DOCTORAL THESIS

Effects of Landscape Patterns on Small Mammal Abundance
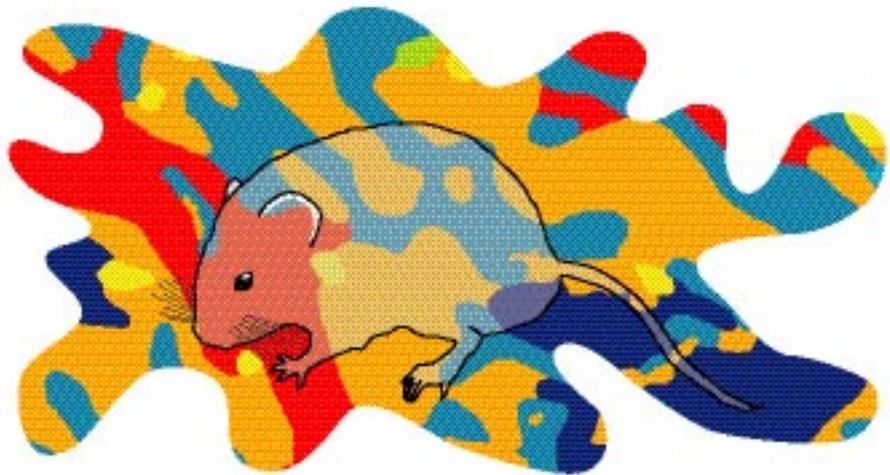
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ACKNOWLEDGEMENTS

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Frauke Ecke, Div. of Applied Geology, LTU, 2003

LIST OF PAPERS

This Doctoral Thesis is a summary and discussion of the following six appended papers to which I refer by their Roman numerals.

I   Ecke, F & Peterson, J. Patterns of model performance in predictive habitat modelling. Submitted to *Landscape Ecology*.

II Ecke, F. Factors affecting performance of GIS-based predictive habitat models. Submitted to *International Journal of Geographical Information Science*.

III Ecke, F., Löfgren, O., Hörnfeldt, B., Eklund, U., Ericsson, P. & Sörlin, D. (2001) Abundance and diversity of small mammals in relation to structural habitat factors. *Ecological Bulletins* 49: 165-171.

IV Ecke, F., Löfgren, O. & Sörlin, D. (2002) Population dynamics of small mammals in relation to forest age and structural habitat factors in northern Sweden. *Journal of Applied Ecology* 39: 781-792.

V   Ecke, F., Hörnfeldt, B., Christensen, P. & Löfgren, O. Habitat selection and population dynamics of small mammals at different spatial scales in a Swedish mountain region. Manuscript.

VI Ecke, F., Christensen, P., Hörnfeldt, B. & Sandström, P. GIS-based identification of important landscape elements for predicting the occurrence of *Clethrionomys rufocanus*. Manuscript.

SUMMARY

Several studies indicate a long-term decline in the numbers of voles in northern Fennoscandia. Altered land use and forest management practices have been proposed as possible causes of the decline. This doctorial thesis aimed to identify, at different spatial scales, landscape patterns that are important for the abundance of small mammals and that might be related to the decline. For this purpose, general trends and aspects of spatial habitat modelling (i.e. spatial modelling of the occurrence, abundance and viability of species) were first reviewed. Secondly, trapping data from three large-extent monitoring programs were related to habitat factors at different spatial scales. For these analyses, a broad range of statistical and GIS (geographic information system) related methods was applied. At the microscale (trap-station, extent ≤ 10 m) and mesoscale (transect, length 90 m), structural habitat factors such as coarse and fine woody debris, umbrella vegetation and structural complexity of the forest floor were identified as important factors influencing small mammal abundance. Small mammal densities were related to the percentage landcover of vegetation types at the micro-, meso-, macro- (subarea/landscape, 1×1, 2.5×2.5 and 2×5 km) and regional scale (overall study area, $20 \times 20 - 80 \times 80$ km). The spatial continuity (non-fragmentation) of old-growth pine forest patches at the landscape scale was positively related to the abundance of *Clethrionomys rufocanus*, the species that showed the most pronounced long-term decline in numbers. The results of the research presented here strongly suggest that altered land use might indeed be involved in the decline in numbers of *C. rufocanus* in managed forest areas in northern Fennoscandia. To reveal and test responses of *C. rufocanus* and other small mammals to changes in landscape patterns in more detail, this work proposes further application of broad scale approaches. These approaches, e.g. GIS-based prediction of areas with currently high abundance of *C. rufocanus* can be tested by field sampling of the type applied in this thesis. Such approaches should consider the key aspects identified in the reviews on GIS-based habitat modelling, e.g. reconciling the scale of the population dynamics of small mammals with the scale (resolution and extent) of the landscape data, the application of different modelling approaches and the performance of sensitivity analysis of models.

SAMMANFATTNING

Flera studier visar på minskande sorkstammar i norra Fennoskandien. En ändrad markanvändning och ett intensifierat skogsbruk har framförts som möjliga orsaker till nedgångarna. Den här avhandlingen hade till syfte att identifiera landskapsmönster på olika spatiala nivåer som är viktiga för smådäggdjursbestånden och som kan vara relaterade till beståndsnedgångarna. För detta ändamål utfördes en litteraturgenomgång av generella trender och aspekter i spatial habitatmodellering, dvs. rumslig modellering av olika arters förekomst, individantal och överlevnadsförmåga. Fångstdata från tre storskaliga övervakningsprogram relaterades till habitatfaktorer på olika spatiala nivåer. För dessa analyser användes ett antal olika statistiska och GIS- (geografisk informationssystem) baserade metoder. På mikro- (fångstpunkt, utsträckning ≤ 10 m) och mesoskalan (transekt, längd 90 m) identifierades strukturella habitatfaktorer som t.ex. fin och grov död ved, skärmvegetation och skogsmarkens strukturella komplexitet som viktiga faktorer för smådäggdjurens individantal. Smådäggdjurens täthet påverkades av den procentuella andelen av olika vegetationstyper på mikro-, meso-, makro- (delområde/landskap, 1×1, 2.5×2.5 och 2×5 km) och regional skala (undersökningsområde, $20 \times 20 - 80 \times 80$ km). Den spatiala sammanhållningen (icke-fragmenteringen) av gamla tallskogsbestånd på landskapsskalan var positivt korrelerat med individantalet bland *Clethrionomys rufocanus*, den art som visade den tydligaste beståndsnedgången i det analyserade materialet. Avhandlingens resultat visar att ändrad markanvändning antagligen är involverad i nedgången av *C. rufocanus* i av skogsbruket påverkade områden i norra Fennoskandien. För att mera detaljerat kunna visa och testa responsen av *C. rufocanus* och andra smådäggdjursarter på landskapsförändringar, föreslås ytterligare användning av storskaliga undersökningsmetoder. Dessa metoder, t.ex. GIS-baserad förutsägelse av områden med i nuläget höga individantal av *C. rufocanus*, kan testas med fältförsök som de visats i denna avhandling. Sådana undersökningar borde ta hänsyn till kärnaspekterna som identifierades i genomgången av GIS-baserad habitatmodelleringen, t.ex. avstämningen av skalan på populationsdynamiken bland smådäggdjur med skalan (upplösning och areal) på landskapsdata, användningen av olika modelleringstyper och genomförandet av modellkänslighetsanalys.

ZUSAMMENFASSUNG

Mehrere Studien deuten auf einen langfristigen Rückgang der Individuenanzahl verschiedener Kleinsäugerarten (*Microtidae*) im Norden Fennoskandiens hin. Geänderte Landnutzung und intensivierter Waldbau wurden als mögliche Ursachen des Rückganges genannt. Diese Doktorarbeit hatte zum Ziel, auf verschiedenen räumlichen Skalen Landschaftsmuster zu identifizieren, die für die Abundanz von Kleinsäugern wichtig sind, und die mit ihrem Rückgang in Verbindung stehen können. Generelle Trends und Aspekte der räumlichen Habitatmodellierung (Modellierung von Vorkommen, Abundanz und Lebensfähigkeit von Arten) wurden dargelegt. Fangdaten von drei großflächigen Überwachungsprogrammen wurden mit Habitatfaktoren auf verschiedenen räumlichen Niveaus in Beziehung gesetzt. Für die Analysen wurde ein breites Spektrum an statistischen und GIS (Geographische Informationssysteme) – basierten Methoden verwendet. Auf der Mikroskala (Fangstelle, Ausdehnung ≤ 10 m) und Mesoskala (Linienprofil, Länge 90 m) wurden strukturelle Habitatfaktoren wie z.B. grobes und feines Todholz, Schirmvegetation und strukturelle Komplexität des Waldbodens als wichtige Faktoren für die Abundanz von Kleinsäugern identifiziert. Individuendichten von Kleinsäugern standen mit dem prozentualen Flächenanteil von Vegetationstypen auf der Mikro-, Meso-, Makro- (Landschaft, 1×1, 2.5×2.5 und 2×5 km) und Regionalskala ($20 \times 20 - 80 \times 80$ km) in Beziehung. Die räumliche Kontinuität (Nichtfragmentierung) von alten Kiefernwaldflächen war positiv mit der Abundanz von *Clethrionomys rufocanus*, der Art mit dem deutlichsten Rückgang in der Individuenanzahl, korreliert. Die Ergebnisse dieser Arbeit deuten stark darauf hin, dass veränderte Landnutzung in der Tat eine Abnahme der Individuenzahl in *C. rufocanus* in forstwirtschaftlich genutzten Gebieten Nord-Fennoskandien bewirkt. Um die Reaktion von *C. rufocanus* und weiterer Kleinsäugerarten auf Veränderungen in Landschaftsmustern detaillierter zu untersuchen, werden in dieser Arbeit weitere großflächige Untersuchungsmethoden vorgeschlagen. Diese Methoden, z.B. die GIS-basierte Identifizierung von Gebieten mit zur Zeit hoher Abundanz von *C. rufocanus* können mit Feldversuchen, wie sie in dieser Arbeit angewandt wurden, getestet werden. Solche Methoden sollten Kernaspekte, wie sie in den Studien der GIS-basierten Habitatmodellierung identifiziert wurden, berücksichtigen. Dazu gehören die Anwendung verschiedener Modellierungstypen und die Durchführung von Analysen zur Modellempfindlichkeit; weiterhin sollte die Skala zur Erhebung der Daten zur Populationsdynamik von Kleinsäugern mit der räumlichen und zeitlichen Auflösung der Landschaftsdaten abgestimmt werden.

1   INTRODUCTION

1.1   Landscape ecology

In the early 1980s, landscape ecology evolved from a descriptive discipline to an accepted quantitative and experimental science (Naveh and Lieberman 1984, Forman and Godron 1986, Hobbs 1999). Modern landscape ecologists study the spatial variation in the structure, function and change of heterogeneous land areas that are composed of interacting ecosystems (Forman and Godron 1986, Forman 1997). In the last decade, landscape ecological studies elucidated the relation between landscape structure (synonymous with landscape patterns) and landscape functioning (synonymous with landscape processes) at different spatial scales (Forman 1997, Risser 1999). Landscape patterns are characterized by the amount and geographical distribution of patch types, patch type diversity and the interspersion, connectivity and fragmentation of patch types (McGarigal and Marks 1995). Landscape processes are related to the dynamics in landscapes: for example, dispersal of species, changes in landscape structure and energy fluxes among landscape elements and ecosystems (Forman and Godron 1986, Forman 1997).

The proportional area of patch types in a landscape, i.e. habitat quantity, is the most commonly applied measure of landscape patterns (e.g. Li et al. 1997, Kobler and Adamic 2000, Luoto et al. 2002). However, species occurrence, abundance and persistence also depend on other characteristics of landscape patterns that might even be of greater importance, e.g. patch area and patch isolation (Hanski 1994; 1999) as well as habitat fragmentation and connectivity (e.g. Bennett 1990, Andrén 1992, Gaines et al. 1992, van Apeldoorn et al. 1992, Andrén 1994, Reunanen et al. 2002).

1.2   Geographic information systems (GIS)

Over the last 20 years, geographically related data on the spatial extent of landscapes and regions has become more available, computer power has steadily increased and GIS software has become more functional and easier to use. In a GIS, spatial digital information is stored in layers and the information can be visualized, combined and reanalyzed (Burrough 1986, Burrough and McDonell 1998). Output layers can be imported into software packages for further statistical analyses or for the quantification of landscape structure (e.g. using FRAGSTATS, McGarigal and Marks 1995). GIS layers of landcover types, soil type, topography and climate are commonly applied for the identification and prediction of habitat and species abundance at broad spatial scales (e.g. Tucker et al. 1997, Dettmers and Bart 1999, Woolf et al. 2002). Remote sensed data, e.g. satellite images are today the primary source of landcover maps. Further, in Fennoscandia, satellite images have been used for the estimation of forest type and forest productivity (Reese et al. 2002). These estimates are applied in landscape ecological studies (e.g. Reunanen et al. 2000, Reunanen et al. 2002). Today, GIS and software packages quantifying landscape structure are indispensable tools in the study of species responses to landscape patterns and processes (e.g. Withers and Meetenmeyer 1999, Skidmore 2002).

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1.3 Spatial scale – extent, resolution and zoning

Ecologists consider spatial scale a dichotomous term referring to a) grain (smallest distinguishable area; synonymous with resolution) and b) extent (overall study area) (Turner et al. 1989, Wiens 1989).

The power of research aimed at the detection of ecological patterns and processes has emerged as scale-dependent (e.g. O'Neill et al. 1986, Turner et al. 1989, Wiens 1989, Turner 1990, Levin 1992, Stoms 1992, Aspinall and Pearson 1993). Several studies have demonstrated information loss on a gradient from fine to coarse grain (Laymon and Reid 1986, Turner et al. 1989, Stoms 1992, Cardillo et al. 1999). Studying the effect of grain on the detection of landscape patterns, Turner et al. (1989) demonstrated that making grain coarser resulted in the loss of rare landscape types. In addition, patterns emerge as noise when grain is too fine and as constants when grain is too coarse (Aspinall and Pearson 1993).

Since the late 1970s, scale effects in landscape ecological studies have been studied in the context of what is referred to as the modifiable areal unit problem (MAUP) (Openshaw and Taylor 1979, Jelinski and Wu 1996, Hay et al. 2001). The MAUP not only deals with arbitrarily changing grain and extent, but also with the zonal or aggregation problem (Figure 1). The zonal problem addresses the consequences of pooling/aggregating data from areal units into different zones without changing grain and extent (Jelinski and Wu 1996, Wu et al. 2002). The effect of changing grain and extent on analytical results have frequently been studied (see above and Prentice et al. 1992, Collingham et al. 2000, Cowley et al. 2000, Wu and Smeins 2000, Wu et al. 2002). The zonal problem as part of the MAUP has however hardly been investigated (Jelinski and Wu 1996).

1.4 Spatial modelling

The number of studies on GIS-based spatially explicit habitat modelling (modelling of e.g. the occurrence, abundance and viability of species) is steadily increasing. Applications of GIS-based predictive models in landscape ecology range from the forecast of the presence (Cherrill et al. 1995b, Van Horssen et al. 1999, Kobler and Adamic 2000, Woolf et al. 2002), abundance (Koutnik and Padilla 1994, Gustafson et al. 2001, Lusk et al. 2002), diversity (Cardillo et al. 1999, Jorgensen and Demarais 1999, Hortal et al. 2001) and viability (Lindenmayer and Possingham 1995, Possingham and Davies 1995) of species, populations and communities, to the study of the impact of climate change on species distributions (Cameron and Scheel 1993, Carey 1996, Iverson and Prasad 1998). However, spatial modelling faces problems related to e.g. the accuracy and precision of the input data (Burrough 1986, Burrough and McDonell 1998), error propagation (Beck 1987), model sensitivity and evaluation (Jørgensen 1994) and available measures of model performance (Fielding and Bell 1997, Congalton and Green 1999). Further, in spatial modelling, one has to choose among an increasing number of available modelling techniques (e.g. overlays, logistic regression, discriminant analysis, machine-learning algorithms, geostatistics). Due to the increasing number of studies on spatial explicit modelling, it appears necessary to consider and elucidate the above-mentioned aspects in more detail. Such an undertaking should help

to improve the performance of spatial habitat models and to enhance the application of spatial modelling in nature conservation and land management.

1.5 Dynamics of small mammal populations

Small mammals are central to the functioning of the terrestrial ecosystems in northern Fennoscandia because they are involved in the dynamics on several trophic levels. They

A

Changing grain

B

Changing extent

C

Zoning

Statistical implications

Making grain coarser results in the loss of rare landscape types (Turner et al. 1989). Increasing grain while keeping extent constant results in decreased variance (Wiens 1989).

Increasing extent while keeping grain constant, results in greater habitat heterogeneity and thus increased variance (Wiens 1989).

Variance decreases with increasing aggregation/zoning (Jelinski and Wu 1996).
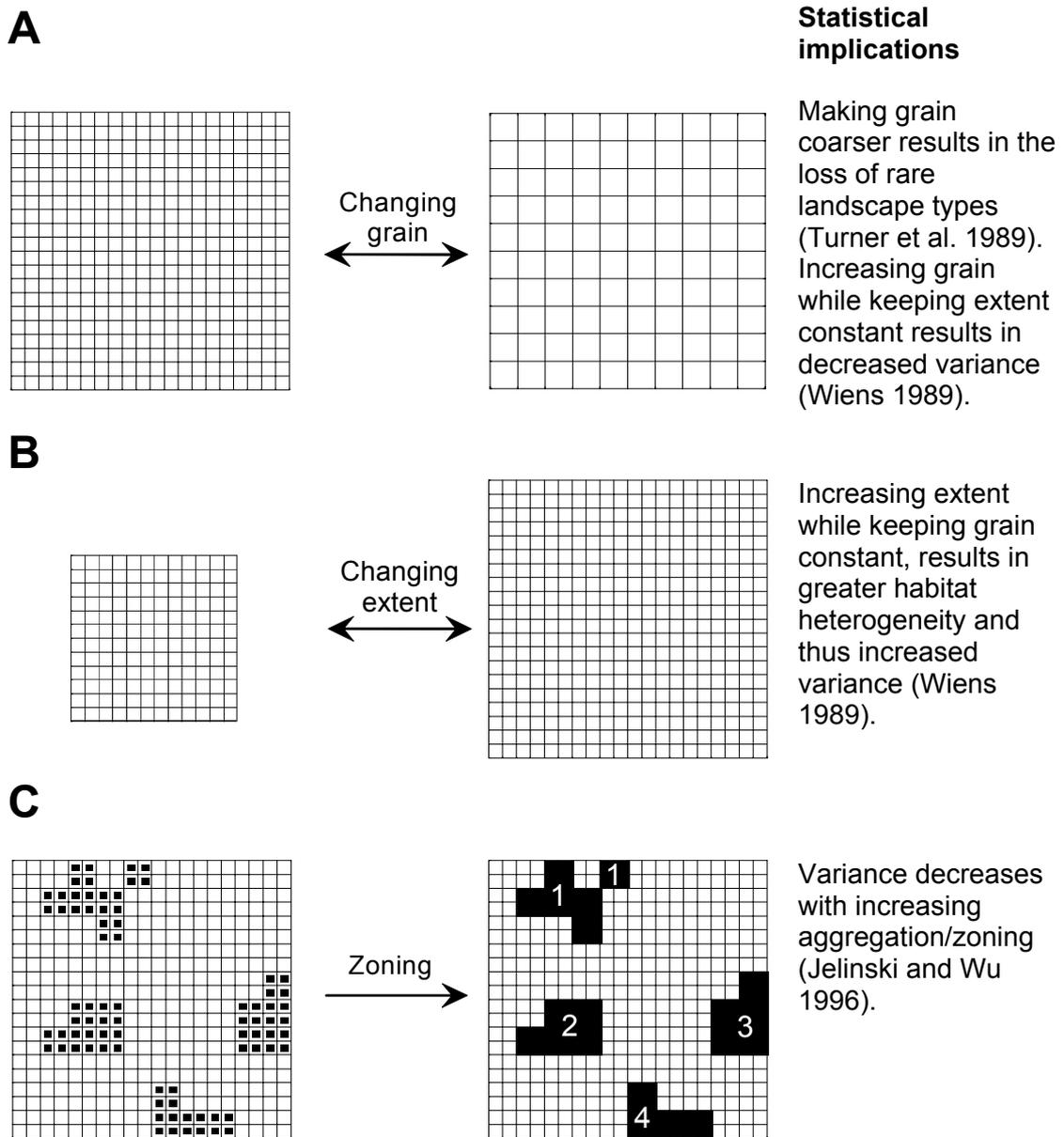
Figure 1. Schematic illustration of the three processes related to the modifiable areal unit problem (MAUP) and their statistical implications: Changing grain while keeping the extent constant (A), changing extent while keeping grain constant (B) and zoning/aggregating data from independent sample units (filled squares) to a higher hierarchical level (C).

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constitute staple food for many mammalian and avian predators (e.g. Englund 1970, Lindström 1982, Erlinge et al. 1983, Hörnfeldt et al. 1990, Tannerfeldt and Angerbjörn 1996), they consume plants, lichens, fungi and invertebrates (e.g. Ericson 1977, Gebczynska 1983, Hansson 1988), and disperse e.g. mycorrhizal fungi (Terwilliger and Pastor 1999) and act as reservoirs and vectors of diseases (e.g. Niklasson et al. 1995). In northern Scandinavia, small mammals exhibit regular/cyclic multi-annual population fluctuations with 3 to 4 years between the cycles (e.g. Hansson and Henttonen 1985, Hörnfeldt 1991; 1994).

There is no general agreement as to which factors regulate the densities of small mammal populations, but predators, food and/or population density have been suggested as some of the important factors (e.g. Krebs and Myers 1974, Hörnfeldt 1994, Stenseth 1999). Habitat factors that provide shelter and/or food are crucial to reproduction and survival of small mammals (e.g. Adler and Wilson 1987, Batzli 1992, Hansson 1997) and should also be important for habitat selection of individuals (Hansson 1978; 1982, Henttonen and Hansson 1984, Adler 1985, Morris 1995; 1996). In boreal forests, shelter is provided by e.g. coarse and fine woody debris (CWD and FWD), vegetation in the field, shrub and tree layer, and boulders (Hansson 1978, Cockburn and Lidicker 1983, Pucek 1983, Chetnicki and Mzurkiewicz 1994, Batzli and Lesieutre 1995, Morris 1997, Johannesen and Mauritzen 1999, Ecke et al. 2001). However, habitat preferences of small mammals in relation to such factors have mostly been studied on fine grains (< 10 m) and on small extents (< 1 sq km). In contrast, density responses of forest-dwelling small mammals to landscape composition have hardly been investigated (but see Angelstam et al. 1987, Delattre et al. 1992).

Studies of small mammal population dynamics have been performed on a broad range of grains and extents (e.g. Krebs and Myers 1974, Stenseth and Ims 1993). Most studies designed to monitor long-term population dynamics over large areas must refer to subsets of snap trapping data. For the purpose of analysis the subsets are commonly aggregated (zoned) to reveal population patterns for larger areas (e.g. Myllymäki *et al.* 1977, Henttonen *et al.* 1985, Hörnfeldt 1994, Steen *et al.* 1996, Bjørnstad *et al.* 1999, Ecke *et al.* 2001). In such cases, zoning generally follows the hierarchical structure of the study design. Ecke et al. (V, 2001) aggregated the data of trap-stations belonging to a transect. Morris (1987) aggregated trap-stations on 9 × 15 trapping grids to subplots of 3 × 3 trap-stations. However, to our knowledge, the effect of such aggregations on the results of the analysis of population dynamics of small mammals has not been dealt with in literature.

Several studies indicate a long-term decline in the numbers of cyclic voles in northern Fennoscandia, especially of the grey-sided vole, *Clethrionomys rufocanus* (Figure 2, Paper VI, e.g. Hörnfeldt 1991, Hanski et al. 1993, Hörnfeldt 1994; 1995, Hansson 1999). Altered land use and forest management practices, together with increased fragmentation of important reproduction habitats have been suggested as possible causes of the decline (Hörnfeldt 1995, Hansson 1999, Hörnfeldt 2003). However, the relationship of different landscape patterns (e.g. habitat fragmentation and connectivity) to densities of *C. rufocanus* has not been studied previously. Further, at finer scales, detailed analyses of the relationship between the population dynamics of small mammals and structural habitat factors (providing shelter) that are altered by forestry are scarce.

2   OBJECTIVES

The objective of this study was to investigate whether landscape patterns affect the abundance of small mammals at different spatial scales.

The focus has been on the following four questions:

- What are the general achievements and challenges in GIS-based habitat modelling?

- What habitat factors are crucial to small mammal abundance at different spatial scales?

- Is the abundance of small mammals determined by the availability of landscape elements and/or landscape structure?

- Are patterns in small mammal abundance more distinctly revealed at particular spatial scales of analysis?

3   MATERIAL AND METHODS

3.1   Literature review

General trends in the patterns of model performance in GIS-based predictive habitat modelling were reviewed and reanalyzed for 40 previously published international
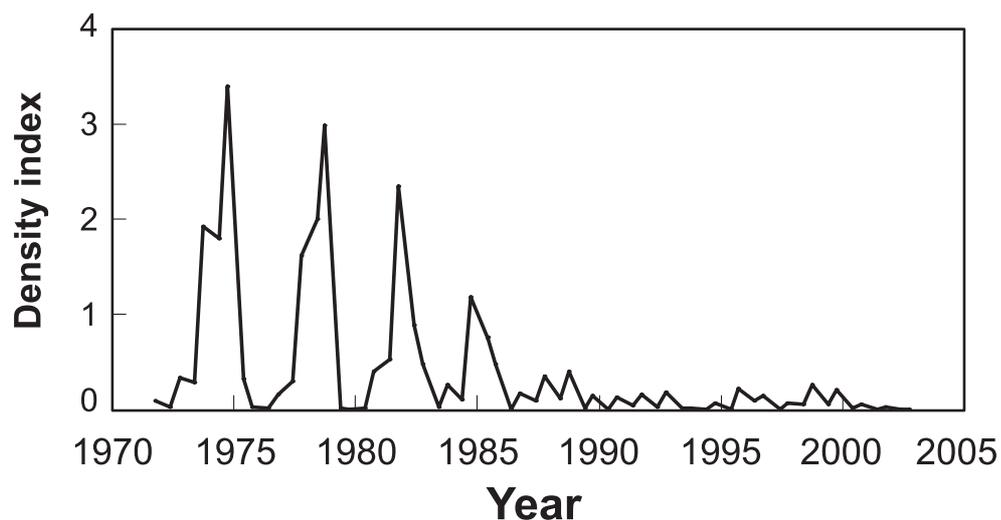

Figure 2. Mean density index for *C. rufocanus* for the whole study area near Umeå. Density indices are given for pooled spring and autumn trappings in 1971 − 2002 (Paper VI).

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studies (Paper I). Emphasis was placed on the relation between model performance and attributes of the predicted parameters, e.g. grain (smallest distinguishable area), extent (overall study area), home range and taxon of studied species, and applied modelling method. Central factors affecting model performance in GIS-based predictive habitat modelling (i.e. predicting the occurrence, abundance or viability of species) were identified and reviewed (Paper II).

3.2   Study areas

The research questions outlined above were studied with data from three broad-scale snap-trapping monitoring programs located in northern Sweden (Figure 3). At the micro- and mesoscale, the relation between structural habitat factors and population dynamics was studied in a mountain region near Ammarnäs, Swedish Lapland and in lowland forests in the rural district of Älvsbyn (Paper III, IV). Trapping data from the Ammarnäs region were further analyzed to elucidate habitat selection and population dynamics at different spatial scales (Paper V). Key habitat sites at the landscape scale of the grey-sided vole *C. rufocanus* were identified in lowland forests near Umeå (Paper VI).

3.2.1 The mountain region (III, V)

According to Sjörs (1999), the mountain region is situated in the northern boreal subzone. However, slopes at higher altitude belong to the subalpine belt (Sjörs 1999). The vegetation period (average daily temperature $> + 5°C$) was about 115 days (Raab and Vedin 1995). Natural sub-arctic birch and coniferous forest of the heath type with either mosses or tall herbs in the bottom and field layer, respectively, dominated at low altitude. At higher altitudes, there was a gradual transition to different types of mires, meadows, heaths and nival snow patches. The field layer of the birch and coniferous forest of the heath type was dominated by *Vaccinium myrtillus* or *Empetrum nigrum* ssp. *hermaphroditum* with elements of herbs, e.g. *Solidago virgaurea* and *Geranium sylvaticum* and ferns, e.g. *Gymnocarpium dryopteris*. Tall herbs, e.g. *Trollius europaeus*, *Cicerbita alpina* and *Aconitum lycotonum* dominated the field layer of the birch and coniferous forest of the meadow type.

3.2.2 The lowland forests near Älvsbyn (IV)

The forests in this region are part of the middle boreal subzone (Sjörs 1999). The vegetation period was ca 140 days and land was covered with snow about 180 days/year (Raab and Vedin 1995). Eighty-three per cent of the rural district of Älvsbyn was covered by forests. Forty-six per cent of this area had forest stands younger than 50 years and 22% had stands older than 100 years (Skogsvårdsstyrelsen 1997). Forested areas were dominated by coniferous forests of the fresh heath type. Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) were the dominating tree species in this forest type. In the field layer, *V. myrtillus* and *V. vitis-ideae* predominated. Further characteristic plant species included *E. nigrum* ssp. *hermaphroditum*, *Deschampsia flexuosa*, *Orthilia secunda*, *Luzula pilosa* and *S. virgaurea*.

3.2.3 The lowland forests near Umeå (VI)

Like the lowland forests near Älvsbyn, the Umeå region is part of the middle boreal subzone (Sjörs 1999). The mean vegetation period was 150 – 160 days and snow cover lasted 150 – 160 days/year (Raab and Vedin 1995). In 1994 the Umeå region was comprised of 34% mixed forests, 21% thinnings/clear-cuts, 19% pine forest, 9% dry fen, 6% water, 6% agricultural land and 3% spruce forest (topographic map (Swedish National Land Survey) and forest parameters (Swedish University of Agricultural Sciences)). Vegetation type composition of coniferous forests in this region resembled that of the lowland forests near Älvsbyn. Due to isostatic rebound after the last glaciation, the study area is divided in an eastern part located below the highest post-glacial coastline and a western part located above the highest post-glacial coastline. Forests on soils located above the highest post-glacial coastline generally have a higher trophic status than forests on wave-washed soils below the highest post-glacial coastline (Lundmark 1986, Engelmark and Hytteborn 1999). There was also a climatic gradient
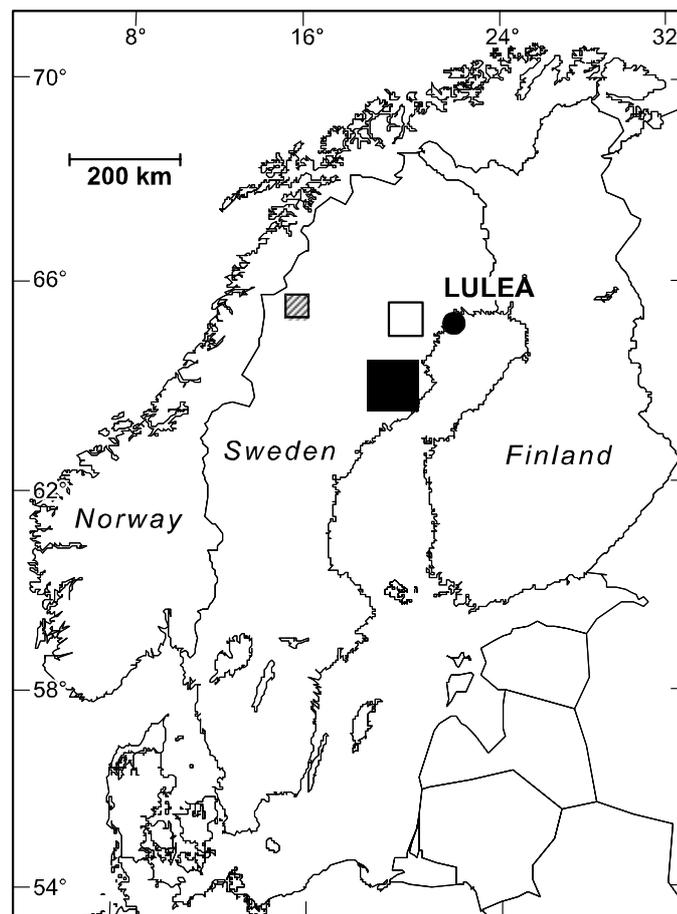

Figure 3. Location of the study area in the mountain region near Ammarnäs in Swedish Lapland (shaded square), and in the lowland forests near Umeå (filled square) and near Älvsbyn (open square). The size of the squares roughly reflects the size of the study areas.

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in the study area. The eastern parts compared with western parts of the study area, for example had a higher average precipitation per year, a higher average temperature per year and fewer days with snow cover (Raab and Vedin 1995).

3.3   The small mammal studies

Snap-trappings were performed along transects twice per year in spring and autumn. In the mountain region and in the lowland forests near Umeå, transects were regularly placed according to the Swedish National Grid (III, V, VI). Transects were therefore located in a range of different vegetation types and forests of different age classes. In contrast, the placing of transects in the lowland forests near Älvsbyn followed a stratified sampling design (IV). In this study, trappings were performed along transects running from immature forests of six different age classes (0 – 50 years) into adjacent mature forests (> 100 years) of the fresh heath type. Trappings were performed at trap-stations spaced at intervals of 10 m along 90 m transects within 1-ha sampling plots (III, V, VI) and of 30 m along transect of 420 m (IV).

Time series from Ammarnäs in 1995 – 1997 (III) and from Älvsbyn in 1998 – 2000 (IV) were analyzed for the relation between structural habitat factors and population dynamics of small mammals at the micro- (trap-station) and mesoscale (transect). In the mountain region, habitat preferences and population dynamics of small mammals were investigated at a range of spatial scales using time series from Ammarnäs in 1995 – 2002 (V). The importance of habitat factors to voles were analyzed at the landscape and regional scale, using trapping data sampled in the Umeå region in 1980 – 1999 (VI). For further details on the trapping methods see Paper III – VI.

3.4   Spatial scales studied

Habitat variables that generally are supposed to influence the dynamics of small mammals were measured and analyzed on a broad range of grains (smallest distinguishable area), extents (overall study area) and zones (aggregation units). The relationship between habitat factors and small mammal abundance was analyzed at the micro-, meso-, landscape/macro- and regional scale. For this purpose, habitat factors were studied in sample plots of 10 × 10 m centred on the trap-stations (III – V, microscale), in transects (length 90 m, mesoscale) (III, V, VI), in subareas (1 × 1, 2.5 × 2.5 and 2 × 5 km, macroscale) (V, VI) and in 20 × 20 – 80 – 80 km, encompassing the overall study area (V, VI, regional scale). To identify suitable sample unit sizes for the analyses of habitat responses of *C. rufocanus* at the landscape scale, sample units of 1 × 1 and 2.5 × 2.5 km centred on the 1-ha trapping plots were analyzed.

3.5   GIS and the analysis of landscape structure

Geographic information systems were applied in three instances. First, in studying the relation between structural habitat factors and population dynamics of *C. glareolus*, GIS were applied to identify suitable study sites (IV). Secondly, a vegetation map of the mountain region was digitized and vegetation type preferences of small mammals were analyzed at different spatial scales (V). Third, important habitat characters to *C. rufocanus* at the landscape scale were identified by combining and analyzing digital

available information on geography, topography, Quarternary deposits geology, landcover types and forest productivity in a GIS (VI). Landscape patterns of the produced GIS layers were analyzed with the FRAGSTATS 3.3 software (McGarigal and Marks 1995) for each 1×1 and 2.5×2.5 km subarea. These analyses included landscape measures that have been found central to the occurrence and abundance of other mammalian species (e.g. Hansen et al. 2001, Lurz et al. 2001, Reunanen et al. 2002). Landscape measures that were analyzed described different types of landscape patterns and included the area percentage of patch types, their connectivity, fragmentation, interspersion, shape and diversity.

3.6   Indices used and statistical analyses

Trapping indices were calculated as the accumulated number of individuals trapped per 100 trap-nights per species, sampling period and sample (III, V, VI), and as the total number of specimens trapped per species and trap-station in 1998 – 2000. The seasonal variation in the abundance of *C. glareolus* was estimated as the rate of change from summer to autumn and from autumn to summer (IV, e.g. Hörnfeldt 1994, Steen et al. 1996). As a rough measure on the occurrence of multi-annual density cycles, the index of cyclicity was calculated (III, V, Williamson 1972, Hansson and Henttonen 1985).

The effect of landscape patterns on the abundance of small mammals was analyzed with uni- and multivariate methods. Some key aspects of the multivariate methods used are given here. Details on the analyses are given in the respective paper. Analyzing the effect of multiple predictors on a dependent variable involves the risk of intercorrelation among the predictor variables (Jongman et al. 1995). Such intercorrelation among predictor variables impedes the assessment of the unique contribution of predictors in explaining the dependent variable. Principal component analysis (PCA) was therefore used to reduce the dimensionality of original data sets to a few essential uncorrelated components (Jongman et al. 1995, Sharma 1996, III, IV, VI). Principal components (PCs) extracted in the PCA were either directly used for further analyses (III, IV) or indirectly by re-extracting significant habitat variables (VI). Applying cluster analysis (Gordon 1999), time series were assigned to different groups that reflected fluctuation patterns (V, Saitoh 1987).

4   RESULTS AND DISCUSSION

In this thesis, patterns in spatial modelling of the occurrence, abundance and viability of species were analyzed (I) and the relevance of factors affecting the performance of habitat modelling was assessed (II). Using empirical data, the effects of habitat and habitat characteristics on densities of small mammals were studied at different spatial scales, from the micro-, meso- and macroscale (landscape scale) to the regional scale (III – VI).

4.1   GIS-based habitat modelling (I, II)

Fine grain data has been proposed to improve model performance in GIS-based habitat modelling (e.g. Pereira and Itami 1991, Cherrill et al. 1995a, Kobler and Adamic 2000). However, review of 40 published studies on GIS-based habitat modelling revealed no

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general trend in the relation between grain size and model performance (I). The review showed that one-species models performed better than multiple-species models. Model performance varied among modelling techniques (I, II) and with the seasonality of the studied system (I). There is a broad range of available techniques for predictive habitat modelling and their number is steadily increasing. The review provides guidelines (including a flow chart) for choosing appropriate techniques for the prediction of species occurrence, abundance and viability, based on the problem to be solved, the properties of the input data, and the assumption of the prediction techniques (II). It is further suggested that non-reconciling the scale of the phenomenon (e.g. population dynamics) with the scale of the instrument (i.e. grain and extent of input data) might hide any relation between the phenomena and predictor variables. When modelling the occurrence of mammalian species, grain size and overall study area should for example be adopted to the home range of the studied species (e.g. Cramer and Portier 2001). In one and the same study, model performance might be judged as either good or poor depending on what measures are used for estimating model performance. Even though the correct classification rate (CCR) is high (e.g. 90%), model performance measured by the positive predictive power might be low (e.g. 40%) (Fielding 2002). Thus, appropriate measures of model performance should be chosen according to the predefined context of model application. Sensitivity might for example be a suitable measure if a manager of nature conservation aims to locate rare species over large areas. This measure only considers predictions in relation to actual occurrence (Fielding and Bell 1997). In contrast, a land manager attempting to identify suitable routes for a new road has to be sure that no threatened species will be affected. In this case, model specificity might be a suitable measure, taking into account predictions in relation to actual absence (Fielding and Bell 1997).

4.2   Abundance of small mammals at the micro- and mesoscale

4.2.1 The importance of vegetation (III – V)

The cover of tall vegetation in the field layer was positively related to the overall abundance of *C. glareolus* (III, IV) (Table 1), *C. rufocanus* (Table 2) and *Myopus schisticolor* (III), to seasonal variation in the abundance of *C. glareolus* (III, IV), and to the occurrence of different functional groups of *C. glareolus* (IV). Vegetation provides not only shelter from (avian) predators (e.g. Batzli and Lesieutre 1995, Morris 1997), but also serves as a food source (Hansson 1985). Thus, cover of umbrella vegetation probably promoted reproduction and/or survival during summer (IV). However, only the abundances of those species that are normally associated with forest habitats, i.e. *C. glareolus*, *C. rufocanus* and M. *schisticolor* (V, e.g. Henttonen and Hansson 1984) showed a positive relation to the cover of umbrella vegetation (III, IV). The abundance of *Microtus agrestis*, *Lemmus lemmus* and *Sorex araneus* was not correlated with the cover of tall vegetation in the field layer (III), which could be explained by the habitat preferences of these species. *L. lemmus* and *M. agrestis* prefer open habitats like mires and meadows (V, e.g. Henttonen et al. 1977, Hansson 1978, Henttonen and Hansson 1984, Hansson 1987). *S. araneus* might have more demanding microclimate habitat requirements than are deduced from vegetation cover data alone.

Table 1. Summary of general responses (+ positive, - negative, ± no response) of the abundance of *C. glareolus* to habitat variables studied in the thesis, at different spatial scales, in upland and lowland forests in northern Sweden. The microscale refers to the extent of trap-stations, the mesoscale to the extent of 1-ha plot transects and the landscape scale to the extent of subareas. Blank fields refer to non-studied responses.

Habitat variable	Spatial scale			
	Upland forests			Lowland forests
	Micro	Meso	Landscape	Micro
Coarse woody debris		+		+
Fine woody debris		+		+
Umbrella vegetation		+		+
Boulders				±
Vegetation type				
Coniferous forest	+	+	+	
Broadleaved forest	+	+	+	
Heath	-	-	-	

The relationship between the temporal variation in vole densities and geographically and climatologically related variables is well acknowledged (e.g. Hansson and Henttonen 1985, Hörnfeldt 1994, Bjørnstad et al. 1998, Lambin et al. 1998, Saitoh et al. 1998). At the mesoscale, the cyclicity index of the densities of *S. araneus*, *L. lemmus* and *C. glareolus* were related to the percentage landcover of vegetation types (V). This result suggests that intervals of 300 m among transects were sufficient to promote different fluctuation patterns.

4.2.2 The importance of structural heterogeneity (III – V)

Structural heterogeneity was estimated as the cover of coarse and fine woody debris (III – V) and structural complexity of the forest floor (IV). The abundance of those species preferring forested habitats, i.e. *C. glareolus*, *C. rufocanus*, *M. schisticolor* and *S. araneus*, was positively related to structural heterogeneity (III – V) (Table 1, 2). Woody debris probably provided shelter in the form of covered runways and nests, and served (directly or indirectly) as a food source when vascular plants, lichens, mosses and fungi had colonized the substrate (Harmon et al. 1986). Decaying trees may also enhance the production of invertebrates (e.g. Samuelsson et al. 1994) which should be beneficial for *S. araneus* and most likely for the omnivorous vole *C. glareolus*. However, the abundances of species mainly occurring in open habitats, *M. agrestis* and *L. lemmus* (e.g. Hansson 1969; 1978, Henttonen and Hansson 1984, Hansson 1987), were not or were negatively correlated to structural heterogeneity (III, V). Considering demographic data, structural heterogeneity did not show any correlation with the occurrence of year-born breeders of *C. glareolus*, but did so for over-wintered breeders, adults and subadults (IV).

Table 2. Summary of general responses (+ positive, - negative, ± no response) of the abundance of *C. rufocanus* to habitat variables studied in the thesis at different spatial scales. The microscale refers to the extent of trap-stations, the mesoscale to the extent of 1-ha plot transects and the landscape scale to the extent of subareas. Blank fields refer to non-studied responses.

Habitat variable	Scale			
	Upland forests			Lowland forests
	Micro	Meso	Landscape	Landscape
Coarse woody debris		+		
Fine woody debris		±		
Umbrella vegetation		+		
Boulders				+
Vegetation type				
Coniferous forest	+	+	+	+
Broadleaved forest	+	+	+	-
Heath	-			

In the mountain region, the cyclicity index of *C. glareolus* decreased with an increased cover of coarse woody debris (III, V). Thus, populations of *C. glareolus* appeared to be more numerically stable the more logs that were present. Most likely, coarse woody debris contributes to the creation of environments that are more heterogeneous. Heterogeneous environments are generally assumed to enhance population stability (e.g. Stenseth 1977, Bondrup-Nielsen and Ims 1988, Hansson 1992). In spite of greater structural heterogeneity in clear-cuts/reforestations than in old-growth forests, winter survival in *C. glareolus* was lower and numerical increases during summers were higher in clear-cuts (IV).

4.2.3 The importance of forest continuity and forest age for C. glareolus *(IV)*

Compared with structural heterogeneity, forest continuity was of minor importance to the population dynamics of *C. glareolus*. However, forest age was negatively correlated to the overall abundance of *C. glareolus*. This result contradicted studies that found the forest-dwelling *C. glareolus* and related *Clethrionomys* spp. to be more common in mature than in young forests (Hansson 1978, Hansson 1999, Sullivan and Sullivan 2001). The abundance of *C. glareolus* was positively correlated with the cover of coarse and fine woody debris and umbrella vegetation as well as with structural heterogeneity. The cover of fine woody debris and umbrella vegetation was negatively correlated to forest age, which might explain the negative relationship between the abundance of *C. glareolus* and forest age.

Year-born breeders of *C. glareolus* were more abundant in reforestations/clear-cuts than in adjacent mature forests. Additionally, the rate of change in numbers of *C. glareolus* during summer was higher, whereas winter survival was lower in reforestations/clear-cuts compared with adjacent mature forests. Consequently, the yearly fluctuations in

numbers of *C. glareolus* were higher in young reforestations/clear-cuts than in middle-aged and old-growth forests. This result is in line with the hypothesis of Van Horne (1983) which suggests that low-quality habitats (here clear-cuts) may support high densities, but that they are mainly occupied by immigrants, whereas high-quality habitats (here old-growth forests) may have lower, but less fluctuating densities of small mammals. Related to this scenario, the forest age related dynamics of *C. glareolus*, e.g. the higher winter survival in old-growth forests than in adjacent clear-cuts, might be explained with a source-sink mechanism. Young individuals, primarily born in old-growth forests in early summer, immigrate into younger forests to breed, where their probabilities for winter survival are poor. A similar mechanism was also suggested by Hansson (1999), who proposed that reforestations might act as sinks for surplus individuals of *C. glareolus* produced in old forests.

4.3   Abundance of small mammals at the landscape and regional scale (III – VI)

Also, at the landscape scale, the abundance of small mammals was related to the availability of vegetation types (Table 1, 2). *S. araneus* was trapped in high numbers in a subarea (2×5 km) that was dominated by birch forest of the heath type (58%), a favourable vegetation type for this species (V). *M. schisticolor* and *C. rufocanus* were absent or trapped in low numbers, respectively, in a subarea with 0% cover of coniferous forest, the preferred vegetation type of both species. In contrast, in subareas with high percentage cover of coniferous forest ($> 24\%$), both species were highly abundant (V). *L. lemmus* was most abundant in a subarea with high percentage cover of the favoured fresh heath. *C. glareolus* preferred coniferous forest and avoided fresh heath. Thus, this species was trapped in low numbers in subareas with low percentage cover of coniferous forest and high percentage cover of fresh heath, respectively (V).

Data on structural habitat factors such as coarse and fine woody debris and structural heterogeneity in the forest floor are not extractable from available remote-sensed data or digitized data from regional forestry files. The population densities of small mammals could thus not be related to the availability of that type of structural habitat factors at the landscape or regional scale. However, extrapolating the relation between forest age/heterogeneity and population dynamics of *C. glareolus* from the forest stand level to the landscape scale, it appeared, that populations of *C. glareolus* might show seasonal instability in landscapes with a high proportion of young forest (IV). In contrast, in landscapes dominated by old-growth forests, structural heterogeneity might enhance temporal stability in the abundance of this species (III, IV).

Marginal and key habitat sites of *C. rufocanus* differed with respect to different habitat variables and related measures at the landscape scale (VI). In accordance with general knowledge on habitat preferences of *C. rufocanus*, the study confirmed the importance of e.g. boulder fields and pine forest for this species (Kalela 1957, Siivonen 1968, Henttonen et al. 1992). However, the study revealed that the abundance of *C. rufocanus* was primarily related to landscape patterns such as patch fragmentation, distance between patches, interspersion among patches, and patch connectivity and diversity, instead of patch quantity (percentage landcover). In particular, the study showed that it was not the percentage landcover of pine forest as such that was important for the abundance of *C. rufocanus*, but the spatial continuity (measured as fragmentation index) of old-growth pine forest (Figure 4).

The connectivity of suitable habitats was also central for the occurrence of the Siberian flying squirrel in northern Finland (Reunanen et al. 2002). If the percentage of available habitat is $< \approx 30\%$, species responses are no longer linearly related to the amount of habitat, and patch size and isolation become major factors influencing species richness and population densities of birds and mammals (Andrén 1994). In the lowland forests near Umeå, pine forest covered 19.0% and old-growth pine forest 6.8% of the study area. Our results revealed a non-linear relationship between fragmentation of old-growth pine forests and *C. rufocanus* densities (Figure 4), suggesting critical fragmentation values for the occurrence and abundance of this species (VI).

4.4 Scale effects in landscape responses of small mammals (V, VI)

Environmentally related variations in small mammal abundance were not detectable on one single scale but on a range of scales. However, when scaling-up/aggregating trapping data from the meso- to the macro- and regional scale, greater variability among transects/sample plots was gradually erased (V).

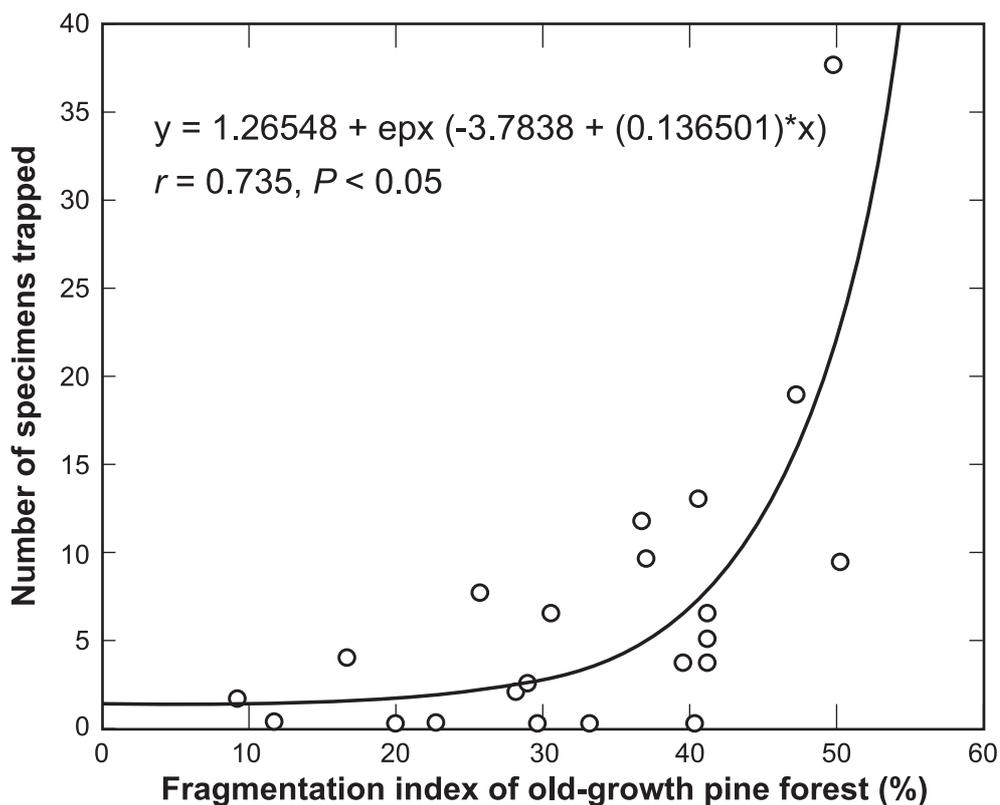**Figure 4**. The number of specimens of *C. rufocanus* trapped in spring 1980 – 1999 in the Umeå region in relation to the fragmentation index of old-growth pine forest for 22 1-ha plots at the 2.5 × 2.5 km scale situated above the highest coastline and $< 20°$ E, analyzed and fitted with an exponential model. Note, that a high fragmentation index indicates low fragmentation of forest patches (Paper VI).

The detection of habitat patterns at the landscape scale depends on the size of the study area (extent) (Wu et al. 2002). The GIS-based identification of important landscape elements for predicting abundance of *C. rufocanus* showed that the 1×1 km scale did not reveal any pronounced relations between densities of this species and landscape patterns (VI). In contrast, landscape responses of *C. rufocanus* were distinctly evident at the 2.5×2.5 km scale. The forest variables applied showed acceptable accuracy first at extents of $\geq 1 \times 1$ km (Reese et al. 2002). Thus, it is reasonable to assume that the accuracy in the analyzed forest variables and the reliability of the results were probably higher at the 2.5×2.5 km scale.

In GIS-based habitat modelling (the spatial explicit modelling of the occurrence, abundance and viability of species), it is important to consider the relation between the geographical position of the study area and the geographic distribution of studied species, since the association between species and their environment may vary spatially (Boone and Krohn 2000, Morrison 2002). The densities of *C. rufocanus* in the lowland forests near Umeå showed a longitudinal gradient (VI). It turned out that the eastern part of the study area ($> 20°$ E) is located at the eastern border of the distribution range of this species in Sweden (Bjärvall and Ullström 1995, Kaneko et al. 1998). In contrast, the 1-ha plots located $< 20°$ E are probably part of the centre of the distribution range of *C. rufocanus* in lowland forests in northern Sweden. Further, the distribution range of *C. rufocanus* in this region coincided closely with the border of the highest post-glacial coastline. Geographic transitions in the dynamics of small mammals (e.g. Saitoh et al. 1998) are supposed to be partly related to climatic variables (e.g. Hansson and Henttonen 1985, Bjørnstad et al. 1998, Stenseth et al. 1998). The study area (VI) also showed climatic gradients (see above). Thus, including only 1-ha plots from the centre of the distribution range, i.e. above the highest post-glacial coastline and $< 20°$ E, in the main analyses probably excluded any bias related to climatic gradients and geographic variations in habitat preferences (cf Boone and Krohn 2000, Morrison 2002).

5   CONCLUSIONS

Geographic information systems (GIS) proved to be indispensable tools for identifying suitable study areas and for the analysis of habitat responses of small mammals at the landscape scale (IV – VI).

In order to improve the performance of GIS-based habitat models and to further promote the implementation of such models in nature conservation and land management, future habitat modelling should a) be performed at multiple scales, b) apply a range of modelling approaches/techniques, c) provide multiple measures of model performance and d) consider model sensitivity (I, II).

This thesis stresses the importance of structural habitat factors and factors related to vegetation for the occurrence/abundance of small mammals in general, and for *C. glareolus* and *C. rufocanus* in particular (Table 1, 2, III – V).

Habitats in old-growth forests were important refuges for over-wintering *C. glareolus* individuals and density fluctuations in this species were greater in young reforestations/clear-cuts than in old-growth forests. Thus, forest management practices such as clear-cutting probably enhance population fluctuations in *C. glareolus* (IV).

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In particular the positive correlation between spatial continuity of old-growth pine forest and densities of *C. rufocanus* strongly suggested that altered land use might indeed be involved in the long-term decline of this species in managed forested areas of Fennoscandia (VI).

6   OUTLOOK

During the course of this thesis, a number of new questions, new hypotheses and future research approaches were identified. They are outlined below.

To analyze effects of spatial scale on the detection of patterns in population dynamics of small mammals in more detail, future studies should choose a sampling design with equal sample size at each scale. Applying a sample design with e.g. *n* = 50 at the micro-, meso-, macro- and regional scale, true scale effects can be distinguished from pseudo scale effects due to statistical problems that arise from varying sample size at different spatial scales when aggregating data to higher spatial levels (V).

When studying landscape responses of *C. rufocanus*, the 2.5 × 2.5 km scale turned out to be superior to 1 × 1 km. However, further spatial scales should be tested to identify whether there is a study area size (extent) that reveals landscape responses of *C. rufocanus* even more distinctly (VI).

Abundance of small mammals was studied in relation to habitat patterns at the landscape scale. However, important identified variables are affected by landscape processes, e.g. fragmentation of old-growth pine forest. Thus, time series of small mammal densities should be related to corresponding time series of landscape changes (VI).

To further reveal the effect of landscape patterns on *C. rufocanus*, future studies can make use of the possibility to predict the occurrence of *C. rufocanus* from the degree of fragmentation of old-growth pine forest at the landscape scale as identified in this thesis (VI).

The non-linear relationship between the fragmentation index of old-growth forest and densities of *C. rufocanus* suggests critical fragmentation thresholds for the occurrence and abundance of this species. The identification of such thresholds should be of tremendous value for managers of nature conservation (VI).

Results indicated that fluctuations in numbers of *C. glareolus* are promoted by clear-cutting. Studied clear-cuts were of approximately the same size. Further studies should investigate whether clear-cuts of varying size induce similar responses in densities of small mammals or if critical area-related thresholds appear in clear-cuts (IV).

Data on structural habitat factors that are altered by forestry, e.g. coarse and fine woody debris, that were important habitat features at the micro- and mesoscale (III – V), are not available at larger scales. However, to assess whether such factors are important for the occurrence of small mammals also at the scale of landscapes and regions, it will be

necessary to develop broad-scale sampling techniques for these variables, preferably based on high-resolution remote sensing.

The results of this thesis strongly suggest that intensified forest management practices might be involved in the long-term decline of *C. rufocanus*. However, long-term declines of this species have also been reported from areas with largely un-managed old-growth forests. Thus, other/alternative causes for the long-term decline have to be identified and tested for these areas.

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