KTH Architecture and
the Built Environment

NETWORK BASED TOOLS AND INDICATORS FOR LANDSCAPE ECOLOGICAL ASSESSMENTS, PLANNING, AND DESIGN

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February 2009

TRITA-LWR.LIC 2045
ISSN 1650-8629
ISRN KTH/LWR/LIC 2045-SE
ISBN 978-91-7415-249-4

Cover image: Ecological network map showing high betweenness centrality of the Common European toad (Bufo bufo) through Stockholm, Sweden.

Licentiate Thesis
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ABSTRACT

Land use change constitutes a primary driving force in shaping social-ecological systems world wide, and its effects reach far beyond the directly impacted areas. Graph based landscape ecological tools have become established as a promising way to efficiently explore and analyze the complex, spatial systems dynamics of ecological networks in physical landscapes. However, little attention has been paid to making these approaches operational within ecological assessments, physical planning, and design. This thesis presents a network based, landscape-ecological tool that can be implemented for effective use by practitioners within physical planning and design, and ecological assessments related to these activities. The tool is based on an ecological profile system, a common generalized network model of the ecological infrastructure, graph theoretic metrics, and a spatially explicit, geographically defined representation, deployable in a GIS. Graph theoretic metrics and analysis techniques are able to capture the spatio-temporal dynamics of complex systems, and the generalized network model places the graph theoretic toolbox in a geographically defined landscape. This provides completely new insights for physical planning, and environmental assessment activities. The design of the model is based on the experience gained through seven real-world cases, commissioned by different governmental organizations within Stockholm County. A participatory approach was used in these case studies, involving stakeholders of different backgrounds, in which the tool proved to be flexible and effective in the communication and negotiation of indicators, targets, and impacts. In addition to successful impact predictions for alternative planning scenarios, the tool was able to highlight critical ecological structures within the landscape, both from a system-centric, and a site-centric perspective. In already being deployed and used in planning, assessments, inventories, and monitoring by several of the involved organizations, the tool has proved to effectively meet some of the challenges of application in a multidisciplinary landscape.

Key words: Least-cost modeling; Functional connectivity; Environmental planning tool; Resilience; Spatial redundancy; Ecological integrity

ACKNOWLEDGEMENTS

First of all, I would like to thank my supervisors Berit Balfors and Ulla Mörtberg for initiating and giving me the opportunity to work on this project. Thank you for giving me helpful comments and suggestions throughout the work. I am also deeply grateful to the members of the advisory board for valuable input and suggestions. Ebbe Adolfsson (Swedish Environmental Protection Agency), Björn-Axel Beier (County Administrative Board of Stockholm), Margareta Ihse (Stockholm University), Oskar Kindvall (Swedish Species Information Center), and Lars-Göran Mattsson (Royal Institute of Technology). Thank you for your engagement and time.

I would also like to thank all that have given me the opportunity to work with real-life cases, testing, discussing, and improving the ideas and tools presented in this thesis: Susanne Östergård, Gunilla Hjorth, Ulrika Egerö, Anja Arnerdal, Helene Nilsson, Ulf Lindahl, and Anna Koffman (Stockholm Municipality); Pernilla Nordström, Anna Silver, Johanna Alton, Rebecca Strömberg, , Håkan Häggström, Lars Carlsson, Anders Nylén, Hanna Dittrich Söderman, and Miguel Jaramillo (County Administrative Board of Stockholm); and last but certainly not least, Bette Malmros (Office of Regional Planning and Urban Transportation). Without all of you, I would be left with nothing but theories.

Thanks to every single person I've been in touch with at the Department of Systems Ecology at Stockholm University, the Stockholm Resilience Centre, and the Beijer International Institute of Ecological Economics at the Royal Swedish Academy of Sciences. There are way too many names to mention you all but you know perfectly well who you are. Thank you so much for bringing new perspectives into my research and for providing such a dynamic and welcoming atmosphere. I would also like to thank Hanna Erixon and Alexander Ståhle at the School of Architecture for interesting discussions about design experiments and application within (landscape) architecture. We are only just scratching the surface here!

Many experts on species and ecology have provided thoughts, information, and data that have been invaluable in the process of modeling. Thank you all.

To my colleagues at the department: thanks for the company and lively discussions during lunch and fika.

More than anything, I would like to thank Katarina for endless love and support, and Selma for giving me the energy and laughter needed to bring this thesis home. You are the constant reminder of what life is all about. Thanks also to my family and friends for well-needed distractions AFK (away from keyboard), mom for faith in my capacity, and dad for great discussions and scientific advice.

Last but not least, thanks to Mr. *Bubo bubo*, the Eurasian Eagle-Owl who kept me company at night the last few weeks of writing this thesis. It's been great having you outside the office, hooting away, and reminding me of how important it is to work for the fantastic nature that can be experienced even in a capital of a million busy humans!

The funding for this research project has been provided by Formas, the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning.

Andreas Zetterberg

Stockholm, February 2009

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LIST OF PAPERS

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

Papers included in the thesis:

I. Mörtberg, U., Zetterberg, A., & Balfors, B. (2009). Urban landscape ecological approaches - Lessons from integrating biodiversity and habitat modelling in planning. Manuscript.

II. Zetterberg, A., Mörtberg, U., & Balfors, B. (2009). Ecological Network Graphs: Linking Graph Theory to Operational Maps in Ecological Assessments, Planning, and Design. Submitted to Landscape and Urban Planning.

Relevant reports referred to but not included in the thesis:

Mörtberg, U. M., Zetterberg, A., & Balfors, B. (2007a). *Landskapsekologisk analys i Stockholms stad: Metodutveckling med groddjur som exempel* (Dnr: 2008-011175-216, bilaga 2). Stockholm: Miljöförvaltningen, Stockholms stad [In Swedish].

Mörtberg, U. M., Zetterberg, A., & Balfors, B. (2007b). Landskapsekologisk analys: Underlag för regionala landskapsstrategier *Det storstadsnära landskapet. Regional landskapsstrategi - en pilotstudie (2007:34), Bilaga 1*. Stockholm: Länsstyrelsen i Stockholms Län [In Swedish].

Mörtberg, U. M., Zetterberg, A., & Gontier, M. (2007). *Landskapsekologisk analys i Stockholms stad: Habitatnätverk för eklevande arter och barrskogsarter* (Dnr: 2008-011175-216, bilaga 1). Stockholm: Miljöförvaltningen, Stockholms stad [In Swedish].

Zetterberg, A. (2007). *Ekologiska förutsättningar för lodjur i Stockholms län* (Rapport 2007:20). Stockholm: Länsstyrelsen i Stockholms län [In Swedish].

1. Introduction

Humans have a profound effect on hydrologic systems, biodiversity, climate, land cover, and biogeochemical cycles, at local, regional, and global scales (Vitousek et al., 1997; Grimm et al., 2008). Land use change represents the primary driving force in the loss of biodiversity world wide, and negative effects reach far beyond the directly impacted areas (Vitousek et al., 1997). This is particularly the case of cities, in which humans depend heavily on ecosystem services scattered across the globe, often occupying areas that are tens to hundreds times that of the cities (Grimm et al., 2008).

Although area wise on a smaller scale, the effects are often evident within the rapidly changing urbanizing regions, where already developed lands become more contiguous over time, while the rural and wildland areas become increasingly more fragmented (Robinson et al., 2005; Hedblom & Söderström, 2008). With increasing exurban development in many parts of the world, both the species richness and the reproduction success of native species are significantly reduced (Hansen et al., 2005). Negative effects of urban development can also be found on the genetic level. For example, Hitchings and Beebee (1998) have found a significant loss of genetic diversity and fitness in smaller, urban populations of the Common Toad *(Bufo bufo)* in comparison with rural populations in the same region.

While apparently having large negative effects on the environment, locally, regionally, and globally, cities also benefit from their internal ecosystem services (Bolund & Hunhammar, 1999). Paradoxically, cities sometimes also harbor valuable native habitat remnants such as natural forests with qualities not normally found in their rural counterparts that are often managed for production. As an example, urban and peri-urban woodlands in Sweden contain significantly higher amounts of components important for biodiversity, such as dead wood, than the non-protected forests outside of these regions, and yet their total area is larger than that of the protected forests nationwide (Hedblom & Söderström, 2008).

The recent increase in awareness of the human impact and dependence on social-ecological systems has resulted in the need to better understand, measure, and predict, potential impacts (both positive and negative) on ecosystems and biodiversity. This need is in part driven by a general understanding among stakeholders regarding the importance of ecosystems and biodiversity, in part by international conventions, regulations, and directives. As a result, there has been an emergence of environmental objectives, environmental assessments, and sustainability considerations within urban and regional planning, and design (Leitao & Ahern, 2002).

Environmental Impact Assessment (EIA; see for example Glasson et al., 2005) and Strategic Environmental Assessment (SEA; see for example Therivel, 2004) have been developed to assess the environmental impacts of proposed projects (EIA), or proposed policy, plan, or program initiatives (SEA). Both EIA, and increasingly also SEA, are strongly regulated tools in many countries (Gontier, 2008). Another movement is reconciliation ecology, where the spatial planning, management, and design of land is carried out in such a way as to increase biodiversity while providing both ecosystem services and economic benefits (Grimm et al., 2008). Land use regimes that address the trade-offs between immediate human needs and the capacity for the long-term sustainability of ecosystem services may successfully meet some of the global environmental challenges (Foley et al., 2005).

Within both physical planning and environmental assessments, there is a need for tools and methods to better handle the ecological aspects in a landscape. This includes analysis, predictions, and evaluations of planning scenarios, the design of better alternatives, and public participation, policy-, and decision making. Since these activities are inherently spatially explicit, and take place in a multidisciplinary landscape, the tools and methods need to be designed with this in mind. There is a rapidly increasing number of such tools, often GIS-based (Guisan & Zimmermann, 2000; Scott, 2002; Guisan & Thuiller, 2005; Tian et al., 2008).

Despite these methodological advances, their use in practice is still limited (Opdam et al., 2001; Gontier et al., 2006; Gontier, 2008). Furthermore, the vast majority of GIS-based tools for biodiversity assessments is developed for single species distribution models (Guisan & Thuiller, 2005; Ferrier & Guisan, 2006), and ecologically relevant theory, as well as process based theory are often lacking (Guisan & Thuiller, 2005; Austin, 2007). In an attempt to move towards a process based systems perspective, there have also been recent advances in the development of network based tools, better suited to study the complex, spatial dynamics across the entire landscape. However, little attention has been paid to making these operational within environmental assessments, physical planning, and design.

1.1. Overall aim and objectives

In this thesis, I set out to bridge the gap indicated above, between the advances in network based landscape ecological approaches, and their effective application in environmental assessments, physical planning, and design. More specifically, the objectives of the project were to:

1. develop an understanding of the state of the art use and effectiveness of network based tools, methods, and indicators within landscape ecological assessments, planning, and design (section 3.1-3.5);
2. analyze strengths and weaknesses of different landscape ecological approaches, and identify the needs for further development to improve their integration in policy making and planning. (chapter 4; section 6.4; Paper I; case studies);
3. modify existing landscape ecological approaches to better fit the specific context of physical planning and assessments (section 6.1-6.3;Paper II);
4. develop a conceptual model for a network based landscape ecological approach that can be effectively used in a GIS (section 6.5-6.6;Paper II);

The thesis is based on two papers, attached in the appendices, and seven commissioned real-world cases, which together address the objectives laid out above. Paper I deals with four of the seven case studies carried out, exploring the effectiveness of an initial GIS-based habitat network tool, and an ecological profile system. Some of the case studies only involve practitioners actively engaged in environmental assessments, monitoring, or physical planning. Others include the participation of a multitude of stakeholders from several disciplines and organizations, for example in the case of the development of a Regional Landscape Strategy for Stockholm County or the Regional Development Plan 2010 for the Stockholm Region (RUFS 2010). A life-cycle based approach to the patch-concept within landscape ecology (section 6.2) is introduced in Paper II, in order to better match the often highly fragmented configuration of ecological resources in the study area. A conceptual model is finally developed (Paper II) allowing the integration of GIS-based, spatially explicit, and geographically defined tools, with graph theoretic indicators of connectivity. The usability of the model is also explored (Paper II), using the Common European toad (*Bufo bufo*) as a profile species, in a regional planning scenario from both a system centric, and a site centric perspective, as well as in a local design scenario.

1.2. Structure of the thesis

The thesis is organized into nine chapters. The introduction in chapter one outlines the general background of the research problem, the research aim and specific objectives of the thesis. A brief overview of how the two papers are interrelated is given above, and the scope and limitations are specified in the next section. Since the thesis is located at the intersection between landscape ecology, network theory, and the effective application within planning and assessments, chapter two introduces some of the methods and concepts used in the respective areas. This chapter is provided for the purpose of orientation for readers with different backgrounds. In chapter three, a review of the state of the art within the relevant topics is presented. Note that, for the sake of clarity, any analysis or criticism presented in this chapter is restricted to the historic and ongoing debate within the respective fields.

The identification of knowledge gaps and an explicit analysis of relevant parts of the review are further treated in chapter four. Based on the review, this chapter specifies and justifies the problem that is addressed in my thesis. Using references to previous research, the problem statement is argued to be both important and not adequately addressed previously. Chapter five introduces the study area and the data that have been used, and chapter six is really where my own contributions start taking shape. In this chapter, the steps considered relevant to solve the problem are presented, bringing in results from the attached papers and further analysis of the case studies. The sections in this chapter follow the order of the objectives specified in section 1.1. The chapter is closely related to a regular results chapter, although some of the relevant methods and a brief discussion are included for the sake of continuity. Details with respect to the methods can be found in the appended papers and referred case studies.

Chapter seven includes a general discussion of the topics treated in the thesis, linking the appended papers and ranging from interpretations of the results to a critical analysis of the methods, approaches and assumptions chosen throughout the project. Chapter eight provides a conclusion of inferences and contributions of knowledge, and chapter nine presents some suggestions for future research.

1.3. Scope and limitations

1.3.1. Biodiversity, ecological integrity, and ecosystems

In less than 20 years biodiversity has become a globally well-known concept among researchers, practitioners, politicians and the general public alike. However, despite the impact and importance of the concept, and its intended use as a practical tool, it is unclear what is meant by biodiversity or how it relates to more traditional concepts such as species diversity (e.g. Hamilton, 2005). A multitude of definitions of biodiversity exists (for lists of definitions, see for example DeLong, 1996; Gaston, 1996; Baydack & Campa, 1999), and the number of definitions and biodiversity-related topics keeps growing. The definitions may seem clear, but policies and decisions involving biodiversity are inherently vague due to the very nature of the concept of diversity. This lack of precision invariably leads to a poor degree of intersubjectivity in communication about results and theories. Furthermore, the concept suffers from unspecificity, with at least three different types of interpretations, which in addition are value-laden. There are even different approaches, and contradictory results regarding objective measurements or implications of biodiversity, within each of the three groups of interpretation.

Despite being useful as a mental construct, I will thus refrain from defining it and leave it to the reader's imagination as the vague concept it is. Neither are there any attempts at finding or using specifically defined metrics as direct indicators of biodiversity in this thesis. There is, however, a review on different species approaches as surrogates of biodiversity, which somewhat relates to the ecological profile system chosen as one of the frameworks in the thesis.

It has been suggested to be more important to focus on the relations between species, functional groups and ecosystem function than on measures of diversity (Bengtsson, 1998; Loreau et al., 2001). In line with this, I have in this thesis chosen to base the work around the concept of "ecological integrity". This can be defined as "the capacity to support and maintain a balanced, integrated, adaptive biological system having the full range of elements (genes, species, assemblages) and processes (mutation, demography, biotic interactions, nutrient and energy dynamics, and metapopulation processes) expected in the natural habitat of a region" (Karr, 1996, p. 101). In other words, ecosystems maintain integrity when both their native components and ecological processes are intact. Note that this intactness does not imply a steady-state but rather includes the dynamics and constant change of ecosystems (De Leo & Levin, 1997). Furthermore, De Leo and Levin argue that the concept also reflects the capability of ecosystems to support services, including aesthetics, that humans value. Although both biodiversity and ecological integrity are normative concepts, Callicott et al. (1999) argue that the latter is "the most comprehensive as well as the most rigorous of current norms in conservation". Higher level perspectives regarding relations between biodiversity, ecological integrity or properties of social-ecological systems are not explicitly analyzed. At the core of my research is an intention of finding tools and methods to better understand, explore, and take into account in physical planning, the complex interactions between species and the physical landscape of which they are a part. Hence, only a limited, one-way perspective of the social-ecological system is handled, implicitly, by ultimately providing a tool for physical planning and assessment activities.

1.3.2. Conservation biology

As previously stated, the overall aim of this thesis is the effective application within physical planning, design, and related ecological assessments, which is quite different from the perspective of conservation biology. While the starting point within conservation biology is safeguarding viable populations of certain species, the urban and regional planning focus is on ecological integrity across the landscape. A central issue within physical planning is the trade-off between different interests, both social, economic, and ecological, to be sustainably implemented in a physical landscape. The methods thus presented in this thesis are an important complement to the methods used within conservation biology, such as detailed spatially explicit population modeling (SEPM; e.g. Dunning et al., 1995; Turner et al., 1995), and population viability analysis (PVA; e.g. Boyce, 1992). Indeed, the methods developed in this thesis may even be useful as a complement within conservation planning as well.

2. METHODS AND CONCEPTS

2.1. Indicators and the science-policy interface

An indicator is an important concept both when formulating targets and goals for the environmental objectives, and when assessing environmental impacts of a plan or policy. They are also used at a higher level when balancing trade-offs in decision making Although the term indicator may not be known to the general public, the concept is used by most people in everyday life to better understand or manage the world we live in. Indicators are simplifications of the complex systems around us, combined into a small set of limited factors that are often, but do not have to be, numeric. Indicators are used in many different contexts, and on many different levels of complexity. As an example, the fuel gauge in a car is a simple type of indicator of how far you can go before the car stops. Indicators are frequently used to aid policy- and decision making on local, regional, national, and international levels, and exist within domains such as health, economy, and environment. Several indicators can be used to illuminate an aspect from different perspectives. As an example, indicators on climate change can include greenhouse gas emission, atmospheric concentrations of carbon dioxide, and the average global temperature.

Indicators are often a calculated index of some kind. The Dow Jones Industrial Average index is an indicator of how the stock market is doing from one perspective. An index can be easy to formulate, appear to be scientific and yet not be particularly relevant outside of a limited range, or even at all. The Body Mass Index (BMI) is often used decide whether a person should be considered overweight. In this case it merely relates to a definition of what overweight is. However, it is also commonly used as an indicator of health, or of the risk for cardiovascular disease, where other factors may (or may not) be far more important.

As has been illustrated above, indicators exist at many different levels, and describe very different aspects of a problem, such as the state, rate-of-change, or some process believed to be important. This is also true of ecological indicators, making it a potentially confusing concept. Ecological indicators are in fact a nested concept with no agreed terminology (Turnhout et al., 2007). As an example, the 16 environmental objectives in Sweden (section 2.2) typically refer to some overall quality, such as 'good-quality groundwater', 'a good built environment', and 'clean air'. The quality objective, 'a rich diversity of plant and animal life', has a target about the 'stopped loss of biodiversity by 2010', which in turn can be assessed through an ecological indicator of diversity such as species richness. There is another source of confusion with respect to ecological indicators and species, where the term indicator species, often a plant species as influenced by Ellenbergs work in the 1950s, is used to indicate some environmental property, such as soil pH (e.g. Diekmann, 2003).

An important point to mention is that quality objectives, such as the Swedish Environmental Objectives, are *not* objective, but instead value-laden. Hence, with respect to intersubjectivity, acceptance, and successful implementation, ecological indicators need to be constructed through negotiation at the science-policy interface (Turnhout et al., 2007). The indicators are normative, and highly dependent on scientific knowledge, but must also be simplified and packaged in such a way that they can be understood and effectively used by all stakeholders. In order to be accepted among the science and policy communities alike, they thus have to be created through boundary work and negotiation at the intersection of these domains (Cash et al., 2003). In such a way scientific knowledge can be translated into useable knowledge such as ecological indicators, and policy questions can be translated into research questions (Turnhout et al., 2007). As a result, the indicators need to be flexible enough to support iterative reshaping throughout the process in order to eventually match the political context while still being scientifically accepted. After all, a scientifically accurate indicator is of no great value if it ends up not being used in policy making or management work.

2.2. Swedish environmental objectives

The Swedish Environmental Objectives "define the state of environment which environmental policy aims to achieve and provide a coherent framework for environmental programs and initiatives at national, regional and local level" (Swedish Environmental Protection Agency, 2009). There are currently 16 environmental quality objectives, of which 15 were adopted by Parliament in 1999, and the 16th, regarding biodiversity, in November 2005. They include overall, national objectives, on the climate, air, acidification, toxins, ozone layer, radiation, water quality, ecosystem types and landscapes, the built environment, and biodiversity. The objectives are broken down into more specific targets, often expressed through indicators (section 2.1), which are used within the framework nationally, regionally, and locally.

2.3. Environmental assessments

As was mentioned in the introduction, environmental assessment frameworks, such as EIA and SEA, are strongly regulated in many countries; both with respect to when and how they need to be carried out and how they should be presented, and followed up. Both the process used when carrying out an EIA or SEA is regulated, as is the structure of the document, the environmental impact statement (EIS), in which the results are presented. A central part of an environmental assessment is the prediction of potential impacts, which is often notoriously difficult, albeit required. Measures on how to mitigate negative impacts should be stated, and within SEA, the state of the impact is required to be monitored. Indicators (section 2.1) are often used when predicting, evaluating, and monitoring impacts.

2.4. Physical planning

In urban planning a wide range of aspects of the built environment of urbanized municipalities and communities are explored, including the social environment, transportation, aesthetics, suburbanization, environmental factors, and safety. Regional planning deals with a much larger geographic region on a less detailed, aggregated level. A successful connection between urban planning and regional planning in situations of suburbanization and sprawl, can support the aims and aspirations of environmental planning and sustainability.

Within urban planning, it is common (often required by law) to develop a comprehensive plan (also called master plan), which in essence is a strategic document providing policy direction for decision-making regarding the several aspects of land use and human activities. Likewise, in some countries, regional planning is manifested in a regional development plan. In some cases, an SEA has to be carried out for comprehensive plans or regional development plans.

Urban and regional planning are commonly referred to as physical planning (or spatial planning). An important aspect of physical planning with respect to this thesis is that it refers to planning with a spatially explicit, geographically defined component. The general idea is to plan the *spatial* configuration of land use and activities in such a way as to achieve the planning objectives. This ultimately results in the plans containing both activities and incentives that aim to influence the distribution of activities and people in the region, and in a set of spatially explicit maps. Indeed, Hall (2002) claims that "it is simply impossible to think of this type of planning without some spatial representation – without a map, in other words". This is of particular interest for the research described in this thesis. Since physical planning activities are carried out and expressed in a physical landscape, it is of great interest for anyone engaged in ecological planning and assessments to understand the relationship between the configuration of this physical landscape and its (social-) ecological properties.

2.5. Landscape ecology

Looking out the window of an airplane, the mosaic-like pattern of the landscape is apparent. Aerial photographs, like Fig. 1a, brought a new perspective into the worlds of regional geography and vegetation science, and out of this new perspective, a new discipline emerged – landscape ecology. The term was coined by the German biogeographer Carl Troll and elaborated in 1950 (Turner, 2005). Central to the discipline is the relation between spatial "patterns" and "processes". Looking at an aerial photograph, a landscape ecologist would typically start to wonder which processes caused the pattern, and this pattern in turn will affect the processes. If one were to shift scales (up or down) several orders of magnitude, the same kind of questions are asked by cell biologist looking at images from a CCD-camera mounted on a microscope, or an astrophysicist studying images from a telescope. One big difference, however, is that the landscape ecologist actually can walk around inside the landscape corresponding to this image, and personally perform a wide range of experiments on site. In reality, the photographic image as such is seldom used. Instead, remote sensing techniques are used to collect spatial data for example through laser scanning or CCD-images from several spectral bands, including both microwave and infra red, which are then manipulated using image analysis techniques. The data sets used can in this way represent a multitude of vegetation classes, wetness, geological structures, or topography. This data is then often stored, analyzed and presented in different ways using Geographic Information Systems (GIS).

Even though there have been many different definitions of landscape ecology (e.g. Risser et al., 1984; Forman & Godron, 1986; Urban

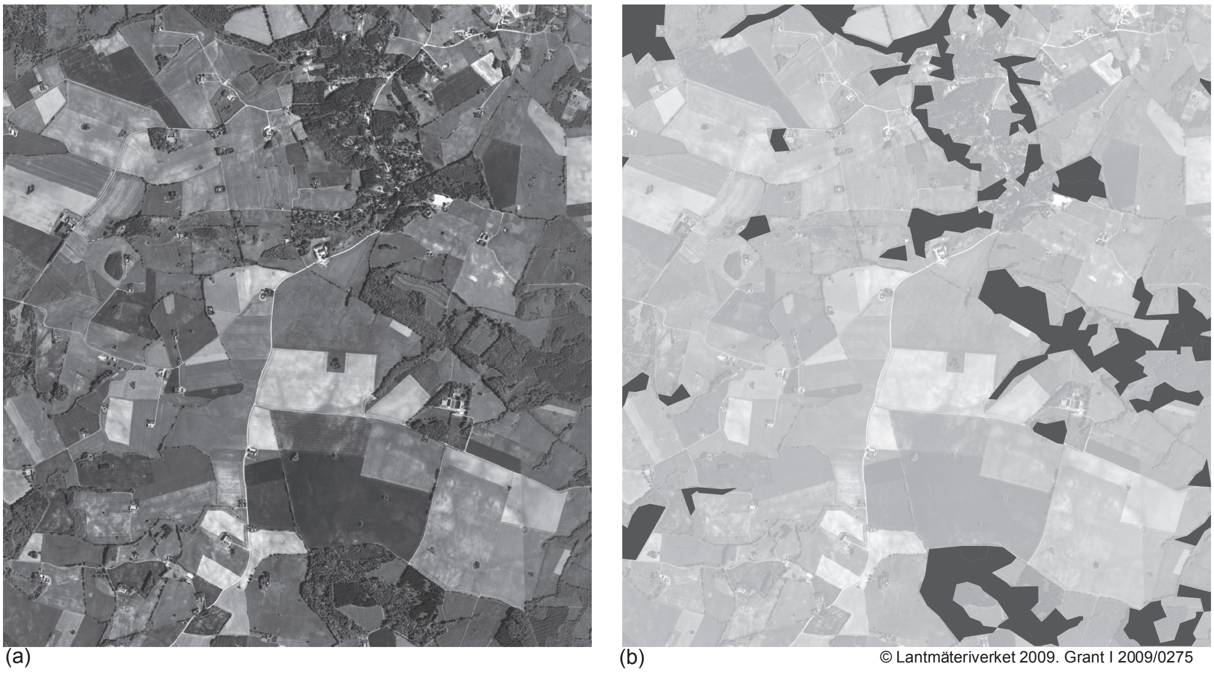


Fig. 1. Comparison of the real world with the patch model used in landscape ecology. (a) Aerial photo near Skurup in southern Sweden showing the patchy landscape. (b) Patches, in this case, corresponding to deciduous forest, all embedded in the matrix.

et al., 1987; Turner, 1989; Pickett & Cadenasso, 1995), they all essentially consider the relations between the spatial heterogeneity of a landscape and ecological processes. There are, however, at least two fundamental schools of landscape ecology: one with its roots in northern Europe, and the other in North America. The European school has more of an anthropocentric view, including humans in the system, and with a clear ambition to aim for application in management and planning. The American school has more focused on analysis of the spatial relations between pattern and process, considering a landscape as a general system that can span from a micro scale of a river bank to entire regions. These two traditions have subsequently spread across the world according to the respective cultural relations (Farina, 2000).

Some of the terms used in landscape ecology are frequently used in this thesis and may require an explanation. The spatially heterogeneous land-mosaic shown in Fig. 1a, almost looks like a patchwork, and the "patch" is a central concept in landscape ecology. The landscape patches of the photograph have different kinds of environmental characteristics, both with respect to the biotic and abiotic elements that they are made up of and the processes that continue to shape them. As such, they are of different suitability for different organisms. A particular organism may only like a certain type of patch and when extracting, or filtering out, these patches, the rest of the landscape in which these patches are embedded is often called the "matrix" (Fig. 1b). The organism under study, whether micro- or macroscopic, flower, moss or animal, usually has seeds, spores or juvenile individuals that eventually spread across the landscape to colonize new patches. This process is referred to as (juvenile) "dispersal". The dispersal between patches takes place through the matrix but often in a non-random fashion, which has led to other concepts. Some organisms tend to use linear elements in the matrix, such as hedgerows, which has led to the "corridor" concept (Forman & Godron, 1981). This is a strictly morphological concept building on the human perception of what may be a suitable linear structure through the matrix. In some cases, smaller well confined landscape elements can be crucial when moving through the landscape, and these are often referred to as "stepping stones".

"Habitat" refers to the different places in the landscape where an organism normally lives. However, this is in fact a complex term. It can be regarded as a collective term for different kinds of habitat, such as breeding habitat, migratory habitat, and foraging (feeding) habitat. These preferential uses of habitat throughout the life-cycle of an organism could be adapted to the patch-matrix model by referring to breeding, migratory, and habitat patches.

In practice, however, this is seldom the case and the majority of studies and models in landscape ecology simply aggregate some land cover classes from a GIS data-set into general habitat patches. In order to better fit the physical planning context and more accurately pinpoint potential impacts of a land use scenario, the patch concept is therefore clearly generalized in this thesis (section 6.2). I consider a patch as being clearly context specific and depending on the time-scale of the landscape model used, a patch can for example be a resource patch, a home range patch, or a population patch.

"Connectivity" is another often used term, and in the thesis this is the most investigated property of ecological integrity. Merriam (1984) introduced the concept of "landscape connectivity" and defined it as "the degree to which absolute isolation is prevented by landscape elements which allow organisms to move among patches". Other definitions have since followed (e.g. Taylor et al., 1993; With et al., 1997), but at the core of the concept lies the degree of flow of organisms and processes through the ecological network (Crooks & Sanjayan, 2006, p. 2). A higher flow means a higher connectivity, which is often desired when maintaining integrity. There are exceptions, however, such as when dealing with disease or invasive species. In these cases, limited connectivity is required to restrict the spread of disease. Different organisms or processes have different degrees of connectivity in the same landscape. The concept is entirely dependent both on the organism or process studied in a landscape, and on the spatial and temporal scales at which the property is studied. This means that metrics of connectivity, as well as definitions, inferences made from experiments, and applications need to be considered in relation to organism, process, and scale. This has led to a considerable amount of debate and confusion, but is indeed no different from the fact that for example the same urban landscape has different connectivity for children in comparison with teenagers.

There are two main approaches to studying connectivity: a "structural" and a "functional" approach (e.g. Tischendorf & Fahring, 2000). The structural (or physical) perspective deals with the physical composition and spatial configuration of elements, such as habitat patches, in the landscape. The functional (or behavioral) perspective deals with the responses of organisms or processes in the landscape. This main division between structural and functional approaches is a recurring theme, not only for connectivity, but in general when studying properties of a landscape. The structural composition of a landscape is often referred to as the "morphology", and in the same way, I argue that a suitable corresponding term for the functional composition is the "physiology" of a landscape.

In this thesis, a functional perspective on the landscape is used instead of the structural, in the sense that it is the geographic extent of the studied ecological process that is considered important. In order to avoid confusion, the term connectivity zone is introduced when referring to a functional corridor. More generally, the connectivity zone refers to any spatially explicit zone in the landscape that is believed to be important in connecting different patches. The term patch is also used in a more general way than the often used habitat patch.

In metapopulation theory the patches correspond to sub-populations that together make up a metapopulation. Within this, sub-populations occasionally go extinct, but are subsequently re-colonized by dispersers from other sub-population patches within the metapopulation (e.g. Hanski, 1998). In cases where this is systematic, the patches with a net loss and a net influx of individuals are called sinks, and the patches with a net out-flux of individuals are called sources (Pulliam, 1988; Pulliam & Danielson, 1991). The metapopulation model is particularly relevant in fragmented landscapes, consisting of many smaller fragments of patches.

2.6. Network flows and graph theory

Networks arise in a wide range of forms and situations. The most obvious setting is in the form of physical networks such as transportation, telecommunication, the Internet or utility networks such as for power or water distribution. There are also non-physical networks such as social networks describing for example the relations between individuals or institutions within a community. The most common problem domain relates to flows within the network, where the movement of some entity (e.g. water, electricity, messages, genes, consumer goods, people, behavior or vehicles) is analyzed (Ahuja et al., 1993). The field of network flows has a rich and long tradition, going all the way back to the mid 1800s and the work of the early pioneers of mechanics and electrical engineering (e.g. Gustav Kirchhoff's circuit laws of 1845). These pioneers formulated many of the key ideas of network flow theory and they established the graph as a useful model representation of networks (Fig. 2).

However, graph theory as a mathematical

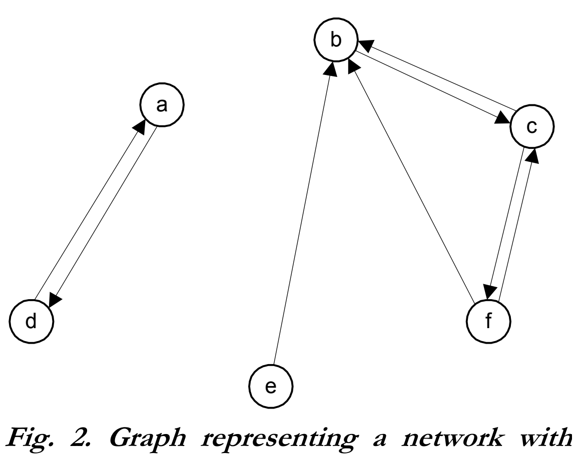


Fig. 2. Graph representing a network with both uni- and bi-directional flows. The graph is disconnected and consists of two sub-graphs defined by the sets (a,d) and (b,c,e,f) with a total of six nodes, and five links, defined by the sets ((a,d), (d,a)) and ((e,b), (b,c), (c,b), (c,f), (f,c), (f,b)).

construct is even older. The first paper on graph theory was published by Euler in 1736, and was inspired by a famous old problem about whether it was possible to take a walk across all the seven bridges of Königsberg, but only crossing each bridge once (Wallis, 2000, p. 23). Euler generalized the problem into any configuration of islands and bridges in a river and the theories are now known as Euler walks. By the way, using this theory, it is not difficult to show that it is impossible to cross the seven bridges of Königsberg exactly once.

The ideas from the early days of Euler, mechanics, and electrical networks, were generalized and used to study one of the most well-known problem areas in network flow theory dealing with minimum cost flows. The first studies considered a special case of the minimum cost flow and were related to a transportation problem ('the travelling salesman problem'). These were, according to Ahuja et al. (1993), originally conducted by Kantorovich (1939), Hitchcock (1941), and Koopmans (1947), (as cited in Ahuja et al., 1993, p. 19).

The minimum cost flow problem was generalized further during the 1950s and great interest arose for specializations such as the maximum flow problem, the shortest path problem and the assignment problem. The pioneers Dantzig (1962, as cited in Ahuja et al., 1993, p. 19), and Ford and Fulkerson (1962, as cited in Ahuja et al., 1993, p. 19) presented groundbreaking work, particularly related to the development of special algorithms for solving these problems. A second revolution in network theory, algorithms and applications has probably come about with the birth of the fastest growing network in the world – The Internet (see for example Hayes, 2000b, 2000a)

The graph model is a fundamental concept within network analysis. A graph, $G(N,L)$, consists of a set of nodes (or vertices), $N(G)$ and a set of links (also called edges or arcs), $L(G)$. The link l_{ij} connects nodes i and j. The term link is used here instead of edge, because edge is an often used term within ecology. In general network analysis the nodes often represent some quantity of production

Table 1 Examples of typical nodes, links, and flows for different types of networks

Type of network	Typical nodes	Typical links	Typical Flows
Water supply network	Pumping stations, lakes, reservoirs, water towers,	Pipelines, aqueducts	Water (comp. w. gas, oil, hydraulic fluids)
Power supply network	Transmission stations, tension towers	Transmission lines	Electric current
Transportation systems	Intersections, airports, rail yards	Highways, rail beds, airline routes	Passengers, freight, vehicles, operators
Mobile phone network	Mobile phones, antennas, base stations	Cables, radio links,	Voice, SMS, MMS, packet data
Integrated computer circuits	Gates, registers, processors	Wires	Electric current
The Internet	Computers, servers, firewalls, routers	Cables (fiber optics, copper), radio links	Web content, e-mails, files, streaming media
Social networks	Persons, communities, nations	Relations (trade, acquaintances)	Goods, behavior
Ecological networks	Habitat patches, stepping stones, overwintering areas	Dispersal paths, corridors, migration routes	Individuals, populations, genes

or consumption, and links represent some relation between these nodes, such as flux, capacity, or probability. See Table 1 for a list of some typical associations for these graph components.

A graph can be both directed (containing at least one uni-directional flow) and undirected (containing bi-directional flows only). A uni-directional flow in an ecological network graph could symbolize the possibility of dispersal in one direction but with no possibility, or a barrier effect in the reverse direction, such as when seeds from a plant are spread through a river but with no possibility of moving back up-stream again.

The graphs can in turn be represented in a computer using a node-link incidence matrix, a node-node adjacency matrix, an adjacency list, or a forward and reverse star. These representations use different amounts of storage space, and have different properties with respect to ease of implementation, efficiency of manipulation, number of developed tools, and algorithms (Gross & Yellen, 2004).

There is a multitude of graph theoretic metrics developed to measure different properties of a network. In this thesis, ten different metrics mainly relating to the connectivity of the network were tested (Paper II). One of these, Betweenness Centrality (Freeman, 1979), was studied in detail. For a graph, $G = (N, L)$, the betweenness centrality $C_B(n)$ for node n is calculated as

$$C_B(n) = \sum_{\substack{i \neq n \neq j \in N \\ i \neq j}} \frac{\sigma_{ij}(n)}{\sigma_{ij}}$$

where σ_{ij} is the total number of shortest geodesic paths (i.e. least-cost paths, see section 2.7), from i to j and $\sigma_{ij}(n)$ is the number of least-cost paths from i to j that actually pass *through* node n. The index essentially finds the nodes routing the highest proportion of the least-cost paths between two randomly chosen nodes in the network, taking all pairs of nodes into account.

2.7. Least-cost modeling

One of the main modeling approaches used throughout this project (Paper I, Paper II, and all of the case studies) is called least-cost modeling (often also referred to as cost-distance modeling). In least-cost modeling, graph theoretic algorithms are used to find the shortest weighted distance from one point in a network to another. This distance is called the least-cost distance, and its corresponding path through the network is called the least-cost path (LCP), or simply the shortest path (SP). The shortest-path problem also has a long history, and is well studied within graph theory (section 2.6).

The modeling approach used in this project, is a variation of the general least-cost problems, and takes advantage of the fact that a 2-dimensional grid, such as a GIS raster, can be seen as a network; each grid cell can be viewed as a node, with a link to its eight neighboring grid cells (four in the cardinal, and four in the diagonal directions). The least-cost path between two nodes can this way be used to represent a geodesic path in between two points (approximated by grid cells) on a projected surface, and thus visualized in a GIS. This path will be the shortest effective distance between two points on a raster, which means that even though the straight line Euclidean distance is a lot shorter, it may be *functionally* shorter for example to follow a detour along a preferred habitat.

Within the raster, the cost-distance value at any point (i.e. grid cell) is the least-cost distance from that point to the closest specified source point. This makes it easy to visualize or otherwise work with georeferenced surfaces, for example when constructing patches made up of cells with a cost-distance value below some threshold corresponding to some ecologically relevant property (section 6.3)

3. Review of state of the art

3.1. Species as indicators of biodiversity

Species are often used as indicators of biodiversity; the rationale being that the fluctuation of the indicator-species population is believed to indicate for example chemical or physical changes or fluctuations of other species in the community (Simberloff, 1998). Species, or groups of species that are considered good biodiversity surrogates are also frequently used as a target species, and their habitat requirements used to analyze the potential landscape support for the species (e.g. Opdam et al., 2008). Metrics based on structural or functional properties of the landscape with respect to these species are then in turn used to infer indicators for biodiversity, sustainability, or ecosystem management. However, concepts such as sustainability, ecosystem management, and even biodiversity are inherently vague and it is therefore difficult (if not impossible) to set meaningful targets (e.g. Simberloff, 1998).

In addition, the methods and criteria for the selection of indicator species, and even what they should indicate, have received critique almost from the very beginning (e.g. Landres et al., 1988). As a result, a number of systematic approaches and attempts to formalize the selection criteria have emerged, such as umbrella species, flagship species, and keystone species (Simberloff, 1998; Roberge & Angelstam, 2004), the focal species approach (Lambeck, 1997), the landscape species approach (Sanderson et al., 2002), and ecological profiles (Vos et al., 2001). The umbrella, flagship, and keystone species approaches result in the selection of a single species. An umbrella is a species believed to have such high requirements, for example large habitat requirements, that saving the umbrella species will automatically save a wide range of other species with lesser requirements. This approach can be questioned when considering that certain insects are better off in naturally fragmented landscapes (Tscharntke et al., 1998). Keystone species are those that are important in regulating or governing the well-being of other species, and are thus believed to target ecosystem properties better. A flagship species is simply a charismatic species that can be used to anchor conservation efforts among stakeholders. However, it need not be an indicator, umbrella or keystone.

For example, the Eurasian lynx *(Lynx lynx)* that was modeled in one of the case studies (Zetterberg, 2007), could be regarded as a flagship species (Linnell et al., 2000). Indeed, the viewers of the most popular nature show on national Swedish television ('Mitt i Naturen'), voted the Lynx as the most popular Swedish animal (Rovdjurscentret De 5 Stora, 2009). Being a predator, however, it is a very controversial flagship species. Furthermore, it is not particularly sensitive with respect to habitat or other resource requirements, and can therefore be questioned as an umbrella species. It does have a keystone function with respect to regulating the density of its prey, and the important secondary effects that follow from this.

Even though they still represent the most common methods for setting targets, the single-species approaches have been criticized, mainly for not representing an acceptable portion of the species within an ecosystem. (Landres et al., 1988; Andelman & Fagan, 2000; Chase et al., 2000; Poiani et al., 2001). Another approach, the focal species approach (Lambeck, 1997), aims at finding a suite of umbrella species in a systematic way so as to better represent an ecosystem. The suite is selected by identifying the most vulnerable species due to high demands with respect to process-, resource-, dispersal-, and area requirements. In reality, however, the choice of focal species has been directed towards well-known species (often birds) not capturing the potential response of other organism groups adequately (Lindenmayer et al., 2002; Lindenmayer & Fischer, 2003). The approach was further criticized by Lindenmayer (2002) for being unsuitable to implement practically, in essence not being operational within planning. The approach requires large amounts of, often unavailable data, and a high level of ecological expertise. In an effort to meet the criticism on subjectivity with respect to the final selection of species, Delphi surveys using expert panels have been used (Hess & King, 2002; Beazley & Cardinal, 2004).

A different perspective on which suite of species to select is provided by the landscape species concept (Sanderson et al., 2002). This approach, although being a kind of focal species approach, differs mainly with respect to the purpose of species selection. While the traditional focal species approach by Lambeck aims at finding the most vulnerable species due to their requirements, the landscape species approach focuses on finding species with spatio-temporal requirements comparable to the human use or transformation of the landscape. Detailed information on the suite of species is then used to analyze the entire landscape needed for their protection with respect to some population level targets, and there is a particular focus on areas at risk for conflicts between the landscape species and human activities. The landscape species concept is thus more aimed at guiding landscape planning than conservation planning.

Opdam et al. (2008), argue that a major problem with all of the approaches above, for their successful application in policy- and decision making, is their lack of flexibility. This flexibility is needed when devising an ecological indicator (Turnhout et al., 2007) in order for its acceptance within planning, assessments and decision making. Opdam et al. argue that there is a need to allow for a dynamic negotiation of the trade-offs for example between aspiration levels of biodiversity, and the corresponding required total area. In response to this need, they have chosen to work with the concept of ecological profiles introduced by Vos et al. (2001), which they call ecoprofiles. This concept groups species in functional classes with respect to three dimensions: the ecosystem type, the ecosystem area requirements, and the dispersal capacity. By mapping the locally relevant species into these functional groups, the trade-offs between biodiversity on one hand, and the corresponding required total area or connectivity (for example modeled as maximum inter-patch distance) on the other, can be explored.

3.2. GIS and maps in ecological planning and assessments

Geographic Information Systems (GIS) are spatial database management and analysis systems that are particularly useful for spatial analysis within ecological assessments, planning, design, and research. They are capable of capturing, storing and managing large spatial datasets, provide a multitude of tools for spatial modeling and analysis, and can efficiently handle spatial data overlays and visualizations for aesthetic analysis, and multidisciplinary stakeholder involvement. There has been a rapid increase in the use of GIS-based methods and models to understand, predict, and visualize the spatial distribution of organisms in a landscape. Many of the popular prediction methods are based on the general linear models (GLM) of multiple regression, but generalized additive models (GAM), Bayesian models, neural networks, and combinations of these are all common (Guisan & Zimmermann, 2000).

However, the use of modeling in ecological assessments remains limited, and the uses of GIS are mainly restricted to analysis through simple data overlays, or presentation through maps (Gontier et al., 2006; Gontier, 2008). While GIS and maps in planning and assessments present considerable benefits for the communication between stakeholders in multidisciplinary landscapes (Theobald et al., 2000), there is a gap between the advances in landscape ecological modeling on one hand, and guidelines, general rules and the application of this knowledge in applied activities, such as landscape evaluation and design, on the other hand (Opdam et al., 2001).

3.3. Landscape ecology: Pattern and process

As was mentioned in section 2.5, an important aspect, in particular in fragmented landscapes such as urban environments, is the relation between pattern and process. However, these relations are not captured in the majority of GIS-based landscape ecological methods used within assessments, planning, or even research today. The two worlds remain separate, with one set of (often GIS-based) methods for finding suitable habitat based on landscape pattern or land cover, and another for studying process based properties, such as within PVA. The landscape support for ecosystem processes depends, not only on the existence of the required resources in a landscape, but also on their spatial configuration and temporal dynamics. For example, different kinds of resources are needed in different life-cycle stages of an organism, and there must be a way to move around between these resources when they are needed.

One of the life-cycle processes that has been studied in particular, with respect to the spatial relations between landscape components, is juvenile dispersal. This research area has been strongly influenced by the fundamental work on island biogeography by MacArthur and Wilson (1967), where relationships are formulated between the sizes of islands (including an infinite size mainland), and the distance between them on one hand, and extinction and colonization on the other. Parts of this work inspired the birth of metapopulation biology by Levins, (1970) (section 2.5), and the introduction of the concept of a metapopulation as a "population of populations which go extinct locally and recolonize". While the theory of island biogeography by MacArthur and Wilson mainly was based on an equilibrium model of the number of species, the metapopulation concept by Levins was more focused on population dynamics. In an attempt to analytically pinpoint parts of this dynamic process, an incidence function was developed (Diamond, 1975). Assuming that the metapopulation dynamics can be described as a stationary Markov process, the incidence function was later turned into a practical patch-occupancy model (Hanski, 1994), only requiring occupancy data from a single point in time. This is an important step forward with respect to validation of models since most data on species that exist are in the form of simple observations (occupancy) at a certain site. At the same time the lack of non-occupancy data is problematic since the fact that a species has not been observed at a site does not necessarily mean that it does not exist there.

Even though classical metapopulation theory is mostly applicable in highly fragmented landscapes (Hanski, 2004), it does point out the importance of considering relations between habitat patches across the landscape. A large negative effect on certain critical patches can affect an entire metapopulation within a region. The awareness of problems with fragmentation in a landscape (e.g. Wilcove et al., 1998) has led to an entire research area attempting to evaluate the degree of fragmentation in a landscape, and sometimes relate this to metapopulation theory. This is often achieved through a *structural approach* to the landscape (section 2.5), using statistical analysis of general morphological attributes such as size, shape, connectivity, isolation, and heterogeneity (e.g. Giles & Trani, 1999).

However, the functional processes are once again not included in these structural approaches, and one can certainly question the ecological relevance of many of their indices. As was mentioned in section 2.5 regarding connectivity, the functional response to a specific morphology of a landscape is different depending on the organism or process studied. Hence a general 'one size fits all' structural index can not exist. Another typical problem for many structural approaches is that several drastically different configurations of the landscape can lead to the same structural index. This is a general problem with most morphological approaches since they are both scale- and scope-dependent. They can even be counter intuitive; as an example, a typical structural approach considers the connectivity to be high if patches are connected to many other patches. Due to this, a landscape with a few, large, high quality patches will have a lower structural connectivity index than a highly fragmented version of the same landscape, where these few larger patches are fragmented into many small patches.

A parallel line of research has followed a *functional approach* rather than the structural, and there are several models that try to relate population processes to landscape pattern (see for example Lindenmayer et al., 1995; Brook et al., 1999). One major drawback with these models focusing on population processes, such as PVA and SEPM, is the large number of parameters and the data requirements. Indeed, one of the main drivers for Hanski when developing the patch occupancy model (1994) was the simple data requirements, and yet even simple occurrence data are hard to find for most species.

In most metapopulation- and patch-matrix-models, the matrix is assumed to be homogenous and often referred to as a 'hostile sea' surrounding the 'habitat islands'. The dispersal success between patches is therefore often expressed as some function of the Euclidean distance between them. In reality, however, the type and configuration of the landscape in between the patches affects both the ease of movement, and for higher organism groups, the behavior (e.g. Wiens et al., 1993). There are also critical components within the matrix that offer, for example, food and shelter. In land use planning, changes within the matrix may influence the organisms just as much as changes within the habitat patches, and there is increasing awareness of the importance of taking this heterogeneity into account (With et al., 1997; Tischendorf & Fahring, 2000; Moilanen & Hanski, 2001; Ricketts, 2001; Tischendorf & Fahrig, 2001; Schadt et al., 2002; Stevens et al., 2004; Dunford & Freemark, 2005; Stevens, Leboulenge et al., 2006; Tanner, 2006; Yamaura et al., 2006; Compton et al., 2007; Wiser & Buxton, 2008). Land use changes within the matrix can also lead to cumulative effects (Bélisle & St. Clair, 2002), which are seldom accounted for.

The least-cost modeling approach (section 2.7) is increasingly being used to incorporate the heterogeneity of the matrix directly from GIS-information into the inter-patch function (Walker & Craighead, 1997; Ferreras, 2001; Graham, 2001; LaRue & Nielsen, 2008). The least-cost model ultimately calculates a functional distance, often referred to as the "effective distance", which can be used in place of the homogenous Euclidean distance. Using genetic approaches, the least-cost model of effective distance has been shown to be significantly more accurate than Euclidean distance or barrier models (Coulon et al., 2004; Vignieri, 2005; Cushman et al., 2006; Stevens, Verkenne et al., 2006; Epps et al., 2007; Mcrae & Beier, 2007).

Another important property of the least-cost modeling approach is that it calculates a geographically explicit least-cost path through the landscape, in addition to estimating the least-cost distance. This is potentially very useful in physical planning as a functional approach to the otherwise often used structural approach of trying to define a 'green corridor' between two patches. An unfortunate interpretation of the least-cost path is that the entire habitat can be eradicated except for the patches themselves, and narrow least-cost paths connecting them, without negatively affecting the species. A measure of connectivity using the least-cost distance would remain unchanged even after such a drastic change of land-use. In reality, the path itself may not even be closely connected with for example the behavioral feasibility for an organism (e.g. Walker & Craighead, 1997; Schadt et al., 2002). Indeed, neither the movement by individuals nor the long term gene flow is restricted to the least-cost path (Theobald, 2006; Mcrae & Beier, 2007). In response to this, there are extensions of the least-cost modeling approach that try to find an entire region, in this thesis referred to as a connectivity zone, between the patches (Theobald, 2006; Theobald et al., 2006). There is another important implementation of the least-cost approach that was briefly described in section 2.7. Instead of simply looking at the least-cost path between two patches, one can highlight all the cells that are below some effective-distance threshold level. This results in entire regions around the patches, and produces maps showing the entire landscape that is potentially within reach from the core habitat patches (Walker & Craighead, 1997; Ray et al., 2002; Adriaensen et al., 2003; Joly et al., 2003; Larkin et al., 2004; Nikolakaki, 2004; Theobald, 2006).

3.4. Network based tools for assessments and planning

As has been previously mentioned, one of the most common tools for network analysis is graph theory and in the last few years, several papers have explored graph-based approaches to modeling species-habitat interactions from a landscape perspective. A graph-theoretic approach to ecological networks can act as an initial, heuristic framework for management, driven in an iterative and exploratory manner, and with very little data requirements (Bunn et al., 2000; Calabrese & Fagan, 2004). It does not require long-term population data, making it an important tool for rapid landscape-scale assessments (Urban & Keitt, 2001), but graph-theory is at the same time dynamic, allowing additional knowledge to be incorporated. Minor and Urban (2007) have illustrated the potential of graph theory as a proxy for SEPM, making it an interesting complement to existing research frameworks.

In section 2.6, it was argued that another attractive property of network analysis and graph theory is their long tradition, well developed and tested tools, as well as efficient algorithms, used in a wide variety of disciplines (e.g. Ahuja et al., 1993; Nijkamp & Reggiani, 2006). Several metrics related to classical network analysis problems, such as maximum flow, connectivity, and shortest paths, have been developed over decades within the world of graph theory, and Bunn et al. (2000) as well as Urban and Keitt (2001) have proposed ecological interpretations for some of these. Some of the proposed graph-based metrics of functional connectivity have also been summarized and evaluated (Pascual-Hortal & Saura, 2006; Saura & Pascual-Hortal, 2007).

In addition to comparing metrics for the *overall* network for different scenarios, graph-based methods can be used to explore important *internal* structures. For example, the importance of a patch with respect to landscape connectivity can be measured by removing one patch (i.e. one node) at a time, and recording the corresponding change, ΔI, of the connectivity index *(I)* (Keitt et al., 1997). This has become a central technique for finding important patches, and has also been used by Urban and Keitt (2001) to find important links within the network. The patches and links contributing the most to overall connectivity can thus be found. Similar techniques have also been used to explore tradeoffs between the total protected area, and the overall connectivity (Rothley & Rae, 2005; Rae et al., 2007).

A simple visualization technique sometimes used within landscape ecology is to present geographically explicit graphs, showing the full extent of the linked patches on top of a map or geographically defined area (Keitt et al., 1997; van Langevelde, 2000; Urban & Keitt, 2001; O'Brien et al., 2006; Zhang & Wang, 2006; Bodin & Norberg, 2007; Fall et al., 2007; Uy & Nakagoshi, 2007). This representation is similar to what Fall et al. (2007) refer to as the ‘spatial graph’, with two-dimensional patches connected by georeferenced one-dimensional paths.

3.5. Ambiguities in the ecological network discourse

The term ecological network seems to have gained wide support among planners, conservationists and policy makers over the past decades. This has been concluded, at least in a European perspective, by Rientjes and Roumelioti (2003), who conducted a survey among conservation ecologists and national or regional policy makers in 31 European countries (107 returned questionnaires; 40.1%). Rientjes and Roumelioti also stated that the concept in general has a potential to appeal to specific stakeholder groups and the general public, experts and laymen, due to its understandable components and the fact that it can be made visible through maps.

Opdam et al (2006) argue that the concept of ecological networks "helps to focus on an ecologically relevant part of the landscape, a part that can be pictured as a concrete structure that appeals to the actors' imagination of what biodiversity needs; facilitates negotiation about feasible goals and required area, configuration and location of ecosystems; can be designed in alternative options with more or less equal sustainability". In addition, the network concept as well as graph theory in general are widely used as a basis for effective communication within other sectors involved in the planning process (Nijkamp & Reggiani, 2006). Even when only considering research involving people here at the Royal Institute of Technology, graph theoretic network examples include transportation networks (Jenelius et al., 2006), traffic simulation (Burghout & Wahstedt, 2007), electric power networks (Holmgren, 2006; Holmgren et al., 2007), social networks (Westlund & Nilsson, 2005; Ernstson et al., 2008; Gronlund et al., 2008; Larsen, 2008), the Internet (Bagula, 2007), and of course the Ecological Network Graph proposed in Paper II. The experience and concepts already developed within these sectors could serve as very valuable sources of inspiration within landscape ecology, with the potential to resolve problems related to tools, methods, metrics, and indicators.

However, the term ecological network is not uniquely defined and has many different uses (Boitani et al., 2007). One refers to a *structural approach*, building on the patch-matrix-corridor paradigm introduced by Godron and Forman (1983), where an ecological network is simplified into morphological landscape elements, such as core areas, buffer zones and corridors (e.g. Jongman, 2004, p. 24). This approach originated from the realization that conservation management needs to be regarded in an integrated way across different scales in an entire landscape, which has lead to the concept of multiple-use modules (MUM) (Noss & Harris, 1986), and later a structural approach to the habitat network (Hobbs, 2002). An implementation of such an ecological network is the Natura 2000 network, which has it's origin in the EU Bird directive of 1979, and the EU Habitat directive of 1991. This is sometimes claimed to be "the largest coherent network of protected areas in the world" (European Commission, 2009). I would however argue that it is still far from the ambition of being coherent, with protected valuable patches indeed, but with a questionable connectivity. Even though the intentions are clear, there is a long way to go for it to even be considered a real network.

Another definition of an ecological network refers to a more general, *functional approach*, where the network is viewed as a set of ecosystems, interacting with the landscape and linked through functional relations between the organisms of the ecosystem (e.g. Opdam et al., 2006). Opdam (2002) also takes on a functional approach for the habitat network concept instead of the more structurally oriented approach taken on by Hobbs (2002). This is closely related to the concept used in general network analysis, where a network is represented by a graph of nodes connected through links.

A third definition is that used within food-web theory (Sole & Montoya, 2001; Montoya et al., 2006), in which the nodes of the ecological network often represent different species, and the links refer to trophic interactions between the species. In this sense, the ecological network within food web theory does not generally have the spatial dimension, like the two first examples of ecological networks, although there are recent advances in the studies of spatial food-webs (e.g. Holt, 2002)

One of the major problems among stakeholders regarding the concept of ecological network is a lack of understanding or different interpretations of concepts such as corridors, key patches, stepping-stones, core areas and buffer zones (Rientjes & Roumelioti, 2003). These problems could perhaps be resolved by harmonizing the terminology and, in some cases, using more general network concepts such as nodes, links, sources, sinks, flow, connectivity, vulnerability, redundancy, and resistance.

4. Problem statement and justification

In light of the review and the objectives of my research project, the problem to be solved can be formulated as *the development of a network based, landscape-ecological tool, and a suggested set of indicators that can be implemented for effective use by practitioners within physical planning and design, and ecological assessments related to these activities.* The tool should be operational, effective, and yet flexible; it should support freedom of choice both of communicative methods for different stakeholders and contexts, and of theoretical metrics, indices, and methods within network theory.

The clear intention of packaging the complexities within landscape ecology for deployment in a physical planning context implies the necessity of a spatially explicit tool, able to effectively meet the challenges of application in a multidisciplinary landscape. Hence the activities that are addressed, such as design, analysis, predictions, assessments, public participation, policy- and decision making, should all be able to use the same spatially explicit landscape as a common reference. Even though there is limited use in practice of suitable tools and methods, such as GIS-based modeling, (Gontier et al., 2006; Gontier, 2008) there is a rapidly increasing number of such tools (Guisan & Zimmermann, 2000; Scott, 2002; Guisan & Thuiller, 2005; Tian et al., 2008).

However, the vast majority of GIS-based tools is developed for single-species distribution models (Guisan & Thuiller, 2005; Ferrier & Guisan, 2006), and ecologically relevant theory, as well as process based theory are often lacking (Guisan & Thuiller, 2005; Austin, 2007). At the same time, there is a widespread understanding of the need to take on an ecosystem approach rather than a species-distribution approach, for successful protection and management of ecological integrity. This urge for an ecosystem approach can for example be seen in the critique on species as indicators of biodiversity (section 3.1), on the lack of ecologically relevant and process based theory (Franklin, 1993; Guisan & Thuiller, 2005; Austin, 2007), and on the focus of measures of species diversity instead of understanding linkages between species, functional groups, and ecosystem function (Bengtsson, 1998; Loreau et al., 2001).

Applying an ecosystem perspective in a spatial context implies a shift from site based assessments to assessments of the entire landscape. It also implies a shift from empirical, structural, and statistical models to spatially explicit mechanistic, functional, and process-based models. Instead of linking ecological pattern to landscape pattern, we would like to link ecological patterns and processes to landscape patterns and processes. Such an approach must recognize the dynamics and complex interactions within the social-ecological system, where physical planning activities are an integral part, and the physical landscape is the common point of reference.

When dealing with complex systems, 'network thinking' is central to understanding (Mitchell, 2006), and network analysis as well as graph theory are commonly used. The enormous increase in easily accessible and manageable data, as well as research on network analysis and complex systems in several fields, has led to a number of recent applications of network thinking within the entire field of biology, from genes to ecosystems (Proulx et al., 2005; Bascompte, 2007). In the last few years, several papers have explored graph-based approaches to modeling species-habitat interactions from a landscape perspective, and although most of these approaches are back at the single-species or focal-species level, some interesting analysis techniques have evolved (section 3.4). In spite of their simplicity, by integrating least-cost modeling with graph theory, these approaches seem to be able to capture the complex processes involved in spatial population analysis in an integrated functional manner.

However, previous network-based research has focused on conservation issues and not on physical planning or ecological assessments related to planning. As a result, little attention has been paid to making these graph-theoretic approaches operational within these practices. Issues related to the successful application of graph theory in planning, policy- and decision making have not been adequately addressed. Examples include the need for negotiation space (Turnhout et al., 2007), or the usefulness of geographically defined maps in multidisciplinary communication (Theobald et al., 2000). Indeed, these issues have been mostly neglected in bridging the gap between spatial planning and landscape ecology in general, and there is a particular need for multidisciplinary tools and methods (Opdam et al., 2001).

In order to be successful, the tools and methods need to be effective within physical planning, and in particular in a context and working environment already in use by planners, such as a GIS. A general aspiration of the research project is thus an effective implementation of the graph theoretic framework within a GIS, which could effectively communicate the problems, results, and challenges among stakeholders of quite different backgrounds in this multidisciplinary landscape. This implementation should ideally allow for the evaluation of planning indicators and at the same time be based on ecologically relevant properties, with a strong connection to the underlying landscape, and aggregated to a higher level that is understandable for stakeholders without thorough ecological knowledge. It should also be based on concepts and a terminology that are generally understandable by ecologists, planners, decision makers and the public alike. The trade-off between simplification and relevancy of scientific knowledge is paramount to a successful implementation (Cash et al., 2003).

My thesis attempts to bridge this gap and meet the challenges by first testing the communicative aspects of geographically defined habitat networks in a GIS, through seven real-world cases using participatory approaches and multi-stakeholder involvement. Four of these case studies are treated in Paper I. A conceptual model is then developed, linking the graph theoretic approaches to the resulting communicative platform in the form of spatially explicit, geographically defined maps in a GIS (Paper II). Finally, an example using a real species in a real landscape within the study area is used to explore the potential and usefulness of this model and ecologically relevant graph theoretic metrics as indicators (Paper II).

It is hoped that this development of a conceptual network based landscape ecological model, and related graph theoretic indicators, can be effectively used in practice, and that the scientific findings can further stimulate the research and the development of new, relevant tools and methods. The shift towards a network perspective could result not only in the much needed operational tools for testing physical planning scenarios, but maybe also give a better understanding of the cause and effect relationships, leading to an improved, guided design, and tighter, iterative interactions between ecological knowledge, and planning, policy-, and decision making.

5. Study area

All of the studies were performed within the county of Stockholm, the capital of Sweden (Fig. 3), during the years 2006-2008. Administratively, the county is divided into 26 municipalities, and the municipality of Stockholm contains the city center. The study area comprises roughly 7000 km^2, and the landscape is heterogeneous with about 60% covered with forest, and the remaining 40% equally broken up by agricultural land, water, and built-up areas. Since the city has grown in a star-shaped form along the main infrastructural routes, green wedge-shaped areas of variable size reach almost all the way into

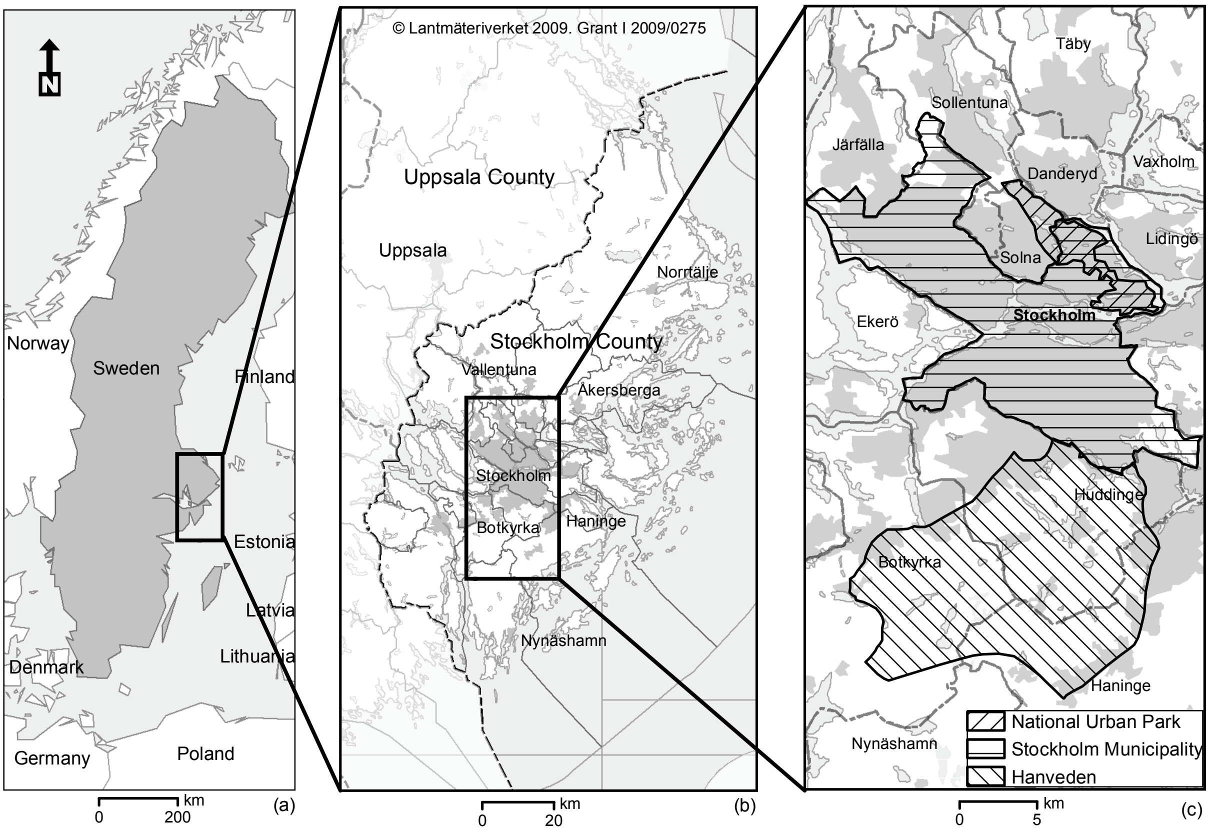


Fig. 3. Study areas. (a) Location of Stockholm County. (b) Extent of Stockholm County, the study area for Paper II, the Regional Development Plan (Paper I), and the Lynx lynx study, . (c) Location of the study areas for the National Urban Park, Stockholm Municipality, and Hanveden (Paper I).

city core. Two million inhabitants live in the area, and the population density varies considerably between the urban, suburban and peri-urban areas. While the average population density for the county is 291 inhabitants per km^2, this figure varies from 4117 in the municipality of Stockholm to 27 inhabitants per km^2 in the municipality of Norrtälje, which is close to the average density of the nation (22 inhabitants per km^2).

6. Moving from problem to solution

6.1. The ecological profile system as a framework and a probe

In an effort to build on previous graph-theoretic advances, while at the same time moving from a single-species approach to a more diversity-oriented functional approach, the concept of ecological profiles (Vos et al., 2001; Opdam et al., 2008) was chosen as an inspirational starting point. One of the reasons was its provisioning of an attractive framework that can guide the inventory of ecologically relevant functional profiles for each planning or assessment case. This inventory can ultimately be used to successively populate the functional, multi-dimensional diagram representing the niches within an ecosystem (Fig. 4). Another reason was the presumed communicative advantage of moving away from a set of specific species and towards a set of abstract functional profiles that could better match the aggregated, high-level perspective of the planner or decision maker.

The overarching organization of ecological profiles is the ecosystem type (or habitat type). An ecological profile for a certain ecosystem type is then ideally constructed by using size, quality, and spatial configuration of ecological resources to match the resource requirements axis (Fig. 4). The resources are usually modeled using patches of different types of land cover. Disturbances within the area are ideally made up of disturbances

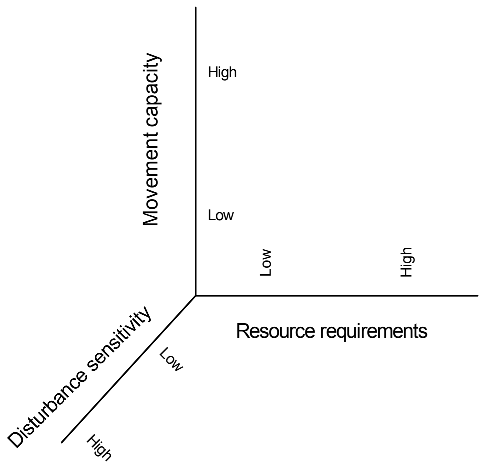


Fig. 4. Parameters for each ecosystem type in the ecological profile system are resource requirements, movement capacity and sensitivity to disturbances. Modified after Vos et al. (2001).

related to urban and regional planning, such as noise, recreational pressure, or pollutants. For dispersal capacity, the maximum juvenile dispersal distance could be used. Based on these initial assessments, the ecological profile diagram is successively populated, and one or several profiles can be chosen for analysis, preferably through a participatory process. In order to be able to exemplify real world expressions of the abstract ecological profile, each profile is finally populated with "profile species", which are real species that fit the functional profile, and are currently, or could potentially be active in the landscape at hand.

The Ecological Profile approach was used in all case studies of Paper I, and the profiles were selected through a participatory approach, involving different kinds of stakeholders from case to case. The parameters used in the modeling of each profile, as well as in the species-specific case of the management plan for the Eurasian Lynx (Zetterberg, 2007), were chosen through expert solicitation (Paper I). A lot of work remains in order to try to validate these parameters, as well as explore their uncertainties. Thus far, several profiles have been constructed and modeled using expert-based parameters and

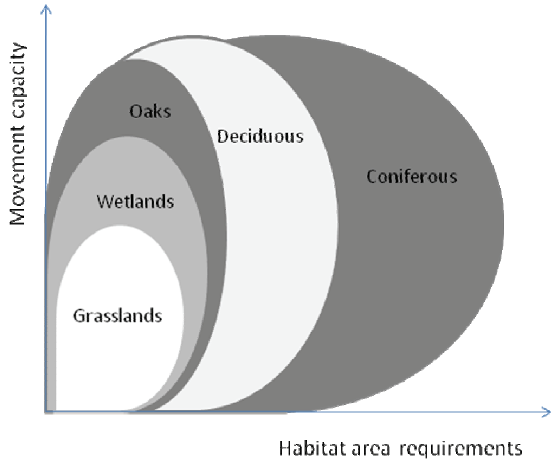


Fig. 5. Schematic illustration of the positioning of ecological profiles developed so far, with respect to ecosystem type

targeting grasslands, wetlands, the oak landscape, deciduous, and coniferous forests (Fig. 5). The amphibian profile for wetlands was in turn used to explore the potential of the Ecological Network Graph model developed and tested in Paper II (see also section 6.6).

6.2. A life-cycle based approach to patches and links

There are several different approaches when trying to model the functional requirements in the landscape of a species, or more generally, of an ecological profile (section 3.3). On one extreme, there is the often used approach of linking pattern and process by simply finding suitable habitat patches and some measure of probability to disperse between these. The patches are then typically found either through expert opinion or using empirical data. In the first case, expert solicitation is used to give information on which classes of land cover that could be considered to be habitat, and if there is any threshold value of lowest acceptable patch size. In the second case empirical observations are matched with statistical modeling of the patches using combinations of parameters such as land cover type, climatic data, topography, hydrology, and distances to roads. The probability of dispersal is typically modeled using a negative exponential function using a species specific parameter, and the Euclidean distance between the patches. On the other extreme, there is the data- and computationally intensive method of using detailed, spatially explicit, individual-based models. In this case, data on life history parameters such as fecundity, mortality, habitat use, and dispersal are required.

The challenge from the perspective of physical planning was to find a suitable trade-off between these two extremes, which could be successfully implemented over larger geographical regions, taking the most significant ecological processes with respect to land use into account. The simpler approach of finding potential patches and the probability of dispersal between these was considered able to capture the most significant ecological processes directly related to the activity of physical planning. It is also a well established approach within landscape ecology (section 3.3), and is particularly suitable when using graph-based methods to model the system, with nodes representing the patches, and links representing the dispersal relations.

Despite being well established within landscape ecology, the habitat/non-habitat form of the much often used patch-matrix paradigm was considered not able to adequately capture ecologically important processes that could potentially be affected by land use change as a result of physical planning activities. Critique has for example been raised on the view of the matrix as simply being a hostile area (section 3.3). I argue that the same reasoning can be extended to the view on patches. The matrix is in reality heterogeneous, containing more or less qualitative elements, and the same is of course true for the patches internally, with resources unevenly distributed within these patches. Furthermore, most organisms are capable of moving between groups of resources, even though they are not spatially contiguous on a land cover map, hence utilizing clusters of

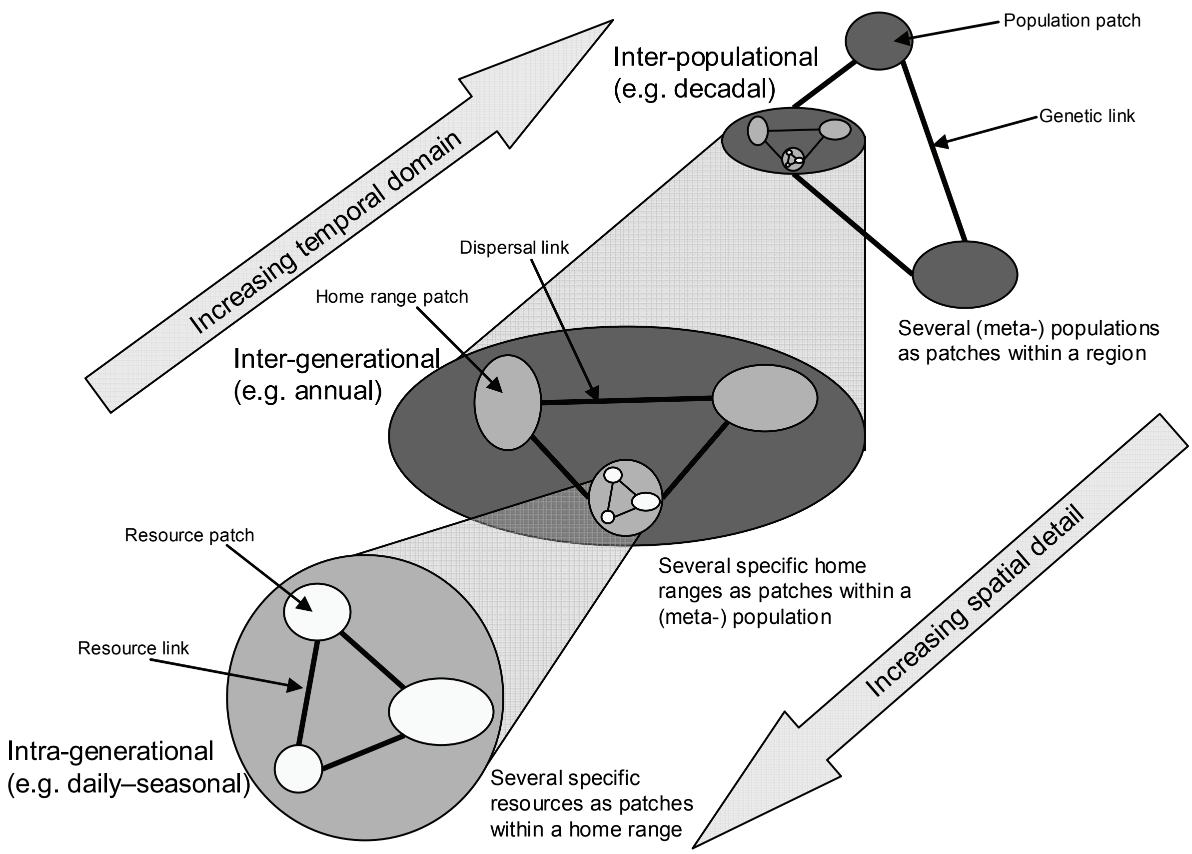


Fig. 6. Schematic overview of how clusters of patches and links gradually build up larger patches, connected by new links as the temporal domain increases. Clusters of resource patches and links make up home-range patches, which are connected by dispersal links. On a longer time scale, these home-range clusters make up population patches, connected by genetic links.

smaller patches. This means that organisms interact with the landscape (e.g. vegetation type, disturbances, topography, hydrology) both *within* and *between* the patches. The resolution of data and computing power of today are more than enough to use other models, better reflecting the interaction between species processes and a heterogeneous landscape. The challenge here is to find a suitable trade-off between the attractive properties of a patch-link paradigm and the detail of the landscape considered when constructing the patches and the links.

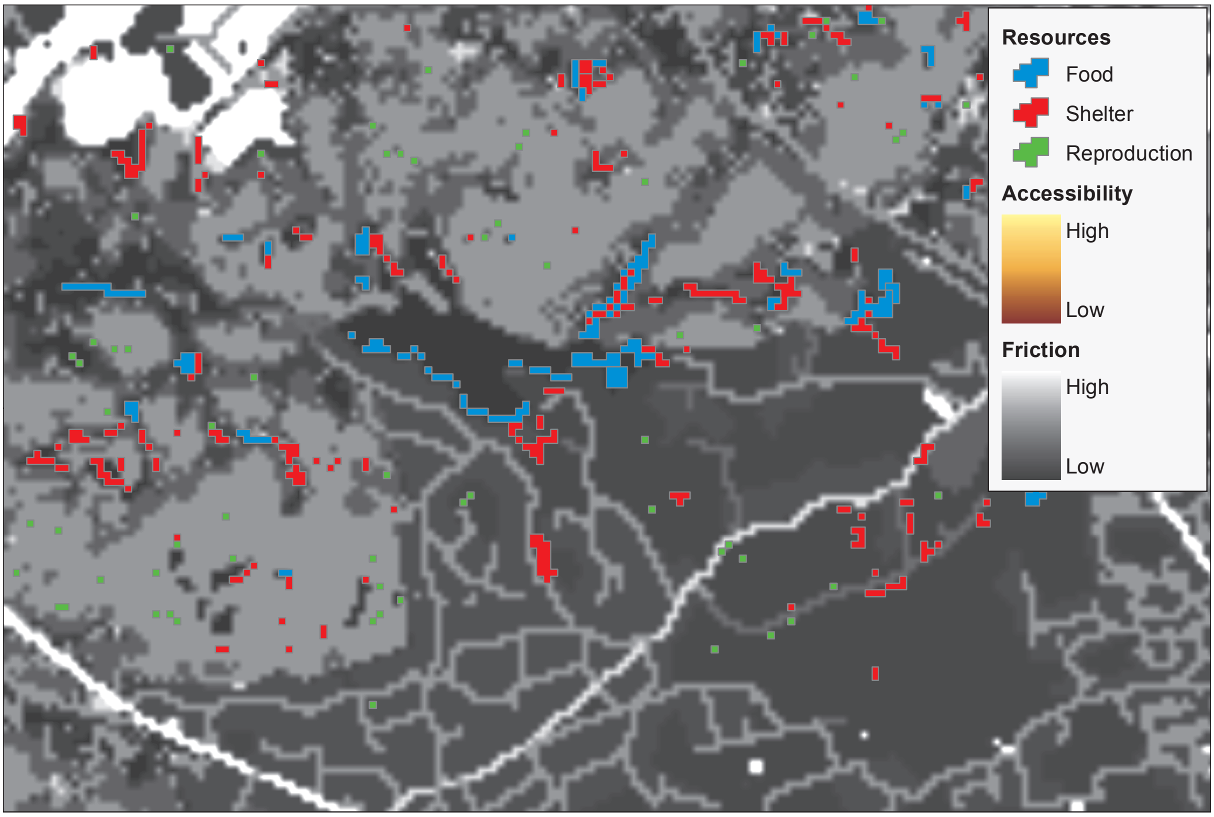
Another seldom emphasized fact is that the size and type of a patch vary with the temporal scale. Theobald (2006) argues that the functional definition of a patch depends on the movement type considered, and that these occur at a range of temporal scales. For example, for a certain organism with temporal dynamics similar to human, the movement type on a daily basis could typically be foraging, and the patches reflecting the corresponding time frame would therefore contain foraging resources. On a yearly basis, the movement types could typically be natal dispersal and genetic exchange, and the patch types would be home range patches (either annual or lifetime). On a centurial basis, the movement type could typically be genetic exchange and the patches would correspond to (meta-) population patches. I argue that the same reasoning is valid for the traditional matrix and corridor concepts; as the temporal scale increases and the patches change type, parts of what was previously considered matrix or connectivity zone are successively incorporated into the patch, and new connectivity zones are formed reflecting the processes relevant at the new time scale (Fig. 6).

In order to generalize this view, a *life-cycle based approach* was designed (Paper II), in which the patches and links were first defined with respect to a temporal scale related to a specified part of the life-cycle. These were then constructed by finding contiguous areas containing all resources *within reach*, needed throughout this selected part of the life-cycle. In the typical modeling case, all resources needed from birth to juvenile dispersal were included in a home-range patch, and the link between the patches then represented juvenile dispersal. For a plant, a patch would for example be closely related to soil type or land cover, for which this general model can be reduced to the simpler habitat/non-habitat model. For higher organisms, however, a patch would need to contain for example resources for reproduction, foraging, and over-wintering. An interesting development of this model would be to include species interactions and move towards a community perspective. In this case, pollinators would be included in the plant model, and the community patch would need to meet their respective spatial, and temporal scales.

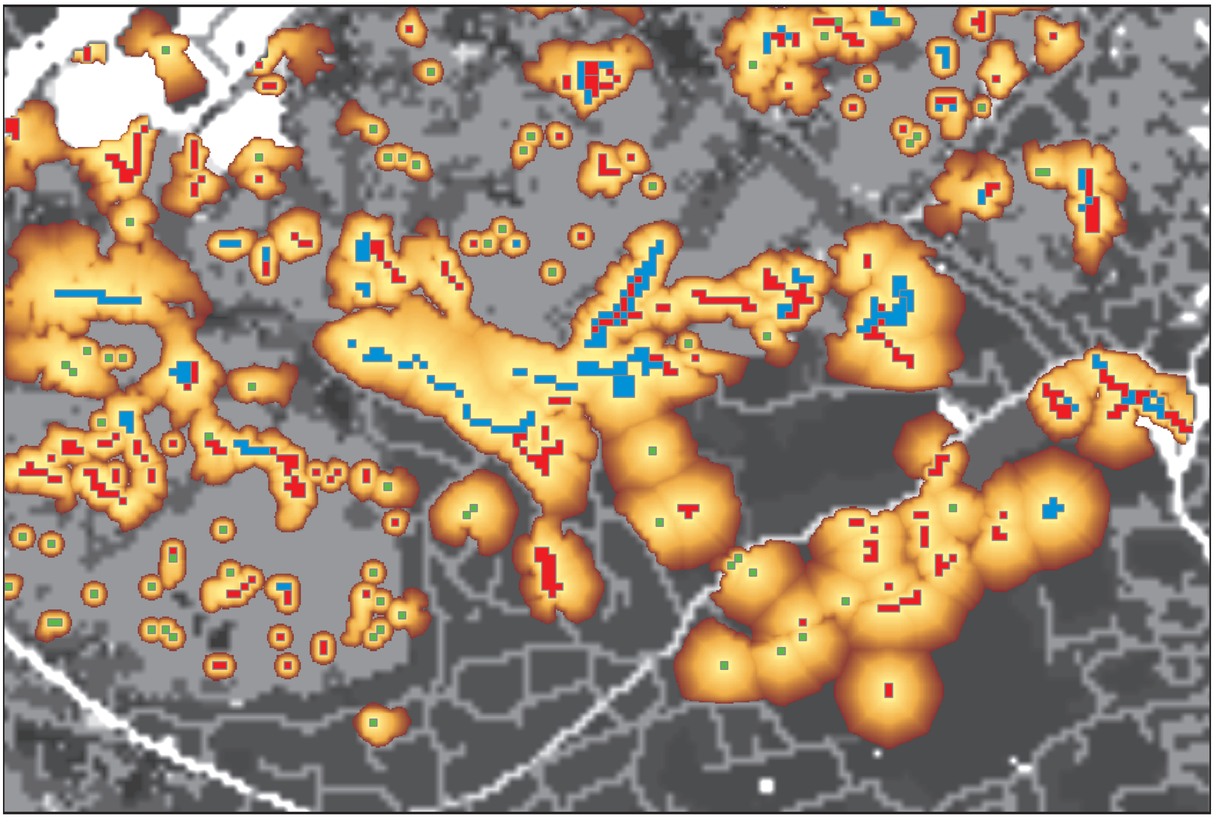
6.3. Least-cost modeling for networks and GIS-maps

Based on a friction map corresponding to the cost of movement across a raster cell (Fig. 7a), the least-cost modeling approach (section 2.7) was used for three different purposes. First of all, it was used to estimate the probability of dispersal as a measure of the link strength in the graph-theoretic analysis (Paper II). Secondly, it was used to model the accessibility of resources, and could thus be used to cluster these resources into home range patches (Paper II). Thirdly, it was used to create a spatially explicit, geographic extent of both the home range patches (Paper I; Paper II; case studies) and the connectivity zones (Paper II). This way, all the required resources within a life-cycle span that were within reach of each other, *including* the part of the landscape needed to move *among* them, could be grouped into geographically defined patches and presented in an “accessibility map” (Fig. 7b).

Another advantage with this choice of method is that tools for least-cost analysis already exist within many of the existing GIS-software packages. For example within ArcGIS Spatial Analyst (ESRI, 2006), the tools ‘cost-distance’, ‘least-cost path’, and ‘least-cost corridor’, can be used to solve many of the related problems. This means that standard GIS-data can be used both as input to, and output from the model, which in turn facilitates the integration of model inputs and results into the existing planning context and



(a) Resources on top of friction map. The darker the color, the lower the friction, and hence the easier to move.



(b) Accessibility map. The resources are clustered into patches using the least-cost distance through the friction landscape.

Fig. 7. Friction map (a), and accessibility map (b). Note the isolation effect in the lower left corner due to the relatively high friction. The highway in the lower right corner and the buildings in the upper left corner also affect the accessibility. Patches that do not contain all the required resources are removed when finally constructing home range patches.

daily working environment. The output from the cost-distance tool in ArcGIS is a GIS-raster giving the least aggregated cost-weighted distance to the nearest source. This produces a continuous map, where the value in each raster cell can be interpreted as the functional, or effective distance (effective distance; e.g. Adriaensen et al., 2003), from the closest source to each point in space.

By setting all required resources as sources in the model, and combining this with the species' friction of movement in the landscape (Fig. 7a), the resulting cost-distance map (Fig. 7b) can be interpreted as the *functional accessibility* of these required resources in the landscape for the studied species. In practice, both the resources and the friction values are constructed by combining available sources of GIS-data (for example land cover, slope, noise, amount of traffic, or altitude) into proxy variables. This way, we approach a functional view, using both life-cycle based requirements and the possibility of navigating *among* these throughout the landscape.

Even though the traditional approach of simply selecting land cover classes sometimes includes different kinds of habitat, there is no guarantee that the same individual can reach these when needed. This is particularly the case in fragmented landscapes.

The resulting maps are referred to as 'habitat network maps', and the approach was used both in Paper I, and all the case studies. In Paper II, least-cost modeling was used a second time to create the connectivity zones corresponding to juvenile dispersal links. In this case, the maps are referred to as "ecological network maps (ENM)" (section 6.5).

6.4. Case studies: Testing the habitat network approach

In order to evaluate the effectiveness of the habitat network approach, seven real-world case studies have been carried out as commissioned projects, and the results from four of these are presented in Paper I. Two cases (Mörtberg, Zetterberg, & Balfors, 2007a; Mörtberg, Zetterberg, & Gontier, 2007) were commissioned by Stockholm Municipality to develop, test, and evaluate the effectiveness of the habitat network maps and ecological profiles within environmental assessments, monitoring, and urban planning. One case (Mörtberg, Zetterberg, & Balfors, 2007b) was commissioned by the County Administrative Board of Stockholm to test the potential of using these tools within the development of Regional Landscape Strategies. Another case (Zetterberg, 2007), also commissioned by the County Administrative Board, aimed at using the habitat network approach to aid the development of a regional management plan for the Eurasian Lynx *(Lynx lynx)* within the county. A fourth case was commissioned by the Office of Regional Planning and Urban Transportation, to aid the formulation of targets, and analyze potential ecological impacts of the planning scenarios within the Regional Development Plan (RUFS 2010). In the remaining two case studies, I did not personally take part, but the analysis of their outcome is included in Paper I.

The basis for the analysis in Paper I was formed around the Landscape Ecological Assessment (LEA) framework (Mörtberg, Balfors et al., 2007). The aim was to study and compare which parts of the LEA-framework were used, how they were used, and whether and how the habitat-network based approach and the LEA-framework could be integrated into the planning process. The LEA-framework is a process based methodological framework aimed at safeguarding proper caretaking of biodiversity within urban and regional planning, with a particular focus on the SEA that is required, for example for certain plans and programs within the European Union (Official Journal of European Communities, 2001). The SEA-process involves tight linkages and iterative cycles between the strategic decision-making and the environmental and sustainability input (Therivel, 2004, p. 15) and the LEA-process supports these linkages through the formulation of landscape targets and related indicators, landscape ecological predictions of impacts, assessments, and an evaluation that feeds back into the strategic decision-making with for example proposed mitigation measures or modified scenarios (Paper I).

The major results from Paper I show that both the ecological profile system and the habitat network maps are useful, both as a predictive tool for impacts in ecological assessments, but also as a communicative tool for participatory approaches. The resulting habitat network maps were useful in aiding a systemic understanding of for example the geographic extent of the resource requirements for the chosen ecological profiles, and have continued being used by the clients even after the project closures. The resulting habitat networks have for example been delivered to the clients, and deployed as GIS-layers in the majority of the cases and are actively used by the respective governmental agencies. Stockholm Municipality is using the habitat network layers within the ongoing planning and environmental assessment activities and they are currently used within the development of the new comprehensive plan of Stockholm Municipality. The County Administrative Board is using the GIS-layer of the Lynx habitat network, both when informing the public, and when planning inventory activities of the Eurasian Lynx.

Another important observation is the importance of a participatory approach, in particular with respect to the formulation of targets and the assessments of impact predictions. The target formulation differed substantially from case to case, in part due to different initial objectives, but also depending on the stakeholders involved in the process. This finding is in line with Turnhout et al. (2007) who, as previously mentioned, argue that the ecological indicators need to be formulated through negotiation and boundary work at the science-policy interface in order to be anchored and accepted by the involved stakeholders. In the case of the Regional Landscape Strategies (Mörtberg, Zetterberg, & Balfors, 2007b), the assessment involved a set of workshops with stakeholders representing scientists from different disciplines, six different municipalities, non-governmental organizations, landscape architects, the County Administrative Board of Stockholm, the Swedish National Road Administration, the Federation of Swedish Farmers, and the Swedish Forest Administration. These workshops led to new input of data, re-iterations of the prediction models and modified, more accurate results that could not have been achieved without the participatory approach. In addition, it helped anchoring the final strategy among the stakeholders. The case of the Regional Development Plan (RUFS 2010) was of particular interest in that the development scenarios were actually re-designed at an early stage to better incorporate the ecological infrastructure. Subsequent landscape ecological modeling and predictions were then carried out, and the main results were incorporated in the reports used in the extensive public participation of the RUFS-process.

In addition to the findings presented above, several new desires were either expressed by the stakeholders or successively formulated within the research project. One was the need to better validate the prediction models, which in turn would require long-term collection of ecological data, an activity which is very rare at present. Another request regards the need for measurable planning indicators and metrics, which can be used for example in comparing planning scenarios, formulating more specific targets, and during follow-up of a plan or project. The indicators should be ecologically relevant and systems oriented in order to better reflect the region-wide landscape-related properties of the ecosystems. There is also the need for tools to better prioritize future land-use between for example areas of ecological importance and areas suitable for housing. A closely related issue is the need to better understand the internal structure of the ecological network. How are the patches within the habitat network map related? Which patches or links are important or critical for the sustainability or the resilience of the ecological infrastructure? Where are the presumed physical connections between the patches manifested as connectivity zones in the landscape? There were problems related to the understanding or interpretation of concepts such as 'habitat network', and 'core areas'. Another problem related to the meaning of a connectivity zone. The functional approach, in essence viewing the landscape through the eyes of another species, was difficult to convey. This was for example the case when connectivity zones showed up across private gardens, church yards, across a street and an allotment garden, instead of along a green corridor of forest.

6.5. Development of an operational graph theoretic model

In response to several of the desires expressed in Paper I, the attention turned to network analysis and graph theory in Paper II. Despite having been proposed as an efficient way to explore and analyze holistic systems properties of ecological networks, landscapes or habitats (section 3.4), little attention has been paid to making these graph-theoretic approaches operational within ecological assessments, planning, and design (chapter 4).

In order to be successfully operational, the graph-based approaches need to be spatially explicit, geographically defined, placed and visualized in a relevant context and scale, and deployed in a working environment already in use by the stakeholders. Simple overlays of maps, relating the spatial whereabouts of potential impacts to geographically defined locations, are an example of an approach that has been showed to be successful in planning and assessments involving multidisciplinary communication (section 3.2). These findings are also in agreement with the findings of Paper I, using the GIS-based habitat network map as a communicative tool and a basis for prediction within ecological assessments and planning.

However, the visualizations of graph-theoretic representations of ecological networks presented thus far are restricted to simple patches of a predefined set of land cover classes considered to be habitat, connected by straight lines, or least-cost paths representing the graph-theoretic links (section 3.4). The extent of the area corresponding to the links, such as the migration zones, juvenile dispersal zones, i.e. connectivity zones, also needs to be considered. This is just as important from the mapping perspective as the geographic extent of the patches. In addition, there are of course several other plausible mapping possibilities and the users engaged in planning, assessments or design activities need to be able to switch between different mappings and visualizations of the graph depending on the context, scale, and situation. One interesting approach has been presented by Theobald et al. (2006), where several different visual and geographically defined representations of nodes, links, patches, and linkages can be mixed.

Recognizing the need for a collective and yet flexible model, Paper II separates the abstract graph-theoretic representation of an ecological network from any visual or geographically defined representation of the network. These representations are instead unambiguously linked to each other, in effect linking process to pattern, and yet allowing for a separate analysis of the two, where appropriate. A common, generalized model is thereby achieved, approaching the ecological landscape at a higher, aggregated level, constituting the basis for a generalized interface between stakeholders.

In order to separate the abstract from the visual representation, two complementary and strongly interlinked concepts are introduced: the Ecological Network Graph (ENG) corresponding to any abstract, graph-based representation of the network, and the Ecological Network Map (ENM), which is a collective term for any spatially explicit, geographically defined representation of the ENG. Each component of the ENG, for example a node, is unambiguously linked to a geographically defined part of the landscape, represented by a component in the ENM, for example the corresponding patch. The ENM is preferably represented within a GIS allowing the incorporation of graph-based network properties into an effective analysis of planning scenarios, and design strategies, as well as a dynamic dialogue among stakeholders within ecological assessments. The spatial graph (Fall et al., 2007) is one of several different kinds of ENM:s (similar to Fig. 8b). A simple geographically defined graph consisting of nodes and links (e.g. Bunn et al., 2000) is another kind of ENM (similar to Fig. 8a).

The separation and unambiguous linking of the abstract, graph-theoretic data structure to

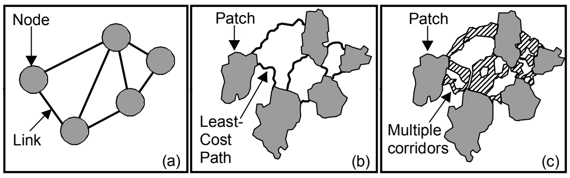


Fig. 8. Three examples of ENMs. a) Traditional representation of a network. b) "Patch-link" representation showing the physical extent of the patches and the least-cost path (LCP). c) Extent of both the patches and multiple connection zones.

the geographically defined and spatially explicit structure allows for several new assessment-, planning-, and design-techniques. Metrics, algorithms, and explorative techniques already established within graph theory can in this way be linked to geographically defined landscape objects in a relevant working environment, such as a GIS. Through graph theory, analysis of critical or otherwise important structures within a network can be found on a scale that is relevant from a management or decision-making perspective (e.g. Keitt et al., 1997; Bunn et al., 2000; Urban & Keitt, 2001). The ability to visualize different aspects of the network using a varying degree of detail depending on the context and scale, as for example when zooming between a regional overview and a detailed local perspective, is a crucial part of making the graph-based approaches operational, placing the local planning and design in a regional network context. The Ecological Network Graph can be represented using several kinds of data structures, such as adjacency matrices or adjacency lists. The ENM can be represented using several visual representations, for example in a GIS. Fig. 8 illustrates three examples of ENM:s.

The traditional representation (Fig. 8a) can be used to highlight important or critical components within the system for conservation purposes, but it could also be useful within the regional planning process. The patch-link representation (Fig. 8b) is analogous with the spatial graph proposed by Fall et al. (2007), and has also been used in conservation planning, and greenway planning (e.g. O'Brien et al., 2006). The third representation (Fig. 8c) is crucial for the implementation of improvements within the design process. The 'Landscape network' proposed by Theobald et al. (2006) has support for all three examples, including a tool for identifying multiple connectivity zones between patches that can be seen in Fig. 8c.

Another important aspect of making the graph-theoretic concepts operational is the ability to deploy these theoretic concepts in a context and daily working environment already in place by planners and designers. The operational maps within the ENM should therefore be implemented in such a way that they can be used seamlessly with other maps, tools and constructs used within the planning and design process, which is often achieved using a GIS.

6.6. Testing the ENG/ENM model using a real-life case

To illustrate the basic principles of working with the proposed operational ENG/ENM-model, an ecological example was performed (Paper II) within the county of Stockholm, the capital of Sweden (Fig. 3), using the European common toad (*Bufo bufo*) as a profile species. The study in Paper II moves one step beyond the issue of conservation of *currently* important structures, and seeks to identify suitable redesigns of the landscape to *improve* its social-ecological qualities. The example also illustrates the potential of using graph theory, not only to find areas that are important from a regional perspective (i.e. a system-centric analysis), but also to find parts of the network that are important from a local perspective (i.e. a site-centric analysis).

The same methods that were used to find the patches in the case study by Mörtberg, Zetterberg, and Balfors (2007a), were scaled up in Paper II to cover the entire County. Least-cost analysis was used to find 1361 potential annual home range patches, based around 22 248 potential reproduction sites within the study area. In order to explore important *internal* ecological structures within the study area, a second least-cost analysis was then run, capturing the potential dispersal zones connecting these home range patches, and ten graph-theoretic indices were calculated for the resulting network. The relative impor-

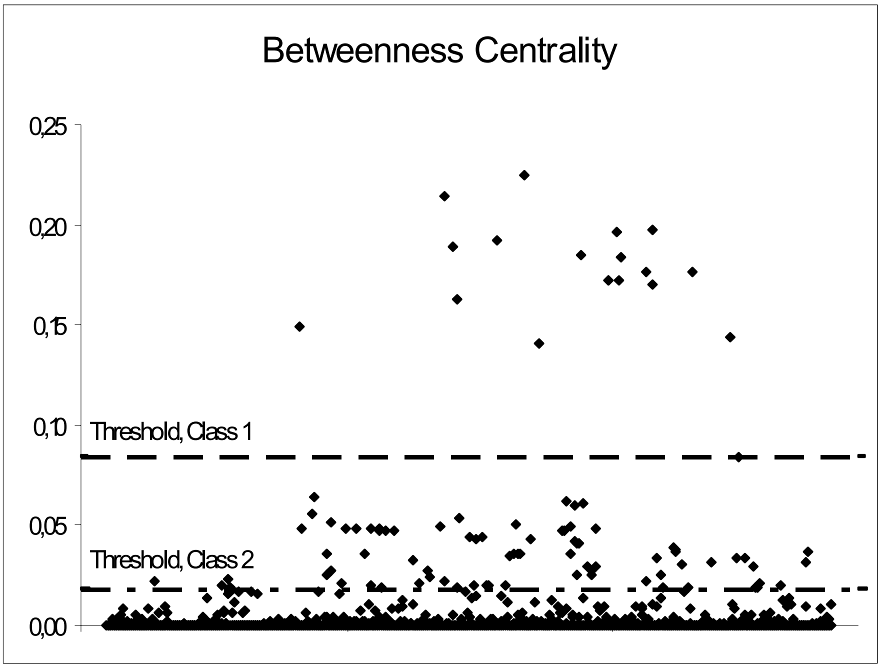


Fig. 9. Betweenness centrality for all 1361 nodes in the ENG of study area in Fig. 2b. The thresholds (class 1 and class 2), created using ArcGIS natural breaks (ESRI, 2006), divide the importance of the nodes into thre distinct classes and the top two were used to illuminate the important patches in Fig 10b).

tance, ΔI , of each patch with respect to each of the ten indices was finally calculated. All of the ten metrics could be used as planning indicators of connectivity to compare urban or regional planning scenarios.

Betweenness Centrality (see section 2.6 for definition), emerged as an index capable of illuminating important smaller stepping stone patches running through the bottleneck of the study area around the heavily urbanized city of Stockholm (Fig. 10). This result is in agreement with Bodin and Norberg (2007) stating that the betweenness centrality index manages to emphasize areas that are thought to be important to the connectivity of the network even when the risk for habitat isolation is low. Minor and Urban (2007) also showed that betweenness centrality could be used to identify stepping stone patches that were not easily identified with a spatially explicit population model.

Fig. 9 plots the betweenness centrality of all the 1361 home range patches, and shows two threshold levels found using 'Natural Breaks' (ESRI, 2006). The additional unambiguous linking of the ENG to the ENM allowed a geographically defined visualization of essentially the same information, which illustrates the power of the conceptual ENG/ENM-model. A result of this linking is shown in Fig. 10 (from Paper II). This is essentially the same information as in Fig 9, but in a GIS with all the 1361 patches to the left (a), and only those above each of the two threshold levels to the right (b). This spatial representation could be useful within regional planning.

In addition, the information about important systemic, regional structures can be brought into a local perspective. This opens up for powerful analysis techniques within urban planning, and design. When zooming in and only studying a few hundred nodes and links instead of several thousands, other ENMs can be used. The marked region in Fig 10 is studied in detail in Fig. 11. Here, two different visualizations are shown, with a node-link map to the left and a patch-link map to the right. Both of these give insight into the relations between the local network structure and the regionally important aspects, and can thus be used to find parts of the network with local or regional improvement potential. The node-link map shows important sources for recruitment as larger nodes and how they are interconnected. The patch-link representation shows the extent of the patches in place of the nodes. In this case, the map shows important patches with respect to regional "betweenness centrality paths". The other patches (striped) can be seen as potential building blocks when managing the ecological network.

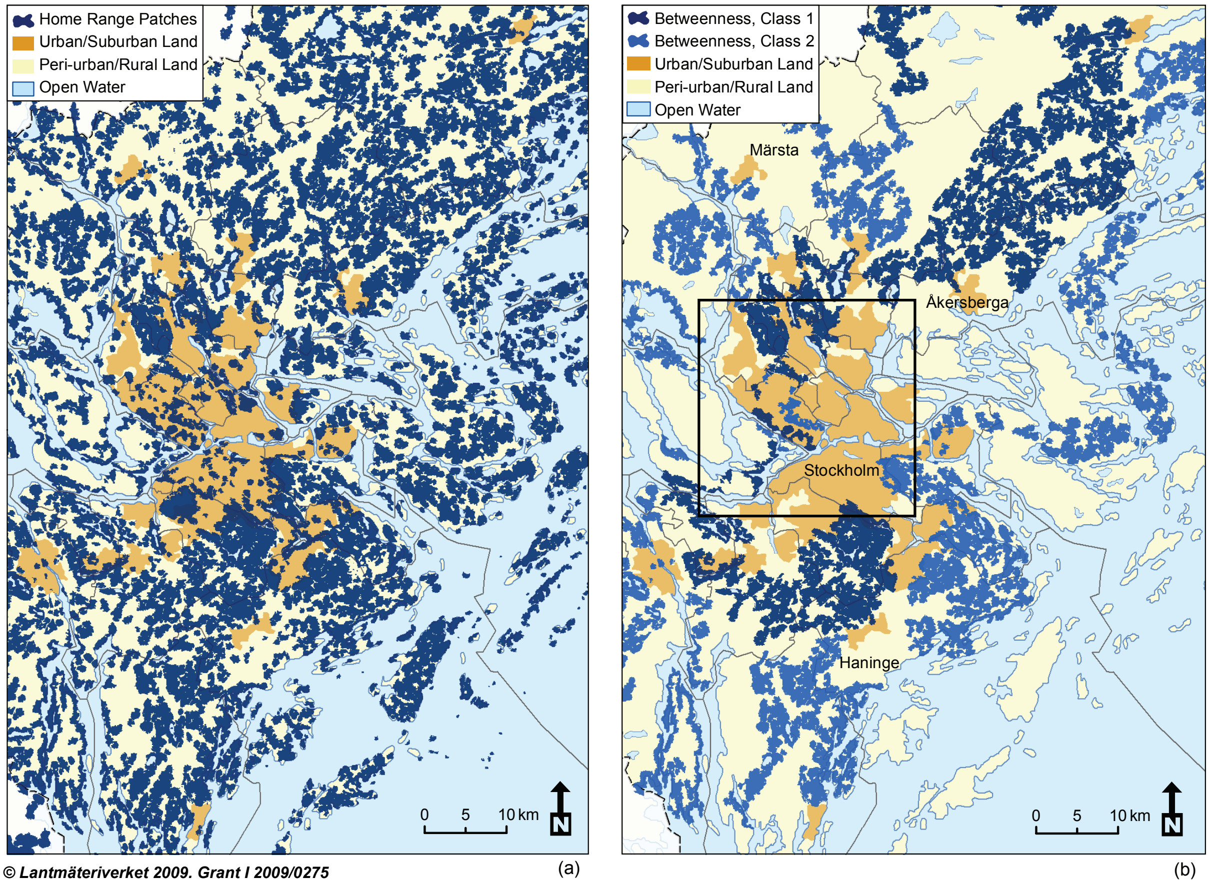


Fig. 10 All of the 1361 patches are shown to the left (a), and the patches considered important (class 1 and class 2) with respect to betweenness centrality, according to Fig. 9, are shown to the right (b). Note the small stepping-stone patches running through the city.

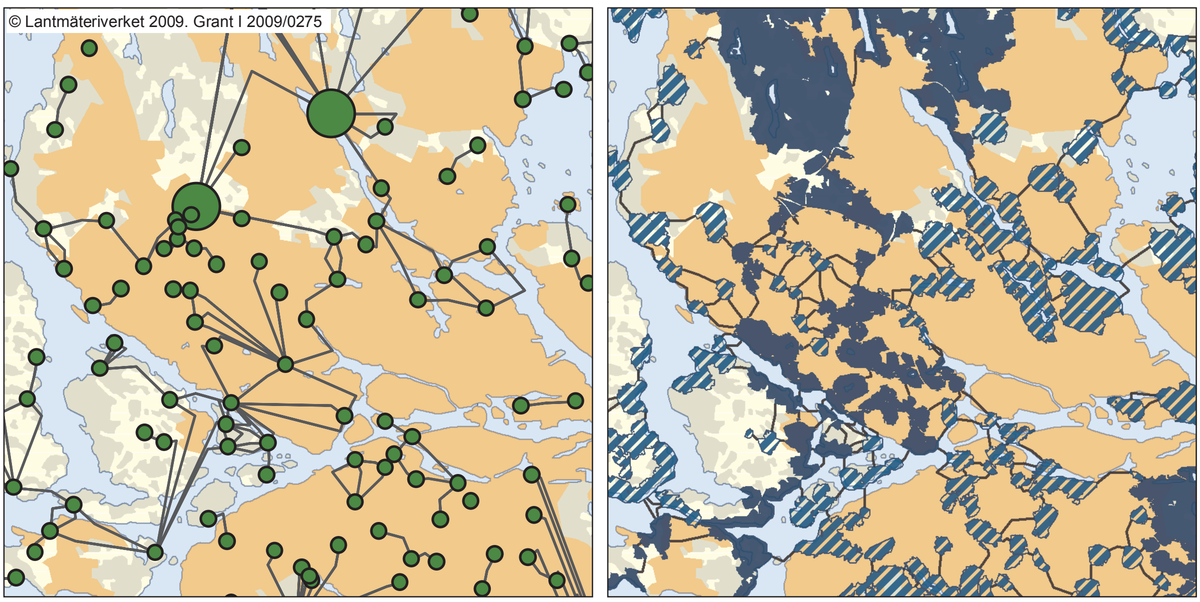


Fig. 11. Close-up of the network. Left: node-link representation. Size of node corresponding to source strength and link-threshold corresponding to one-year dispersal. Right: patch-link representation. Solid patches have high betweenness centrality, and striped patches are below class 1 and 2 threshold level. Link-threshold corresponding to three-year dispersal.

To explore this potential further, a local, urban study, followed by a more detailed study, both within the municipality of Stockholm, were carried out in Paper II. While the regional study aimed at finding important ecological structures through the region, the local study illustrated examples of managing "improvement potential"; both for the ecological resilience of the entire network by increasing spatial redundancy, and for mitigating the isolation of the National Urban Park within the municipality of Stockholm (Paper II). In addition, the effect of a redesign, involving the construction of three new spawning ponds within an area suggested as suitable for improvement potential, was studied by re-running the ENM after modifying the input data.

7. General discussion

7.1. Ecological profiles or real species?

The two main reasons for choosing the ecological profile approach were its provisioning of a framework for profile inventory, and the communicative advantage of using an abstract profile instead of specific species when involving non-ecologists (section 6.1). In reality it turned out to be quite difficult to separate the abstract profile from specific species throughout the entire process, from selecting, to working with, or communicating the ecological profile. In the phase of setting targets and formulating ecological profiles, the ideal methodology was to first formulate suitable profiles based on an aspiration level with respect to landscape requirements, and then populate the profile with real 'profile species' that could be used as examples. However, this methodology has been difficult to follow. The actual participatory process has instead started off with agreeing on relevant ecosystem types for each case, and then, through local expertise, finding examples of species that are vulnerable within the current landscape with respect to those ecosystem types. Real species have then finally been grouped into functional profiles matching their landscape requirements.

This is in effect closely related to the focal species approach (Lambeck, 1997), or the landscape species approach (Sanderson et al., 2002). It resembles the landscape species approach by initially focusing on an anticipated land-use change, but does not try to find specific species with high area requirements and a demand for many different ecosystem types across the entire landscape. It resembles the focal species approach in trying to find a suite of ecological profiles that, altogether, are believed to include the requirements of many species, but it does not try to find specific species whose requirements are believed to encompass the requirements of many other species with lower requirements. It is simply a way of organizing the functional requirements space.

Another difference from the traditional focal species approach is the use of abstract ecological profile names, intended to avoid the use of specific species in the communication with non-ecologists. As it turned out in the case studies of Paper I, however, both the abstract ecological profile and specific profile species were used depending on the context. When starting off with a specific species, there was a clear risk of limiting the discussion. The systems perspective could get lost in favor of discussions about the relevance of protecting that particular species. On the other hand, when starting off with communication centered on an ecological profile, the reality of that abstract profile could be questioned, and the real-world profile species were needed to give credible examples. This is in agreement with Opdam et al. (2008), who initially assumed that the virtual ecoprofile would be easier to work with due to for example reduced complexity, but that the stakeholders "attributed imaginary value to real species". Indeed, in their case study, the stakeholders *preferred* to use the real species in the communication, even though they lost the systems perspective in doing so. This imaginary value of real species may in fact be the reason why the ecological profiles ended up being constructed via real species, instead of the other way around as was initially intended. The results from Paper I show that both the ecological profile, the specific profile species, and the corresponding habitat network maps were needed and complemented each other in the participatory process. The ecological profile aided in the understanding of the ecosystems perspective. The habitat network maps aided in the understanding of the spatio-temporal systems perspective, and the profile species were needed for acceptance as well as a real, common imagination point of reference.

7.2. A Landscape perspective and environmental objectives

Despite difficulties in applying the methodology as first intended, I argue that a clear advantage of the ecological profile approach came out of the overarching organization by ecosystem type. This shifts the perspective from species as such towards the landscape as a starting point, which better matches the activities within physical planning, and its related assessment and decision-making activities. It also matches environmental objectives that are often formulated in terms of ecosystem types. For example, several of the 16 Swedish environmental quality objectives are formulated using expressions such as 'thriving wetlands', 'sustainable forests', 'a varied agricultural landscape', 'flourishing lakes and streams', and 'a magnificent mountain landscape' (Swedish Environmental Protection Agency, 2009). Hence, during the participatory process of formulating planning indicators and targets, ecological profiles matching those of the environmental objectives or their more specific environmental targets could maybe be more easily anchored among the stakeholders. Indicators related to these profiles would in this case also better match several parts of the environmental assessment process and the subsequent follow-up, such as monitoring.

7.3. Species-landscape or species-species interactions?

From a species-landscape point of view, Opdam et al. (2008) argue that the proposed ecoprofile matrix was important in facilitating both the communication, and negotiation among the stakeholders. Having a simple matrix with easy-to-understand parameters such as 'total area requirements' along one dimension, and 'inter-patch distance' along the other, made it easier for ecologist to communicate the ecological needs for an ecoprofile within each ecosystem type. They further argue that it was successful during the negotiation of a reasonable aspiration level, where changes in total protected area and maximum inter-patch distance easily pinpointed the portion of the ecoprofile matrix that would be included in the protection scheme. This would provide the desirable ease of understanding and flexibility needed during negotiation within the science-policy interface (Turnhout et al., 2007).

I argue, however, that it is probably more fruitful to base the negotiation around the actual predicted *spatial requirements and outcome* of the model; using the map one can clearly illustrate the trade-off between spatial properties 'where, why, and which species', rather than the non-spatial properties 'area, inter-patch distance, and portion of the ecoprofile matrix'. Although this approach would require the involvement of ecological expertise to run an initial model iteration, the boundary objects (boundary object; Turnhout et al., 2007) for negotiation, formed through the habitat network maps (Paper I) or ecological network maps (Paper II), are probably easier to understand than the more abstract generic parameters used in the ecoprofile matrix. In addition, moving away from a simpler model based on a generic approach, to a more context specific flexibility of the model, would produce a higher ecological relevancy, which may be important for a successful anchoring during the negotiation process. These hypotheses need to be investigated further.

Another important point with respect to ecological relevancy is that it may in fact be the interactions between different species that are far more important to consider than the interactions between a functional ecological profile and the landscape. Much of the work on spatial population dynamics and its relation to landscape properties such as the amount and quality of habitat, and the fragmentation of the landscape, including the work in Paper I and II, does not take these species interactions into account. Some of the case studies in Paper I took on a multi-species or 'many ecological profiles' approach, but none of them attempted at including inter-species or intra-species interactions.

Within metapopulation ecology, the importance of interactions such as interspecific competition has been studied (Iwasa & Roughgarden, 1986; Bengtsson, 1991), and in (meta-) community ecology, it is recognized that different types of interactions and ecological processes dominate at different spatial scales (e.g. Leibold et al., 2004). Studies of complex network interactions within food-web theory suggest that species interactions are a lot closer than previously believed, and that the removal of certain species can in fact restructure the entire species community (Sole & Montoya, 2001; Montoya et al., 2006). Depending on the strengths of species interactions with other species or their resources, the loss of a single species can theoretically even produce a secondary cascade of species extinctions (Christianou & Ebenman, 2005; Eklöf & Ebenman, 2006).

This research arena is not without debate, however, and there are sometimes strong deviations between model predictions and empirical results, some of which can be explained by including a spatial dimension (Van de Koppel et al., 2005). In essence, this would drive the research towards including both species-landscape, and species-species interactions, producing an ever increasing level of complexity. Another complicating factor is the temporal mismatch between pattern and process; there can be a time-lag of several decades or even centuries between land use or land management changes, and significant effects on species distributions both in urban (Löfvenhaft et al., 2004) and rural (Lindborg & Eriksson, 2004) landscapes. Ultimately, the question is about simplifying the ecological complexity enough to allow for effectiveness, flexibility, and understanding among stakeholders, while still being ecologically relevant and credible (Cash et al., 2003).

7.4. Species systems, ecosystems, or social-ecological systems?

Even though it is already computationally possible, and with more ecological knowledge may also be practically possible to model a very high level of complexity and spatial dynamics, including inter-species, intra-species, and species-landscape interactions, the key question remains. What is it that we really want to achieve and be able to take into account within physical planning and environmental assessments? Within conservation biology this key question is somewhat easier to answer and is often expressed in terms of viable populations of selected species, although the term viable can certainly be debated as well as the lack of a social-ecological systems perspective in the modeling activities, including for example management or governance issues. Within the realm of physical planning or higher level environmental quality objectives, the key questions are much vaguer. Objectives often refer to ill-defined, value laden concepts such as the level of biodiversity, sustainable social-ecological systems, ecosystem functioning, and ecological integrity.

There seem to be clear links between some of the major constituents of these concepts, for example between species richness and ecosystem properties such as nutrient cycling, productivity, and decomposition rates (Loreau et al., 2001). However, trying to use such criteria to create operational relations between ill-defined and vague concepts, such as biodiversity and ecosystem functioning, is problematic (Bengtsson, 1998), and has led to intense debate and controversy over the years. Due to the inherent value laden nature of these high level concepts, I do not foresee an operational solution to such an approach. Despite this apparent dead-end, I agree with Noss (1999) in that we must continue to act on current knowledge, and learn through adaptive management, hopefully without too much damage along the way. Scientific progress within smaller parts of the system, such as the tools and methods presented in this thesis that focus on the species-landscape interactions, are important contributors to this knowledge. One of the main challenges within the systems analysis, that has received little attention, is finding better methods for linking and integrating the models between the micro, meso, and macro scales (Ostrom, 2007).

7.5. Effective application of landscape ecological assessments

One of the aims with the case studies of Paper I was to acquire general knowledge about the effectiveness, understanding, and trust of the steps in the LEA framework. The participatory approach that was used in the case studies ended up not only serving the intended purpose of anchoring the methodology and potential impact results among stakeholders, but also providing better data input, more accurate model predictions, and a better understanding among the stakeholders of the science behind the models. The last part is important for the effective application of the assessments, since stakeholders may not support what they do not understand (Theobald et al., 2000; Cash et al., 2003). The participatory steps of the framework also provided input regarding improvements of understandability and usability as proposed by Turnhout (2007), some of which were used in Paper II. This supports the idea that landscape ecology must co-evolve with spatial planning to be successful (Ahern 1999, as cited in Opdam et al., 2003). In particular, local expertise was found to be important in providing more accurate data and validating the predictions of potential impacts by the landscape ecological models. Indeed, there are attempts at devising collaborative GIS- methods to incorporate local and technical knowledge into the already existing knowledge bank and GIS-data (Balram et al., 2004).

Despite the positive response indicated in the case studies and in Paper I, the effectiveness has not been formally tested. Neither have the graph based approaches, metrics, or the ENG/ENM-model developed in Paper II. These were designed with the aim of being operational in planning assessments and design; some of the potential was explored in Paper II, but their operational effectiveness needs to be formally tested as well.

Although the spatial maps proved to be useful to communicate predictions, a better understanding of the complex nature of the ecological infrastructure, and as negotiation tools, the power of the map as a concrete artifact that could be misused or infect the dialogue was evident. Even though for example the uncertainty in these models was communicated, the exact location of for example a border between habitat network and non-habitat network could end up being intensively debated, both by those who felt that an area should be included in the habitat network, and those that felt that an area of their interest was intruded by the habitat network. Even the choice of color for illustrating the habitat network turned out to be important, and the 'wrong' color could lead to politically charged situations. It seems clear that deceivingly accurate and objective maps of this kind are very strong communicative tools and, as such, they *will* be used politically, sometimes even to promote conflicting ideas.

7.6. Resilience, robustness, and redundancy

Within urban and regional planning and design, it is of interest to know which areas are suitable to develop without a large negative impact on the ecological integrity. One way of achieving this is to look for redundancies in the ecological network. However, one has to keep in mind that the resilience of the ecological network is degraded when removing spatial redundancy in the network (Janssen et al., 2006). Indeed, one of the results in Paper II illustrated how to *increase* resilience by finding areas suitable for *creating* spatial redundancy in important structures. A deeper understanding of the ecological network structure helps to select areas where redundancy can be increased as well as areas that are of less ecological importance and where redundancy could be decreased, allowing for other functional aspects of the landscape, such as housing.

However, there are intricate and complex trade-offs to watch out for, and a tool for finding redundancies (Paper II) can lead to counterproductive effects. Even though the robustness of the model can be improved with respect to a number of proposed planning scenarios and uncertainty in parameters, it does not automatically imply that the social-ecological system is resilient. Indeed, the more efficiently we plan, even though the intention is planning for sustainability, the more rigid the structure of the system may become. In effect, this can dramatically degrade the resilience of the social-ecological system, making it even more vulnerable to sudden changes (Holling, 1987). This apparent paradox calls for a shift in mental models, where we accept the limitations of the human ability to plan and adopt steady-state inspired policies, and move towards an adaptive governance of the multidisciplinary landscape which we are a part of (Folke, 2006).

Yet, even within adaptive governance and management, we are still faced with a need to prioritize elements of nature, in particular in urbanizing regions with expensive land and increasing pressure on the remaining lots of undeveloped land! Choices *have* to be made and in an environment such as a heavily urbanizing area, changing the land use of an area that has already been engulfed by the urbanization process is not possible, hence restricting the options within adaptive management. In such an environment, I argue that being able to strategically plan for spatial redundancy (Paper II), may uphold some of the spatial resilience in the form of ecological memory within the system (Bengtsson et al., 2003).

A suite of carefully selected ecological profiles (Paper I) may also promote resilience if an overlapping of function through species redundancy within scales, can be reinforced across scales (Peterson et al., 1998). This species redundancy, distributed across a range of spatio-temporal functional scales, can be an important factor contributing to response diversity (Elmqvist et al., 2003), which is an important component in the sustainment of ecological resilience and ecosystem services.

7.7. Sources, sinks, and barriers

In many ecological applications of least-cost modeling, the friction values are often related to a mixture of energy expenditure, behavioral aspects, and mortality risks (e.g. Ray et al., 2002; Adriaensen et al., 2003; Joly et al., 2003; Theobald, 2006). As a consequence, areas with high mortality are assigned a higher friction value, which in effect results in a reduction of the accessible patch area in the habitat network map. In network analysis, a more appropriate approach could be to link the mortality risks to a reduction of the surviving number of propagules flowing through the network. In Paper II, the mortality risks were separated from energy expenditure, only acknowledging energy expenditure as being part of the effective distance. This opens up for other methods for handling the mortality risks, such as probability-related models, which in turn can result in both a better geographic representation of the potentially accessible patch, and a separate analysis of how to mitigate mortality risks.

As an example, roads are often considered to be barriers (e.g. Forman & Alexander, 1998), but I argue that, in many landscape ecological cases, several roads should instead be regarded mainly as population sinks within the network (population sinks; Pulliam, 1988) instead of barriers. A sink can then be modeled using a node with consumption (i.e. negative value) instead of production. This is particularly the case for the common European toad in Paper II, because some toads (and many other amphibians) may have no problem crossing certain roads, and often do not even avoid crossing. Once on a road, however, there is a substantial risk of being killed (e.g. Fahrig et al., 1995; Hels & Buchwald, 2001). In order to better reflect this in environmental assessments, this loss of individuals due to certain roads being sinks should be emphasized and not disguised by regarding the problem simply as a case of fragmentation due to roads as barriers. By not including the mortality in the friction value used for least-cost analysis, the network map clearly illustrated the potential sinks, and could thus be used to guide a more ecologically sustainable design of the landscape. Indeed, a short term solution could in fact be to *create* barriers along the roads that currently act as sinks in the landscape.

7.8. Dealing with subjectivity, errors, and uncertainty

Although the ecological profiles, graph theoretic networks, and habitat network maps were created within the realm of natural science, using models, parameters, statistics and multi-dimensional diagrams, they are of course far from objective. In both Paper I and Paper II, as well as the report on the Eurasian Lynx (Zetterberg, 2007), several of the parameters used for modeling the habitat network maps were gathered using expert judgment, a method which introduces subjective uncertainties. These uncertainties could possibly be bracketed using bounding habitat suitability maps, as suggested by Ray and Burgman (2006), but the models should ideally be validated. The fact that both resolution and detail in the datasets often vary among different administrative units can also introduce artifacts in the results.

The ecological profile is also a highly subjective construct. As an example, how does one really define habitat requirements? Is it simply area requirements of some habitat, quality-weighted or not, or is it dependent on the internal configuration of different resources? The life-cycle based approach that was suggested in Paper II is a step in a more detailed direction. This potentially narrows down the vagueness of the profile dimensions, albeit still subjective, but it makes modeling more complicated and model validation more costly due to the increase in validation data requirements. There is also a clear trade-off between increase in detail and potential accuracy on one hand, and the decrease in communicative power due to more complexity. Opdam et al. (2008) simplify the parameters into a matrix of total area requirements, and inter-patch distance for each ecosystem type.

However, I argue that when modeling species, be it single or several, it is crucial to capture the parameters that may be significant in illustrating the impacts on critical parts of the system, which means that the choice of parameters is highly context and case dependent. I hypothesize that the benefits of an increase in detail and flexibility of parameters, such as higher ecological relevance, outweigh the potential communicative loss due to an increase in complexity. It may even end up *improving* the total understanding of the system among multidisciplinary stakeholders, even those with little or no ecological knowledge, compared to easy-to-understand but ecologically questionable simplifications.

A drawback of a more context dependent and detailed ecological approach is the need for expert knowledge. On the other hand, the need for, and use of expert knowledge is not unusual in planning and decision making when assessing for example, potential impacts on traffic systems, commerce, social equity or health related issues. In order to meet the need for an iterative planning process, the results from the initial expert output could be transformed into an intermediate knowledge structure, usable by for example non-ecologist planners in exploring, testing and changing potential effects of different scenarios. The final proposed scenarios resulting from this process could then again be re-modeled by experts. Another source of subjectivity is within the evaluation of the results, which can also be handled using expert panels (Geneletti, 2005, 2007).

On a more general level, both the habitat network maps in Paper I, and the graphs and network metrics in Paper II, are susceptible to great uncertainty at this stage due to the uncertainty related to landscape data (Rae et al., 2007), uncertainty related to the model structure and the methods used to create the graph, and due to lack of knowledge about the ecology of the modeled species. Notwithstanding their limitations due to uncertainties, both the habitat network models and the graph theoretic models are useful as heuristic frameworks to explore the ecological infrastructure. The graph theoretic analysis can be driven with very little data (Bunn et al., 2000; Urban & Keitt, 2001), and critical parts of the network can still be identified, for example using patch importance indices found through patch removal (Keitt et al., 1997) and searching for thresholds, as was done in Paper II. Similar techniques have been used to explore tradeoffs between a patch's contribution to overall connectivity and its corresponding increase in protected area (Rothley

& Rae, 2005), or to analyze critical thresholds in connectivity with respect to dispersal distance (e.g. Keitt et al., 1997).

8. Conclusions

The habitat network tool that was introduced and tested in the case studies was shown to be useful in the urban and regional planning projects, as well as for the management of the Eurasian lynx. Areas within the city of Stockholm, in which suggested developments of the planning scenarios were detrimental to habitat networks, were successfully localized. This information on areas of conflict was subsequently used for decision support. An attempt at quantifying habitat loss and the splitting of habitat networks was able to predict negative impacts of the four planning scenarios tested in the Regional Development Plan (RUFS 2010).

A strong indication of the effectiveness of the habitat network tool is the fact that it has recently been successfully implemented by several of the clients. Indeed, the results of the commissioned cases within the research project, such as the GIS-layers of habitat networks, are actively used in planning, assessments, inventories, and monitoring by Stockholm Municipality, the County Administrative Board of Stockholm, and the Office of Regional Planning and Urban Transportation. The case studies also showed that the GIS-based habitat networks were useful as communicative tools in participatory approaches involving several different kinds of stakeholders. In these, both the ecological profile, and the corresponding habitat network map as well as the specific profile species were needed and complemented each other in the participatory process. The ecological profile and the habitat network aided in the understanding of the systems perspective, and the profile species helped by appealing to the imagination of the stakeholder, and by providing real examples of the profile needed for acceptance of the profile concept.

The case studies expressed a need for ecologically relevant systemic metrics that can be used as indicators within planning and assessment activities. There was also a need to prioritize among areas within the habitat networks and to clearly distinguish ecologically critical structures *within* the network. Another desire that was expressed was the ability to highlight structures that can be used to *improve* the network through an effective redesign of the landscape.

The proposed ENG/ENM-model presented in Paper II, was designed to meet these needs. Through the design of an operational model, linking graph theory to operational maps, graph-theoretic methods can be included in a GIS. This facilitates a context dependent, spatially explicit, and geographically defined network analysis in a working environment already in use by planners and designers. Inherent in network analysis and graph theory is the ability to capture complex interactions and emergent phenomena across the entire network, in ways that could never be achieved by structural or statistical approaches. It has the potential of finding the critical interactions within some part of the network that make the difference between two completely different outcomes.

Indeed, these aspects were explored by illustrating how the model could be used in finding important regions within a network, as well as how to, either increase resilience through spatial redundancy, or direct housing development to redundant areas. In addition, it was illustrated how the tool can be used in urban design to improve the ecological quality, both from a systems perspective, and a site perspective. The ENG/ENM-model places the graph theoretic toolbox in a geographically defined landscape, providing completely new insights for physical planning, and environmental assessment activities.

It is hoped that the results and developments presented in this thesis will improve the knowledge transfer through the science-policy interface by facilitating the use of landscape ecological aspects in assessments, planning and design, as well as providing insight into the needs for effective application.

9. Future research

There is a strong need for further development and testing of ecologically relevant, graph-based metrics. Most graph-based metrics that are currently used are direct adaptations of classical counterparts from other disciplines. A general requirement is that the metrics can be validated. This will be a major challenge, but an interesting way of validating both the proposed landscape ecological models and the graph-based metrics is through genetic approaches. It is for example argued that the betweenness centrality index introduced in this thesis could be tested this way. An ecological interpretation of betweenness centrality is that it may indicate areas with long-term genetic variety. The index identifies the patches routing the highest proportion of the shortest effective dispersal paths between two randomly selected patches. Since the algorithm is influenced by all patches, including those that are far from each other and thus probably more genetically different, patches with the highest betweenness may indicate the genetically most diverse paths through the network. In the meantime, at least the uncertainty of any metric due to the uncertainty in model structure and input parameters can be explored through forward uncertainty analysis.

Another way of validating the model is to use empirical observations when possible. Recent availability of new data opens up for interesting possibilities regarding the habitat network model. For example, in the case study on the ecological conditions for the Eurasian lynx in Stockholm County, the model was used to predict areas of potential colonization by lynx within three years. Now, two years after the study, a large scale inventory of lynx in three adjacent counties has recently been completed, and preliminary results indicate that a large portion of the predicted areas have been colonized.

When focusing on landscape-species interactions, it is easy to forget the importance of interactions between the species. There have recently been some interesting developments within the field of spatial food-webs, but there is a need to also consider non-trophic dynamics; both antagonistic dynamics, such as competition, and parasitism, and mutualistic ones, such as pollination.

Although it is argued that the graph based landscape ecological approaches can be effectively applied in physical planning and environmental assessments, this has not been formally tested. The validity of this argument would benefit from further case studies focusing on aspects such as usability, understandability, credibility, and negotiation flexibility. A number of communicative aspects could be tested; in particular the trade-off between accurate results and few parameters. Which is easier to understand, or more credible, and for which stakeholders? What kinds of boundary objects in the science-policy interface are effective for negotiation? Should they for example be based on general numeric parameters such as the trade-off between the total protected area and number of potentially affected species? Or around the trade-offs between the predicted, explicit, spatial location and the actual species that may be affected? A major challenge will be finding a good trade-off between the communicative aspects and the ecological relevance.

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