. 1994. A primer for the Monte Carlo Method. - CRC Press LLC.

Sutherland, W. J. 1998. The importance of behavioural studies in conservation biology. - Animal Behaviour 56: 801-809.

Taylor, P. D., et al. 1993. Connectivity is a vital element of landscape structure. - Oikos 68: 571-572.

Thulke, H.-H., et al. 1999. From pattern to practice: a scaling-down strategy for spatially explicit modelling illustrated by the spread and control of rabies. - Ecological Modelling 117.

Tischendorf, L. 1997. Modelling individual movements in heterogeneous landscapes: potentials of a new approach. - Ecological Modelling 103: 33-42.

Tischendorf, L. and Fahrig, L. 2000. How should we measure landscape connectivity? - Landscape Ecology 15: 633-641.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Annu. Rev. Ecol. Syst. 20:171-197.

Ulfstrand, S. 1996. Behavioural ecology and conservation biology. - Oikos 77: 183.

Vuilleumier, S. and Metzger, R. 2003. A new landscape model for animal movement and behaviour assessment. - *Submitted.*

Wissel, C. 2000. Grid-based Models as tools for Ecological Research. - In: Dickmann, U., Law, R. and Metz, J. A. J. (eds.), The Geometry of Ecological Interactions Simplifying Spatial Complexity. Cambridge University Press, pp. 94-115.

With, K. A., et al. 1999. Movement responses to patch structure in experimental fractal landscapes. - Ecology 80: 1340-1353.

With, K. A. and Crist, T. O. 1995. Critical thresholds in species' responses to landscape structure. - Ecology 76: 2446-2459.

With, K. A., et al. 1997. Landscape connectivity and population distributions in heterogeneous environments. - Oikos 78: 151-169.

Wu, H., et al. 2000. Modelling animal movement as a persistent random walk in two dimensions: expected magnetitude of net displacement. - Ecological Modelling 132: 115-124.

Wyszomirski, T., et al. 1999. Simple mechanisms of size distribution dynamics in crowded and uncrowded virutal monocultures. - Ecological Modelling 115: 253-273.

Zollner, P. A. 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. - Landscape Ecology 15: 523-533.

Zollner, P. A. and Lima, S. 1999. Illumination and the perception of remote habitat patches by white-footed mice. - Animal Behaviour 58: 489-500.

Chapter 6

Genetic differentiation in a fragmented landscape: Dispersal model applied to *Crocidura russula*[2]

Abstract

Spatially-explicit modelling allows the simulation of individual dispersal with movement behaviour and species interactions with heterogeneous landscapes. It provides a quantification of dispersal processes according to landscape structures. The validation of parameter estimates of such models (such as distances between habitat patches according to the paths used) is a crucial issue in this field. As differentiation between populations can be quantified by genetics[2], coupling it with individual dispersal simulation is of great interest to analyse the ability of both to reproduce real dispersal.

In this context, we simulate dispersal of the greater white-toothed shrew (*Crocidura russula* (Hermann, 1780)) in a highly fragmented landscape in Switzerland according to several alternative hypotheses considering several behaviours, dispersal distances and number of habitat patches. Simulation results were compared to genetic measures of differentiation among populations. Based on this, we attempt to:

(i) explain genetic variability due to landscape heterogeneities from estimates obtained by modeling approaches, and

(ii) compare its ability to explain genetic variability with the explanation obtained by geographical distances.

---

[1] *Note: this chapter will be submitted to an international journal*
Co-author: Pierre Fontanillas, Nicolas Perrin

[2] *For genetic terminology please refer to Appendix A*

Introduction

Dispersal has large implications in conservation, ecology, population genetics, ethology, and evolution (Stenseth and Lidicker 1992). Its demographic consequences may consist in stabilizing densities and determining the spatial structure of populations that can enlarge or maintain a viable metapopulation (Hanski 1999, Hanski and Ovaskainen 2000). Additionally, it is a vector of gene flow that is essential for long term conservation by reducing the chances of inbreeding (Ralls et al. 1986, Wolff 1994, Pursey and Wolf 1996) and, by genetic diversity enhancement, it provides sufficient capacity for a species to adapt to its environment (Paradis et al. 2002).

Animal dispersal differs from gene dispersal in that the former refers to the overall process of flow of individuals between habitat patches (Hanski 1999) while gene dispersal depends on subsequent gene incorporation into a new generation according to reproduction (Endler 1977, Gaines and McClenaghan 1980, Barton 1992).

In a landscape, a heterogeneous environment surrounds habitat patches, which vary in suitability (Forman 1995). The dispersal ability can be deterred or prevented by landscape features and spatial structures which may guide or potentially inhibit movement, depending on the behaviour and resource needs of the species (Fahrig and Merriam 1985, Turner 1989, Kozakiewicz and Szacki 1995, Peles et al. 1999). By modifying dispersal, landscape fragmentation and heterogeneity affect metapopulation (Hanski 1999) and gene flow (Barton 1992, Couvet 2002). Hence, understanding how movement patterns are affected by the spatial structure of an environment is a key question (Wiens 1995), meaning that a simple relationship between colonization and geographical distance from the source does not apply (Hansson 1991).

Inference between landscape heterogeneities and dispersal among populations can be estimated by three main complementary approaches: field experiments (tracking), modelling approaches and genetic approaches (genetic models).

Field experiments may allow an estimate of rates of movement among discrete populations as well as estimates of dispersal parameters with capture-recapture or mark-resight data or tracking measures (Bennetts et al. 2001). Those require a large quantity of data, which grows with the variability of dispersal behaviour between and within species (Hestbeck 1982, Smith and Peacock 1990, Koenig et al. 1996, Wolff 1999). Those experiments are moreover limited by the fact that tracking an individual organism is time consuming, expensive and difficult to analyse (Koenig et al. 1996, Tischendorf 1997). Those practical constraints strongly limit the use of such an approach.

The modelling approach is a promising field for animal dispersal simulation (Berger et al. 1999, Grimm et al. 1999, Hall and Halle 1999). With today’s computer performances, it allows the simulation of animal behaviour of varying complexity (Blackwell 1997, Carter and Finn 1999, Moorcroft et al. 1999, Nally 2001) and dispersal in an explicit heterogeneous landscape (Downing and Reed 1996, Beecham and Farnsworth 1998, Lorek and Sonnenschein 1999). They provide a quantification of dispersal processes related to landscape heterogeneities (Tyre et al. 1999, Bennetts et al. 2001, Berggren et al. 2001). In this field, spatially explicit representation of landscape needs to be addressed at the appropriate scale of resolution (Peles et al. 1999) and has to depict the landscape features that may direct movements. Only such models can represent dispersal processes in a realistic way.

The genetic approach provides a quantification of genetic variation among populations, which can be used to analyse genetic differentiations due to isolation. The latter is usually estimated with geographical distances (Barton 1992, Cockburn 1992, Hanski 2001). Under some assumptions, the genetic difference between populations can be quantified with genetic models (Slatkin 1995, Takezaki and Nei 1996, Nei and Kumar 2000, Mallet 2001, Whitlock 2001, Balloux and Goudet 2002, Balloux and Lugon-Moulin 2002). They can give robust and widely applicable estimates (Barton 1992).

In this study, we assume that landscape heterogeneities affect dispersal and thus explain the genetic differentiation among population better than geographical distance. To validate this hypothesis, we analyse the contribution of a spatial modelling approach to reproduce dispersal of the greater white-toothed shrew, *Crocidura russula* (Hermann, 1780). By adopting hypotheses on dispersal behaviours, dispersal distances and the number of habitat patches encompassed, we will see that the model connectivity measures can explain the genetic differentiation of *C. russula* and that those measures add explanations to the one provided by the usual Euclidian distance.

We use a spatially explicit dispersal model that reproduces an animal's interaction with landscape features (Vuilleumier and Metzger 2003, Vuilleumier and Perrin 2003). The model generates ecological distances (considering travel paths) between habitat patches. All are compared with three measures of genetic variability obtained with seven autosomal microsatellite loci (Fontanillas et al. 2003).

Material and methods

Crocidura russula ecology

Crocidura russula is a small insectivorous mammal. This species is anthropophile in the central and occidental part of Europe (Fatio 1869, Hainard 1961) due to its energetic needs (Richter 1963). The ecological distribution of *C. russula* is associated with inhabited areas, where they settle in gardens and hedges. In Switzerland, *C. russula* rarely appear at elevation over 1000 m, are obligatorily anthropophile above 600 m, and are commonly seen at lower altitudes (400-600 m) (Genoud 1982, 1995).

During dispersal, an animal's range of perception is an important factor in its movement (Lima and Zollner 1996). Little information is known on the perceptual range of small mammal species (Peles et al. 1999). According to Branis and Bura (1994) the structure of the shrew's eye predisposes it to normal vision. Its small size, however, presumably reduces and constrains the range, sensitivity and resolution capacities of vision. Shrews can thus be considered visually unspecialised (generalized) mammals. The ecological niche of shrews apparently exerts little selective pressure for vision; therefore its eyes have retained small dimensions and limited functional capacities (Branis and Bura 1994). From evidence, it is reasonable to believe that its perceptual range lies within 3-30 m (Peles et al. 1999).

Figure 33: The greater white-toothed shrew, Crocidura russula (Hermann, 1780). Photo by David Hosking

The dispersal process between habitat patches in *C. russula* seems to be due to overcrowding and recolonization opportunities and doesn't appear to be sex-biased (Perrin and Goudet 2001, Fontanillas et al. 2003). *C. russula* cover in 24 hours under natural conditions (uncorrelated to thermal condition) a distance of 568 ± 240 m (Genoud and Hausser 1979, Genoud 1981). Nevertheless, some observations prove that small mammals are actually able to cover much greater distances than previously believed (Kozakiewicz and Szacki 1995). Further studies suggest that a behavioural adaptation to a fragmented landscape might induce differential movements and increase distance movement in heterogeneous landscape compared to a homogeneous (Kozakiewicz 1993). To our knowledge, the distance covered by *C. russula* during colonisation of a habitat patch has never been established.

Genetic measurements

If we consider a metapopulation composed by populations, we can analyse the difference between populations by genetics. Four main genetic forces act on a population: genetic drift, mutation, selection and migration. For example, if two or more populations are separated or partially separated from each other, then the allele frequencies at a locus in two or more populations may differ. This difference is due to the random drift and/or differential selection in the two environments. That will cause a homogenisation of the allele frequency within the population but a differentiation among populations. This difference can be used to determine the genetic relatedness and the migration rates between the populations. Genetic distance between two populations is defined in terms of allele frequencies for all loci in the genome (Nei 1987). For an introduction to genetic processes in metapopulation see *appendix 1*.

The genetic data used are allelic frequency estimated for seven autosomal microsatellite loci (for details see Fontanillas et al. (2003)). According to the assumption of the selective neutrality of each locus and the independent assortment of the allele, we use them to quantify the difference between populations. The latter is estimated by measure: (i) Manhattan metric, (ii) F-Statistic and (iii) Nei *et al.'s* (1983) D_A genetic distance.

(i) Manhattan metric

The "Manhattan metric" C_M (Nei 1987) is a version of the Czekanowski's (1909) distance (*equation 9*).

$$C_M = \sum_{j=1}^{r} \sum_{i=1}^{m} \left| x_{ij} - y_{ij} \right| \qquad \textit{Equation 9}$$

With

x_{ij}, y_{ij} : Frequency of the *i*th allele at the *j*th locus in population X and Y, respectively
m_j : Number of alleles at the *j*th locus
r : Number of loci

Manhattan metric is primary used for population classification (Nei 1987), particularly when the studied populations are closely related. As there are many loci, the average of C_M over the loci is used.

(ii) The F-statistic

The F-statistic (Wright 1965) are parameters and statistical tools used to describe the variance of allele frequencies by hierarchical partitioning. F_{st} is one of the F-statistics which measures the proportion of the total genetic variability due to genetic differentiation between populations. Therefore F_{st} represents a measure of the Wahlund effect (Wahlund 1921), which can be stated in terms of the variance in allele frequency (Wright 1943, 1965). According to a finite number of populations, pairwise F_{st} (Cockerham and Weir 1993, Weir 1996) can be estimate, which give genetic differentiation among populations. Pairwise F_{st} provided by P. Fontanillas, University of Lausanne, (for details see Fontanillas et al. (2003)) will be used for the analysis.

(iii) Nei et al's (1983) D_A genetic distance

Among genetic forces acting on a population, if no migrant interferes and there is a selective neutrality of each locus, drift and mutation cause divergence of the allele frequency in a subpopulation. Based on these assumptions, several formulae have been proposed for estimating genetic distance (or similarity); which vary in terms of their underlying genetic models, see Takezaki and Nei (1996) for details. Among them we use the Nei *et al's* (1983) D_A (*equation 11*).

$$D_A = 1 - \frac{1}{r}\sum_{j}^{r}\sum_{i}^{m_j}\sqrt{x_{ij}y_{ij}} \qquad \textit{Equation 10}$$

Where

x_{ij}, y_{ij} : Frequency of the ith allele at the jth locus in population X and Y, respectively
m_j : Number of alleles at the jth locus
r : Number of loci

Genetic differentiation is quantified by genetic distance measures presented in previous sections: *Manhattan metric* C_M, the *pairwise* F_{st} and the Nei *et al's* (1983) D_A distance.

Shrew dispersal modeling

Shrew movements and land use occur at a local scale, while the metapopulation dynamics and gene flow occur at the metapopulation scale. Thus, the dispersal model must provide a representation of both small movement patterns and general colonization processes. Moreover, at the local scale, *C. russula* interact with and use small landscape features during dispersal. These features must explicitely be represented. To achieve this, we use a new feature-oriented landscape model developed by (Vuilleumier and Metzger 2003), which is coupled with an animal model that reproduces behavioral traits of species (Vuilleumier and Perrin 2003).

In the feature-oriented landscape model, two main spatial entities, irregular in shape and dimension, are used: cells (polygons) and frontiers (polylines). Cells represent homogenous areas of land use and frontiers regroup linear landscape features (such as river shores, hedges and road sides) and edges between land use areas (such as forest borders and edges between open fields). Each entity has attributes according to modelling needs (typology, metrics, shape) and contains the information on their related entities (topological and typological relations). The feature-oriented landscape model provides information to create chains of spatial entities, which form the individual paths. In the animal model, procedures generate successive choices of landscape entities according to the individual landscape elements used and the cognitive abilities.

The animal and landscape model is used and adapted according to the following assumptions on shrew dispersal:

(i) Habitat patches are inhabited areas.

(ii) An individual has no knowledge of the landscape area between habitat patches.

(iii) When leaving its habitat patch, *C. russula* aims at finding a new habitat patch.

(iv) *C. russula* uses linear structures (hedges, road borders) during movement between habitats to avoid predation (exposure in open field).

(v) An ecological distance (dispersal distance) limits *C. russula's* dispersal, which is defined as the length of the travel path.

(vi) During dispersal, the successive choices of frontiers are based on their cognitive abilities. Two main hypotheses are tested:

- *Random: C. russula* is unable to use any information concerning the landscape; i.e., it moves randomly on linear features.
- *Near-sighted: C. russula* moves on linear features and perceives its neighbouring environment to direct its path during dispersal.

The latter assumption implies a choosing procedure during dispersal. To achieve this, a probability to be selected is assigned to each landscape feature. This probability encodes the attraction to a landscape linear structure. Depending on the cognitive abilities tested and how *C. russula* perceives landscape features; frontiers are characterized by their length and their attractiveness. Attractiveness was determined according to expert judgment (see *table 8 and matrix 1* below).

Table 8 Attractiveness assigned to landscape linear feature entities

Landscape entities categories	***Attractiveness***
Hedges, highways, first, second, third, fourth, fifth and sixth category category road, railroad	3
Bridges, rivers and streams	0
Fruit trees	1

Matrix 1: Attractiveness assigned to borders between different land uses

	A	B	C	D	E	F	G
A	1						
B	1	1					
C	5	5	1				
D	1	1	1	1			
E	1	1	5	1	1		
F	1	1	5	1	1	1	
G	10	10	10	10	10	10	1

With

Cell type	***Categories***
Fruit tree	A
Swamp	B
Forest, scattered forest, and bush	C
Lake and rivers	D
Cultivated land	E
Quarry, fallen rocks, rocks, vineyards	F
Inhabited area	G

Study area

The study area is a highly fragmented landscape situated in western Switzerland (*figure 34*). It covers around 260 square kilometres, in which 32 potential habitat patches have been identified in an altitude range of 390-930 m. To be in accordance to the border condition for the dispersal-modelling phase, the study area has been extended in the northeast and the southwest part. Otherwise, Lake Geneva (374 m) and the Jura mountains limit the other sides of the study area (where no *C. russula* are present).

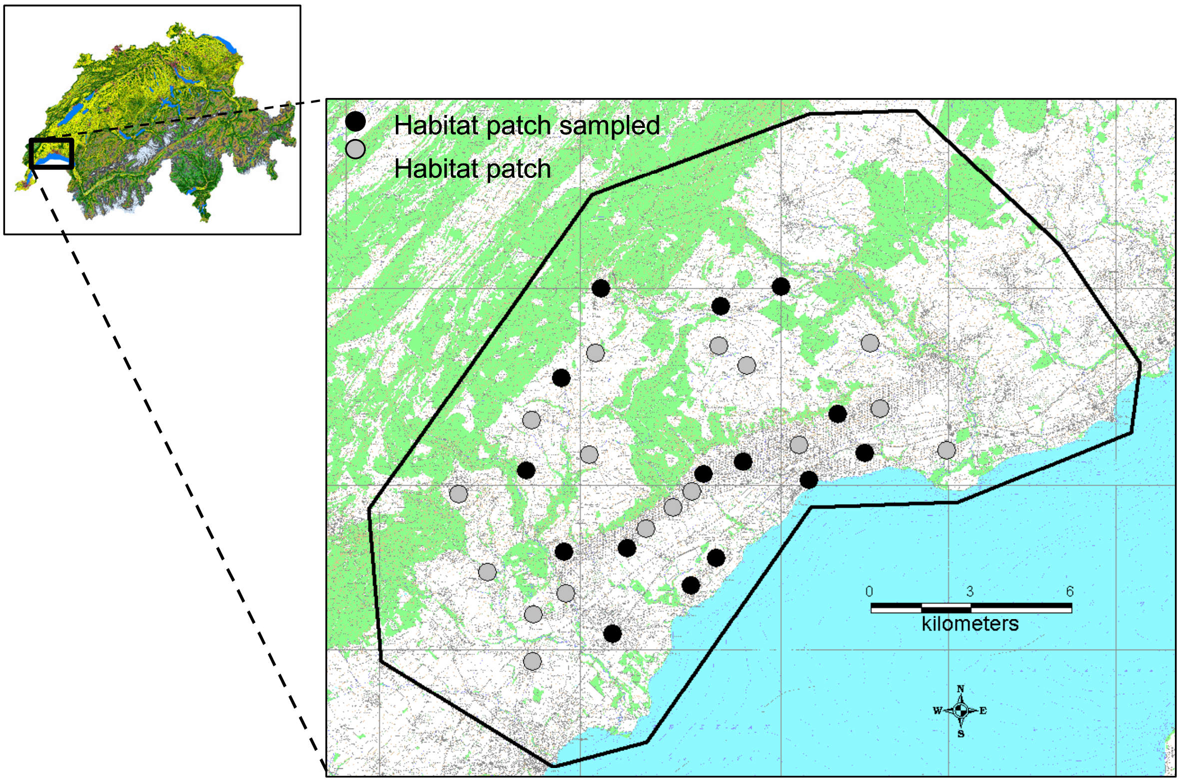


Figure 34: Study area and habitats patches sampled in black ● *and unstamped in grey* ● *used for the analysis.*

Sampled populations

Among the 32 potential habitats identified, only 15 have been sampled (*figure 34*). Sampling took place in 1999 and 2000 from June to August, in each of the 15 habitat patches. For localization and trapping details see Ehinger et al. (2002) and Fontanillas et al. (2003). 170 individuals were captured and were recorded for seven autosomal microsatellite loci (for details see Fontanillas et al. (2003)).

Simulation setup

We perform two series of simulations enclosing 15 and 32 habitats patches, respectively. The first series corresponds to genetic data availability; the second considers all potential habitat patches, which are the villages within the study area that may interfere in the dynamic of the metapopulation.

According to the movement strategies, ecological distance assigned, and number of habitat patches encompassed, seven simulations are planned (*Table 9*).

Table 9: Simulations performed

Scenarios	***Strategy***	***N. of habitat patches***	***Dispersal distance (km)***
R32-100	Random	32	100
R32-15	Random	32	15
R15-100	Random	15	100
R15-15	Random	15	15
N32-100	Near-sighted	32	100
N32-15	Near-sighted	32	15
N15-15	Near-sighted	15	15

Dispersal simulations have been performed as follows: from each patch, 50 000 individuals are released in the landscape. They move along the linear structure of the landscape depending on their choosing procedures. The individuals attempt to disperse until they reach a new habitat patch and while the maximum dispersal distance has not be exceeded. Maximum dispersal distance assigned are 15 km (according to plausibility) and 100 km (to generate maximum connections between habitat patches), they do not correspond to a direct dispersal but to a rare long-distance dispersal event, which may occur during a long period (colonisation processes).

The estimates extracted from the simulations are the distances D_{xy}. They correspond to the distance required to reach a habitat patch *y* from a habitat patch *x*. This distance is a function of the path travelled. They are computed for each successful disperser. In other words, this measure captures the effect of landscape structure and heterogeneity in terms of distance. Over *n* distances obtained by successful dispersers between two habitat patches; the median value obtained is used. This value is called ecological distance. This value is asymmetric, i.e. D_{xy} may differ from D_{yx}, and gives the intensity of the connection between two habitat patches. In the case that no dispersers reach patch *x* from patch *y*, D_{xy} is assumed to be the shortest distance joining patch *x* and *y* via a patch *k*, therefore $D_{xy} = D_{xk} + D_{ky}$.

Genetic and simulation approaches compared

The evaluation of the ability of the simulation approach to reproduce *C. russula* dispersal and to explain genetic differentiation among populations is performed with tests of associations using the Mantel test (Manly 1991, 1997) (see *appendix 2* and http://www.fas.umontreal.ca/biol/casgrain/). To carry out such a test, the Ecological distance obtained by the modelling approach (asymmetric matrix) is turned into a symmetric matrix by averaging the two triangular half-matrices. The statistical significance of the correlation based upon ranks (Spearman correlations) between genetic divergence and measures of connectivity was evaluated by 9999 permutations for the Mantel test. We compute the correlation coefficient provided by the Euclidean distance and compare it using the Fisher r-to-z transformation (see *appendix 2*) with the correlation provided by ecological distances.

To better understand the implications of spatial assumptions related to the simulation model (dispersal distance and number of habitats patches), the values of the ecological distance generated are compared according to the number of patches used in the simulation (15 and 32 habitat patches).

Results

The Spearman correlation coefficients obtained by comparison of geographical and ecological distances for all simulations performed (scenarios) are presented in *table 10.* The correlation coefficients of determination were computed with the Mantel test. For all matrices the significance of incongruence probability (χ^2 , 9999 perm.) is > 0.0001, never exceeding 0.006.

Table 10: Resemblance among the symmetric distance matrices: Matrix of Mantel correlations based upon ranks (Spearman correlations)

	Geographical Distance	R15-15	R15-100	R32-15	R32-100	N15-15	N32-15	N32-100
Manhattan distance	0.55	0.60	0.66	0.52	0.64	0.61	0.60	0.65
F_{st}	0.41	0.50	0.56	0.39	0.56	0.49	0.49	0.56
Nei distance	0.59	0.67	0.71	0.56	0.69	0.65	0.64	0.69

Table 10 shows that the geographical distance is related with a correlation value reaching respectively 0.55, 0.41 and 0.59 for the genetic variability measured with the Manhattan metric, the pairwise F_{st} and the Nei *et al.'s* (1983) genetic distance. Correlations are highest with the R15-100 strategy, 0.66, 0.56 and 0.71, respectively. It can be shown that Nei *et al.'s* (1983) genetic distance

systematically provides a better correlation compared to other genetics distances while the F_{st} value provides the worst.

Comparison of these correlation coefficients to those obtained with geographical distances show a significant difference for the F_{st} and Nei *et al's* (1983) genetic distance (*table 11*). In these cases, the R15-100 simulations provide the highest value of correlation for the Nei distance. *Figure 35* presents the relation between the ecological distance obtained with the R15-100 strategy and the three genetic differentiation estimations. The figures show a strong relation between both values.

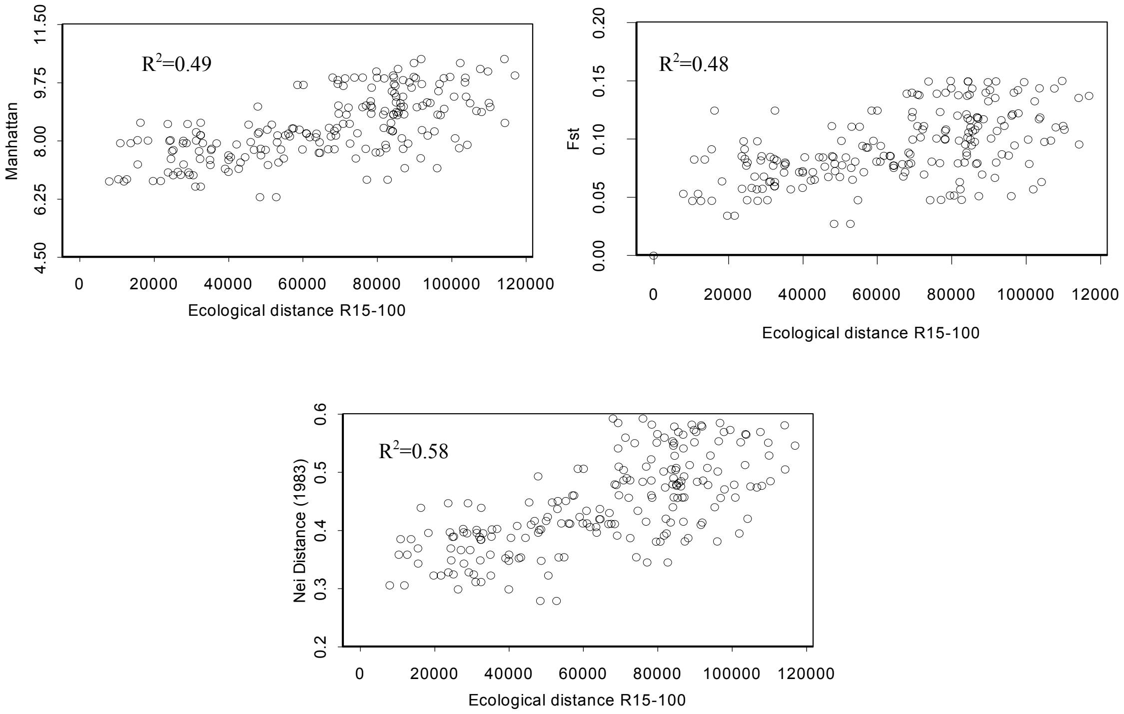


Figure 35: Pattern of the relationship between ecological distance and genetic differentiation estimations for the near strategy (with R^2 corresponds to a linear regression).

It can be seen in *table 11* that cognitive abilities assigned corresponding to the "Near-sighted" strategy, whatever dispersal distance assigned, do not differ significantly from the "Random" strategy. However, values obtained with a dispersal distance corresponding to 100 km seems to present a better explanation (correlation coefficient greater than 0.4) than those obtained with a 15 km dispersal distance. Unfortunately, significance of the difference between these correlation coefficients has only been established for the F_{st} value.

Table 11: Significance of the difference between correlation coefficients obtained with geographical distance using the Fisher r-to-z transformation

	R15-15	R15-100	R32-15	R32-100	N15-15	N32-15	N32-100
Manhattan distance	0.430	0.066	0.660	0.142	0.342	0.430	0.099
F_{st}	0.230	**0.038**	0.802	**0.038**	0.289	0.289	**0.038**
Nei distance	0.162	**0.027**	0.638	0.073	0.303	0.395	0.073

Discussion

According to the results presented above, *C. russula* genetic differentiation between habitat patches is best explained by ecological distance generated by a dispersal model taking into account landscape arrangement and heterogeneities and assuming a very large dispersal distance. But, there is no significant differences between results due to examined movement strategies. This can be explained by the strong effect of the landscape arrangement on dispersal processes, as an individual moves according to the linear structure in the landscape and even a random strategy does not yield a diffusive dispersal. It must be noticed that the maximum dispersal value retained in the simulations is unrealistic given the low dispersal ability of *C. russula* (Balloux et al. 1998). In fact this distance leads to a quantification of connectivity instead of a true dispersal process. The more distant the habitat patch is, the better the estimation of the genetic differentiation of *C. russula*. Thus, a better explanation seems to be provided by the model if the genetic variability is higher between distant habitat patches. According to our results, Nei *et al.'s* (1983) genetic distance seems to be the best measure of genetic differentiation due to isolation. Further investigations in this field promise interesting results for analysing genetic differentiation in a metapopulation.

There are still limitations in modelling and comparison with genetic distance due to individual dispersal assumptions. According to Stenseth and Lidicker JR (1992) in our spatial modelling approach, we use “dispersal” to mean one-way movements of individuals away from their habitat patches with no return. With our model we do not have any information on the fitness of successful dispersers and the within-population spatial structure. Of course, most of the time, the movement or dispersal of whole organisms causes gene flow from one population to another (Mallet 2001), but to provide a good representation of gene flow among populations, gamete dispersal has to be simulated. As we do not consider population dynamics, no information on effective migrants from habitat patches can weight the results obtained with the model. This might lead to an incorrect estimation of the ecological distance between populations.

Additional factors may affect the landscape dispersal pattern and dispersal ability in a fragmented landscape. They have not been considered and may explain partially the genetic variability between habitat patches. Dispersal varies considerably among species with respect to life history (Koenig et al. 1996, Lima and Zollner 1996), degree of species speciation (Wolff 1999), spacing behaviour (density, territoriality sex-based dispersal) (Hestbeck 1982, Koenig et al. 1996, Wolff 1997, 1999) and sociality as conspecific attraction (Smith and Peacock (1990)). All can enhance or reduce the colonisation processes and add additional barriers, which may have demographic consequences (Wolff 1999). Dispersal processes are also dependent on species' intrinsic factors (condition, reproduction, life expectancy) (Lidicker and Stenseth 1992) and on ultimate factors (selective forces, evolution of behaviour, fitness traits) (Lidicker and Stenseth 1992). Including all factors as the specific *C. russula* breeding system (Cantoni and Vogel 1989) and female-based dispersal of *C. russula* (Favre et al. 1997, Balloux et al. 1998, Fontanillas et al. 2003) is not realistically interpretable and therefore those factors have not been considered in our first simulation approach. Developments in this field might lead to a better interpretation of factors affecting genetic dispersal.

Another limitation is caused by the rapid landscape change in such a human-dominated area. In fact the genetic differentiation obtained corresponds to gene flow that might have occurred at a time when the landscape arrangement was different form the actual one.

According to our results and the previous remarks, performed simulations seem to represent well the influence of landscape heterogeneity on genetic differentiation. The landscape model linked with an animal model responds to the need to study animal responses to landscape features at a fine scale (Peles et al. 1999), as well as the need to analyse dispersal process in a metapopulation scale taking into account animal interactions with landscape features (Reed and Dobson 1993, Curio 1996, Lima and Zollner 1996, Ulfstrand 1996, Sutherland 1998, Caro 1999, Reed 1999, Anthony and Blumstein 2000). Therefore, with simple movement rules and behavioural assumptions, the genetic differentiation among populations in a fragmented can be estimated. This research improves dispersal simulations by tacking into account landscape heterogeneities and arrangement, which are critical factors at both the local and metapopulation scales.

Finally, beside the numerous assumptions in the spatial and genetic modelling approaches and considering the large number of parameters that have not been considered in this analysis, we can conclude that our model provides a reproduction of the dispersal of shrew in a fragmented landscape that explains genetic differentiation and provides stable and reproducible results.

Conclusion

The dispersal model integrating landscape features specificity and species-specific responses to landscape structure constitutes an improvement in the animal dispersal simulation field. Further research is required to determine more precisely for many species the landscape use, dispersal abilities, behaviour and the impact of other factors such as life history and sociality in dispersal processes. In such case, this approach could give important information on connectivity between habitat patches and thus on gene flow. By adding a part of the complexity of the dispersal process, the one due to landscape heterogeneity, the presented model has proved to explain genetic differentiation between populations and to be interpretable. This would not have been the case, if all potential factors, had been incorporated.

Calibration and validation of dispersal models with field experiments is difficult due to the feasibility of data collection (Koenig et al. 1996, Tischendorf 1997). Therefore our results show that genetics can bring important contributions in model calibration and interpretations. They offer a new field of investigation for spatially-explicit dispersal simulation validation, even if, due to the complexity of the processes involved, the genetic measures are not yet completely adapted and unified.

References

Anthony, L. L., and D. T. Blumstein. 2000. Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce N-e. Biological Conservation 95:303-315.

Balloux, F., and J. Goudet. 2002. Statistical properties of population differentiation estimators under stepwise mutation in a finite island model. Mol. Ecol. 11:771-783.

Balloux, F., J. Goudet, and N. Perrin. 1998. Breeding systems and genetic variance in the monogamous, semi-social shrew, *Crocidura russula*. Evolution 52.

Balloux, F., and N. Lugon-Moulin. 2002. The estimation of population differentiation with microsatellite markers. Mol. Ecol. 11:155-165.

Barton, N. H. 1992. The genetic consequences of dispersal. Pages 37-59 *in* N. C. Stenseth and W. Z. J. Lidicker, editors. Animal Dispersal: small mammals as a model. Chapman & Hall, London.

Beecham, J. A., and K. D. Farnsworth. 1998. Animal foraging from an individual perspective: an object oriented model. Ecological modelling 113:141-156.

Bennetts, R. E., J. D. Nichols, J.-D. Lebreton, R. Pradel, J. E. Hines, and W. M. Kitchens. 2001. Methods for estimating dispersal probabilities and related parameters using marked animals.

Pages 3-17 *in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. Dispersal, Oxford.

Berger, U., G. Wagner, and W. F. Wolff. 1999. Virtual biologist observe virtual grasshoppers: an assessment of different mobility parameters for the analysis of movement patterns. Ecological Modelling 115:119-127.

Berggren, A., A. Carlson, and O. Kindvall. 2001. The effect of landscape composition on colonization success, growth rate and dispersal in introduced bush-crickets Metrioptera roeseli. Journal of Animal Ecology 70:663-670.

Blackwell, P. G. 1997. Random diffusion models for animal movement. Ecological Modelling 100:87-102.

Branis, M., and H. Bura. 1994. Visual and hering biology of the shrews. Pages 189-200 *in* J. F. Merrit, G. L. Kirkland JR, and R. K. Rose, editors. Advances in the biology of shrews, Pittsburgh.

Cantoni, D., and P. Vogel. 1989. Social organisation and mating systems of freeranging greater white-toothed shrews, Crocidura russula. Animal Behaviour 38:205-214.

Caro, T. 1999. The behaviour-conservation interface. Trends in Ecology and Evolution 14:366-369.

Carter, J., and J. T. Finn. 1999. MOAB: a spatially explicit, individual-based expert system for creating animal foraging models. Ecological Modelling 119:29-41.

Cockburn, A. 1992. Habitat heterogeneity and dispersal: environmental and genetic patchiness. Pages 65-95 *in* N. C. Stenseth and W. Z. J. Lidicker, editors. Animal Dispersal: small mammals as a model. Chapman & Hall, London.

Cockerham, C. C., and B. S. Weir. 1993. Estimation of gene flow from F-statistics. Evolution 47:855-863.

Couvet, D. 2002. Deleterious effects of restricted gene flow in fragmented populations. Conservation Biology 16:369-376.

Curio, E. 1996. Conservation needs ethology. Trends in Ecology and Evolution 11:260-263.

Downing, K., and M. Reed. 1996. Object-oriented migration modelling for biological impact assessment. Ecological modelling 93:203-219.

Ehinger, M., P. Fontanillas, E. Petit, and N. Perrin. 2002. Mitochondrial DNA variation along an altitudinal gradient in the greather white-tooted shrew, Crocidura russula. Mol. Ecol. 11:939-945.

Endler, J. A. 1977. Geographic Variation, Speciation, and Clines. Princeton University Press,, Princeton, New Jersey.

Fahrig, L., and G. Merriam. 1985. Habitat patch connectivity and population survival. Ecology 66:1762-1768.

Fatio, V. 1869. Faune des vertébrés de la Suisse. I. Histoire naturelle des mammifères. H. Georg.

Favre, L., F. Balloux, J. Goudet, and N. Perrin. 1997. Female-biased dispersal in the monogamous mammal Crocidura russula: evidence from field data and microsatellite patterns. Proc. R. Soc. Lond B:127-132.

Fontanillas, P., E. Petit, and N. Perrin. 2003. Estimating sex-specific dispersal rates with autosomal markers in hierarchically-structured populations. *Submitted.*

Forman, R. T. T. 1995. Land mosaics: the ecology of landscapes and regions, Cambridge University Press edition, Cambridge, Massachusetts.

Gaines, M. S., and L. R. McClenaghan. 1980. Dispersal in small mammals. Annual Review of Ecology and Systematic:163-196.

Genoud, M. 1981. Contribution à l'étude de la stratégie énergetique et de la distribution écologique de Crocidura russula (soricidae, insectivora) en zone tempérée. Université de Lausanne, Lausanne.

Genoud, M. 1982. Distribution écologique de Crossidure russula et d'autres Soricidés (Insectivora, Mammalia) en Suisse romande. Bulletin de la Société Vaudoise des Sciences Naturelles 76:117-131.

Genoud, M. 1995. Crocidure russula. Pages 49-53 *in* J. Hausser, editor. Mammifères de la Suisse. Birkhäuser-Verlag, Basel.

Genoud, M., and J. Hausser. 1979. Ecologie d'une population de Crocidura russula en milieu rural montagnard (Insectivora, Soricidae). Terre et vie 33:539-553.

Grimm, V., T. Wyszomirski, D. Aikman, and J. Uchmanski. 1999. Individual-based modelling and ecological theory: synthesis of a workshop. Ecological Modelling 115:275-282.

Hainard, R. 1961. Mammifères suavages d'Europe. I. Insectivores, Chéiroptères, Carnivores., Neuchâtel.

Hall, S., and B. Halle. 1999. Modelling activity synchronization in free-ranging microtine rodent. Ecological Modelling 115:165-176.

Hanski, I. 1999. Metapopulation Ecology. Oxford University Press, Oxford.

Hanski, I. 2001. Spatially realistic models of metapopulation dynamics and their implication for ecological, genetic and evolutionary processes. Pages 139-156 *in* J. Silvertown and J. Antonovics, editors. Integrating Ecology and evolution in a spatial context.

Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. Nature 404:755-758.

Hansson, L. 1991. Dispersal and connectivity in metapopulations. Biological Journal of the Linnean Society 42:89-103.

Hestbeck, J. B. 1982. Population regulation of cyclic mammals - The social fence hypothesis. Oikos 32:157-163.

Koenig, W. D., D. Van Vuren, and P. N. Hooge. 1996. Detectability, philoparty, and the distribution of dispersal distances in vertebrates. Trends in Ecology and Evolution 11:514-517.

Kozakiewicz, M. 1993. Habitat isolation and ecological barriers: the effect on small mammal populations and communities. Acta Theriologica 38:1-30.

Kozakiewicz, M., and J. Szacki. 1995. Movements of small mammals in a landscape: patch restriction or nomadism? Pages 78-94 *in* W. Z. Lidicker, editor. Landscape approaches in mammalian ecology and conservation, Minneapolis, Minesota.

Lidicker, W. Z. J., and N. C. Stenseth. 1992. To disperse or not to disperse: who does it and why? Pages 21-36 *in* N. C. Stenseth and W. Z. J. Lidicker, editors. Animal Dispersal: small mammals as a model. Chapman & Hall, London.

Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution 11:131-135.

Lorek, H., and M. Sonnenschein. 1999. Modelling and simulation software to support individual-based ecological modelling. Ecological Modelling 115:199-216.

Mallet, J. 2001. Gene Flow. Pages 337-360 *in* I. P. Woiwod, D. R. Reynolds, and C. D. Thomas, editors. Insect Movement: Mechanisms and Consequences: proceedings of the Royal Entomological Society's 20th Symposium. CABI Publishing, Oxon.

Manly, B. F. J. 1991. Randomization and Monte Carlo Methods in Biology, 1st edn. Chapman & Hall edition, London.

Manly, B. F. J. 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology, 2st edn. Chapman & Hall edition, London.

Moorcroft, P. R., M. A. Lewis, and R.-L. Crabtree. 1999. Home range analysis using a mechanistic home range model. Ecology 50:1656-1665.

Nally, R. M. 2001. Interaction strengths and spatial scale in community ecology: simulated quadrat-sampling and confinement experiments involving animals of different mobilities. Ecological modelling 144:139-152.

Nei, M. 1987. Molecular evolution genetics. Columbia University Press, New York.

Nei, M., and S. Kumar. 2000. Molecular Evolution and Phylogenetics. Oxford Universtity press.

Paradis, E., S. R. Baillie, and W. J. Sutherland. 2002. Modeling large-scale dispersal distances. Ecological Modelling 151:279-292.

Peles, J. D., D. R. Bowne, and G. W. Barrett. 1999. Influence of Landscape Structure on Movement Patterns of Small Mammals. Pages 41-62 *in* G. W. Barrett and J. D. Peles, editors. Landscape Ecology of Small Mammals. Springer-Verlag, New York.

Perrin, N., and J. Goudet. 2001. Inbreeding, kinship, and the evolution of natal dispersal. Pages 123-142 *in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. Dispersal. Oxford University Press Inc., New York.

Pursey, A. E., and M. Wolf. 1996. Inbreeding avoidance in animals. TREE:201-206.

Ralls, K., P. H. Harvey, and A. M. Lyles. 1986. Inbreeding in Natural Population of Birds and Mammals. *in* M. E. Soulé, editor. Conservation Biology. Sinauer Associates Inc, Sunderland, MA.

Reed, J. M. 1999. The role of behavior in recent avian extinctions and endangerments. Conservation Biology 13:232-241.

Reed, J. M., and A. P. Dobson. 1993. Behavioral constraints and conservation biology- Conspecific attraction and recruitment. Trends in Ecology and Evolution 8:253-256.

Richter, H. 1963. Zur Verbreitung des Wimperspitzmäuse (*Crocidura* Wagler, 1832) in Mitteleuropa. Abh. Ber. Staatl. Mus. Tierk. Dresden 26:219-242.

Slatkin, M. 1995. A Measure of Population Subdivision Based on Microsatellite Allele Frequencies. Genetics Society of America 139:457-462.

Smith, A. T., and M. M. Peacock. 1990. Conspecific attraction and the determination of metapopulation colonization rates. Conservation Biology 4:320-323.

Stenseth, N. C., and W. Z. J. Lidicker. 1992. The study of dispersal: a conceptual guide. Pages 1-20 *in* N. C. Stenseth and W. Z. J. Lidicker, editors. Animal Dispersal: small mammals as a model. Chapman & Hall, London.

Sutherland, W. J. 1998. The importance of behavioural studies in conservation biology. Animal Behaviour 56:801-809.

Takezaki, N., and M. Nei. 1996. Genetic Distances and Reconstruction of Phylogenetic Trees From Microsatellite DNA. Genetics Society of America 144:389-399.

Tischendorf, L. 1997. Modelling individual movements in heterogeneous landscapes: potentials of a new approach. Ecological Modelling 103:33-42.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Annu. Rev. Ecol. Syst. 20:171-197.

Tyre, A. J., H. Possingham, and D. Lindenmayer. 1999. Modelling dispersal behaviour on a fractal landscape. Ecological Modelling 14:103-113.

Ulfstrand, S. 1996. Behavioural ecology and conservation biology. Oikos 77:183.

Vuilleumier, S., and R. Metzger. 2003. A new landscape model for animal movement and behaviour assessment. *Submitted*.

Vuilleumier, S., and N. Perrin. 2003. Cognitive ability and colonisation success in a real landscape: A modelling approach. *Submitted.*

Weir, B. S. 1996. Genetic data analysis, Sinauer, Sunderland, MA.

Whitlock, M. C. 2001. Dispersal and the genetic properties of metapopulations. Pages 452 *in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. Dispersal, Oxford.

Wolff, J. O. 1994. More on juvenile dispersal in mammals. Oikos 71:349-352.

Wolff, J. O. 1997. Population regulation in mammals: An evolutionary perspective. J. Anim. Ecol 66:1-13.

Wolff, J. O. 1999. Behavioral Model Systems. Pages 11-40 *in* G. W. Barrett and J. D. Peles, editors. Landscape Ecology of Small Mammals. Springer-Verlag, New York.

Wright, S. 1943. Isolation by distance. Genetics:114-138.

Wright, S. 1965. The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution 19:395-420.

Chapter 7

Synthesis and general conclusions

Planning ecological networks to avoid species and population extinction is presently carried on in many countries throughout the world (see for example (Bennett 1999) and review by (Bennett and Wit 2001)). Unfortunately and since scientific and practical knowledge in this field is lacking, their real consequences are difficult to evaluate (Verboom et al. 1993). Reckoned as a major process (Wiens 1995, Diffendorfer et al. 1999), animal dispersal in fragmented landscape (meaning that individuals move from one habitat patch to another) is one of the processes that needs to be well understood to provide effective ecological networks. Scarcity of available data makes it difficult to handle this process and thus leads to further difficulties to estimate the various factors involved within this process (searching and movement behaviour, animal dispersal abilities). This thesis proposes methods, models, analysis and applications aiming at increasing practical and scientific knowledge in the field. They concern the explicit modelling of dispersal and thus, imply, at first, a technical challenge taking into consideration the need of effective models for both management and scientific purposes, and second, an ecological challenge due to the strong needs of realistic modelling, of spatial localisation and of the generation of effective estimates to describe the processes involved.

The presented method developed with standard GIS software shows that the simulation of diffusive dispersal processes allows a straightforward design of ecological networks according to animal movement constraints in a fragmented landscape. This method has proved to be an effective management tool at different scales and provides widespread opportunities for application. The method developed within this thesis based on expert judgments has been used to: (i) identify ecological networks for game species (Gatabin et al. 2001, Luyet 2001) and amphibians (Zanini 2001, Morard 2003), (ii) estimate the effects of roads on ecological networks (Benyahia 2001, Waegli 2002), (iii) to evaluate landscape planning scenarios (Zanini 2003), and (iv) to calculate least cost distances between habitat patches (*figure 36*). Nevertheless, this method, as well as other major actual models used to simulate animal dispersal, has technical and scientific limitations. Technical limitations concern the model's inability to simulate complex interactions between landscape features and dispersers as well as the simulation time and data volume needed. Scientific limitations are mainly due to the underlying assumptions that consider animal dispersal without cognitive abilities and use a simplistic and inadequate representation of landscape features.

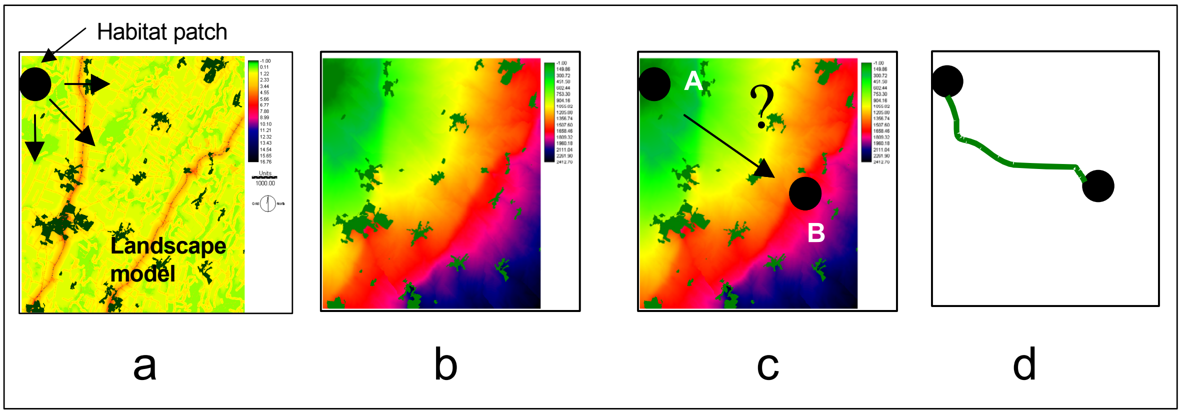


Figure 36: Illustrations of the procedures to find the least distance between two points according to a surface of constraints. With the dispersal model presented in chapter 3, it is possible to identify the least cost path between two points in a landscape. According to a landscape model (surface of constraints) where friction values are assigned to each pixel (figure 36a), it is possible from an area in the landscape (habitat patch) to generate a least cost surface (figure 36b). Movement cost between two pixels A and B is computed according to the distance between pixels weighted by the friction value of the pixels crossed. Then, algorithms provided by Idrisi® software compute the least cost between the habitat patch and another point within the landscape and spatially identify the corresponding path (figure 36c and d).

To simulate dispersal in a realistic way, overcoming the limitations above, both the landscape and animal models are reconsidered. In the landscape model, the landscape features have to be represented according to their influence on dispersal processes, which may be due to their form, intrinsic properties or visibility. In the animal model, behaviour (preference for particular landscape features) and dispersal ability (dispersal distance, ability to cross landscape structures or to use cues to direct searching) should be simulated. In order to carry out such a task, the development of a new conceptualisation of dispersal possesses in an individual-based approach and formalisation of a landscape feature representation are both required. Their implementation in an object-oriented programming approach (in the Borland® Delphi™ environment with the Object Pascal language and in MapBasic® and MapInfo Professional® developmental environment) has demonstrated their ability to simulate complex interactions between entities: in our case, individual and landscape. The dispersal model therefore:

- allows simulation of dynamic processes depending on topological and typological properties of landscape features and processes where distant and/or close relations between entities are involved,

- provides a spatial identification of paths according to their frequency in use and new quantification of colonisation probability, distance (ecological cost) and flow of individuals between habitat patches within a metapopulation,
- allows the simulation of various dispersal strategies, landscape uses, and behaviours and cues of disperser, and
- can be used to investigate the consequences of species behaviour, dispersal abilities and landscape use on metapopulation persistence in a realistic landscape.

According to our knowledge, none of the actual methods provide a quantification of either the belonging of a habitat patch to a metapopulation or a quantification of metapopulation dynamics induced by landscape structures and species behaviour. Therefore, the model provides new investigation possibilities within this field.

From a theoretical point of view, the dispersal model:

- can be used to examine both local and global aspects of dispersal processes by providing a simulation of species interactions with heterogeneous landscapes and a quantification of the influence of dispersal strategies on metapopulation structures and dynamics.
- Quantifies metapopulation dynamics due to landscape and identifies the number and intensity of habitat patches connected within a metapopulation (both are usually difficult to determine) and therefore, offers a new method of metapopulation analysis.

As a major result, the relation between ecological costs and colonisation successes among specific habitat patches (*figure 37)* provides quantification of species viability according to behaviour and dispersal ability. Investigations therefore lead to a better understanding of the many factors affecting species viability within a metapopulation settled in a fragmented landscape area.

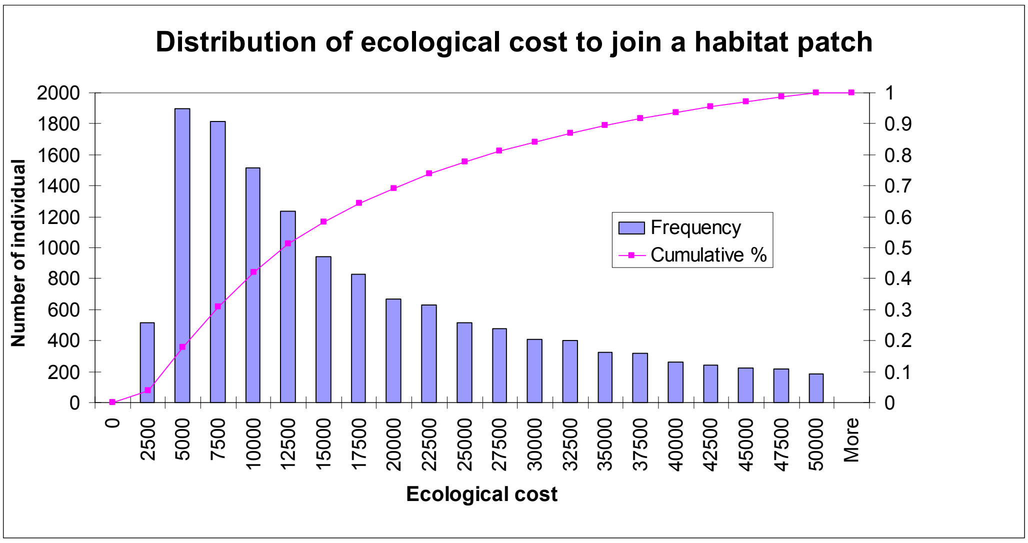


Figure 37: Histogram representing the distribution of ecological cost between two habitat patches. According to the estimation of the ability of a disperser to pay a "cost", it is possible to determine the associated colonisation probabilities.

The theoretical application that attempts to evaluate the potential influence of animal cognitive abilities on landscape uses, on species distribution and on metapopulation dynamics has shown that behaviour represents a fundamental aspect to take into consideration when dealing with dispersal processes. Behaviour induces different landscape uses and thus causes various dynamics and structures at the metapopulation level. Results show that the increase of colonisation probability with the species ability to 'pay' a cost and the variability of paths used are not confirmed except under randomised movement assumptions (*figure 38*). According to the variability of landscape uses and travel costs, the related colonisation probabilities of species may present different sensitivities to landscape changes or management measures. However, they can be estimated by measures generated by the model.

From a practical point of view and according to the lack of information on the effect of landscape heterogeneities and species behaviour on landscape use patterns, modelling movement behaviours in heterogeneous landscapes may:

- contribute to a better understanding of dispersal processes as well as factors that may have important implications,
- offer assistance to planners for critical management decisions or to scientists for investigation planning,
- be applied to species when measures are available to calibrate the model, and
- allow "what if" scenarios related to landscape changes or specific species studies.

The developed models in this thesis offer a wide range of opportunities for applications such as the determination of species viability and the number and degree of connections of habitat patches according to a species' ability to disperse. The spatial identification of major connections with the associated costs may help scientists as well as landscape managers to prevent or reinforce animal dispersal. While planning ecological networks, this may also help in determining land-use conflicts or hot spots for dispersal. Thanks to their spatial dimension, the present developments provide connection identification and assessment of effects of landscape modifications on wildlife.

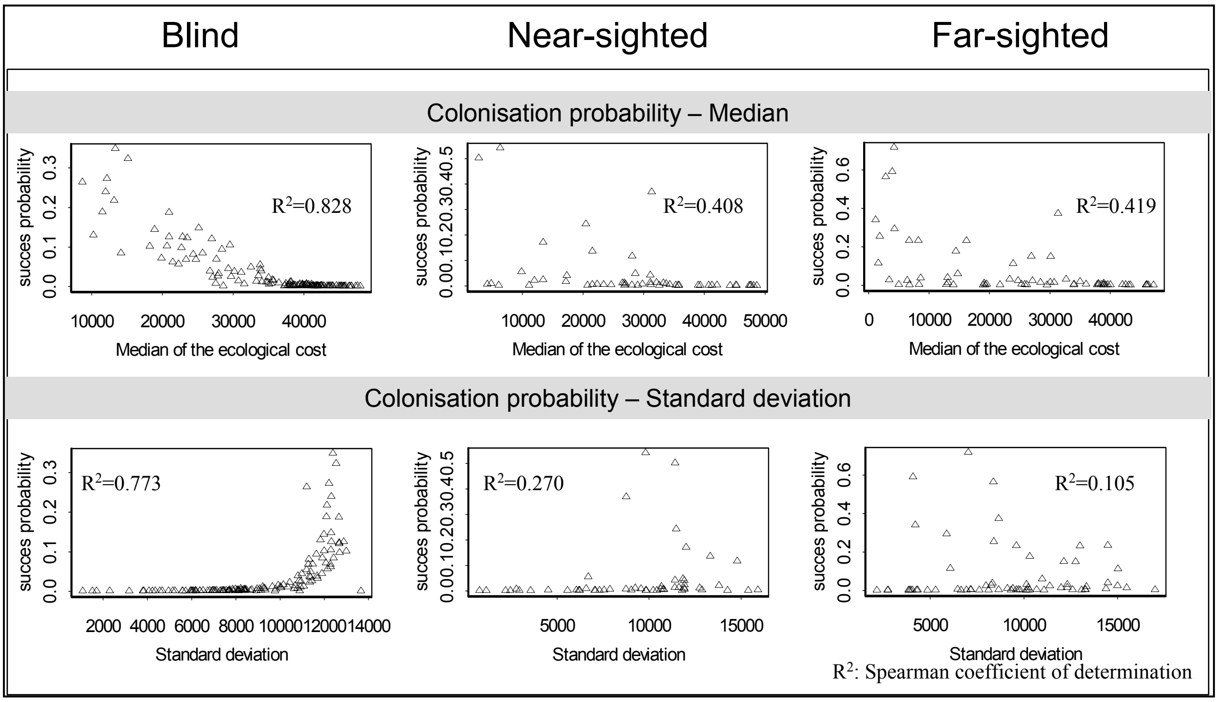


Figure 38: Plot of the colonisation success probability and the (a) median and (b) standard deviations of the distribution of ecological costs. Whatever the cost and standard deviation (variability of the paths used), success may occur with near-sighted and far-sighted strategies. That is not the case for the blind strategy.

However, limitations in application are mainly due to the lack of knowledge concerning the relationship between the data to be used and the studied species (for example: scale and categories of landscape features present in dispersal processes or affecting animal behaviour) and their availability. Difficulties that occur when applying such a model may be due to

- the spatial identification of habitat patches
- the assumption that the species is involved in metapopulation system,
- searching-strategy assumptions that assign a specific movement strategy and cues (here only visual cues are simulated, others may be more important),

- neglecting significant factors that may play an important role (sociability, for example),

- the temporal scale of the process involved, which is difficult to establish with rapid changes in landscape, and finally,

- the dependency of the results on expert judgment, the value assigned to a landscape model (value of friction, attractiveness and cost) and the value assigned to an animal model (cognitive abilities).

Even though species are becoming more traceable, significant problems in developing dispersal models remain, mainly due to the lack of knowledge in factors involved and also due to the difficulty of validating such models. For example, the model developed provides a quantification of landscape incidence by colonisation probability. In order to obtain the effective number of dispersers in a metapopulation, this probability must be weighted by the number of effective emigrants to quantify effective dispersers and provide a quantification of the effective flow of individuals between habitat patches. Therefore, the model must incorporate an estimation of the population dynamics within each habitat patch.

For validation procedures, a promising field is genetics. Our application shows that the use of genetics as a validation tool is not straightforward, which is mainly due to the complexity of the processes involved. Measures of genetic distances between populations derived from simplified models (which are based on numerous assumptions), lead to difficulties in interpreting what is really measured. Modeling approaches, as developed in this thesis, consider only the estimation of population connectivity due to landscape heterogeneities and animal behaviour while genetics measures do include differentiation due to landscape heterogeneity (isolation) and other factors such as the reproductive system and demography. To draw a relation between both approaches, models have to consider driving forces of gene flows as, for example, reproduction and sex-biased dispersal. Nowadays, landscapes are often changing rapidly so that the temporal aspects of genetic differentiation may add difficulties when interpreting the results. Despite such difficulties, this approach provides a better estimation of species behaviour and better explanation of genetic differentiations among populations than geographic distances. These results highlight the fact that exchanges of individuals between habitat patches depend on species movement behaviour and on landscape heterogeneity and arrangement. They do point out the importance of landscape as a factor affecting genetic differentiation among populations. Additionally, they demonstrate the flexibility and ability of such models to be used for a specific species.

Models developed in this research are operational and useful to analyses dispersal processes, however there are still some analyses, developments and investigations that would be interesting to complete, as in the following non-exhaustive list.

- Models developed in chapter 4 and applied in chapters 5 and 6 provide the frequency of landscape features used and identify dispersal pattern (ecological networks or corridors) of species in heterogeneous landscape according to species behaviour and abilities. Hence, additional analysis may help to understand the spatial implication of dispersal. A comparison of the results obtained with the simplified method developed in Chapter 3 and with those obtained with the developed model may quantify the gain of information of the latter.

- Spatial analysis of landscape feature arrangements (as provided by Fragstat (McGarigal and Marks 1995)) may help in determining the character of landscape heterogeneity, which should draw a relation between landscape pattern and connectivity.

- Estimation of the effective colonisation rate by adding to the model a habitat patch identification procedure and estimation of the carrying capacity and population dynamics.

- Paths generated by the model are Markov chains. Thus, dispersal processes may be characterized by Markov processes, whose underlying properties may help in interpreting results and also add information on landscape heterogeneities incidence on dispersal processes.

- Values such as cost or attractiveness, are assigned to landscape entities and their values defined with the help of expert judgements. Because of the difficulty in validating such values, a sensitivity analysis would be worthwhile to perform. It could be carried out, for example, with Monte Carlo methods (Rubinstein 1981) and should lead to a better quantification of the model's response to changing entity values.

- Others model extensions, in particular searching strategies, could be incorporated: integrating other cues to direct searching, enhancing visual cues or integrating partial learning. Additionally, factors such as resource availability, territoriality, co-specific attraction or predation ability, that may deeply affect the dispersal process, could also be considered. However, such developments may dramatically increase parameters, which may be difficult to obtain. Nevertheless, thanks to the model's implementation strategy, all these factors can be easily implemented.

Another important perspective, which is also of major interest regarding this model, is to apply it to a species for which tracking has been performed or genetic distances among populations are available; thus behavioural aspects of the species may be calibrated. Moreover, persistence of these species may be analysed as well. Additional applications to plant species or birds may also be of interest, but they definitively depend on the availability of data.

In conclusion, the present research provides new models of simulating dispersal on a new landscape representation according to various species movement behaviour and search strategy modelling. They provide estimations of metapopulation dynamics and structures due to landscape heterogeneities and species behaviour and abilities to disperse.

In order to carry out such model developments, GIS, landscape ecology, metapopulation ecology, animal behaviour and genetics have been investigated. Proposed developments could give important information and allow a better understanding of dispersal processes, which may help to understand the scientific implications of the processes by providing new investigations and plans for critical management decisions. These models have proved to be useful in many analyses and constructive applications in landscape ecology and metapopulation ecology, but also conservation biology and landscape management.

References

Bennett, A. F. 1999. Linkages in the Landscape: The role of corridors and connectivity in wildlife conservation. IUCN, Gland, Switzerland and Cambridge, UK.

Bennett, G., and P. Wit. 2001. The development and application of ecological networks: A Review of proposals, plans and programmes. AIDEnvironment and IUCN, Amsterdam.

Benyahia, N. 2001. Evaluation du réseau écologique de la région de Grandson (VD), Projet de semestre. Travaux d'étudiants Laboratoire d'hydrologie et aménagements, Lausanne.

Diffendorfer, J. E., M. S. Gaines, and R. D. Holt. 1999. Patterns and impacts of movements at different Scales in Small Mammals. Pages 63-88 *in* G. W. Barrett and J. D. Peles, editors. Landscape Ecology of Small Mammals. Springer-Verlag, New York.

Gatabin, C., R. Prélaz-Droux, and S. Vuilleumier. 2001. Projet AGICE, Rapport intermédiaire. Rapport de projet Laboratoire d'hydrologie et aménagements, Lausanne.

Luyet, V. 2001. Elaboration d'une conception d'évolution du paysage pour la plaine du Rhône : développement méthodologique et application, travail de diplôme. Travail de diplôme GECOS, EPFL, Lausanne.

McGarigal, K., and B. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Protland, US.

Morard, E. 2003. Les sites de reproduction d'amphibiens de la plaine de l'Orbe. Travail de diplôme de biologie Laboratoire de la biologie de la conservation, Université de Lausanne, Lausanne.

Rubinstein, R. Y. 1981. Simulation and the Monte Carol Methods. John Wiley and Sons, New York.

Verboom, J., J. A. J. Metz, and E. Meelis. 1993. Metapopulation models for impact assessment of fragmentation. *in* C. C. V. a. P. Opdam, editor. Landscape Ecology of a Stressed Environment. Chapman and Hall, London.

Waegli, A. 2002. Évaluation du réseau écologique de la région du Chablais. Travaux d'étudiants Laboratoire d'hydrologie et aménagements, Lausanne.

Wiens, J. A. 1995. Landscape mosaic and ecological theory. Pages 1-26 *in* L. L. Hansson, Fahrig and G. Merriam, editor. Mosaic Landscapes and Ecological Processes. Chapman and Hall, London.

Zanini, F. 2001. Modélisation d'un réseau écologique et prototype SIG cantonal pour la gestion des données sur les amphibiens. Travail de diplôme EPFL, Lausanne.

Zanini, F. 2003. Indice de perméabilité du paysage aux déplacements de la faune à affinité forestière et de la faune amphibie, projet Gesorbe. Rapport interne Laboratoire d'hydrologie et aménagements, Lausanne.

Appendix A

Genetics in metapopulations

Species are typically subdivided into local populations. These populations may be connected by dispersal and form a metapopulation. Among populations, allele[1] frequency[2] may vary due to the environmental context and population dynamics. Thus, we can analyse genetic differentiation among them. Four main genetic forces act on a population: (i) *Genetic drift*, (ii) *Mutation*, (iii) *Selection* and (iv) *Migration* that are explained below.

Genetic drift (Calow et al. 1998) is due to a random fluctuation of gene frequencies in a population, and is caused by a random sampling of gametes[3] and/or genotypes[4] in reproduction. According to Mendel's law[5] of segregation, gamete production is a stochastic process and genotype frequencies in subsequent generations fluctuate even in perfectly constant environments, as well as in the absence of any selection. Drift induces a fixation and

---

[1] Alleles (Calow et al. 1998): Two or more forms of a gene occupying the same locus on a chromosome. In somatic cells of diploid organisms each gene is represented by two alleles, except for the genes contained in sex chromosomes in the heterogametic sex.

[2] Allele frequency (Calow et al. 1998): Genetic variation in a population at a locus A implies the presence of more than one allele at that locus. For two alleles A1 et A2, the frequency (p) of allele A1 is given by: P = [(2 * number of A1A1 homozygotes) + (number of A1A2 heterozygotes)] / (2 * total number of individuals). For diploid organisms, the genetical mechanics of evolution are given by allele frequency changes.

[3] Gametes (Calow et al. 1998): Sexual reproductive propagule that is haploid (single set of unpaired chromosomes)

[4] Genotype (Calow et al. 1998): the genetic constitution of organisms

[5] The laws of Mendel concerning inheritance are the laws of segregation (Mendel's first law (1) Traits are controlled by pairs of genes, (2) These genes segregate during the formation of the reproductive cells, thus passing into different gametes) and the law of independent assortment (Mendel's second law: When a trait is controlled by two or more pairs of genes simultaneously, they segregate independently (partially correct)) (Calow et al. 1998).

a loss of alleles and thereby can cause a delay in genetic variability. In the absence of new mutations, the heterozygosity[6] h, in a population of diploid[7] organisms decreases due to drift as:

$$h(t) = h(0)(1 - \frac{1}{2N_e})^t \qquad \textit{Equation A 1}$$

with time *t* measured in generation and N_e denoting the effective population size (population that reproduces). This process can be viewed most easily as a pool of 2 N_e genes with equal probability of being transmitted. If the selection operates, drift causes deviations from the expected shift in genotype frequencies.

Mutation refers to any spontaneous, random change in the genome. It will prevent the elimination of deleterious alleles by selection; a balance between drift and new mutations will be reached at the equilibrium of heterozygosity (Calow et al. 1998).

Selection means to choose one or a few from a greater number, selection is occurring whenever 2 alleles have different chances of survival or have different chances of leaving offspring. Thus, selection is a process that reduces heterozygosity.

Migration promotes a new pool of alleles which tends to increase heterozygosity at a population scale. If migrants are coming from other subpopulations, they will cause a homogenisation of the allele frequency among the metapopulation (Hastings and Gavrilets 1999).

Among genetic forces acting on a population, if no migrants interfere and there is a selective neutrality of each locus, drift and mutation cause the divergence of the allele frequency among subpopulations and the homogenization of the allele frequency within the population. This difference can be used to determine the genetic relatedness and the migration rates between populations. Under some stringent assumptions, we can measure the genetic variability (a description of the state of populations) and obtain an estimate of gene flow (meaning the movement of genes).

Several formulae have been proposed for estimating the genetic distance (or the genetic similarity); which vary in terms of their underlying genetic models; see Takezaki and Nei (1996) for details.

---

[6] Heterozygosity (Calow et al. 1998): Estimate the probability that any individual is heterozygous at any of a specified set of loci. A zygote is the product of the fusion of an egg and a sperm. It contains two copies of each chromosome, one from each parent. Egg and sperms cells, on the other hand, each contain only one copy of each chromosome.

[7] Diploid (Calow et al. 1998): That contains two sets of chromosomes (one set donated from each parent).

Genetic differentiation can first be estimated by simple measures of distance between series of allele frequency. In this field we can find the Euclidian distance, which calculates the root sum-of-squares of differences and the Czekanowski's (1909) distance, which measures the sum of the absolute differences (*equation A 2*)

$$C_z = \frac{1}{m} \sum_{i=1}^{m} \left| x_i - y_i \right| \qquad \textit{Equation A 2}$$

A version of this measure is the ***Manhattan metric***

$$C_M = \sum_{i=1}^{m} \left| x_i - y_i \right| \qquad \textit{Equation A 3}$$

With

x_i, y_i : Frequency of the *i*th allele in population X and Y, respectively
m : Number of alleles

When there are many loci, the average of C_z or C_M over the loci is used.

C_z and C_M are primarily used for population classification, particularly when the populations studied are closely related. They satisfy the triangle inequality. But, C_z and C_M have some undesirable properties:

C_z : the maximum value of C_z depends on the number of alleles. If two populations are polymoriphic but share no common allele, C_z becomes < 1.

C_M : is 0 when two populations are identical but always 2 when they have no shared alleles; to adjust C_M we can divide it by 2.

Other measures characterize the genetic drift and the mutation equilibrium in a population by two main mathematical models of mutation: the Infinit Allele Model (IAM) and the Stepwise Mutation Model (SMM).

The Infinit Allele Model assumes that a new mutation gives rise to new electrophoretically distinguishable allele. In the Stepwise Mutation Model allele mutation is assumed to create a new allele by the gain or loss of 1 repeat unit. These models can be applied if they fulfill the following assumptions:

1. Selective neutrality of each locus. In order to detect the selection we can compare the observed genotype frequencies to those expected from the prediction of Hardy-Weinberg

equilibrium[8]. Two kinds of deviations can occur: (1) excess of heterozygotes due to overdominant selection or occurrence of outbreeding or (2) excess of homozygotes due to selection, null allele, inbreeding or Wahlund's effect[9].

2. The presence of "null alleles" (not detected via PCR analysis).
3. The independent assortment of the loci.

There are numerous genetic distance measures based on IAM, for example shared allele distance (Chakraborty and Jin, 1993), Nei et al's (1983) distance (DA), Nei's (1973) minimum genetic distance (Dm), Nei's (1972) standard genetic distance (Ds), Latter's (1972) distance, Roger's (1972) distance, Prevosti et al's (1975) distance, Sanghvi's (1953) distance, Reynold's genetic distance (1983) and Cavali-Sforza and Edwards' (1967) chord distance. The most widely used measure is Nei's (1972) standard genetic distance (Nei et al. 1983) defined as follows:

$$D_S = -\ln[J_{xy} / \sqrt{J_X J_Y}\,] \qquad \textit{Equation A 4}$$

With

$$J_x = \sum_j^r \sum_i^{m_j} {x_{ij}}^2 / r, \quad J_y = \sum_j^r \sum_i^{m_j} {y_{ij}}^2 / r, \quad J_{xy} = \sum_j^r \sum_i^{m_j} y_{ij} x_{ij} / r$$

Where

$J_{xy} / \sqrt{J_X J_Y}$ is the normalized identity of genes between two populations.

x_{ij}, y_{ij} : Frequency of the *i*th allele at the *j*th locus in population X and Y, respectively
m_j : Number of alleles at the *j*th locus
r : Number of loci

This measure is intended to estimate the average number of codon substitutions per locus.

---

[8] *Hardy-Weinberg law* (Calow et al. 1998): *Hardy-Weinberg law* consists of two parts:
The first part states that if there is no evolutionary forces (Mutation, selection, drift or migration) acting on allele frequencies (ideal population); they do not change. It applies to diploid as well as haploid or n-ploid species. The second part states that if, moreover, there is random mating, the genotype frequencies attain equilibrium frequencies in a single generation in a diploid species.

[9] *Wahlund effect*: Heterozygote deficit due to population subdivision. A subdivided population contains fewer heterozygotes than predicted despite the fact that all subdivisions are in Hardy-Weinberg equilibrium (Biology Teaching Organization).

The main genetic distance measures based on SMM are the following (Goldstein et al. 1995): average square distance (ASD) (Goldstein et al. 1995b; Slatkin 1995), Shriver et al.'s (1995), Lev A. Zhivotovsky's (1999).

Takezaki and Nei (1996) and Nei and Kumar (2000) have compared by simulation the genetic distances presented above (distance based on IAM and SMM). As previously mentioned by Nei et al. (1983), they show that the D_A (*equation A 5*) distance is more efficient than other distance measures in obtaining the true topology underlying varying genetic models. Their high efficiencies are due to their small coefficients of variation.

$$D_A = 1 - \frac{1}{r}\sum_{j}^{r}\sum_{i}^{m_j}\sqrt{x_{ij}y_{ij}} \qquad \textit{Equation A 5}$$

Where

x_{ij}, y_{ij} : Frequency of the *i*th allele at the *j*th locus in population X and Y, respectively
m_j : Number of alleles at the *j*th locus
r : Number of Loci

Nei *et al's* (1983) D_A distance is between 0 and 1, the value 1 being obtained when two populations share no common alleles. Since the maximum value of this measure is 1, it is nonlinearly related to the number of gene substitutions. When D_A is small, however, it increases roughly linearly with evolutionary time. This measure is then independent of the mutational models (Nei 1987, Takezaki and Nei 1996). This measure is adapted from the Nei's (1972) standard genetic distance (Nei 1972), which is based on Bhattacharyya's Angular Transformation (Bhattacharyya, 1946) measure and on the chord distance (Cavalli-Sforza 1967). Bhattacharyya (1946) suggested that the extent of differentiation of population could be measured in terms of the angle between two hyperspheres. Two populations can be represented on the surface of a multidimensional sphere, where the q allele are a q-dimentional hypersphere with radius 1 and each axis represents the square root of the allele frequency.

Genetic approaches can bring an important contribution to quantify and analyse a metapopulation structure and dispersal process. According to the complexity of the processes involved, genetic measures are not yet completely adapted and unified, and discrepancies between genetic and demographic estimates subsist. This is mainly due to the restrictive assumptions underlying the models such as the neutrality of genetic markers, demographic stability and mutation (Rousset 2001). In spite of the difficulties in interpreting results, they offer a new field of investigation for model calibration and interpretations.

References

Calow, P. E.-i.-c., E. Board:, D. A. Falk, J. Grace, P. D. Moore, B. Shorrocks, and S. C. Stearns, editors. 1998. The Encyclopedia of Ecology and Environmental Management, Blackwell Science edition.

Cavalli-Sforza, L. L. 1967. Phylogentic analysis: models and estimation procedures. Amer. J. Hum. Genet.:233-257.

Goldstein, D. B., A. R. Linares, L. L. Cavalli-Sforza, and M. W. Feldman. 1995. An evaluation of genetic distances for use with microsatellite loci. Genetics 139:463-471.

Hastings, A., and S. Gavrilets. 1999. Global dispersal reduces local diversity. Proc. R. Soc. Lond B 266:2067-2071.

Nei, M. 1972. Genetic distance between populations. American Naturalist 106:283-291.

Nei, M. 1987. Molecular evolution genetics. Columbia University Press, New York.

Nei, M., and S. Kumar. 2000. Molecular Evolution and Phylogenetics. Oxford Universtity press.

Nei, M., F. Tajima, and Y. Tateno. 1983. Accurancy of estimated Phylogenetic Trees from Molecular Data. J. Mol. Evol.:153-170.

Rousset, F. 2001. Genetic approaches to the estimation of dispersal rates. Pages 18-28 *in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols, editors. Dispersal. Oxford University Press Inc., New York.

Takezaki, N., and M. Nei. 1996. Genetic Distances and Reconstruction of Phylogenetic Trees From Microsatellite DNA. Genetics Society of America 144:389-399.

Appendix B

Mantel Test (Manly 1991)

When problems involve the consideration of possible relationships between distance matrices, observations are not independent and are spatially autocorrelated. Thus, it is not possible to measure association (correlation) with traditional hypothesis tests. In this case, Mantel's (1967) randomisation test allows a measure of correlation between dissimilarity matrices and evaluates the significance of the statistic. By permuting rows and columns in one of the matrices, it determines the distribution of the measure of association.

Considering two square symmetric matrices A and B with zero diagonal terms (distance matrices), the correlation between all the off-diagonal elements is the same as the correlation between the *m=n(n-1)/2* elements in the lower triangular part only, this correlation being given by

$$r = \frac{\sum a_{ij}b_{ij} - \sum a_{ij}\sum b_{ij}/m}{\sqrt{\left[\left(\sum a_{ij}^2 - \left(\sum a_{ij}\right)^2/m\right)\left(\sum b_{ij}^2 - \left(\sum b_{ij}\right)^2/m\right)\right]}} \qquad \textit{Equation B 1}$$

where all the summations are over the lower triangular elements (i.e. i<j). The term altered by changing the order of the elements in one of the matrices is the sum of the products

$$Z = \sum a_{ij}b_{ij} \qquad \textit{Equation B 2}$$

The Z value is computed with the matrices A and B and then compared to the Z value obtained by permutation. It is possible to use the normal approximation for the randomized distribution of Z to test the significance of an observed value. There are *n!* possible permutations for the order of n items. According to Manly (1997) generally 1000 randomisations is a realistic minimum for estimating a significance level of about 0.05.

The Mantel test was originally developed to examine associations between dissimilarity matrices, and this test has been expanded with correlation versions and permutation tests (Dietz 1983, Smouse et al. 1986, Sokal and Rohlf 1995).

Test of the difference between two correlation coefficients

In order to determine if there is a difference between two correlation coefficients ($Ho: R_1=R_2$), which are assumed to be normally (bivariate) distributed, a Fisher Z-transform can be applied. The procedure computes a confidence interval on the difference between two independent correlations. The Fisher Z-transform converts both correlation coefficients R_1 and R_2 in z_{f1} and z_{f2} as:

$$z_{f1} = \frac{1}{2}\ln\left(\frac{1+R_1}{1-R_1}\right)$$

Equation B 3

and the difference

$$z = \frac{z_{f1} - z_{f2}}{\sqrt{\left(\frac{1}{n_1-3} + \frac{1}{n_2-3}\right)}}$$

Equation B 4

where n_1 and n_2 are the sample sizes, is approximately standard normal distributed. Then, the z value can be used to determine the level of significance.

References

Dietz, E. J. 1983. Permutation tests for association between two distance matrices. Syst. Zool. **32**:21-26.

Manly, B. F. J. 1991. Randomization and Monte Carlo Methods in Biology, 1st edn. Chapman & Hall edition, London.

Manly, B. F. J. 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology, 2st edn. Chapman & Hall edition, London.

Smouse, P. E., J. C. Long, and R. R. Sokal. 1986. Multiple regression and correlation extensions of the Mantel test of matrix correspondence. Syst. Zool. **35**:627-632.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry, New-York.

Curriculum Vitae

VUILLEUMIER SÉVERINE

Date & Place of Birth: the 29th December 1973, St-Imier
Nationality: Swiss Nationality, Tramelan, BE
E-mail address: severine.vuilleumier@epfl.ch

SCIENTIFIC INTERESTS

Dispersal process, Movement behaviour, Metapopulation dynamics and genetics, Gene flow, Landscape ecology, Ecological networks, Modelling, GIS development

EDUCATION

Since oct. 2000 **Research assistant / Ph. D. student**

Swiss Federal Institute of Technology, Institute of Environmental Science and Technology, Lausanne.
Development of a spatially-explicit model for dispersal simulation integrating landscape features, animal behaviour and metapopulation dynamics.

1994-1999 **Bachelor and Master's in Rural Engineering, Major in Environmental Science**.

Swiss Federal Institute of Technology, Lausanne, Switzerland
Master's Thesis: Conception of a GIS for NGO information exchange and spatial analysis of pressure acting on Lemur, realized in Madagascar.

1994 **High School Diploma - Scientific Section**

Pierre Viret High School, Lausanne , Switzerland

WORK EXPERIENCE

1999-2003 **Graduate research assistant / Research engineer**

Swiss Federal Institute of Technology, Hydrology and land management laboratory, Lausanne

- Software development
- Analysis of metapopulation persistence in fragmented landscape
- Mapping of ecological networks for landscape planning
- Evaluation of the protection of nature and landscape inventories
- Teaching assistant for the lectures "GIS and biodiversity" and "Dispersal process" and for Post-graduate studies in Biological Sciences and for 8th semester students
- Supervisor of 5 weeks field campaign during the 8th semester

CONTINUED EDUCATION

2001	Winter School on Mathematical Modelling in Biology proposed by the European Science Foundation, Nice, France. 22-31 January
	Course on Object-oriented programming, *Swiss Federal Institute of Technology*,
	Workshops on Advanced and Operational Spatial Data Analyis, Prof M. Kanevski, Lausanne, Switzerland. 18-19,25-26 May
2000	Der Ökologishe Umbau von Tourismuszentren – eine Herausforderung für den Alpenraum im neuen Europa, Triesenberg, Liechtenstein. 24-25 August

COMPUTER SKILLS

GIS	MapInfo Professional, IDRISI, ArcView
Development	Pascal (Delphi), MapBasic, SQL, Splus, MatLab

LANGUAGES

French	Mother tongue
English	read, spoken, written, good
German	read, spoken, written, good

PERSONAL INTERESTS

Nature	General interest in ecology, biology, environment and natural history
Sports	Horse-riding, hiking, trekking
Travelling	Nepal, Madagascar, Ecuador, Canada, Uganda and Peru

Scientific publications

Vuilleumier, S., P. Fontanillas and N. Perrin (2003). *Genetic differentiation in a fragmented landscape: A spatially-explicit dispersal model applied to greater white-toothed shrew. In Preparation*

Vuilleumier, S., R. Metzger (2003). *A feature-oriented landscape model for animal movement and behaviour assessment. Submitted*

Vuilleumier, S., N. Perrin (2003*). Cognitive ability and colonisation success in a real landscape: A modelling approach. Submitted*

Vuilleumier, S., and R. Prélaz-Droux (2002). *Map of ecological networks for landscape planning.* Landscape and Urban Planning 58(2-4): 157-170.

Proceedings and Conferences

Vuilleumier, S. (2003) "*A landscape model for animal movement and connectivity*", The 18th Annual Symposium, International Association for Landscape Ecology-US Chapter, Banff Centre, Alberta, Canada April 2-6, 2003

Vuilleumier S. (2002). "*Assessment of the influence of cognitive ability on colonisation success in a real landscape".* Ecology Conference on Extinction Thresholds: insights from ecology, genetics, epidemiology and behaviour, in Helsinki, Finland, the 2 - 5 September.

Gatabin C., R. Prélaz-Droux and S. Vuilleumier (2002) *Analysis of environmental constraints on agriculture for an integrated land planning*, Proc. of ISOMUL Conference 2002, Bellingham WA USA

Gatabin, C., R. Prélaz-Droux and S. Vuilleumier, (2001). *Analyse du contexte agricole pour un aménagement du territoire intégré*. In 8th National meeting of the portuguese association for regional development (APDR), Villa Real, Portugal.

Vuilleumier, S. and R. Prélaz-Droux (2000). *Evaluation of the efficiency of inventories of protected areas*. Proceedings of 3rd international workshop on Sustainable land use planning, Wageningen University The Netherlands.

Prélaz-Droux, R. and S. Vuilleumier (2000). *Map of ecological potentialities for landscape planning*. Proceedings of 3rd international workshop on Sustainable land use planning, Wageningen University The Netherlands.

Seminars

"*Assessment of the influence of cognitive ability on metapopulation in a real landscape, a modelling approach*" Séverine Vuilleumier, November 11, 2002, Institute of Ecology, University of Lausanne, Switzerland

"*Aménagement et risque écologique: cartographie des potentiels écologiques*", Séverine Vuilleumier, 7 et 8 septembre 2000, Journées scientifiques du DGR, Gruyères, Switzerland.

Reports

Gatabin, C., R. Prélaz-Droux, Vuilleumier, S. (2001). *Projet AGICE - Rapport intermédiaire*. Rapport EPFL et Etat de Vaud. Lausanne: 60p + annexes.

Gatabin, C., R. Prélaz-Droux, Vuilleumier, S. (2001). *Projet AGICE - Résumé du Rapport intermédiaire*. Rapport EPFL et Etat de Vaud. Lausanne

Vuilleumier, S. and R. Prélaz-Droux (2000). *Projet AGICE - Identification des potentialités du développement des réseaux écologiques* : Application à la plaine de l'Orbe. Lausanne, CH, EPFL et Etat de Vaud: 24p + annexes.

Vuilleumier, S., O. Paschoud, et al. (1999). *Evaluation de l'efficacité de l'Inventaire des Monuments Naturels et des Sites (IMNS).* Lausanne, IATE/Hydram, EPFL et Etat de Vaud (SFFN-CN): 80p + dossier d'annexes.

Software and extension

Animal Dispersal (Delphi)

Feature-oriented landscape model (MapBasic)

Awards

U.S. - IALE Foreign Scholar Travel Award. The 18th Annual Symposium, International Association for Landscape Ecology-US Chapter, Banff Centre, Alberta, Canada April 2-6, 2003