PREDICTING ABUNDANCE, SPECIES RICHNESS AND ASSEMBLAGES OF WOODLAND SNAILS USING ENVIRONMENTAL VARIABLES

THESIS CANDIDATUS SCIENTIARUM

Thor Inge Vollan
Section of Animal Ecology
Department of Zoology
University of Bergen, Norway
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Front page: An adult *Arianta arbostorum* found at Åsane in Hordaland, Norway. Photo by Thor Inge Vollan.

TABLE OF CONTENTS

ABSTRACT

The abundance and diversity of woodland snails (Gastropoda: Pulmonata) were investigated in a large-scale study in Geitaknottane Nature Reserve in Kvam County (Norway). Snails were collected in 132 squares (50 X 50 meters) in an area of approximately 1,5 km^2. Six sifting samples (1-3 liters) were taken from the litter in each square, and environmental variables were also recorded. Detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) were applied to relate the relative abundance and diversity of snails to the most important environmental variables measured. A total of 11478 individuals in 30 species from 12 families were found in the area. The range of snail species was from 2 to 22 per square, and the number of individuals per square ranged from 1 to 788. The significant environmental variables considered were productivity, aspect, gorge, cliff area, mire, scree area, pollarded trees, topographic position, vegetation type and number of dry calcium-indicating moss species. The main axes in CCA were interpreted as representing richness of nutrients (axis 1) and humidity (axis 2). These axes explain respectively 62% and 12% of the species-environment relation in the analyses. Several groups of species was indicated by ordination, and by interpreting these groups placement in the ordination diagrams several predictions about optimal habitats and environmental tolerance were made.

KEYWORDS

Land snails, biodiversity, abundance, forest, prediction, multivariate analysis, Norway.

1 INTRODUCTION

The human impact on Norwegian forests has increased during intensive forestry the last 500 years. Introduction of alien tree species has altered the composition of the forest, from being dominated by pine and deciduous species, to a high abundance of spruce and other exotic species. Continuous fellings has changed the age structure of the trees, with the loss of old and coarse trees being one of the most evident consequences. Another factor of great impact is the removal of downed and decaying stages of dead trees, with adverse effects on the organisms living in this habitat. This has led to a cascading change in composition of various animal, plant and fungi communities. To secure a well-founded conservation strategy of forest habitats, knowledge about the ecology and preferences of inhabiting species is of crucial importance. The present study focuses on the abundance and diversity of land gastropod species in a woodland habitat at the west coast of Norway.

The phylum Mollusca is the second most species-rich phylum, only surpassed by the phylum Arthropoda (e.g. Kerney *et al.* 1979). Land snails (i.e. with shell) and slugs (i.e. without shell) belong to the order Gastropoda, compromising some 30 000 described species and considered the most successful of the molluscan classes (Ruppert & Barnes 1994; Barker 2001). Most of these species belongs to the order Stylommatophora. According to a recent review by Olsen (2002), the total number of land snail species in Norway is 96, of which 77 are snails and 19 are slugs. There are approximately 55 snail species and 11 slug species occuring naturally in Norwegian woodland habitats (Solhøy *et al.* 1975; Solhøy *et al.* 1998).

The abundance of land snails is thought to be dependent on various aspects of the environment (e.g. von Proschwitz 1993; de Winter & Gittenberger 1998; Johannessen 2000). Although land snails can be found in a wide range of habitats (e.g. snails from the family Helicidae is found from deserts to wet tropical forests), the highest diversity probably occurs in warm temperate forests (Peake 1978). Different requirements of the species may lead to characteristic species compositions in distinct habitats. To avoid drying up, snails need to restrict their movements to humid places and periods. The consequences of this is that most species are nocturnal and most active in wet weather (Riddle 1993). The properties of the soil are also key elements in the snails' choice of habitat. Occurrence of calcium (Ca) in the soil is crucial for the construction of the shell and other physiological processes. A poor access to Ca may lead to thinner and more fragile shells, which in turn can make them more vulnerable to predators (Voelker 1959). Ca is also a neccesary element in the formation of eggshells of most snails (Tompa 1976). The diversity of snail species often increases along with the amount of Ca in the soil and the associated increase in pH (e.g. Gärdenfors et al. 1995; Johannessen & Solhøy 2001). Ca is often found as easily accessible citrate in deciduous forests. In areas without Ca in the bedrock and soil or areas where deciduous tree species is not present, Ca is often found as a less accessible oxalate complex (Wäreborn 1982). Shortage of Ca may also lead to the abscence of many species, whereas deciduous woodland upon sedimentary rock rich in Ca is widely recognized as the richest of land snail habitats, while areas with rocks, cliffs and scree are thought to be inhabited by characteristic species (Kerney et al. 1979).

Snails feed mainly on dead organic matter, but some species also forage on living plants, algae, fungi and lichens, and a few species are carnivorous. At high densities in rich deciduous forests, the snails may play an important role in decomposition, especially at the initial stage of division of the litter (Boycott 1934; Mason 1970). Carnivorous snails in the families Zonitidae and Vitrinidae frequently eat other species of snails and their eggs (Kerney et al. 1979). They also act as predators on eggs and larvae of terrestrial arthropods and other invertebrates. Snails, especially of the family Helicidae, are an important source of food for many bird species. Some rodents also include snails, e.g. *Cepaea* spp. and *Arianta arbustorum.* in their diet (Cameron 1969). Field micee (*Apodemus sylvaticus*) and hedgehogs (*Erinaceus europaeus*) have been observed eating snails (T. Solhøy pers. comm.).

Biodiversity became an area of interest in the ecological sciences in the early 1980's. By definition the term 'biodiversity' includes diversity of life on different levels; within species (genes), between species and of ecosystems (e.g. UNEP 1995; Begon et al. 1996; Gaston & Spicer 1998). Lately, biodiversity has been one of the main areas of interest in ecological research, partly due to the Convention on Biological Diversity, which was ratified in December 1993. The focus on biodiversity has lead to significant developments in the ecological sciences. Applied ecology, like conservation and wildlife management, has also benefited greatly from it.

Snails has been investigated in several biodiversity studies (e.g. Waldén 1981; Wäreborn 1982; von Proschwitz 1993; Cowie et al. 1995; Davies et al. 1996; Tattersfield 1996; Emberton 1997; de Winter & Gittenberger 1998; Solhøy et al. 1998; Barker & Mayhill 1999; Myrseth

1999; Cameron et al. 2000; Johannessen 2000; Schilthuizen & Rutjes 2001), partly because some species are considered to be effective environmental indicators, but also because their mobility is low (Solhøy et al. 1998).

Community ecology is a rather young science, with neglible research before 1900 and almost no quantitative work until around 1950 (Greig-Smith 1980). A lot of the recent works has concentrated on modelling community processes and patterns. The nature of ecosystems is complex, i.e. they consist of many interacting components, both biotic and abiotic. A common way of analyzing the relation between species composition and environmental variables is by using multivariate statistics, which is a mathematical way of examining numerous variables simultaneously (e.g. Gauch 1982a; Manly 1994). There are several analyses used in community ecology, and one common and important constraint of these analyses is their dependence on a solid and consistent background material (regarding both collected species and environmental data). Ordination-methods are a group of multivariate analyses often used to reveal patterns in community structure. In large sets of species data, ordination can be used to summarize and display these data in ordination diagrams. When no environmental variables are included, ordination is called an indirect gradient analysis or unconstrained ordination (ter Braak 1995a). If environmental variables are included, the analysis is known as a canonical or constrained ordination, which is a direct gradient analysis. Various computer programmes for multivariate analysis in community ecology exist. For the analysis in this study, CANOCO (ter Braak 1988) was used, as it was considered the most suitable software solution for multivariate analysis in context of this study.

The main objectives of this study is:

- To investigate the distribution, relative abundance and diversity of woodland snails within a 1,5 km^2 area in Geitaknottane Nature Reserve in Western Norway
- To examine the factors related to the distribution of the moderately abundant species
- To find relations between the distribution of woodland snail species and environmental factors that can be easily meaured
- To explore methods to predict the composition of snail communities and individual snail species on a local scale using environmental variables

2 MATERIALS AND METHODS

2.1 STUDY AREA

The study site is a part of Geitaknottane Nature Reserve in Kvam (Hordaland county in Norway). It covers approximately 1,5 km² and is situated at 60°07' N and 5°52' E. Map series M711 no. 1215 II (Varaldsøyna) covers the area.

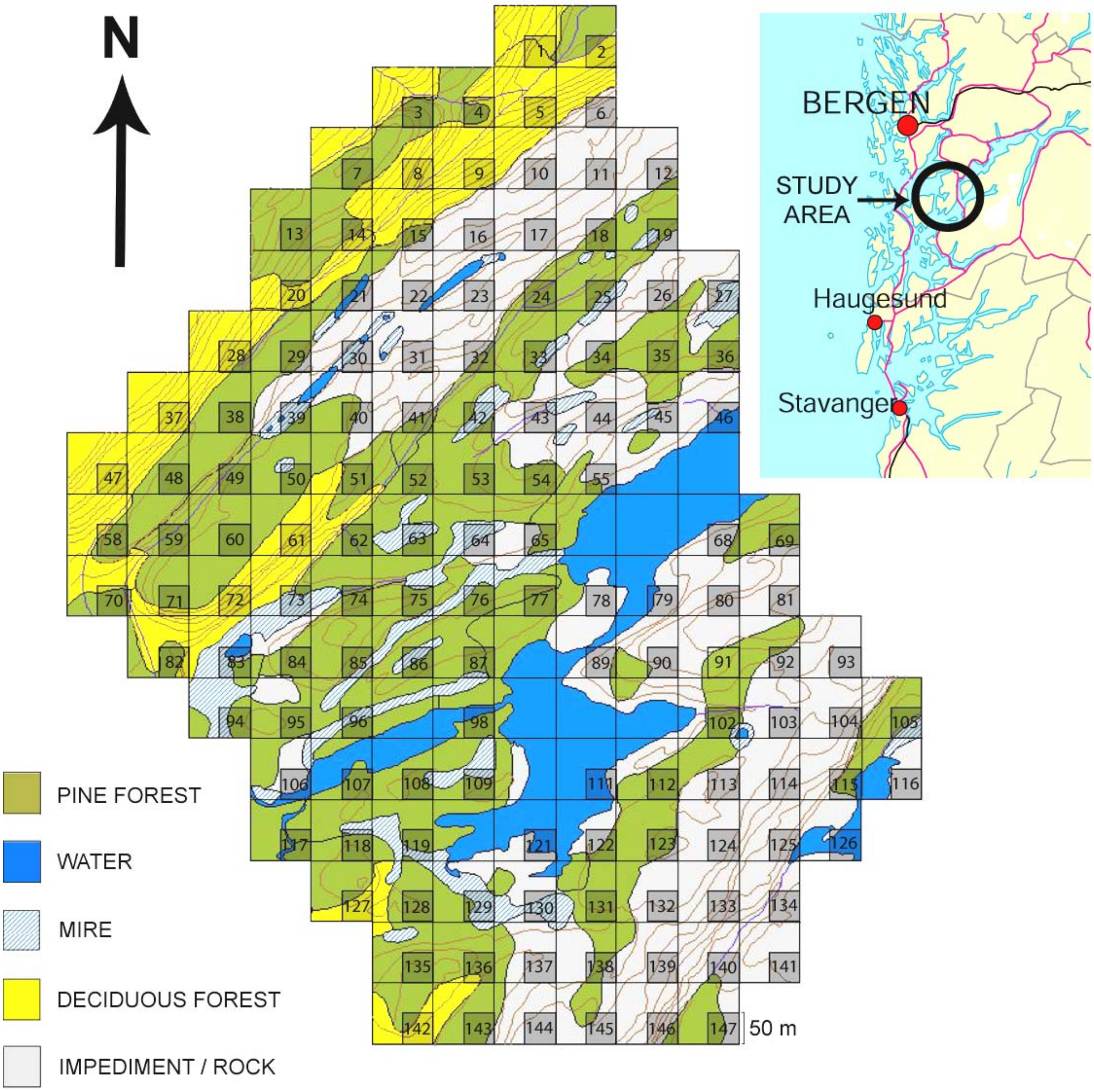

Figure 1. Map of the study site in Geitaknottane Nature Reserve, Hordaland County, Western Norway. The numbered squares are the 50 X 50 m areas sampled in the project. Scale 1:10 000. Contour intervals 10 m.

2.1.1 TOPOGRAPHY AND GEOLOGY

The approximate altitudal range of the study area is from 120 meters above sea level (a.s.l.) to 300 m a.s.l. Lake Sveavatn is situated at 172 m a.s.l. in the middle of the area. Most of the bedrock in the area is composed of greenstone and schist, while the northern part consists of calcium-rich mica schist (Foslie 1955). In this transition zone there is a rather sharp compositional change of the vegetation. Due to the alkaline properties of the rock species, most of the weathered material is rich in nutrients.

2.1.2 CLIMATE

The area is characterized by relatively warm summers (with average July temperatures of 14,8°C), long autumns and mild winters (with average February temperature of 0,6°C) (see Table 1). The climate is oceanic and strongly influenced by humid air drifting in from the fiords in the west and south. Annual precipitation is high, approximately 2000 mm, but nevertheless lower than in areas situated north and south of the study area. These factors implies a long period of plant growth, from early spring to late autumn (Moe 1995).

Table 1. Weather data from Omastrand Climate Station during the period of sampling. Temperatures in Celcius degrees (C°) and precipitation in millimeters (mm). "Normal" refers to the mean of the period 1960 to1990. Data from the Norwegian Meterological Institute (Det Norske Meterologiske Institutt, DNMI).

	May	Jun.	Jul.	Aug.	Sept.	Okt.	Nov.
Normal temperature	10,3	13,7	14,8	14,3	10,9	8,0	4,0
Temperature in 1997	9,6	15,9	17,7	18,1	11,2	5,8	5,1
Normal precipitation	109	132	139	181	304	318	309
Precipitation in 1997	77	40	65	122	362	288	81

Overall, the 1997 summer was considerably drier compared to a normal one. The mean temperatures were also much higher in July and August as well. September and October had much more rain than the five other months in the sampling period.

2.1.3 VEGETATION

Large proportions of the area are covered with scots pine (*Pinus sylvestris*) forest, but the forest cover is sparse considering the modest altitude of the area. One of the reasons for this may be the thin layer or absence of soil on the ridges and hills. The age of many pine trees are

200-300 years, and at some locations there are pine forests untouched by forestry for at least the 50-100 last years (Moe 1995). Birch (*Betula pubescens*) is the most common deciduous tree species in Geitaknottane. Bogs and small ponds occur scattered throughout the area. Locations with deeper soil and better growth conditions often show traces of old fellings. In these forests, there are specimens of large and coarse pine trees with diameters of 50-60 cm and heights of approximately 20 m. The age of one tree in the productive part of the forest were estimated to 135 years, and some trees of elm and ash has stems with a diameter of over 1 m.

The plant diversity in the area is high. An inventory (Gjerde 1998b) did register 297 species of vascular plants, 385 species of mosses, 43 species of polypore fungi and 86 species of macro-lichens. A total of 48 rare species (23 species listed in the IUCN red list and several species rare both regionally and in Europe) were recorded in the study area. As an example, the fern *Osmunda regalis* is found at only two other Norwegian localities (Moe & Sætersdal 1995). For further vegetation descriptions of the area, see Moe (1995).

2.1.4 HISTORY OF VEGETATION AND HUMAN INFLUENCE

The deciduous tree species elm (*Ulmus glabra*) and ash (*Fraxinus exelcior*) were pollarded to approximately 1930, the grass on the mires has been cut in the last century, and there has been frequent fellings until the 1950's. Geitaknottane became a nature reserve (coniferous forest reserve) in 1997, and a part of it is also a herptile reserve for the endangered crested newt *Triturus cristatus* (Dolmen 1993). The regulations in the area allow grazing by cattle and sheep, and the area is frequently used for this purpose. There has also been mining activity in a small part of the area in the beginning of the twentieth century.

2.1.5 PREVIOUS STUDIES

The flora and fauna of Geitaknottane Nature reserve has been subject to several inventories and scientific studies. Myrseth (1999) analysed a smaller part of the present dataset for her Cand. scient.-degree, the spiders in the same area has been studied by Pommeresche (1999) and Carter (1999) has investegated the effects of pH on snail diversity in Geitaknottane. Studies on other animal groups in the area includes e.g. investigations of the crested newt by Myklebust (1998), Hage (1999), Hobæk et al. (2000) and Gutiérrez (2002). Skogforsk (The Norwegian Forest Research Institute, NFRI) has been in charge of one of the largest

Norwegian biodiversity inventories, also undertaken partly in this area (Blom 1998; Gjerde 1998a; Gjerde & Ihlen 1998; Gundersen & Rolstad 1998a, 1998b; Skartveit & Pommeresche 1998; Solhøy *et al.* 1998; Sætersdal 1998; Blom 1999; Skartveit *et al.* 1999; Storaunet 1999; Sætersdal 1999; Gjerde & Baumann 2002; Storaunet 2002; Sætersdal 2002; Skartveit *et al.* 2003; Sætersdal *et al.* 2003; Thuenes *et al.* 2003).

2.2 SAMPLING

The sampling was carried out at the study site in Geitaknottane from 12 May to 7 November 1997. An area of approximately 1,5 km^2 was divided into 147 quadrates (100 m X 100 m). Snails and other invertebrates were sampled from squares measuring 50 X 50 m in the southeastern corner of the quadrates. Environmental data were recorded in the same areas. Due to inaccessible areas and some squares containing just water, 15 squares were omitted from the data set. Hence, the number of squares used for analyses is 132.

Six sifting samples were collected from each square. Special care was taken to sample all the different microhabitats suitable for snails. Each sample consisted of 1,0-3,5 liters of sifted litter material. The ground litter was sifted in the field to separate the snails and other fine-grained fragments from the coarser organic material in the samples. This was done by shaking the litter over a sieve with 7mm mesh. The proportion that did not go through the mesh was thrown away after being examined for large snails. All sifted material was transported to the laboratory in cloth bags and dried. The dried matter was sieved through a 2mm mesh. The finer fraction was examined with a binocular microscope (Wild M3 Heerburg) at 6-12X magnification, while the coarser material was examined with a table mounted magnifying glass (3X magnification). All snails were picked out by a team of 12 students, and then identified by E. W. Myrseth (39 squares) and T. Solhøy (94 squares). T. Solhøy verified all identifications.

2.3 ENVIRONMENTAL VARIABLES

NFRI recorded environmental data during the same period as the snails were collected. The variables assumed relevant for the distribution of snail species is listed in Table 2. In the following analyses, these are the variables used to represent the environment.

Table 2. Environmental variables registered in the survey. The first column contains the abbreviations used in the statistical analyses; the second column gives a brief explanation of the variable. An extended description is given in the text below the table. The full set of environmental variables for each square can be found in Appendix 6.3.

Name of variable	Brief explanation
H40	Height of trees at the age of 40 years
ASPECT	A measure of exposure to sunlight
GORGE	Occurence of gorge
LOGCLIFF	Area of cliffs (log-transformed)
MIRE	Percent cover of mire
LOGSCREE	Area of scree (log-transformed)
POLLARD	Number of pollarded trees
TOPOPOS	The dominating topographic position
ANTPERC	Percentage of ants
VEGIND	Vegetation types ranged after richness
MOSSDRY	Number of calcium-indicating mosses on dry rocks
MOSSWET	Number of calcium-indicating mosses on wet rocks

Description of the registered environmental variables:

H40: This variable is a measure of the potential productivity of the forest. Its value indicates the height of forty-year-old trees in meters. Trees on productive soil usually have a higher H40-value than a tree on poor soil.

ASPECT: The dominating aspect of a square, ranging from north-east (=1) to south-west (=8), measured as deviation from NE. Increases with a factor of 1 for every ≈25° away from NE. Thus, squares highly exposed to sun radiation get a high value.

GORGE: If there are gorges present in a square, the value 1 is assigned. The value 0 is used to indicate non-presence of gorges.

LOGCLIFF: Area of cliffs in a square. The value of this variable is log-transformed to avoid large area to have a disproportionally large influence on the results from the multivariate analyses (Lepš & Šmilauer 2003).

MIRE: Percentage area of a square covered by mire.

LOGSCREE: The area of scree in a square. Log-transformation is used to correct the effect of large areas.

POLLARD: Number of pollarded trees in a square. Zero-values indicate no pollard trees. If trees in the square have been pollarded, a value from 1 to 3 is assigned.

TOPOPOS: Indicates the main topographic position in a square. The lowest value is given to areas on top of slopes and facing south. 1 = On the level, flat; 2 = Upper part of slopes facing south; 3 = Lower part of slopes facing south; 4 = Upper part of slopes facing north; 5 = Lower part of slopes facing north; 6 = Bottom part of slopes or gorges.

ANTPERC: Amount of ants in a square.

VEGIND: Ranking of vegetation types, reflecting the general richness of the vegetation. A high value denotes richer vegetation than a low value. Heather-bog, bilberry-scots pine forest = 1; bilberry forest = 2; forest with large and small ferns = 3; low-herb forest = 4; deciduous woodlands = 5.

MOSSDRY: Number of Ca-indicating moss species present on dry places in a square.

MOSSWET: Number of Ca-indicating moss species present on wet places in a square.

2.4 STUDY SPECIES

All the investigated species are snails with shell (phylum Mollusca: order Gastropoda: subclass Pulmonata). Slug species were not included in the study, although such species were found in the area (see results section 3.1). The main reasons for omitting slugs from the analyses, is the fact that they are almost ubiquitous and considered to have a low value as indicator species (T. Solhøy pers. comm.). The species included in the study is listed in Table 3, and an outline of the distribution and ecology of the species can be found in Appendix 6.8.

2.5 DATA ANALYSES OVERVIEW

To find basic properties of the species diversity in the area, summary statistics and graphical display of the data were used. This was done partly as a descriptive analysis, and partly as a guideline for the multivariate analyses.

A species' response to its environment (e.g. acidity, nutrients or humidity) may be linear, unimodal or polymodal (i.e. have several optimas) (ter Braak 1995a). In this study, a multivariate ordination method, detrended correspondence analysis (DCA) (Hill & Gauch 1980), was applied to decide whether to use methods that deal with linear or unimodal species responses. The output from DCA indicates the amount of species turnover along extracted axes, expressed as gradient length measured in standard deviations units (SD). This test suggested a fairly long gradient length (≈ 3 SD) of the two first axes. According to ter Braak & Prentice (1988), the results suggests unimodal methods to be used. Two unimodal ordination methods (detrended correspondence analysis DCA and canonical correspondence analysis CCA) were applied to examine the distribution of the collected snail species. The DCA is an indirect gradient analysis, while the CCA is a direct gradient analysis. Shorter gradients (< 1,5 SD) may be analyzed with a principal component analysis (PCA) and a redundancy analysis (RDA).

To allow comparison between different squares (with different sample volumes), the abundances are converted to density (i.e. individuals/100 liters).

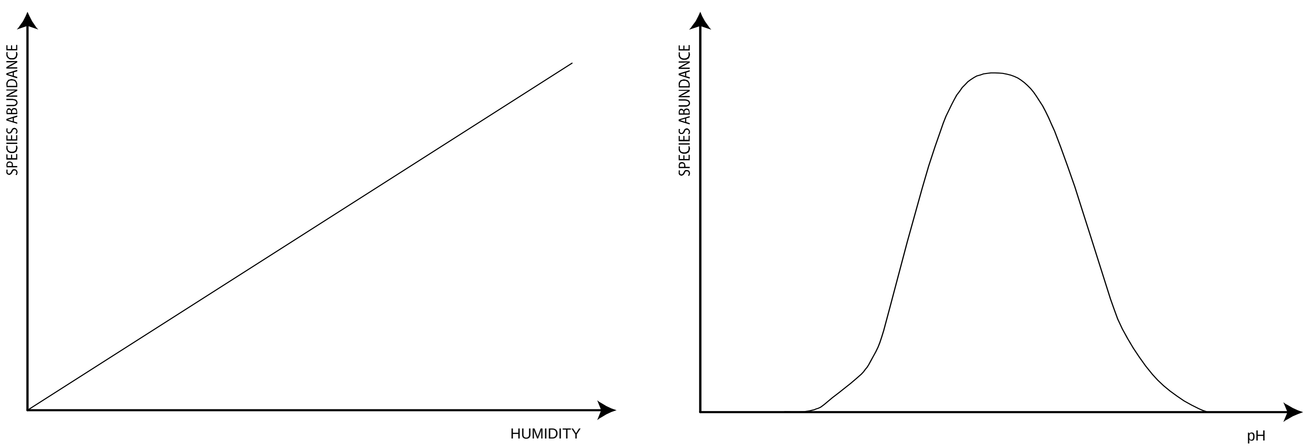

Figure 2. Two examples of different species response curves. The linear response to the left and unimodal to the right. Different methods can be use to detect response type, and they also require different statistical approaches (linear or unimodal methods). If isolated, the increasing and decreasing phase of the unimodal curve can also be interpreted as linear.

2.5.1 INDIRECT GRADIENT ANALYSIS (DCA)

To investigate major gradients and to reveal any underlying patterns in species composition, an indirect gradient analysis (detrended correspondence analysis, DCA) was carried out. The software settings for this analysis and the direct gradient analysis is listed in Appendix 6.7.

2.5.2 DIRECT GRADIENT ANALYSIS (CCA)

The CCA is a direct gradient analysis, and was used to relate the species data to the environment (ter Braak 1986). Although there exists an detrended version (DCCA) of this analysis, the CCA is considered a much more robust method regarding the arch effect than its unconstrained counterpart, the CA (Palmer 1993; McCune 1997).

Monte Carlo permutation tests are a way of solving complex statistical problems by random sampling from simulated populations on a computer (Sokal & Rohlf 1995). During the run of CCA, Monte Carlo permutation tests were used to test the significance of environmental variables. In ordination methods they are used to test the significance of the null hypothesis ("Species are unrelated to the environmental data in question"). Thus, if the test gives a significant result for a certain variable, this indicates that there is less than 5% chance that its relation to the species composition is due to chance. For futher reading on Monte Carlo methods, see Besag & Diggle (1989), Good (1994) or Manly (1997).

The lowest number of permutations needed can be calculated (Lepš & Šmilauer 2003). In this study, the computer power was not restricted and there was no design-related limitations regarding the number of theoretical permutations. Considering this, the number of permutations was maximized (9999 permutations, which is the highest number permitted in CANOCO).

2.5.3 TRANSFORMATION OF SPECIES DATA AND ENVIRONMENTAL DATA

It is well known that rare species may have an unpropotionally large influence on analysis in unimodal models (ter Braak & Šmilauer 1998). A way of reducing this problem is to downweight rare species as a separate step in the analyses in CANOCO. To avoid unproportionally much influence from the species occuring in very low numbers, downweighting of these species were applied both in the indirect and direct gradient analyses (Lepš & Šmilauer 2003).

The environmental variables (scree-area and cliff-area) were log-transformed to correct the effect of area (ter Braak & Šmilauer 1998). This was done prior to analyses in CANOCO.

2.5.4 SOFTWARE

The thesis was written in Microsoft Word 2000. For the multivariate analysis, CANOCO 4.0 and 4.5 by Cajo terBraak were used. Figures of the output from CANOCO were produced with CanoDraw 3.1 and CanoPost 1.0 by Petr Šmilauer. StatSoft Statistica 6.1 and Microsoft Excel 2000 were used for descriptive statistics. SPSS Sigmaplot 8.0, Adobe Photoshop 7 and Adobe Illustrator 10 were also used to produce figures and graphics.

3 RESULTS

3.1 GENERAL RESULTS

The total number of living snails included in this study was 11478, distributed on 30 species in 12 families. This is well above 50% of all the shell-snail species occuring naturally in Norwegian forests (Solhøy *et al.* 1998; Olsen 2002). All species belonged to the order Stylommatophora, except *Carychium minimum* and *C. tridentatum*, which belongs to the more primitive order Basommatophora. (Primitive in a taxonomic sense, referring to the single pair of tentacles with an eye at the tentacle base, in contrast to the double pair of tentacles with terminal eyes in Stylommatophorans (Ruppert & Barnes 1994)). The number of individuals of each species ranged from 1 (*Vertigo pygmaea*) to 2528 (*Columella aspera*). In addition *Zoogenestes harpa* were recorded only by dead shells and *Vertigo alpestris* was recorded in one square (no. 37) by a special investigation on the snail micro-distribution by Myrseth (1999). *Galba truncatula* were found in mires but omitted because it is conventionally classified as a limnic species. Hence, 33 terrestrial snail species have been recorded in the area so far.

The abundance of species varied highly throughout the study site. *Columella aspera* was almost omnipresent, and was found in all squares except one. Other highly abundant species in terms of occurence were *Nesovitrea hammonis, Euconulus fulvus* and *Punctum pygmaeum,* which all appeared in more than 100 squares. *Carychium tridentatum* were found in a higher maximum number per square than *E. fulvus*, but occured in fewer squares. The least frequent and thus rare species, occuring in less than 10 squares, were *Cochlodina laminata*, *Vertigo lilljeborgi*, *Discus ruderatus*, *Lauria cylindracea*, *Balea perversa*, *Ena obscura*, *V. pusilla*, *V. ronnebyensis* and *V. pygmaeum*.

Eleven species of slugs were also found in the area, viz. *Arion ater*, *A. circumscriptus*, *A. fasciatus*, *A. intermedius*, *A. silvaticus*, *A. subfuscus*, *Deroceras laeve*, *D. reticulatum*, *Limax cineroniger*, *L. marginatus* and *L. tenellus*. This represents all the slug species occuring naturally in Norwegian forests (T. Solhøy pers.comm.).

A list of the collected species can be found in Appendix 6.2, and abbreviations used in multivariate analyses and in some of the figures is provided in Table 3. The species in the list is ranked in order of total abundance.

Table 3. Occuring species in the snail material collected in Geiaknottane Nature Reserve. The list is sorted after the total number of individuals. The total number of individuals collected of each species is given, as well as their percentage of the total number. As a measure of occurence and abundance, the number of squares containing a species is used, along with its maximum occurence number.

Abbreviation	Scientific Name	Family	Total ind. found	Percent of total ind.	Number of squares	Max ind. / square
COLASP	Columella aspera	Vertiginidae	2528	22,02 %	131	197
PUNPYG	Punctum pygmaeum	Endodontidae	2089	18,20 %	103	190
NESHAM	Nesovitrea hammonis	Zonitidae	1630	14,20 %	127	66
CARTRI	Carychium tridentatum	Ellobiidae	1504	13,10 %	52	366
EUCFUL	Euconulus fulvus	Euconulidae	813	7,08 %	112	101
VITCON	Vitrea contracta	Zonitidae	573	4,99 %	57	67
COCLUB	Cochlicopa lubrica	Cochlicopidae	421	3,67 %	47	96
AEGPUR	Aegopinella pura	Zonitidae	420	3,66 %	40	89
COLEDE	Columella edentula	Vertiginidae	263	2,29 %	17	34
SPELAM	Spermodea lamellata	Vallonidae	195	1,70 %	52	44
DISROT	Discus rotundatus	Endodontidae	164	1,43 %	30	22
OXYALL	Oxychilus alliarius	Zonitidae	164	1,43 %	76	11
CARMIN	Carychium minimum	Ellobiidae	147	1,28 %	11	54
VERSUB	Vertigo substriata	Vertiginidae	139	1,21 %	32	23
AEGNIT	Aegopinella nitidula	Zonitidae	124	1,08 %	16	28
ACAACU	Acanthinula aculeata	Acanthinulidae	56	0,49 %	13	19
ARIARB	Arianta arbostorum	Helicidae	43	0,37 %	22	15
NESPET	Nesovitrea petronella	Zonitidae	43	0,37 %	16	8
VERLIL	Vertigo lilljeborgi	Vertiginidae	35	0,30 %	7	15
VITPEL	Vitrina pellucida	Zonitidae	35	0,30 %	16	7
CLABID	Clausilia bidentata	Clausiliidae	34	0,30 %	28	2
CEPHOR	Cepaea hortensis	Helicidae	14	0,12 %	13	2
LAUCYL	Lauria cylindracea	Pupillidae	14	0,12 %	3	8
DISRUD	Discus ruderatus	Endodontidae	10	0,09 %	3	8
COCLAM	Cochlodina laminata	Cochlicopidae	7	0,06 %	7	1
VERRON	Vertigo ronnebyensis	Vertiginidae	5	0,04 %	2	3
VERPUS	Vertigo pusilla	Vertiginidae	3	0,03 %	2	2
BALPER	Balea perversa	Clausiliidae	2	0,02 %	2	1
ENAOBS	Ena obscura	Enidae	2	0,02 %	2	1
VERPYG	Vertigo pygmaea	Vertiginidae	1	0,01 %	1	1

The abbreviations used in statistical analyses is formed by six capital letters, the first three letters in the genus name and the tree first letters in the species epithet. These short names are required as input to CANOCO, but they also makes the diagrams easier to read, compared to the use of full name or substituting numbers.

The varying occurence of different species might be expressed as percentage occurence of all squares (Figure 3). As can be seen from this figure, only two species were found in nearly all the squares, an additional three species were found in more than 50% of the squares, while as much as 17 species occured in less than 20% of the squares.

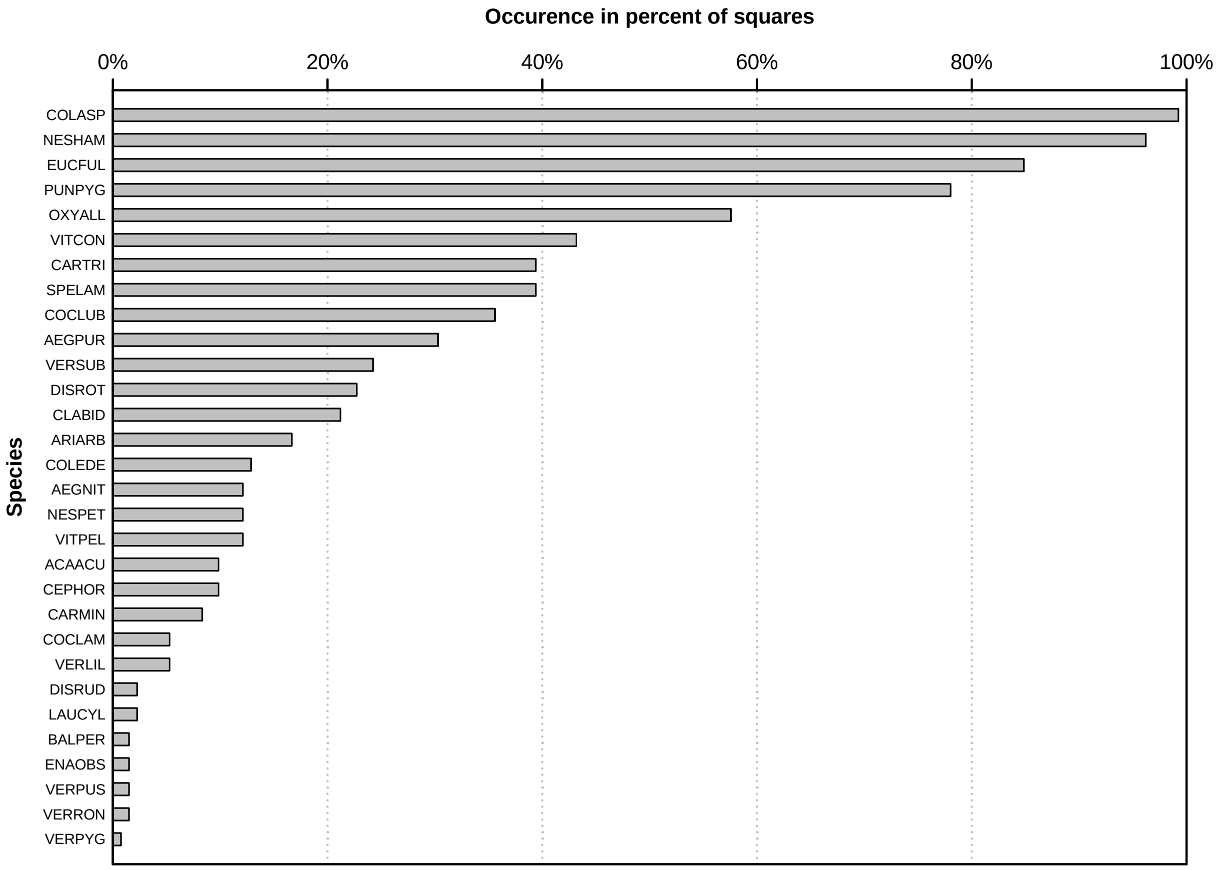

Figure 3. This figure displays how many squares the individual species occured in. Numbers are in percent of the total 132 squares included in the study. For explanation of the abbreviations, see Table 3.

Some general properties of the samples and squares are listed in Table 4. As mentioned earlier, the density (individuals per liter sifted material) is the standard unit used in the analyses. When comparing the mean and median for individuals found per square, it becomes apparent that the median is significantly lower than the mean.

Table 4. Descriptive statistics for snail species collected in the 132 squares.

	Species pr. square	Individuals pr. square	Density (Ind/liter)
Minimum	1	2	0,14
Maximum	22	788	57,51
Mean	7,88	86,95	6,48
Median	7	40	2,77
Standard deviation	± 4,66	± 118,90	± 9,35

The number of species present in each square varied from 1 to 22. Thus, no squares contained more than 73% of the total number of species present in the study. A detailed view of the situation is provided in Figure 4. There are 19 squares containing 5 species, and there is a decreasing trend towards the extremes. This indicates a general pattern where most of the squares have a species richness well below the middle of the range, which is 11 species per square.

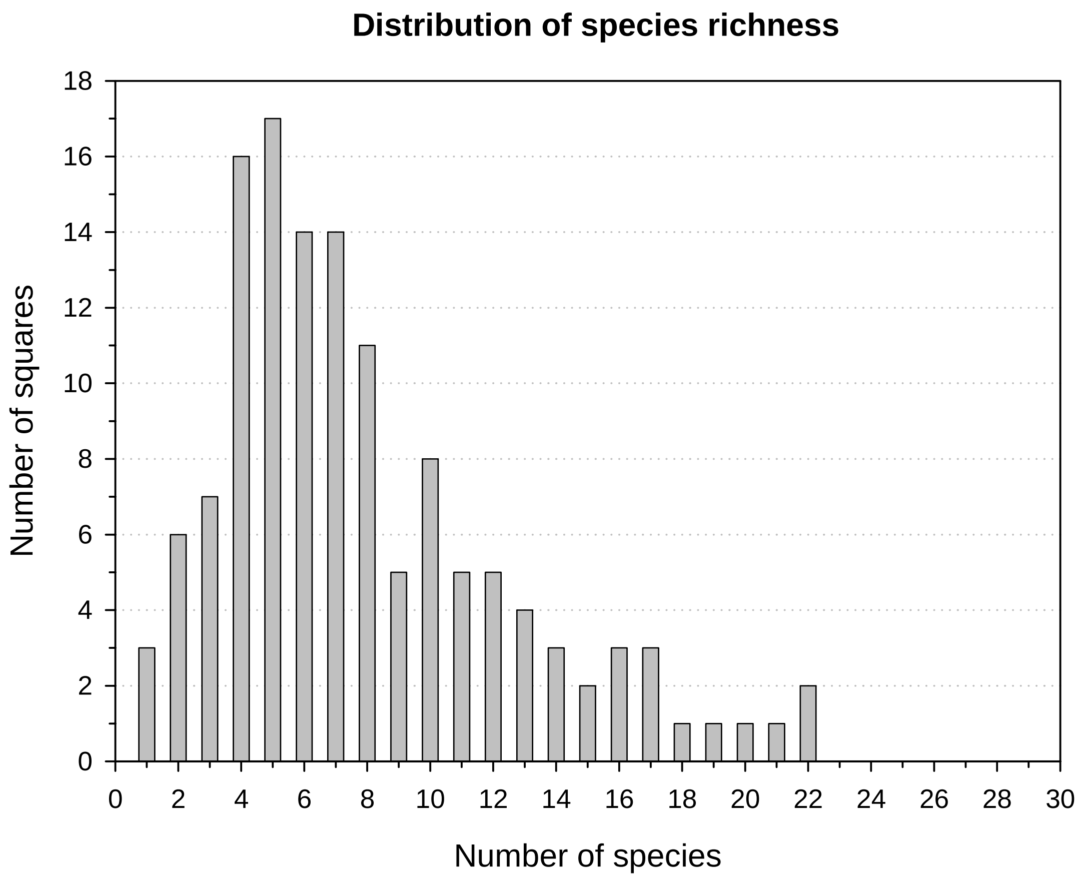

Figure 4. The diagram shows how many squares that contain a certain number of species.

When focusing on the richest squares (i.e. those with most species), it is noteworthy that most of these are squares having a high abundance of rich deciduous tree species (viz.

alder, hazel, ash, aspen, lime and elm). The poorest squares are those with high dominance of pine.

To illuminate the connection between the number of snail individuals and the number of species in the samples, Figure 5 exhibit a strong log-linear association (R^2 = 0,752) between these two parameters. In general, this means that a sample with high density of individuals are more likely to contain more species than a low density sample.

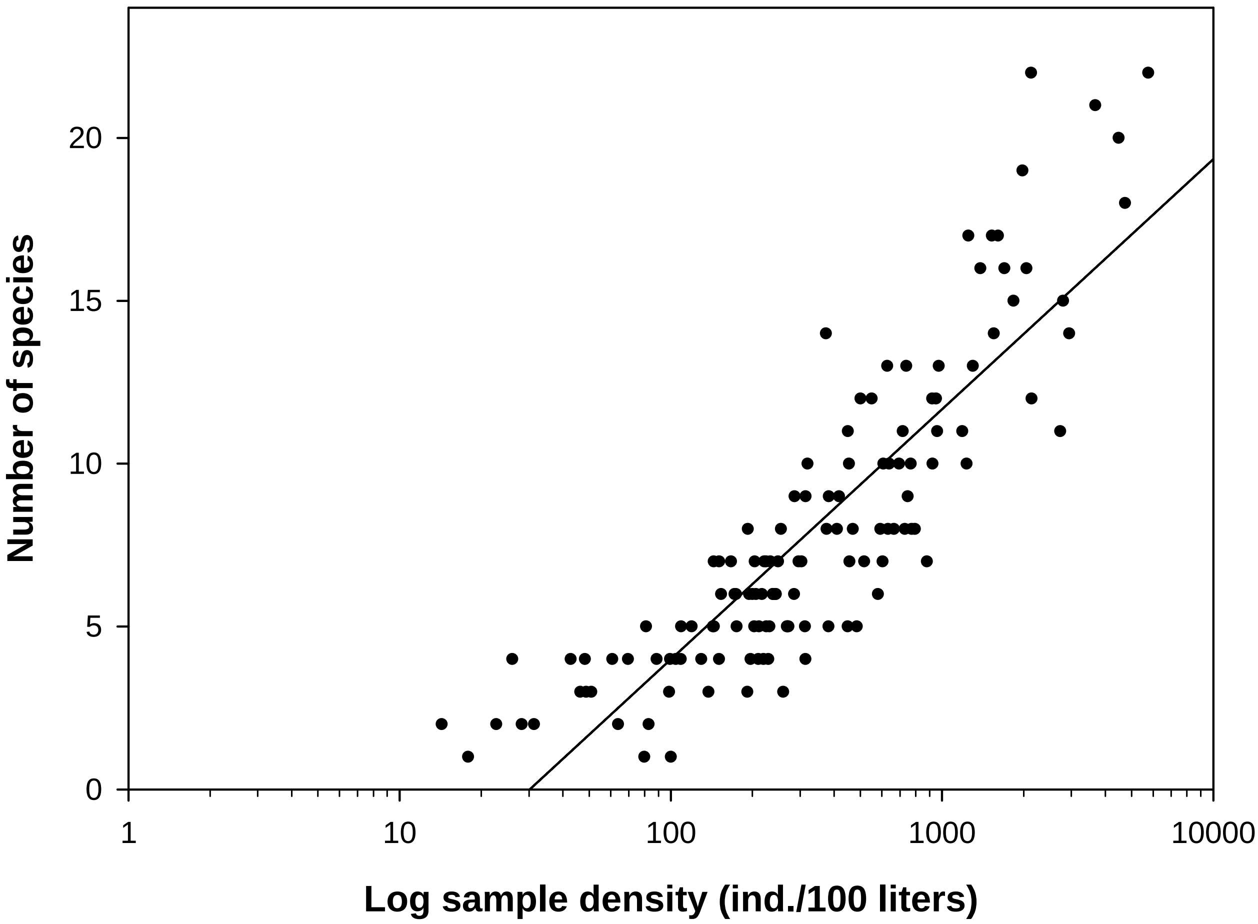

Figure 5. This plot shows how the density of snails in the samples affects the number of species recorded. The x-axis is log-transformed, as the rate of new species recorded is expected to drop when the sample size increases. R^2-value is 0,752.

3.2 RESULTS FROM MULTIVARIATE ANALYSES

In the following sections, the results from multivariate statistical tests are presented. A summary arranged in tables and two ordination diagrams are presented along with possibles interpretations. Concise explanations of terms are provided in Appendix 6.1.

3.2.1 INDIRECT GRADIENT ANALYSIS (DCA)

The results from the detrended correspondence analysis (DCA) indicated rather long gradients of axis 1 and axis 2, approximately 2.8 SD for both. This suggests the use of unimodal ordination methods, i.e. correspondence analysis (CA or DCA) and canonical correspondence analysis (CCA). A scatterplot of a CA revealed an arch-effect, which justifies detrending of the analysis (Peet *et al.* 1988). Thus, the results from the DCA were also used as an indirect gradient analysis after the preliminary tests.

Table 5 summarizes the results from the DCA. "Total inertia" indicates the total variation in the data set, and "variance explained" for an axis can be calculated after the following formula:

$$\text{variance explained (\%)} = \frac{\lambda_i * 100}{\text{Total inertia}} \qquad \text{,where } \lambda_i \text{ is the eigenvalue of axis } i$$

Table 5. Results from indirect ordination (DCA), including eigenvalues, gradient length, explained variation and total inertia.

	DCA axis			
	1	**2**	**3**	**4**
Eigenvalue (λ)	0,367	0,156	0,086	0,043
Length of gradient (SD)	2,797	2,811	2,062	1,710
Variance explained	30,0 %	12,8 %	7,1 %	3,5 %
Total inertia		1,221		

A quite high proportion (42,8%) of the species variation can be explained by the two first axes. This gives a good spatial distribution of the species along the axes (ter Braak 1995a). Interpretations of the axes will be given in the next section on direct gradient analysis.

If the scores from the DCA are used to make an ordination diagram (Figure 6), the species distribution maximums can be displayed. The distance between them indicates the degree of similarity in patterns of abundance and distribution. Species located near each other in the ordination space will have a more similar distribution than species far apart. The site scores might also be plotted in the same ordination diagram. Sites close to each other are expected to have similar species composition, and they will be assumed to have a high abundance of the nearby species. The high number of sites in this study makes it inconvenient to plot sites in the same diagram as the species.

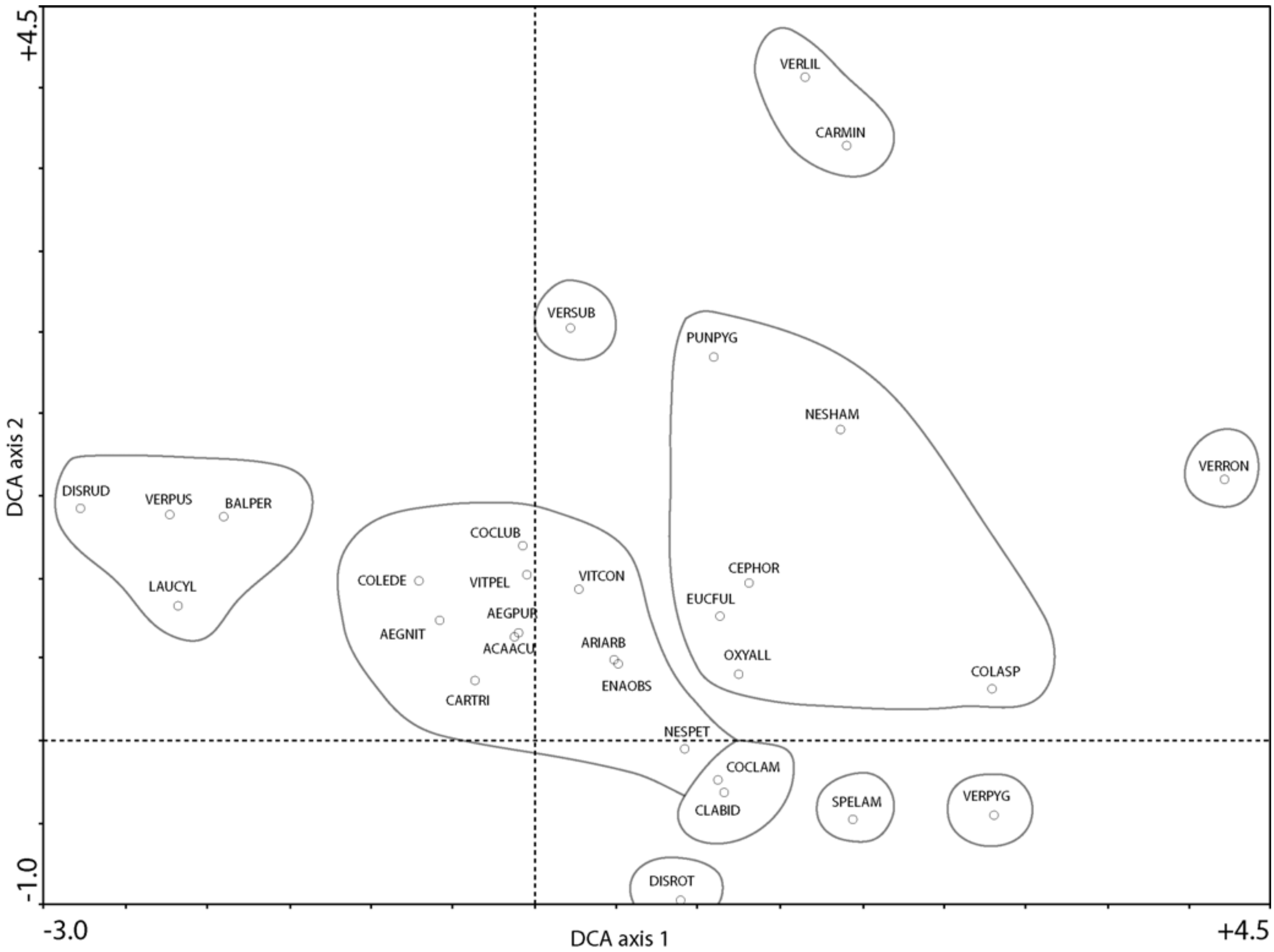

Figure 6. DCA-diagram displaying the peak abundance of all snail species investigated. The groups are drawn on basis of the indirect and direct ordination of the species and appendices 6.2 and 6.3.

If the distribution of the species in the DCA-ordination diagram is compared to their abundance, a certain pattern appears. Most of the rare species (regarding occurence, see Table 3 and Figure 3) can be found along the edges of the diagram. Examples are *Vertigo ronnebyensis*, *Discus ruderatus*, *Balea perversa*, *Lauria cylindracea*, *V. pygmaea*, *Carychium minimum* and *V. lilljeborgi*.

3.2.2 DIRECT GRADIENT ANALYSIS (CCA)

The canonical correspondence analysis is a tool to understand relationships between species abundances and environmental factors (ter Braak 1995b). In this study, the abundances of 30 snail species were analysed together with 12 environmental variables. Ten of these variables were found to be significant using Monte Carlo permutation tests, and a summary of the test results is listed in Table 6.

Table 6. Summary of the Monte Carlo permutation test performed during the run of CCA..

Variable	Interset correlation		t-value		Marginal	Additional		
	Axis 1	Axis 2	Axis 1	Axis 2	Variance	Variance	P-value	VIF
MOSSDRY	0,85	0,05	9,61	3,58	26 %	26 %	0,0001	2,58
VEGINDEX	0,74	-0,12	3,57	1,03	21 %	5 %	0,0001	9,21
LOGCLIFF	0,31	-0,33	-2,78	-4,04	6 %	4 %	0,0001	1,68
MIRE	-0,32	0,37	-0,79	5,18	7 %	3 %	0,0036	1,62
GORGE	0,26	-0,17	0,45	-0,79	5 %	2 %	0,0030	2,37
POLLARD	0,19	-0,02	-2,08	2,45	4 %	2 %	0,0166	1,80
H40	0,69	-0,13	0,17	-3,21	18 %	2 %	0,0146	6,76
ASPECT	0,38	-0,04	3,30	-0,72	6 %	1 %	0,0181	1,47
LOGSCREE	0,67	-0,15	0,37	1,31	17 %	1 %	0,0280	6,83
TOPOPOS	0,42	-0,15	-0,50	0,03	8 %	1 %	0,0235	2,59
MOSSWET *	-	-	-	-	-	-	0,1245	-
ANTPERC *	-	-	-	-	-	-	0,6860	-

* denotes the non-significant environmental variables

To select a group of environmental variables that explains the species distribution almost as well as the full set of environmental variables, the t-values of the regression coefficients can be examined and compared with a table of critical values of the t-distribution (Zar 1999). Considering this, the variables GORGE, LOGSCREE and TOPOPOS may be interpreted as variables with little influence on the species distribution in the ordination space. Nevertheless, they are included in the CCA biplot (Figure 6) since they were found to be significant through the Monte Carlo permutation tests, which are assumed to be a more reliable significance test than than the t-value (ter Braak & Šmilauer 1998).

If the results of the DCA and the CCA are compared, it is possible to tell how well the environmental variables explain the inherent variation in the species abundance. This can be verified by comparing how much of the variance is explained by the first two axes in both DCA (Table 5) and CCA (Table 7), but also by comparing the ordination diagrams from the analyses (Figure 6 and 7). The first axis in DCA explains 30.0% of the variance, whereas the first axis in CCA explains 24,4%. Hence, the first CCA axis explains 5,6% less of the variance, which should be considered a quite small reduction. Gradients extracted in the DCA ordination are confirmed to a high degree by the CCA.

Table 7. Results from direct ordination (CCA) of the snail species and environmental variables.

	CCA axis			
	1	**2**	**3**	**4**
Eigenvalue (λ)	0,298	0,058	0,042	0,032
Length of gradient (SD)	0,911	0,591	0,646	0,622
Variance explained species data	24,4 %	4,8 %	3,4 %	2,6 %
Variance expl. species - environment	61,5 %	12,1 %	8,6 %	4,6 %
Total inertia		1,221		

Together, the first two axes of the CCA account for 73,6% of the total variation explained by the environmental variables (see Table 7). If axis 3 and 4 is included, the variance explained is 88,8%. Thus, a biplot of the first two CCA-axes will retain most of the information from the CCA, regarding the relationship between the snail species and the environmental variables.

Figure 7 is a biplot of the direct ordination. The axes represents linear combination of the ten significant environmental variables. Axis 1 is interpreted as a gradient in productivity/nutrient-richness, going from poor (left) to richer (right) conditions. Axis 2 seems to be related to factors involving moisture/humidity.

The diagram can be interpreted by the biplot-rule (ter Braak & Šmilauer 1998), which states that the species points in proximity correspond to species often occurring together. The environmental variable arrows each points in the expected direction of the steepest increase of values of the variable, and angles between arrows indicate correlations between the individual variables. The species symbols can be projected perpendicularly onto the line overlaying the arrow of particular environmental variable. These projections can be used to approximate the optima of individual species in respect to values of that variable. Species projection points are in the order of the predicted increase of optimum value for that variable.

A large part of the environmental variables show some degree of intercorrelation. This is mainly the variables positively related to productivity (along axis 1). On the other hand, vectors for mire and cliffarea points the opposite direction, indicating a high degree of negative relationship between these two variables. The reported VIF-values for VEGIND, LOGSCREE and H40 (see Table 6) are highest, but still considerably lower than the limit of "perfect correlation" (viz. VIF > 20) proposed by ter Braak & Šmilauer (1998).

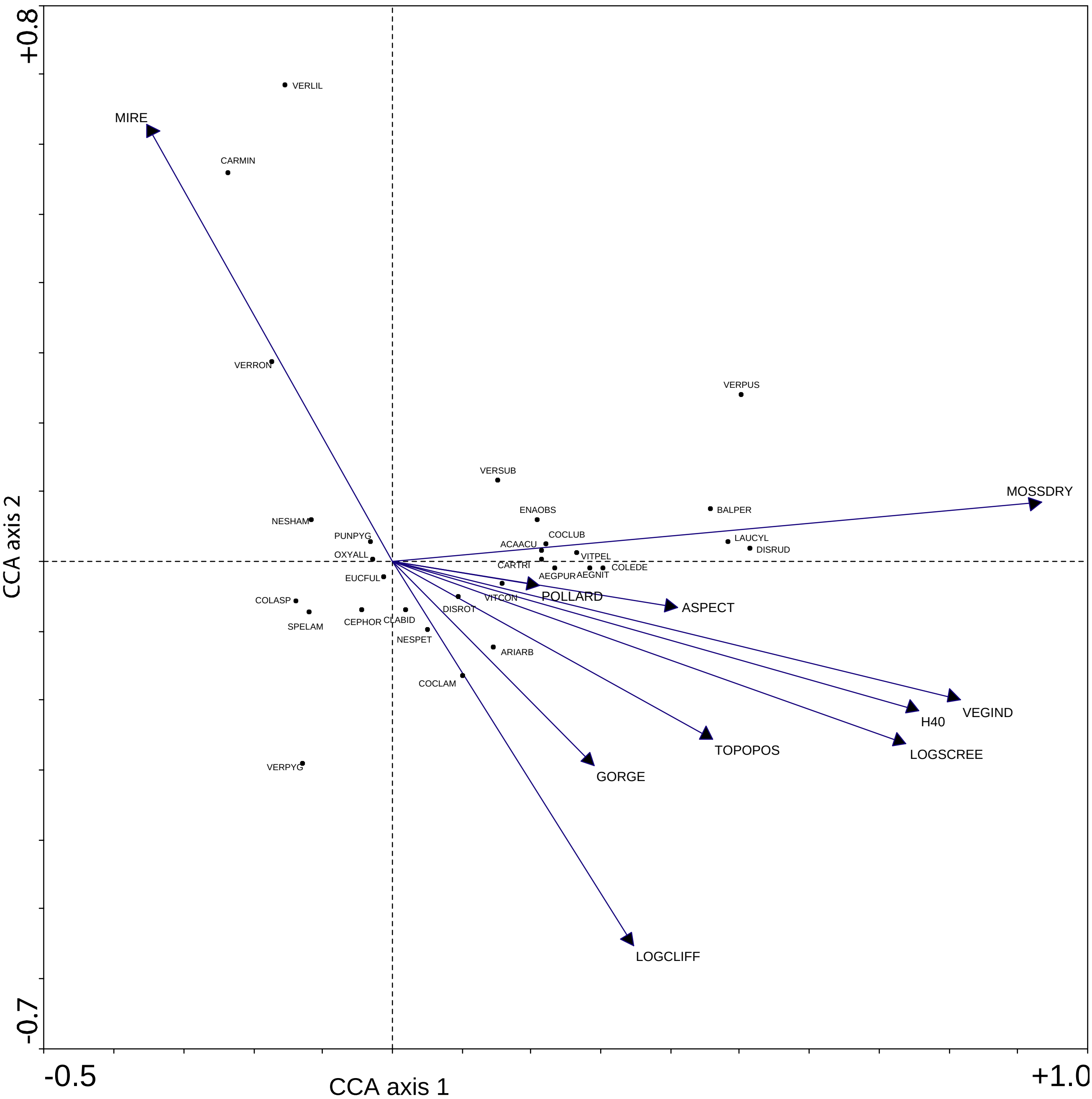

Figure 7. CCA ordination diagram (biplot) showing the variation in abundance of species (dots) related to environmental variables (arrows). Explanation of abbreviations is provided in Tables 2 and 3.

The most abundant species, in terms of occurence, can be found around the center of the diagram. Their optima is found around the average values of the environmental variables, and considering their omnipresence, interpreted as species with a great tolerance.

Habitat requirements of the snail species with reference to the ordination diagrams:

- The species *Vertigo lilljeborgi* and *Carychium minimum* were strongly associated with mires of quite eutrophic state.
- One species, *Vertigo ronnebyensis* was found in only two sites, with southfacing aspect, rather oligotrophic vegetation and wet to dry micro-habitats.
- The species mostly or exclusively selecting dry screes or rock walls on calcareous substate were *Balea perversa*, *Lauria cylindracea*, *Vertigo pygmaea, Clausilia bidentata*, and to a certain extent *Cochlodina laminata.* The two last mentioned species could also be collected from deciduous trees, especially older ashe and elm trees.
- Four species can be grouped as stenotopic and very local and rare litter species of screes and steeper slopes in deciduos forest, viz. *Vertigo alpestris, Vertigo pusilla, Ena obscura* and *Discus ruderatus.*
- As many as 10 species can be classified as almost stenotopic of deciduous forest : *Achantinula aculeata, Columella edentula, Vitrea contracta, Aegopinella nitidula, Aegopinella pura, Vertigo substriata, Carychium tridentatum, Cepaea hortensis, Coclicopa lubrica* and *Vitrina pellucida.* If they did occur in more oligotrophic squares dominated by pine, they were associated with stands of deciduous trees, gorges or cliffs with ledges or a combination of these three factors.
- Associated mostly with deciduous woodland and high productive pine forest were the five species *Spermodea lamellata, Nesovitrea petronella, Discus rotundatus* and *Arianta arbustorum*. This applied also to *Zoogenetes harpa*, although found only as dead individuals.
- Five species (viz. *Columella aspera, Punctum pygmaeum, Euconulus fulvus, Nesovitrea hammonis* and *Oxychilus alliarius*) can be classified as ubiquous since they occured in between 60 and 100% of all the squares.

4 DISCUSSION

The following subjects will be discussed in the next sections:

- The weather during the sampling period and possible consequenses
- Sampling methods and identification of snail species
- Recording of environmental variables and their relevance for this study
- Advantages and limitations of the ordination methods
- Results of the direct and indirect ordinations
- Interpretations of the variation in species richness between squares
- Prediciting power of the environmental variables

4.1 WEATHER CONDITIONS, SAMPLING AND IDENTIFICATION

Few other land snail studies have been conducted at the same large scale as this study. Together with the registered environmental variables, this provides a reliable foundation for drawing conclusions with regard to the species' different environmental requirements and tolerances.

This study should be evaluated as an investigation of snail species in relation to their environment, with focus on spatial distribution. Processes concerning the time aspect may also be of great influence, but the material from this inventory does not allow such hypotheses to be explored. Therefore, I will focus the discussion on possible predictors of species richness, occurence and abundance, in the context of their surroundings at the time of sampling.

According to Cameron (1982), the life cycles of most shell-bearing snails are not well known. He presents evidence for *Discus rotundatus* having an annual life cycle, while *Aegopinella nitidula*, *Carychium tridentatum* and *Cochlodina laminata* generally follow a biennal life cycle. Cameron also suggests a trend where large species breed in the summer and smaller species breed in the autumn. Several studies (e.g. Mason 1970; Gärdenfors 1992; Gärdenfors *et al.* 1995) add weight to the point of view that snail populations show negligible variations during the summer months. Mason (1970 and references therein) also supports the general comprehension that woodland snail species have a breeding period that extends through the season. However, they suggest a slight population growth of *Punctum pygmaeum* towards the end of the autumn.

The sampling period for this study was May to November 1997. Regarding temperature and precipitation, this year was differering from the normal (Table 1). The mean monthly temperature was substantially higher, and there were conciderabliy less precipitation than usual. An exception is September, which had more rain and just marginally higher temperature compared to the normal. The time span of collection was seven months, which also implies daily variation in humidity, temperature and other factors that affect the occurrence of snails. This may have forced the snails to withdraw from the litter, and into more sheltered sites in the soil, in gorges or among rocks (e.g. Cameron 1970; Kerney *et al.* 1979; Wäreborn 1982; Dallas *et al.* 1991).

As the only sampling method used for the collection of snails in this study were sifting samples, the abundance of tree-climbing species (Grime & Blythe 1968; Kerney *et al.* 1979), viz. *Arianta arbustorum*, *Clausilia bidentata*, *Cochlodina laminata* and *Balea perversa,* might have been underestimated. None of these species are exclusively tre-climbing, but *B. perversa* is seldom found in the litter, this may be the reason why it was only found in two squares. However, in Norway and Sweeden, *B. perversa* is mainly associated with calcareous rocks where it feeds on lichens (Solhøy pers. komm. Baur 1997).

The sampling method used in this study is mainly used for collecting as *many* species of snails within each square as possible, rather than to give a correct *abundance* estimate (Waldén 1998). This means that the number of sampled individuals will be affected by the amount of litter sampled and the way the sampling is carried out. But as the same sampling method was applied in all the squares, a comparison between these are not unrealistic. Samples were taken where the different species were assumed to occur, and care was taken to sample as many microhabitats as pratically possible.

Most of the Norwegian snails are very small (1-5 mm), and the juvenile stages are even smaller (Solhøy *et al.* in Gjerde & Baumann 2002). This makes the extraction and identification of the snails difficult and time-consuming. However, considering the background of the persons involved in the process, one must assume that all snails are correctly identified. Due to difficulties associated with picking snails from the sifted material, some speciemens may not have been detected. This is especially true for the smallest species and juveniles, which can be hard to separate from the sifted litter material. Thus, an underestimation of the smaller species might be expected. Johannessen (2000) suggests an underestimation of about 5-20% of the smallest and indiscernible species, while little underestimation is expected regarding the large species. T. Solhøy and T. von Proschwitz (pers. komm.) suggest that less than one percent will escape notice if the sorting is done at a high magnification and by an experienced person.

There are some identification problems that need to be pointed out (see Kerney *et al.* 1979; Kerney *et al.* 1983):

- The separation of *Carychium minimum* and *C. tridentatum* is a straight forward task in adult specimens. But the differentiation of the smallest juveniles are difficult, and there may exist some misidentification in the material.
- Two species of *Cochlicopa spp.* exist in deciduous woodland in Western Norway, viz. *Cochlicopa lubrica* and *C. lubricella.* The separation of the two species can be problematic, particularly in juveniles. Most of the *Cochlicopa spp.* material from Geitaknottane belongs to *C. lubrica* and all specimens have been classified as such, but the occurrence of *C. lubricella* can not be ruled out locally in drier scree areas.
- *Nesovitrea hammonis* exists in one brown and one colourless or faint greenish morph. This last morph is coastal in distribution in Western Norway and has not so far been recorded from the Geitaknottane area. The shell of *Nesovitea petronella* is closely similar to *N. hammonis*, but never brown. The separation of *N. hammonis* and *N. petronella* in the study area was therefore quite unproblematc.
- *Vitrea contracta* and *V. crystallina* are very similar species. Both have been recorded in Western Norway, but *V. contracta* seems to be much more common. The material from Geitaknottane was classified as only *V. contracta*, but the occurrence of *V. crystallina* can not be ruled out.

4.2 DATA ANALYSIS AND INTERPRETATION

By using the density of individuals instead of occurence/absence, a more detailed description of the data material can be achieved (ter Braak 1995a). This will give a more reliable estimation of the species optimas. In this study, density was chosen as unit because of the different sample numbers and volumes among the squares. This was considered the simples and most direct way of transforming the individual counts to a unit that allowed comparison between squares. A variety of transformation methods for use in ordination methods exists (e.g. Legendre & Gallagher 2001), but as there were no apparent need for further treatment of the raw data, such transformations were judged as unnecessary.

The diversity index N_2 (Hill 1973) is the inverse of the Simpson diversity index, and can be used to determine which species to include in ordinations. It has been suggested to make species with N_2-values smaller than 2,0 supplimentary in the analyses (ter Braak & Šmilauer 1998; Johannessen 2000) because these are typically species that occur in very few squares and as few individuals. Since the influence of the species with low N_2-value was tested and shown to have no effect on the results in this case, all species were included.

There are numerous different methods for multivariate analysis in use in ecological sciences today. Ordination is a method to arrange species and samples in a low-dimensional space, where similar entities are close by and unequal entities far apart. Principal components analysis (PCA) is recognized as an especially objective ordination technique that does not require subjective weighting by the user, and produces species and sample scores simultaneously (Gauch 1982a). But as the first multivariate analyses indicated a unimodal response of the species (see Table 5), measured as a gradient length of approximately 3 standard deviations, unimodal methods were chosen. In other terms this means that the species turnover along the ordination axis is approximately 75%, as 1 standard deviation represents roughly a 25% species turnover (Hill & Gauch 1980; Eilertsen *et al.* 1990). A gradient with 100% turnover can thus be interpreted as a gradient with no species in common between the extremes.

To analyse the data material in this study the two unimodal ordination methods, detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) were chosen after considering various aspects of the data structure. The use of DCA differs from PCA in that there is no systematic relation between the second and higher axes to any of the lower axes. The scores of the second axis are divided into segments to ensure an even distribution along the higher axes in DCA. This means that there is no arch effect (an artefact found in other ordination methods, like reciprocal averaging, correspondence analysis (CA) and PCA). The arch effect was indicated in this data material by producing a scatterplot of site scores in an undetrended CA. This was one of the causes to choose DCA as an indirect ordination technique instead of a CA. The use of DCA has recieved a fair amount of critique (e.g. Minchin 1987; Wartenberg *et al.* 1987; James & McCulloch 1990), mostly on background of the detrending of scores along the second axis. This is understood as a mathematically inelegant way of treating data, and some of the authors claim that removal of an arch effect is wrong, as the arch might be an inherent property of the species and site ordination. On the other hand, there has been published a lot of articles (e.g. Hill & Gauch 1980; Peet *et al.* 1988; Eilertsen *et al.* 1990; Ejrnæs 2000) supporting the use of the detrended correspondence analysis. These works suggest that even though DCA has certain drawbacks and also some assumptions to be met, it is a reliable and solid ordination method for comparing the distribution of species. Considering this, I find the DCA the most suitable method for indirect ordination in this study. If no arch effect had been detected, a CA had probably been the better choice.

Canonical correspondence analysis is a method where two matrixes (species and environmental data) are analyzed simultaneously to reveal any common structures among them. The robustness of the CCA is dependent upon several factors, the most important being unimodality of species responses. Noise in the ecological data does not seriously affect the CCA, but noise in the environmental data may do so. Highly correlated environmental variables might pose a problem in regression analyses, but in the CCA this is considered rather unimportant for the distribution of species and site scores in the ordination space (Palmer 1993; McCune 1997).

The null hypothesis is that the response (the species composition) is independent of the environmental variables (Lepš & Šmilauer 1999). Monte Carlo permutation tests are used to simulate the distribution of the values that occur in the original data matrix (ter Braak & Šmilauer 1998). By doing this, it is possible to test whether the connection between the separate environmental variables and the species' distribution is significant (i.e. not likely to occur by chance). In this investigation, 10 of the 12 original environmental variables were found significant. The number of permutations were maximized and should therefore produce a reliable measure of significance.

4.3 GENERAL DISCUSSION

There are no Norwegian woodland snails in the IUCN Red List at the moment, partly because there is little knowledge about their ecology and distribution. However, as mentioned in section 3.1, there are some species found in this study which are considered vulnerable (Gundersen & Rolstad 1998a). These species are *Vertigo ronnebyensis, Ena obscura, Aegopinella nitidula, Spermodea lamellata* and *Lauria cylindracea*. *Aegopinella nitidula* and *Spermodea lamellata* were found in relatively high numbers, which may indicate that some of the vegetation types or other aspects of the environment in this area is particularly suitatable for these species.

It is taken for granted that earlier events (e.g. forest fires, climate or vegetation changes) may have influenced the observed patterns, hence a certain level of disturbance is expected a priori. A certain amount of noise is also expected from biases in collection procedures, daily weather changes etc., but the ordination methods used here has been shown to be resistant to this kind of noise (Gauch 1982b; McCune 1997).

Species thought to be associated with cliffs and calcium are *Clausilia bidentata*, *Vertigo pygmaea*, *Lauria cylindracea* and *Balea perversa*. In the areas more deficient in nutrients, *Vertigo lilljeborgi* and *Carychium minimum* are common species. *Ena obscura* is rare in woodland habitats, and in this study it was found in only two squares. In old natural forests, *Spermodea lamellata* is more abundant than in areas where the nutrient content is low.

4.4 DISTRIBUTION

As much as about half of the species have been found in only 15 % or less of the squares. Some of these are rare because of a paucity of suitable habitats, some are rare because they are on the edge of their distribution, some are genuinely rare even in their supposed optimal habitat and one is rare because of a more consealed life.

- Paucity of suitable habitats: *Vertigo lilljeborgi* and *Carychium minimum* are rare because there are few eutrophic mires in the areas. *Vertigo pygmaea, Lauria cylindracea* and *Balea perversa* are rare due to the lack of suitable open, exposed calcareous cliffs.
- The following species are rare because they have an eastern distribution in Norway: *Zoogenetes harpa, Discus ruderatus, Nesovitrea petronella* and *Vertigo ronnebyensis.*

- Five species are genuinely rare even in the most eutrophic deciduous woodland: *Vertigo alpestris, Vertigo pusilla, Ena obsura, Cochlodina laminata* and *Acanthinula aculeata.*
- The species *Vitrina pellucida* is active in the litter mainly in the autumn and lives more concealed in the soil in most of the sampling period.
- Two species mostly associated with old abandoned grassland with associated bushy vegetation, gardens and other man-made habitats are *Cepaea hortensis* and *Arianta arbustorum*.

4.5 COMMENTS ON THE DIVERSITY OF SNAILS WITHIN THE STUDY AREA

In this study, more than 55% of the snail species with shell occuring naturally in Norwegian forests were recorded. This is a higher number than in other comparable studies (Myrseth 1999; Johannessen 2000). The study of Myrseth was carried out in the same area, but recorded "only" 25 species. One reason for this lower number is the limited selection of squares used in her study. Johannessen recorded the same number of species as Myrseth in his study, but this study was done in another part of the country, within an area of predominantly acidic bedrock. As the number of species in a sample is expected to rise along with the number of species recorded (see Figure 5), the total species number for the area investigated may be higher than indicated.

Most of the squares (56%) have a species richness of between 4 and 8 species (Figure 3). As the total number of species were 30 and the highest species richness was 22 species per square, most of the squares must be considered quite poor, regarding species richness.

The species *Columella aspersa*, *Nesovitrea hammonis*, *Euconulus fulvus* and *Punctum pygmaeum* occured in nearly 80% or more of the squares, and must be considered species with a very wide environmental tolerance. *Carychium tridentatum* was found in under half of the squares, but in high individual numbers, which indicates a higher degree of patchy distribution than the four most abundant species mentioned. On the other end of the scale we find rare species like *Vertigo pygmaea, V. ronnebyensis, V. pusilla, Ena obscura, Balea perversa, Lauria cylindracea* and *Discus ruderatus,* which all occured in less than 3% of the squares.

4.6 ENVIRONMENTAL VARIABLES

A discussion on the different environmental variables that were found significant is given in this section. Most of the conclusions are based on the two ordination diagrams. Regarding the VIF-values, only the higher ones (indicating strong intercorrelation) are commented.

4.6.1 CALCIUM-INDICATING MOSSES ON DRY SURFACES - MOSSDRY

Although present in only 16 squares, the number of calcium-indicating moss species on dry surfaces (MOSSDRY) is one of the variables with a high explanatory value. If the data files are studied, it becomes clear that the squares containing calcium-indicating mosses on dry surfaces are also charachterised by high species richness and a high level of productivity (H40). The number of calcium-indicating mosses have the highest value of both marginal and additional variance (Table 5), indicating that this variable is the most important one, regarding explanation of the species composition. Snail species that are closely connected to this variable are *Balea perversa*, *Lauria cylindracea* and *Discus ruderatus*. These species are known to be associated with scree and cliffs with calcareous substrate.

A short remark on calcium-indicating mosses on wet surfaces: The variable MOSSWET turned out not to be significant in the permutation tests. One reason for this might be that these wet mosses are associated with mire and other very wet habitats with unfavourable conditions for most snail species.

4.6.2 VEGETATION INDEX - VEGIND

The vegetation index is composed of five different vegetation types found in the area, ranged after richness. This variable is positively and quite closely correlated with the variables H40 and LOGSCREE along the first axis in the CCA diagram (Figure 7). It has the highest VIF (9,21) of the environmental variables (see Table 6), and this intercorrelation is probably due to an increased productivity in the higher vegetation classes. The vegetation index has a high value of marginal variance, emphasizing the importance of this variable. As indicated by Boycott (1934) and Mason (1970), the more favourable condition of these high productivity forests may lead to a higher species richness of both snails and other litterdwelling organisms. It can be predicted from the environmental vegetation index that the highest species richness will be found in squares with rich deciduous tree species. The litter in pine, spruce and oak forests is often acidic, and few species of snails are found here (mostly *C. aspera, N. hammonis, E. fulvus, P. pygmaeum* and *O. alliarius*) (Solhøy et al. 1998).

4.6.3 AREA OF CLIFFS - LOGCLIFF

The vector for this variable in the CCA diagram points in the opposite direction of the MIRE vector. This indicates a strong negative correlation between the two variables. Species associated with this variable are *Cochlodina laminata*, *Nesovitrea petronella*, and to a certain extent also *Clausilia bidentata* and *Arianta arbustorum*. The log-transformation of this variable was done to downweight the influence of very large areas of cliffs, which may have biased the results in an unwanted way. The variable is quite closely linked to the variable GORGE. See Appendix 6.9 for pictures of two different types of cliffs, viz. rich and poor in nutrients.

4.6.4 PERCENTAGE OF MIRE - MIRE

The species *Carychium minimum* and *Vertigo lilljeborgi* are found mainly in eutropic mires. *Vertigo ronnebyensis* also seems to be closely associated with this variable, but this species position in the ordination diagram should not be given too much weight since the species is found at only two locations with one individual at each location. Mires are generally unfavourable habitats for most snail species, as they represent a potential risk of drowning (Boycott 1934), but rich fens may contain 10-15 species in Norway (T. Solhøy pers.com.). In short, this means that nearly all but the most hydrophilic species of snails tend to avoid wet mires.

4.6.5 OCCURENCE OF GORGES - GORGE

Gorges are habitats distinguished by high humidity, crevices, shade and often a high cover of mosses. In the direct ordination, this variable was found significant through permutation tests, but a low t-value (Table 6) indicates that the influence of this variable is weak, and often counteracted by other factors. One reason for this might be sampling errors because some gorge walls may have been overlooked, and some gorges are inaccessible. The species associated with the occurence of gorge are mainly the same species as those associated with cliffarea.

4.6.6 POLLARDED TREES - POLLARD

In earlier times, trees in the study area were pollarded to provide more food for sheep and cattle staying indoor at winter. Only deciduous trees were pollarded, and mainly the species elm (*Ulmus glabra*) and ash (*Fraxinus excelsior*). This lead to a denser and wider crown of the tree, which in turn has lead to a larger amount of leaves falling to the ground in areas with pollarded trees. The larger amount of litter formed in these areas may make the conditions more favourable for the snails. The vector for pollarded trees is short, indicating a weaker explaining power, regarding species composition. As it is almost parallel to the first CCA axis, it is highly related to factors of nutrient richness.

4.6.7 PRODUCTIVITY - H40

Other studies (e.g. Myrseth 1999; Johannessen 2000) has shown that productivity is one of the most important factors determining the species richness of snail species. With a VIF-value of 6,76, it shows a high degree of intercorrelation with the variables VEGIND and LOGSCREE. The marginal variance value is high (18%), indicating that the productivity index is an important variable in the direct ordination of the species.

4.6.8 EXPOSURE TO SUNLIGHT – ASPECT

Slopes facing south-west are most exposed to sunlight, making these areas favourable for the vegetation. It is assumed that this variable has a potential of misinterpretation, since the heterogenity of the landscape may lead to a great variation of aspects even witin a square. The variable was found significant in the Monte Carlo permutation tests (Table 5), but care should be taken when interpreting the species composition using this variable. As many of the other variables, it is strongly associated with factors involving richness of nutrients.

4.6.9 AREA OF SCREE – LOGSCREE

The occurence of scree is considered important as shelter for snails (e.g. Boycott 1934; Mason 1970; Kerney *et al.* 1979; Solhøy *et al.* 1998). It provides a shelter from unfavorable climatic conditions (e.g. humidity and temperature), and may provide a more stable environment. The VIF-value is high (6,83), and indicates as earlier mentioned an intercorrelation between this variable and H40 and VEGIND. The marginal variance is high (Table 5), and thus a high explanatory power is indicated.

4.6.10 TOPOGRAPHIC POSITION – TOPOPOS

The topographic position of the square has a vital importance for the amount of sunlight recieved, but also for the humidity of the soil. A flat area on the top of a hill is generally drier and more exposed to sunlight than an area at the bottom of a slope. In the sloping parts the nutrients will accumulate in the lower parts, also called the slope effect (Valovirta 1968). This will lead to a wetter and more nutrient rich area in the lower parts of the slope. The TOPOPOS vector in the CCA ordination is not pointing in the expected direction, but seems to indicate that the more nutrient rich parts are the driest parts. A reason for this may be that the slope effect has a lower influence on the vegetation and nutrient richness than the exposure to sunlight.

4.7 INTERPRETATION OF THE ORDINATION AXES

The first axis in the CCA diagram seems to be closely related to factors associated with nutrient richness, while the second can be interpreted as a gradient in humidity related factors. This is similar to many other studies from the area (Myrseth 1999; Pommeresche 1999; Sætersdal *et al.* 2003), and might be expected as these two factors are some of the essensial factors regarding the distribution of vegetation. As many of the variables are connected to nutrient richness, it is recommended to consider these factors as a group, instead of isolated variables with separated effects. If the two ordination diagrams are considered jointly, predictions of different species groups can be made.

4.8 CONCLUSIONS

A summary of the most important findings from the study is given below:

- The data material used in this study is a reliable basis for investigation of snail species and their relation to the surrounding environment.
- The climate during the sampling period was quite different compared to the normal temperature and precipitation for earlier years.
- The sampling method used is not strictly quantitative, but it is one of the few well established methods for semi-quantitative sampling of snails.
- Identification was carried out by trained and experienced persons, thus a reliable identification of the numerous individuals is assumed.
- Unimodal responses of the species were indicated by the introductory multivariate analyses, thus the two ordination methods DCA and CCA were chosen.
- The two first axes of the DCA and the CCA explained the inherent variance in the data set well, but there were still some variation that these analyses could not explain.
- The first axis of the DCA and the CCA was interpreted as a gradient in nutrient related factors, whereas the second axis in both analyses were interpreted as a gradient in humidity related factors.
- 10 of the 12 included environmental variables were found significant using Monte Carlo permutation tests at maximum number of permutations. The significant variables were number of calcium-indicating mosses, vegetation index, area of cliffs, percentage of mire, occurence of gorges, pollarded trees, forest productivity, exposure to sunlight, area of scree, and dominating topographic position of the square.
- Four of the environmental variables had a high marginal variance, viz. number of calcium-indicating mosses, vegetation index, forest productivity and area of scree. This indicates high explanatory power.
- If the two ordination diagrams are used, the occurence of several groups of species can be predicted with regard to the environmental variables. Some species occur in nearly all habitat types, while others are confined to specific environmantal conditions.

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5 REFERENCES

Barker G.M. & Mayhill P.C. (1999) Patterns of diversity and habitat relationships in terrestrial mollusc communities of the Pukeamaro Ecological District, Northeastern New Zealand. *Journal of Biogeography* **26:** 215-238.

Barker G.M. (2001) Gastropods on land: Phylogeny, diversity and adaptive morphology. in: *The biology of terrestrial molluscs*. G.M. Barker. CABI Publishing, Wallingford. 558 pp.

Begon M., Harper J.L. & Townsend C.R. (1996) *Ecology - Individuals, populations and communities*. Oxford, Blackwell Sciences Ltd. 1068 pp.

Besag J. & Clifford P. (1989) Generalized Monte Carlo significance tests. *Biometrika* **76:** 633-642.

Blom H. (1998) Registrering av moser i studieområdet Geitaknottane, Kvam i Hordaland. *Aktuelt fra skogforskningen* **3:** 14-15.

Blom H. (1999) Artsmangfold og fordeling av moser. En forløpig gjenomgang av materialet fra seks studieområder. *Aktuelt fra skogforskningen* **6:** 4-6.

Boycott A.E. (1934) The habitats of land mollusca in Britain. *Journal of Ecology* **22:** 1-38.

Cameron R.A.D. (1969) Predation by Song Thrushes Turdus Ericetorum (Turton) on Snails Cepaea Hortensis (Mull.) and Arianta Arbustorum (L.) near Rickmansworth. *Journal of Animal Ecology* **38:** 547-553.

Cameron R.A.D. (1970) Effect of Temperature on Activity of 3 Species of Helicid Snail (Mollusca- Gastropoda). *Journal of Zoology* **162:** 303-309.

Cameron R.A.D. (1982) Life Histories, Density and Biomass in a Woodland Snail Community. *Journal of Molluscan Studies* **48:** 159-166.

Cameron R.A.D., Mylonas M. & Vardinoyannis K. (2000) Local and regional diversity in some Aegean land snail faunas. *Journal of Molluscan Studies* **66:** 131-142.

Carter C. (1999) *The Distribution of Terrestrial Snails in Geitaknottane Nature Reserve, Norway*. Term paper. Department of Zoology, University of Bergen. 55 pp.

Cowie R.H., Nishida G.M., Basset Y. & Gon S.M. (1995) Patterns of land snail distribution in a montane habitat on the island of Hawaii. *Malacologia* **36:** 155-169.

Dallas H.F., Curtis B.A. & Ward D. (1991) Water Exchange, Temperature Tolerance, Oxygen-Consumption and Activity of the Namib Desert Snail, Trigonephrus Sp. *Journal of Molluscan Studies* **57:** 359-366.

Davies P., Gale C.H. & Lees M. (1996) Quantitative studies of modern wet-ground molluscan faunas from Bossington, Hampshire. *Journal of Biogeography* **23:** 371-377.

de Winter A.J. & Gittenberger E. (1998) The land snail fauna of a square kilometer patch of rainforest in southwestern Cameroon: High species richness, low abundance and seasonal fluctuations. *Malacologia* **40:** 231-250.

Dolmen D. (1993) Herptilreservat Rindalsåsene. Forslag til verneområde for amfibier og reptiler. NTNU Vitenskapsmuséet, Trondheim. 40 pp.

Eilertsen O., Økland R.H., Økland T. & Pedersen O. (1990) Data Manipulation and Gradient Length Estimation in DCA Ordination. *Journal of Vegetation Science* **1:** 261-270.

Ejrnæs R. (2000) Can we trust gradients extracted by Detended Correspondence Analysis? *Journal of Vegetation Science* **11:** 565-572.

Emberton K.C. (1997) Diversities and distributions of 80 land-snail species in southeastern-most Madagascan rainforests, with a report that lowlands are richer than highlands in endemic and rare species. *Biodiversity and Conservation* **6:** 1137-1154.

Foslie S. (1955) Kisdistriktet Varaldsøy - Ølve i Hardanger og bergverksdriftens historie. *Norges Geologiske Undersøkelser* **147:** 1-106 + pl. I-IV.

Gaston K.J. & Spicer J.I. (1998) *Biodiversity - An Introduction*. Oxford, Blackwell Science. 113 pp.

Gauch H.G. (1982a) *Multivariate Analysis in Community Ecology*. New York, NY, Cambridge University Press. 298 pp.

Gauch H.G. (1982b) Noise reduction by eigenvector ordinations. *Ecology* **63:** 1643-1649.

Gjerde I. (1998a) Miljøregistrering i skog - biologisk mangfold. Status for forskningsdelen av prosjektet. *Aktuelt fra skogforskningen* **3:** 4-5.

Gjerde I. (1998b) Hotspot-overlapp mellom ulike artsgrupper. *Aktuelt fra skogforskningen* **3:** 27-28.

Gjerde I. & Ihlen P.G. (1998) Lav på hassel i edelløvskog og furuskog. *Aktuelt fra skogforskningen* **3:** 21-22.

Gjerde I. & Baumann C. (2002) Miljøregistrering i skog - biologisk mangfold. Hovedrapport. 104 pp.

Good P. (1994) *Permutation tests: A practical guide to Resampling methods for testing hypotheses.* New York, Springer-Verlag. 344 pp.

Greig-Smith P. (1980) The development of numerical classification and ordination. *Vegetatio* **42:** 1-9.

Grime J.P. & Blythe G.M. (1968) An investigation of the relationship between snails and vegetation at the Winnats Pass. *Journal of Ecology* **57:** 45-66.

Gundersen V. & Rolstad J. (1998a) Truete arter i skog. En gjennomgang av rødlistearter i forhold til norsk skogbruk. Norsk institutt for skogforskning. 137 pp.

Gundersen V. & Rolstad J. (1998b) Nøkkelbiotoper i skog. Norsk institutt for skogforskning (NISK). 61 pp.

Gutiérrez M.A.U. (2002) *The Crested Newt (Triturus cristatus) in Geitaknottane Nature Reserve, Western Norway: A study on population number estimates and belly pattern variations in four ponds.* Term paper. Department of Zoology, University of Bergen. 116 pp.

Gärdenfors U. (1992) Effects of Artificial Liming on Land Snail Populations. *Journal of Applied Ecology* **29:** 50-54.

Gärdenfors U., Waldén H.W. & Wäreborn I. (1995) Effects of soil acidification on forest land snails. *Ecological Bullentins* **44:** 259-270.

Hage M. (1999) *The Northern Crested Newt (Triturus cristatus) in the Geitaknottane Nature Reserve: diet, body size and population estimates.* Cand. scient. thesis. Department of Zoology, University of Bergen. 116 pp.

Hill M.O. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology* **54:** 427-432.

Hill M.O. & Gauch H.G. (1980) Detrended correspondence analysis: An improved ordination technique. *Vegetatio* **42:** 47-58.

Hobæk A., Hage M., Solhøy T. & Myklebust O.A. (2000) Vannkvalitet og stor salamander i Geitaknottane naturreservat, Hordaland. Norsk institutt for vannforskning (NIVA). 31 pp.

James F.C. & McCulloch C.E. (1990) Multivariate analysis in ecology and systematics: Panacea or Pandora's box? *Annual Review of Ecology and Systematics* **21:** 129-166.

Johannessen L.E. (2000) *Distribution of Terrestrial Snails in Relation to Environmental Variables in a Nemoral Mixed Oak Forest at Havsåsen, Kristiansand.* Cand. scient. thesis. Department of Zoology, University of Bergen. 119 pp.

Johannessen L.E. & Solhøy T. (2001) Effects of experimentally increased calsium levels in the litter on terrestrial snail populations. *Pedobiologia* **45:** 234-242.

Kerney M.P., Cameron R.A.D. & Riley G. (1979) *A field guide to the land snails of Britain and North-west Europe*. London, Collins. 288 pp.

Kerney M.P., Cameron R.A.D. & Jungbluth J.H. (1983) *Die landschnecken Nord- und Mitteleuropas*. Hamburg, Verlag Paul Parey. 384 pp.

Legendre P. & Gallagher E.D. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* **129:** 271-280.

Lepš J. & Šmilauer P. (1999) Multivariate Analysis of Ecological Data. University of South Bohemia, Ceské Budejovice. 110 pp.

Lepš J. & Šmilauer P. (2003) *Multivariate analysis of ecological data using CANOCO*. Cambridge, Cambridge University Press. 269 pp.

Manly B.F.J. (1994) *Multivariate Statistical Methods - A Primer*. London, Chapman & Hall. 174 pp.

Manly B.F.J. (1997) *Randomization, Bootstrap and Monte Carlo Methods in Biology*. London, Chapman & Hall. 399 pp.

Mason C.F. (1970) Snail populations, beech litter production, and the role of snails in litter decomposition. *Oecologia* **5:** 215-239.

McCune B. (1997) Influence of noisy environmental data on canonical correspondence analysis. *Ecology* **78:** 2617-2623.

Minchin P.M. (1987) An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* **69:** 89-107.

Moe B. (1995) Geitaknottheiane: Vegetasjon, flora og verneverdi. Fylkesmannen i Hordaland, Miljøvernavdelinga, Bergen. 13 pp.

Moe B. & Sætersdal M. (1995) Kongsbregne, Osmunda regalis, planten som har ført en bortgjemt tilværelse i Hordaland. *Blyttia* **4:** 177-189.

Myklebust O.A. (1998) *Vasshabitat- og åtferdsstudie av stor salamander (Triturus vulgaris) i Geitaknottane naturreservat, Ytre Hardanger.* Cand. scient. thesis. Department of Zoology, University of Bergen. 84 pp.

Myrseth E.W. (1999) *Utbredelsen av skallbærende terrestre snegl i relasjon til miljøvariabler. Geitaknottane naturreservat, Kvam i Hardanger.* Cand. scient. thesis. Department of Zoology, University of Bergen. 86 pp.

Olsen K.M. (2002) Landsnegler i Norge - en oppsummering og en presentasjon av tre nye arter, *Oxychilus navarricus* (Bourguignat, 1870)*, Lucilla singleyana* (Pilsbry, 1890) og *Hawaiia minuscula* (Binney, 1840). *Fauna* **55:** 66-77.

Palmer M.W. (1993) Putting things in even better order: The advantage of canonical correspondence analysis. *Ecology* **74:** 2215-2230.

Peake J. (1978) Distribution and ecology of the Stylommatophora, 429-527 pp. in: *Pulmonates (2A)*. V. Fretter and J. Peake. Academic Press Inc., London. 540 pp.

Peet R.K., Knox R.G., Case J.S. & Allen R.B. (1988) Putting things in order: The advantages of detrended correspondence analysis. *The American Naturalist* **131:** 924-934.

Pommeresche R. (1999) *Diversitet, samfunnsstrukturer og habitatpreferanser hos epigeiske dderkopper (Araneae) i ulike vegetasjonstyper innen Geitaknottane naturreservat, indre Hordaland.* Cand. scient. thesis. Department of Zoology, University of Bergen. 76 pp.

Riddle W.A. (1993) Physiological Ecology of Land Snails and Slugs. in: *The Mollusca - Ecology*. W.D. Russel-Hunter. Academic Press, Inc., London. **6**. 431-462 pp.

Ruppert E.E. & Barnes R.D. (1994) *Invertebrate zoology*. Orlando, Saunders College Publishing. 1070 pp.

Schilthuizen M. & Rutjes H.A. (2001) Land snail diversity in a square kilometre of tropical rainforest in Sabah, Malaysian Borneo. *Journal of Molluscan Studies* **67:** 417-423.

Skartveit J. & Pommeresche R. (1998) Evertebratar i skogbotnen - Edderkoppar og biller. *Aktuelt fra skogforskningen* **3:** 11-13.

Skartveit J., Solhøy T., Pommeresche R. & Myrseth E.W. (1999) Artsmangfold hjå bakkelevende evertebrater i ulike vegetasjonstyper i Kvam. *Aktuelt fra skogforskningen* **6:** 11-15.

Skartveit J., Sætersdal M., Gjerde I., Solhøy T., Blom H., Ihlen P.G., Myrseth E.W., Pommeresche R. & Aas O. (2003) Small-scale variation in invertebrate and plant biodiversity in scots pine forest in Western Norway. In prep. pp.

Sokal R.R. & Rohlf F.J. (1995) *Biometry*. New York, W. H. Freeman and Company. 887 pp.

Solhøy T., Hauge E. & Meidell B. (1975) Årsrapport fra fagområdet terrestrisk zoologi, Bind III. 100 pp. In: Edelløvskog på Vestlandet, Evertebrater, Bind I-III. Hauge, E., Meidell, B. and Solhøy, T. Zoologisk Museum, Universitetet i Bergen, Bergen. 275 pp.

Solhøy T., Skartveit J. & Eide E.W. (1998) Evertebrater i skogbunnen - Terrestre skalldekte snegl. *Aktuelt fra skogforskningen* **3:** 8-12.

Storaunet K.O. (1999) Skogshistorie-indikatorer i MiS-prosjektet. *Aktuelt fra skogforskningen* **6:** 21-23.

Storaunet K.O. (2002) Hogstaktivitet og artsmangfold i boreal skog - Fra studieområdene Gartland (Grong), Oppkuven (Ringerike)og Heimseteråsen (Sigdal). *Aktuelt fra skogforskningen* **8:** 20-23.

Sætersdal M. (1998) Indikatorer for utvelgelse av viktige områder for biologisk mangfold. *Aktuelt fra skogforskningen* **3:** 28-29.

Sætersdal M. (1999) Indikatorer for biologisk mangfold og utvelgelse av arealer basert på komplementaritet. *Aktuelt fra skogforskningen* **6:** 24-25.

Sætersdal M. (2002) Forutsetninger for bruk av indikatorarter for artsrikhet. *Aktuelt fra skogforskningen* **8:** 24-26.

Sætersdal M., Gjerde I., Blom H., Ihlen P.G., Myrseth E.W., Pommeresche R., Skartveit J., Solhøy T. & Aas O. (2003) Vascular plants as a surrogate species group in complimentary site selection for bryophytes, macrolichens, spiders, carabids, staphylinids, snails, and wood living polypore fungi in a northern forest. *Biological Conservation* **In press**.

Tattersfield P. (1996) Local patterns of land snail diversity in a Kenyan rain forest. *Malacologia* **38:** 161-180.

ter Braak C.J.F. (1986) Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67:** 1167-1179.

ter Braak C.J.F. (1988) CANOCO - an extesion of DECORANA to analyse species-environment relationships. *Vegetatio* **75:** 159-160.

ter Braak C.J.F. & Prentice I.C. (1988) A Theory of Gradient Analysis. *Advances in Ecological Research* **18:** 271-317.

ter Braak C.J.F. (1995a) Ordination. in: *Data analysis in community and landscape ecology*. R.H.G. Jongman, C.J.F. ter Braak and O.F.R. Van Tongeren. Cambridge University Press, Cambridge. 91-173 pp.

ter Braak C.J.F. (1995b) Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic sciences* **55:** 255-289.

ter Braak C.J.F. & Šmilauer P. (1998) *CANOCO Reference manual and User's Guide to CANOCO Version 4 for Windows*. Ithca, NY, Microcomputer Power. 352 pp.

Thuenes K.H., Skartveit J. & Gjerde I. (2003) The canopy arthropods of old and mature pine *Pinus sylvestris* in Norway. *Ecography* **26:** 490-502.

Tompa A.S. (1976) A comparative study of the ultrastructure and mineralogy of calcified land snail eggs (Pulmonata: Stylommatopora). *Journal of Morphology* **150:** 861-871.

UNEP (1995) *Global Biodiversity Assessment*, Cambridge University Press. 1031 pp.

Valovirta I. (1968) Land molluscs in relation to acidity on hyperite hills in Central Finland. *Annales Zoologici Fennici* **5:** 245-253.

Voelker J. (1959) Der chemische Einfluss von Kalziumkarbonat auf Wachstum, Entwicklung und Gehaüsebau von Achatina fulica Bowdich (Pulmonata). *Mitteilungen aus dem Hamburgischen Zoologischen Musum und Institut der Universität Hamburg* **57:** 37-78.

von Proschwitz T. (1993) Habitat selection and distribution of ten virginid species in the province of Dalsland (SW. Sweden). *Malakologische Abhandlungen* **16:** 177-212.

Waldén H.W. (1981) Communities and diversity of land molluscs in scandinavian woodlands. I. High diversity communities in taluses and boulder slopes in SW Sweden. *Journal of Conchology* **30:** 351-371.

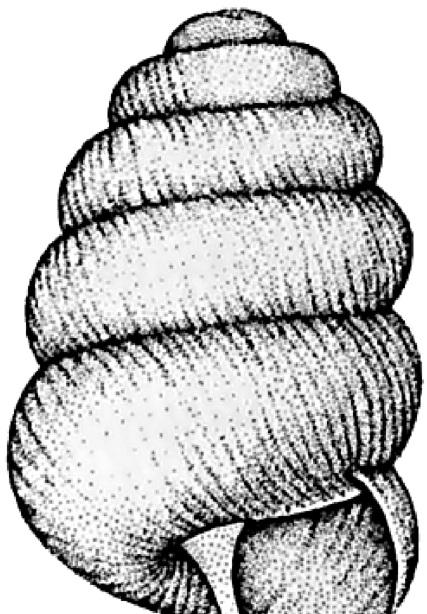
Waldén H.W. (1998) Studier över skogbruksåtgärdernas inverknad på snäckfaunans diversitet. Skogsstyrelsens förlag. **2**. 61 pp.

Wartenberg D., Ferson S. & Rohlf F.J. (1987) Putting things in order: A critique of detrended correspondence analysis. *The American Naturalist* **129:** 434-448.

Wäreborn I. (1982) *Environments and molluscs in a non-calcareous forest area in southern Sweden.* Dissertation. Department of Animal Ecology, University of Lund. 84 pp.

Zar J.H. (1999) *Biostatistical Analysis*. London, Prentice-Hall International Ltd. 663 pp.

APPENDICES



Columella aspera

The most abundant species in the study

6 APPENDICES

6.1 GLOSSARY AND ACRONYMS

Alpha (α)-diversity:
The diversity or richness of a species within a particular habitat, community, local area or individual sample.

Beta (β)-diversity:
The richness of species in a specified geographical region (regional diversity). A measure of the rate and extent of change in species along a gradient from one habitat to others.

CCA:
Canonical Correspondence Analysis, a direct ordination method. Also called constrained ordination. This method is used to relate environmental variables to the investigated sites and species with unimodal responses.

DCA:
Detrended Correspondence Analysis, an indirect ordination method for species with unmodale responses along environmantal gradients. Also called unconstrained ordination. A method used to ordinate sites and species along abstract environmental gradients (axes). The DCA is a *detrended* version of correspondence analysis (CA), and reduces the arch-effect often produced by CA.

Eigenvalue:
The variance accounted for by an axis. If divided by the total inertia of an analysis, the percentage variation accounted for by the specified axis is found. Thus, it is a measure of how well an axis explains the inherent variance in the data material.

Gamma (γ)-diversity:
The richness of species across a range of habitats within a geographical area or in widely separated areas, dependent upon both the alpha diversity of the local habitats and the extent of the beta diversity between them.

Habitat:
The space used by an organism, together with all the species with which it coexists, and the landscape and climate elements that affect it; the place where an animal or a plant usually lives and reproduces.

Indicator species:
A species whose status provides information on the overall condition of the ecosystem and of other species in that ecosystem. Species that flag conditions in biotic or abiotic conditions. They reflect the quality and changes in environmental conditions as well as aspects of community composition.

IUCN:
International Union for Conservation of Nature and Natural Resources.

m a.s.l.:
Meters above sea level.

PCA:
Principal Component Analysis. A linear unconstrained ordination method.

RDA:
Redundancy Analysis. A linear constrained ordination method.

Species diversity:
The number and variety of species found in a given area in a region.

Species richness:
The number of species found within a region. A part of the species diversity.

6.2 RAW DATA SNAILS

Appendix 6.2. Collected snail species. Abbreviations from Table 3. All numbers are counts, and sample volume is in liters.

SQUARE	VOLUM	ACAACU	AEGNIT	AEGPUR	ARIARB	BALPER	CARMIN	CARTRI	CEPHOR	CLABID	COCLAM	COCLUB	COLASP	COLEDE	DISROT	DISRUD	ENAOBS	EUCFUL	LAUCYL	NESHAM	NESPET	OXYALL	PUNPYG	SPELAM	VERLIL	VERPUS	VERPYG	VERRON	VERSUB	VITCON	VITPEL
1	9,3	3	9	31	15	0	0	81	1	2	0	18	26	33	9	0	0	46	0	32	8	5	19	5	0	0	0	0	8	63	2
2	11,2	0	0	9	1	0	0	9	0	0	0	0	28	0	3	0	0	7	0	7	5	4	5	0	0	0	0	0	1	24	0
3	13,4	0	0	0	0	0	0	0	0	1	0	0	35	0	0	0	0	0	0	4	0	0	2	0	0	0	0	0	0	0	0
4	8,3	0	3	4	2	0	0	13	0	1	1	1	34	1	1	0	0	12	0	11	0	1	24	0	0	0	0	0	1	5	0
5	8,4	0	0	6	0	0	0	0	0	1	1	0	140	0	0	0	0	23	0	19	0	1	29	1	0	0	0	0	0	7	1
6	11,1	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	4	0	1	6	0	0	0	0	0	0	5	1
7	15,5	0	2	3	0	0	0	0	0	0	0	0	36	0	0	0	0	8	0	11	0	0	50	12	0	0	1	0	0	0	0
8	12,3	0	5	24	1	0	0	67	1	2	0	5	25	17	8	0	0	101	0	34	0	11	190	9	0	0	0	0	13	67	1
9	10,5	4	0	22	0	0	0	48	0	0	0	5	80	7	1	0	0	17	0	20	2	4	51	8	0	0	0	0	4	20	0
10	14,8	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	1	0	1	0	0	2	0	0	0	0	0	0	0	0
11	12,6	0	0	0	0	0	0	1	0	0	0	0	14	0	0	0	0	3	0	8	0	1	3	0	0	0	0	0	0	0	0
12	11,2	0	0	0	0	0	0	1	0	0	0	0	16	0	0	0	0	2	0	6	0	1	1	0	0	0	0	0	0	0	0
13	19,2	7	7	5	0	0	0	35	0	0	0	2	33	1	3	0	0	16	0	17	0	3	187	1	0	0	0	0	1	7	1
14	17,7	0	0	6	2	0	0	80	1	2	0	2	3	16	6	1	0	26	0	13	2	5	69	0	0	0	0	0	5	31	0
15	14,7	0	0	1	0	0	0	0	0	1	0	0	15	0	0	0	0	4	0	7	0	1	9	1	0	0	0	0	0	3	0
16	15,4	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0
17	14	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
18	14,7	0	0	1	0	0	0	19	0	0	0	0	16	0	0	0	0	4	0	6	1	3	48	0	0	0	0	0	1	3	0
19	15,3	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	2	0	4	0	1	0	0	0	0	0	0	0	0	0
20	12,7	4	4	16	0	0	0	33	0	1	0	8	64	8	0	0	0	16	0	21	1	2	64	5	0	0	0	0	1	12	0
21	13,1	0	0	0	0	0	0	0	0	0	0	3	18	0	1	0	0	1	0	3	0	1	0	0	0	0	0	0	0	0	0
22	13,1	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	1	0	4	0	1	0	0	0	0	0	0	0	0	0
23	14,4	0	0	0	0	0	0	15	0	0	0	1	10	0	0	0	0	3	0	9	0	0	12	2	0	0	0	0	0	2	0
24	14,7	1	0	19	0	0	0	27	0	0	0	2	31	1	1	0	0	17	0	29	0	2	46	9	0	0	0	0	0	6	0
25	11,9	0	0	0	0	0	0	0	0	0	0	0	13	0	7	0	0	4	0	5	0	3	0	0	0	0	0	0	0	0	0
26	15,2	0	0	0	0	0	0	0	0	0	0	0	29	0	0	0	0	1	0	8	0	1	19	0	0	0	0	0	0	0	0
27	15,8	0	0	0	0	0	0	3	0	0	0	1	58	0	1	0	0	5	0	23	0	4	22	3	0	0	0	0	1	0	0
28	13,2	1	3	16	4	0	0	45	0	1	0	3	15	13	0	0	0	19	0	6	0	5	23	1	0	1	0	0	4	5	0
29	15,6	0	0	1	0	0	0	0	0	0	0	0	12	0	6	0	0	3	0	1	0	2	3	2	0	0	0	0	0	0	0
30	11,8	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0
31	16,6	0	0	0	0	0	0	8	0	0	0	0	13	0	3	0	0	4	0	7	0	5	8	2	0	0	0	0	1	2	0
32	13,4	0	0	1	0	0	0	0	0	1	0	0	19	0	6	0	0	6	0	8	6	2	11	5	0	0	0	0	1	1	0
33	16,7	0	0	0	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0	12	0	1	0	0	0	0	0	0	0	0	0
34	18,9	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	6	0	12	0	1	0	4	0	0	0	0	0	0	0
35	17,3	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	1	0	4	0	1	0	0	0	0	0	0	0	0	0
36	18,4	0	0	8	1	0	0	53	0	1	0	8	27	0	0	0	0	5	0	19	0	4	31	4	0	0	0	0	0	14	0
37	15,1	2	8	20	2	0	0	39	0	1	1	25	11	33	22	0	0	25	0	21	0	5	37	7	0	0	0	0	7	31	2
38	12,8	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	3	0	3	0	3	2	0	0	0	0	0	0	1	0
39	11,9	0	0	0	0	0	0	0	0	0	0	0	19	0	0	0	0	3	0	2	0	1	0	0	0	0	0	0	0	0	0
40	15,1	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	2	0	6	2	1	0	0	0	0	0	0	0	0	0

SQUARE	VOLUM	ACAACU	AEGNIT	AEGPUR	ARIARB	BALPER	CARMIN	CARTRI	CEPHOR	CLABID	COCLAM	COCLUB	COLASP	COLEDE	DISROT	DISRUD	ENAOBS	EUCFUL	LAUCYL	NESHAM	NESPET	OXYALL	PUNPYG	SPELAM	VERLIL	VERPUS	VERPYG	VERRON	VERSUB	VITCON	VITPEL
41	13,9	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	6	0	1	0	1	0	0	0	0	0	0	0
42	11,5	0	0	0	0	0	3	0	0	0	0	0	17	0	2	0	0	3	0	13	0	2	5	2	0	0	0	0	0	1	0
43	11,9	0	0	2	0	0	0	6	0	0	0	0	11	4	0	0	0	9	0	12	0	2	3	4	0	0	0	0	0	1	0
44	9,2	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	1	0	5	0	0	1	0	0	0	0	0	0	0	0
45	18,5	0	0	0	0	0	0	0	0	0	0	0	18	0	0	0	0	4	0	9	0	3	1	0	0	0	0	0	0	2	0
47	17,8	19	10	35	1	1	0	79	1	1	1	42	8	21	12	1	0	29	0	16	0	5	51	4	0	0	0	0	7	33	2
48	14,6	0	0	0	1	0	0	0	0	0	0	0	10	0	0	0	0	1	0	7	0	1	1	1	0	0	0	0	0	0	0
49	16,8	0	0	0	0	0	0	0	0	0	0	0	28	0	1	0	0	1	0	1	2	0	7	0	0	0	0	0	0	0	0
50	17,3	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	1	0	5	0	1	2	0	0	0	0	0	0	0	0
51	11,9	0	0	17	0	0	0	27	0	1	0	7	28	32	17	0	0	20	0	22	0	1	28	1	0	0	0	0	3	8	6
52	16,9	0	0	0	0	0	0	1	0	0	0	0	16	0	0	0	0	7	0	11	0	1	4	1	0	0	0	0	0	2	0
53	16	0	0	0	0	0	0	0	0	0	0	0	7	0	1	0	1	4	0	8	0	1	0	1	0	0	0	0	0	0	0
54	17,3	0	0	0	0	0	0	0	0	0	0	0	23	0	0	0	0	3	0	8	0	0	4	0	0	0	0	0	0	0	0
55	14,7	0	0	0	0	0	0	5	0	0	0	0	9	0	0	0	0	0	0	24	0	0	24	0	0	0	0	0	0	4	0
58	18,1	0	0	0	0	0	0	0	0	1	0	0	26	0	0	0	0	4	0	4	0	1	3	0	0	0	0	0	0	1	0
59	12,3	0	0	2	0	0	0	33	0	1	0	2	48	0	22	0	0	7	0	33	2	1	35	2	0	0	0	0	2	1	0
60	16,4	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	4	0	0	1	0	0	0	0	0	0	0	0
61	13,7	7	28	40	1	0	0	366	0	1	0	96	3	33	3	8	1	8	8	12	1	6	73	0	0	2	0	0	23	61	7
62	16,3	0	0	0	0	0	0	0	0	0	0	0	54	0	1	0	0	8	0	14	0	2	22	1	0	0	0	0	0	0	1
63	15,1	0	0	0	0	0	0	0	0	1	0	0	4	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
64	13,2	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	1	0	5	0	0	0	0	0	0	0	0	0	0	0
65	17,8	0	0	0	0	0	0	9	1	0	0	0	11	0	0	0	0	5	0	21	0	2	16	1	0	0	0	0	0	2	0
68	10,9	0	0	0	0	0	0	0	0	0	0	0	15	0	0	0	0	3	0	4	0	0	11	0	0	0	0	0	0	1	0
69	11,9	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	3	0	1	0	1	4	0	0	0	0	0	0	0	0
70	18,2	0	3	0	0	0	0	27	0	0	0	2	36	1	0	0	0	1	0	17	1	0	14	0	0	0	0	0	0	14	0
71	15,3	0	0	0	0	0	0	0	0	0	0	0	28	0	0	0	0	1	0	3	0	0	3	0	0	0	0	0	0	0	0
72	14	3	22	89	1	1	0	131	1	1	1	68	17	34	5	0	0	13	5	18	0	4	46	0	0	0	0	0	10	39	5
73	11	0	0	11	1	0	7	17	0	0	0	9	16	8	2	0	0	9	0	13	3	3	41	0	6	0	0	0	4	26	1
74	11,8	0	0	0	2	0	0	0	0	0	0	1	36	0	1	0	0	6	0	18	0	2	20	2	0	0	0	0	0	0	0
75	14,5	0	0	0	0	0	0	0	0	0	0	0	47	0	13	0	0	5	0	16	0	1	2	0	0	0	0	0	0	0	0
76	17,8	0	0	0	0	0	0	0	0	0	0	0	21	0	0	0	0	2	0	15	0	0	1	0	0	0	0	0	0	1	0
77	15,8	0	0	0	0	0	0	2	0	0	0	0	20	0	0	0	0	1	0	15	0	0	6	0	0	0	0	0	1	0	0
78	14,3	0	0	0	0	0	3	19	0	0	0	2	15	0	0	0	0	6	0	14	0	0	5	3	0	0	0	0	0	0	0
79	10,9	0	0	0	0	0	0	0	1	0	0	0	17	0	0	0	0	3	0	4	0	1	6	1	0	0	0	0	0	0	0
80	11	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	3	0	4	0	1	1	0	0	0	0	0	0	0	0
81	14,2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
82	16,1	0	2	1	1	0	0	0	0	1	1	0	13	0	3	0	0	3	0	6	5	1	20	0	0	0	0	0	0	2	1
83	15,6	0	0	0	0	0	9	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	9	0	15	0	0	0	0	0	0
84	16	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	4	0	8	0	0	6	4	0	0	0	0	0	1	0
85	18,9	0	0	0	0	0	0	0	0	0	0	0	45	0	0	0	0	9	0	24	0	1	4	2	0	0	0	0	0	1	0
86	19,2	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	1	0	7	0	0	1	0	0	0	0	0	0	0	0
87	16,9	0	0	1	0	0	0	3	0	0	0	1	12	0	0	0	0	3	0	19	0	0	3	0	0	0	0	0	0	0	0
89	10,8	0	0	0	0	0	0	0	0	0	0	0	19	0	0	0	0	0	0	4	0	0	5	0	0	0	0	0	0	0	0
90	8,8	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
91	16,6	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0

SQUARE	VOLUM	ACAACU	AEGNIT	AEGPUR	ARIARB	BALPER	CARMIN	CARTRI	CEPHOR	CLABID	COCLAM	COCLUB	COLASP	COLEDE	DISROT	DISRUD	ENAOBS	EUCFUL	LAUCYL	NESHAM	NESPET	OXYALL	PUNPYG	SPELAM	VERLIL	VERPUS	VERPYG	VERRON	VERSUB	VITCON	VITPEL
92	15,1	1	0	0	0	0	0	12	0	0	0	0	17	0	0	0	0	2	0	12	0	0	43	0	0	0	0	0	4	0	0
93	16,4	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	0	0
94	13,4	0	0	0	0	0	54	0	0	0	0	0	8	0	0	0	0	1	0	13	1	0	79	1	5	0	0	0	2	1	0
95	17,5	0	0	0	0	0	0	0	0	0	0	0	19	0	0	0	0	4	0	10	0	2	0	2	0	0	0	0	0	0	0
96	14,8	0	0	0	0	0	4	0	0	0	0	0	7	0	0	0	0	4	0	10	0	0	0	0	0	0	0	0	5	0	0
98	15,8	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	4	0	4	0	2	0	0	0	0	0	0	0	0	0
102	11,8	0	0	2	0	0	0	5	0	0	0	3	17	0	0	0	0	1	0	6	0	0	1	1	0	0	0	0	0	1	0
103	13,8	0	0	0	0	0	0	4	0	0	0	1	8	0	0	0	0	0	0	8	0	0	6	2	0	0	0	0	0	2	0
104	18	0	0	0	0	0	0	19	0	0	0	1	44	0	0	0	0	10	0	39	0	0	23	1	0	0	0	2	0	0	0
105	14,2	3	0	2	1	0	0	0	0	1	0	2	32	0	0	0	0	3	0	26	1	0	8	7	0	0	0	0	0	2	1
106	12	0	0	0	0	0	20	0	0	0	0	0	12	0	0	0	0	4	0	22	0	1	4	0	6	0	0	0	2	0	0
107	16,2	0	0	0	0	0	0	4	0	0	0	3	7	0	0	0	0	1	0	14	0	1	3	0	0	0	0	0	0	0	0
108	15,7	0	0	1	0	0	0	0	0	0	0	0	6	0	0	0	0	2	0	20	0	0	4	1	0	0	0	0	0	0	0
109	14,4	0	0	0	1	0	0	0	0	0	0	0	10	0	0	0	0	4	0	6	0	2	2	0	0	0	0	0	0	0	0
112	11,8	0	0	3	1	0	0	1	0	0	0	11	34	0	0	0	0	13	0	15	0	0	58	2	0	0	0	0	1	1	0
113	15,5	0	0	0	0	0	0	0	0	0	0	0	19	0	0	0	0	4	0	12	0	1	6	0	0	0	0	0	0	0	0
114	13,2	0	0	0	0	0	0	2	0	2	0	6	5	0	0	0	0	3	0	15	0	0	6	0	0	0	0	0	0	0	0
115	12,3	0	1	5	0	0	0	2	2	0	0	16	197	0	1	0	0	24	0	33	0	3	32	44	0	0	0	0	0	1	1
116	11,2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
117	14,2	0	0	4	0	0	31	1	0	0	0	9	8	0	0	0	0	8	0	50	0	2	12	1	1	0	0	0	2	9	0
118	16,3	0	0	1	0	0	0	1	1	0	0	0	28	0	0	0	0	6	0	35	0	4	15	4	0	0	0	0	0	4	0
119	16,7	0	0	0	0	0	0	0	1	0	0	0	31	0	0	0	0	6	0	33	0	1	30	3	0	0	0	0	0	6	0
122	12,1	0	0	2	1	0	0	49	0	0	0	1	23	0	0	0	0	11	0	16	0	0	4	1	0	0	0	0	1	7	0
123	12,8	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
124	18	0	0	0	0	0	0	0	0	2	0	1	4	0	0	0	0	2	0	22	0	0	4	0	0	0	0	0	0	0	0
125	10,2	1	0	0	0	0	0	4	0	1	0	8	34	0	0	0	0	11	1	7	0	1	4	0	0	0	0	0	0	1	0
127	16,8	0	0	0	0	0	0	0	0	0	0	0	13	0	0	0	0	5	0	13	0	0	2	0	0	0	0	0	0	0	0
128	17,6	0	0	2	0	0	0	0	0	0	0	0	23	0	2	0	0	7	0	28	0	0	6	1	0	0	0	0	0	3	0
129	14,2	0	0	0	0	0	3	0	0	0	0	0	4	0	0	0	0	2	0	5	0	0	14	0	1	0	0	0	4	0	0
130	10,9	0	0	0	0	0	5	8	0	1	0	2	4	0	0	0	0	8	0	11	0	0	6	0	1	0	0	0	1	2	0
131	15,3	0	0	1	0	0	0	23	0	0	0	2	23	0	0	0	0	19	0	30	0	3	31	7	0	0	0	0	0	2	0
132	14,4	0	0	0	0	0	0	12	0	0	0	5	11	0	0	0	0	6	0	52	0	0	14	1	0	0	0	0	0	4	0
133	12,4	0	0	0	0	0	0	0	0	0	0	2	28	0	0	0	0	1	0	8	0	0	66	2	0	0	0	0	2	0	0
134	8	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
135	16,2	0	0	0	0	0	0	1	0	0	0	1	12	0	0	0	0	1	0	5	0	1	6	0	0	0	0	0	0	0	0
136	13,2	0	10	4	0	0	0	28	0	0	0	14	20	0	0	0	0	16	0	66	0	2	92	0	0	0	0	0	16	12	2
137	16	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	8	0	0	12	0	0	0	0	0	0	0	0
138	12,2	0	0	0	0	0	8	0	1	0	0	4	10	0	0	0	0	8	0	26	0	0	6	0	0	0	0	0	0	0	0
139	13	0	0	0	0	0	0	0	0	1	0	4	14	0	0	0	0	6	0	38	0	0	0	0	0	0	0	0	0	0	0
140	13,8	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
141	9,4	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0
142	11,1	0	7	1	1	0	0	6	1	2	0	4	23	0	0	0	0	3	0	11	0	1	18	0	0	0	0	0	0	4	0
143	11,8	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	1	0	2	0	0	4	0	0	0	0	3	0	0	0
144	11,2	0	0	0	0	0	0	18	0	0	0	0	4	0	0	0	0	4	0	2	0	0	2	0	0	0	0	0	0	0	0
145	11,1	0	0	0	0	0	0	2	0	0	0	1	3	0	0	0	0	2	0	8	0	0	1	0	0	0	0	0	0	0	0
146	10,9	0	0	1	1	0	0	0	1	0	1	6	30	0	0	0	0	2	0	11	0	2	2	2	0	0	0	0	0	1	0
147	14,5	0	0	0	0	0	0	0	0	0	0	0	11	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0

Appendix 6.2 continued. Collected snail species. All numbers is in percentage of the total abundance. The table is ranked after species richness of the square.

SQUARE	COLASP	NESHAM	EUCFUL	PUNPYG	OXYALL	VITCON	CARTRI	SPELAM	COCLUB	AEGPUR	VERSUB	DISROT	CLABID	ARIARB	COLEDE	AEGNIT	NESPET	VITPEL	ACAACU	CEPHOR	CARMIN	COCLAM	VERLIL	DISRUD	LAUCYL	BALPER	ENAOBS	VERPUS	VERRON	VERPYG	Species
47	2	4	8	13	1	9	21	1	11	9	2	3	0	0	6	3		1	5	0		0		0		0					22
61	0	2	1	9	1	8	46		12	5	3	0	0	0	4	4	0	1	1					1	1		0	0			22
72	3	4	3	9	1	8	25		13	17	2	1	0	0	7	4		1	1	0		0			1	0					21
1	6	8	11	5	1	15	19	1	4	7	2	2	0	4	8	2	2	0	1	0											20
37	4	7	8	12	2	10	13	2	8	7	2	7	0	1	11	3		1	1			0									19
8	4	6	17	33	2	12	12	2	1	4	2	1	0	0	3	1		0		0											18
14	1	5	10	26	2	11	30		1	2	2	2	1	1	6		1			0				0							17
28	9	4	12	14	3	3	27	1	2	10	2		1	2	8	2			1									1			17
73	9	7	5	23	2	15	10		5	6	2	1		1	5		2	1			4		3								17
4	30	10	10	21	1	4	11		1	3	1	1	1	2	1	3						1									16
13	10	5	5	57	1	2	11	0	1	2	0	1			0	2		0	2												16
20	25	8	6	25	1	5	13	2	3	6	0		0		3	2	0		2												16
9	27	7	6	17	1	7	16	3	2	8	1	0			2		1		1												15
51	13	10	9	13	0	4	12	0	3	8	1	8	0		15			3													15
59	25	17	4	18	1	1	17	1	1	1	1	12	1				1														14
82	22	10	5	33	2	3				2		5	2	2		3	8	2				2									14
115	54	9	7	9	1	0	1	12	4	1		0				0		0		1											14
24	16	15	9	24	1	3	14	5	1	10		1			1				1												13
105	36	29	3	9		2		8	2	2			1	1			1	1	3												13
117	6	36	6	9	1	7	1	1	7	3	1										22		1								13
142	28	13	4	22	1	5	7		5	1			2	1		9				1											13
2	27	7	7	5	4	23	9			9	1	3		1			5														12
32	28	12	9	16	3	1		7		1	1	9	1				9														12
36	15	11	3	18	2	8	30	2	5	5			1	1																	12
136	7	23	6	33	1	4	10		5	1	6					4		1													12
146	50	18	3	3	3	2		3	10	2				2						2		2									12
5	61	8	10	13	0	3		0		3			0					0				0									11
112	24	11	9	41		1	1	1	8	2	1			1																	11
122	20	14	9	3		6	42	1	1	2	1			1																	11
125	47	10	15	5	1	1	5		11				1						1						1						11
130	8	22	16	12		4	16		4		2		2								10		2								11
18	16	6	4	47	3	3	19			1	1						1														10
27	48	19	4	18	3		2	2	1		1	1																			10
31	25	13	8	15	9	4	15	4			2	6																			10
43	20	22	17	6	4	2	11	7		4					7																10
70	31	15	1	12		12	23		2						1	3	1														10
94	5	8	1	48		1		1			1						1				33		3								10
118	28	35	6	15	4	4	1	4		1										1											10
131	16	21	13	22	2	1	16	5	1	1																					10
15	36	17	10	21	2	7		2		2			2																		9
42	35	27	6	10	4	2		4				4									6										9
65	16	31	7	24	3	3	13	1												1											9
74	41	20	7	23	2			2	1			1		2																	9
102	46	16	3	3		3	14	3	8	5																					9
7	29	9	7	41				10		2						2														1	8
23	19	17	6	22		4	28	4	2																						8
29	40	3	10	10	7			7		3		20																			8
52	37	26	16	9	2	5	2	2																							8
62	52	14	8	21	2			1				1						1													8
78	22	21	9	7			28	4	3												4										8
104	32	28	7	17			14	1	1																				1		8
106	17	31	6	6	1						3										28		8								8
119	28	30	5	27	1	5		3												1											8
128	32	39	10	8		4		1		3		3																			8
132	10	50	6	13		4	11	1	5																						8
48	45	32	5	5	5			5						5																	7
53	30	35	17		4			4				4															4				7
58	65	10	10	8	3	3							3																		7
79	52	12	9	18	3			3												3											7
85	52	28	10	5	1	1		2																							7
87	29	45	7	7			7		2	2																					7
92	19	13	2	47			13				4								1												7
103	26	26		19		6	13	6	3																						7
107	21	42	3	9	3		12		9																						7
114	13	38	8	15			5		15				5																		7
129	12	15	6	42							12										9		3								7
133	26	7	1	61				2	2		2																				7
135	44	19	4	22	4		4		4																						7
138	16	41	13	10					6											2	13										7
6	37	15		22	4	19												4													6
11	47	27	10	10	3		3																								6
12	59	22	7	4	4		4																								6

SQUARE	COLASP	NESHAM	EUCFUL	PUNPYG	OXYALL	VITCON	CARTRI	SPELAM	COCLUB	AEGPUR	VERSUB	DISROT	CLABID	ARIARB	COLEDE	AEGNIT	NESPET	VITPEL	ACAACU	CEPHOR	CARMIN	COCLAM	VERLIL	DISRUD	LAUCYL	BALPER	ENAOBS	VERPUS	VERRON	VERPYG	Species
21	67	11	4		4				11			4																			6
38	45	14	14	9	14	5																									6
45	49	24	11	3	8	5																									6
49	70	3	3	18								3					5														6
75	56	19	6	2	1							15																		6
77	44	33	2	13			4				2																					6
84	41	21	10	15		3		10																								6
108	18	59	6	12				3		3																					6
109	40	24	16	8	8									4																	6
124	11	63	6	11					3				6																		6
145	18	47	12	6			12		6																						6
25	41	16	13		9							22																		5
26	50	14	2	33	2																										5
34	30	36	18		3			12																								5
40	39	33	11		6												11														5
50	36	36	7	14	7																										5
55	14	36		36		6	8																								5
68	44	12	9	32		3																									5
69	47	6	18	24	6																										5
76	53	38	5	3		3																									5
80	25	33	25	8	8																										5
83	3	6		25																	25		42								5
95	51	27	11		5			5																								5
96	23	33	13								17											13										5
113	45	29	10	14	2																										5
139	22	60	10						6				2																		5
143	41	12	6	24																									18		5
144	13	7	13	7			60																								5
3	83	10		5									2																		4
10	56	11	11	22																											4
16	25	25	25		25																										4
19	70	17	9		4																										4
22	54	31	8		8																										4
35	50	33	8		8																										4
39	76	8	12		4																										4
41	56	33			6			6																								4
44	30	50	10	10																											4
54	61	21	8	11																											4
71	80	9	3	9																											4
86	55	35	5	5																											4
91	63	13	13		13																										4
93	29	43	14											14																		4
98	29	29	29		14																										4
127	39	39	15	6																											4
30	33	50		17																											3
33	59	38			3																										3
60	38	50		13																											3
63	57	29											14																		3
64	54	38	8																												3
89	68	14		18																											3
137	9	36		55																											3
17	50				50																										2
81	50	50																													2
90	50												50																		2
123	50		50																												2
141	33	67																													2
147	92	8																													2
116		100																													1
134	100																														1
140	100																														1
	131	127	112	103	76	57	52	52	47	40	32	30	28	22	17	16	16	16	13	13	11	7	7	3	3	2	2	2	2	1	

6.3 Raw data environmental variables

Appendix 6.3. Raw data for the environmental variables recorded in the study area. Explanations given on pages 11-12.

SQUARE	H40	Aspect	Gorge	LogCliff	Mire	LogScree	Pollard	Topopos	Antperc	Vegind	Mosswet	Mossdry
1	17	7	1	2,26	10	3,00	0	6	0	5	3	3
2	14	4	1	2,08	0	2,70	0	5	0	5	9	0
3	14	1	1	2,00	0	3,18	0	6	0	5	14	0
4	17	7	1	2,00	0	3,00	1	6	0	5	9	0
5	14	2	0	2,26	0	3,04	0	5	0	4	6	0
6	6	2	0	0,00	0	0,00	0	3	0	1	7	0
7	11	7	0	0,00	0	0,00	0	1	0	1	1	0
8	17	7	1	1,71	0	3,00	3	6	0	5	6	2
9	14	2	0	0,00	0	3,00	0	5	0	4	11	0
10	4	2	0	0,00	0	0,00	0	1	0	1	3	0
11	4	7	0	0,00	0	0,00	0	2	0	1	6	0
12	8	7	0	1,32	20	0,00	0	3	0	1	1	0
13	8	7	0	0,00	0	0,00	0	2	0	1	4	1
14	14	7	1	2,05	0	2,70	1	6	0	5	4	1
15	14	2	0	0,00	0	2,85	0	3	0	4	8	0
16	4	2	0	0,00	0	0,00	0	3	0	1	3	0
17	4	7	0	0,00	5	0,00	0	2	0	1	2	0
18	8	5	0	2,30	20	0,00	0	6	0	1	8	0
19	8	5	0	0,00	10	0,00	0	3	0	1	5	0
20	14	7	1	2,30	0	2,70	3	6	0	5	5	0
21	8	5	0	2,30	10	0,00	0	6	0	2	1	0
22	4	8	0	0,00	5	0,00	0	6	0	1	1	0
23	4	7	0	0,00	5	0,00	0	2	0	1	2	0
24	8	7	1	2,76	0	2,00	0	6	0	4	10	0
25	8	2	0	2,00	10	0,00	0	6	0	1	1	0
26	4	2	0	1,32	15	0,00	0	1	0	1	2	0
27	8	7	0	1,49	40	0,00	0	3	37	1	2	0
28	14	7	1	0,00	0	3,00	3	6	0	5	9	5
29	6	5	0	1,91	20	0,00	0	6	0	1	6	0
30	4	7	0	2,48	10	0,00	0	6	0	1	3	0
31	4	8	0	0,00	20	0,00	0	2	0	1	6	0
32	8	7	1	2,30	10	0,00	0	6	0	1	7	0
33	8	5	0	2,85	20	0,00	0	6	0	2	3	0
34	8	5	0	1,91	10	0,00	0	4	0	1	0	0
35	8	7	0	0,00	20	0,00	0	4	0	1	2	0
36	6	8	0	2,48	0	0,00	0	5	0	1	3	0
37	14	7	1	2,78	0	3,30	1	6	0	5	6	5
38	8	8	0	0,00	0	0,00	0	1	0	1	6	0
39	6	5	0	1,32	40	0,00	0	6	0	1	2	0
40	8	5	0	0,00	20	0,00	0	4	0	1	1	0
41	8	7	1	0,00	10	0,00	0	6	0	1	3	0

SQUARE	H40	Aspect	Gorge	LogCliff	Mire	LogScree	Pollard	Topopos	Antperc	Vegind	Mosswet	Mossdry
42	8	5	0	2,55	40	0,00	0	6	0	2	9	0
43	4	8	1	0,00	10	0,00	0	3	0	1	7	0
44	4	7	0	0,00	30	0,00	0	3	0	1	1	0
45	4	7	0	2,30	20	0,00	0	3	0	1	6	0
47	14	7	1	2,30	0	3,30	1	5	0	5	8	5
48	8	5	0	2,30	0	0,00	0	1	0	2	3	0
49	6	5	1	2,30	0	2,48	0	6	0	2	9	2
50	6	5	0	0,00	30	0,00	0	1	0	2	0	0
51	11	7	1	2,30	5	0,00	0	6	0	4	9	5
52	8	7	0	1,32	20	0,00	0	3	0	2	3	0
53	8	4	0	0,00	10	0,00	0	3	0	1	0	0
54	8	7	0	2,00	10	0,00	0	3	0	1	1	0
55	6	7	0	0,00	10	0,00	0	3	0	1	2	0
58	8	4	0	0,00	0	0,00	0	6	0	2	2	0
59	8	7	1	1,91	20	0,00	0	6	0	4	8	1
60	6	5	0	0,00	0	0,00	0	4	0	1	5	0
61	17	7	0	2,30	0	3,04	0	5	0	5	4	8
62	8	8	1	0,00	20	0,00	0	3	0	2	6	0
63	6	8	0	0,00	20	0,00	0	1	0	1	2	0
64	6	8	0	0,00	20	0,00	0	1	0	1	5	0
65	6	8	0	0,00	10	0,00	0	3	0	1	3	0
68	4	2	0	0,00	10	0,00	0	5	0	1	4	0
69	11	2	0	0,00	0	0,00	0	5	0	2	4	0
70	14	8	0	0,00	0	0,00	0	6	0	5	5	0
71	6	5	0	3,26	0	0,00	0	1	0	1	0	0
72	14	7	0	3,23	0	3,30	0	5	0	5	6	8
73	17	7	0	0,00	60	0,00	0	6	0	4	0	2
74	11	1	1	2,90	10	0,00	0	5	0	1	15	1
75	8	1	0	1,91	10	0,00	0	4	0	2	3	1
76	6	5	0	2,45	40	0,00	0	1	0	1	12	0
77	8	5	0	1,49	0	0,00	0	3	0	1	4	0
78	8	5	0	0,00	50	0,00	0	1	0	1	6	0
79	4	2	0	2,60	0	0,00	0	4	0	1	3	0
80	4	2	0	2,00	20	0,00	0	5	0	1	4	0
81	4	2	0	0,00	10	0,00	0	4	0	2	3	0
82	17	5	0	2,60	0	2,78	3	5	0	5	3	4
83	6	5	0	0,00	50	0,00	0	1	0	1	0	0
84	8	6	0	0,00	15	0,00	0	3	0	1	1	0
85	8	7	1	2,48	30	0,00	0	6	0	1	3	0
86	8	5	0	1,71	30	0,00	0	1	0	1	3	0
87	8	5	0	0,00	20	0,00	0	1	0	1	0	0
89	4	2	0	3,00	20	0,00	0	4	0	1	5	0
90	4	2	0	0,00	0	0,00	0	1	0	1	0	0
91	8	7	0	0,00	0	0,00	0	2	0	1	0	0
92	4	8	0	0,00	10	0,00	0	3	0	1	2	0
93	4	7	0	0,00	0	0,00	0	2	0	1	1	0

SQUARE	H40	Aspect	Gorge	LogCliff	Mire	LogScree	Pollard	Topopos	Antperc	Vegind	Mosswet	Mossdry
94	6	3	0	0,00	30	0,00	0	6	0	1	5	0
95	8	5	0	2,19	20	0,00	0	4	0	1	8	0
96	6	5	0	0,00	30	0,00	0	1	0	1	2	0
98	8	5	0	0,00	0	0,00	0	1	33	1	5	0
102	6	6	1	2,66	40	0,00	0	6	0	1	17	0
103	4	4	0	2,18	5	0,00	0	4	0	1	5	0
104	4	8	0	0,00	0	0,00	0	2	0	1	0	0
105	11	7	1	0,00	50	0,00	0	6	0	1	2	0
106	4	5	0	0,00	40	0,00	0	2	0	1	2	0
107	8	5	0	1,32	0	0,00	0	1	42	1	5	0
108	8	5	0	0,00	10	0,00	0	1	92	1	9	0
109	8	5	0	1,41	20	0,00	0	4	45	1	7	0
112	8	5	0	0,00	10	0,00	0	2	0	1	6	0
113	4	2	0	0,00	0	0,00	0	1	0	1	3	0
114	4	7	0	2,26	0	0,00	0	2	0	1	3	0
115	6	7	0	2,48	10	0,00	0	3	0	1	6	0
116	4	5	0	0,00	10	0,00	0	1	0	1	1	0
117	8	3	0	1,32	50	0,00	0	6	0	1	3	0
118	8	5	0	1,32	20	0,00	0	4	0	2	10	0
119	8	5	0	1,41	30	0,00	0	1	100	1	6	0
122	8	5	0	0,00	0	0,00	0	2	0	1	7	0
123	8	2	0	0,00	10	0,00	0	1	12	1	4	0
124	4	7	0	0,00	10	0,00	0	2	0	1	2	0
125	4	7	0	2,78	0	0,00	0	3	0	1	2	0
127	6	3	0	2,00	0	0,00	0	1	100	1	1	0
128	8	5	0	0,00	15	0,00	0	2	0	1	3	0
129	5	5	0	2,00	80	0,00	0	1	0	1	5	0
130	4	5	0	0,00	20	0,00	0	1	0	1	6	0
131	6	5	0	0,00	0	0,00	0	3	70	1	0	0
132	4	8	0	0,00	10	0,00	0	2	0	1	1	0
133	4	7	0	2,30	0	0,00	0	3	0	1	6	0
134	4	7	0	2,78	0	0,00	0	6	0	1	3	0
135	8	5	0	0,00	20	0,00	0	4	0	1	4	0
136	8	1	0	0,00	15	0,00	0	1	0	3	3	0
137	4	1	0	0,00	10	0,00	0	1	0	1	2	0
138	6	5	0	0,00	20	0,00	0	1	20	1	0	0
139	4	5	0	2,00	0	0,00	0	2	0	1	3	0
140	4	7	1	2,70	0	0,00	0	6	0	1	4	0
141	4	5	0	0,00	0	0,00	0	1	0	1	0	0
142	14	7	1	3,11	0	2,70	3	6	0	5	9	0
143	8	5	0	0,00	30	0,00	0	1	90	1	0	0
144	4	7	0	3,08	10	0,00	0	1	0	1	1	0
145	5	8	0	0,00	10	0,00	0	1	0	1	1	0
146	4	7	1	3,30	20	0,00	0	6	0	1	6	0
147	6	2	0	0,00	0	0,00	0	2	0	1	2	0

6.4 LOG-FILE TRANSCRIPT FROM CANOCO

Program CANOCO Version 4.0 April 1998 - written by Cajo J.F. Ter Braak
Copyright (c) 1988-1998 Centre for Biometry Wageningen, CPRO-DLO
Box 100, 6700 AC Wageningen, the Netherlands.
CANOCO performs (partial) (detrended) (canonical) correspondence analysis,
principal components analysis and redundancy analysis.
CANOCO is an extension of Cornell Ecology program DECORANA (Hill,1979)

For explanation of the input/output see the manual or
Ter Braak, C.J.F. (1995) Ordination. Chapter 5 in:
Data Analysis in Community and Landscape Ecology
(Jongman, R.H.G., Ter Braak, C.J.F. and Van Tongeren, O.F.R., Eds)
Cambridge University Press, Cambridge, UK, 91-173 pp.

*** Type of analysis ***

Model	Gradient analysis		
	indirect	direct	hybrid
linear	1=PCA	2= RDA	3
unimodal	4= CA	5= CCA	6
„	7=DCA	8=DCCA	9
	10=non-standard analysis		

Type analysis number
Answer = 7

*** Data files ***
Species data : C:\DOCUME~1\THORIN~1\MYDOCU~1\Hovedfag\Canoco\snail.dta
Covariable data :
Environmental data :
Initialization file:

Number of segments = 26
Nonlinear recaling of axes
Rescaling threshold = .00
Number of axes in biplot = 2
Diagnostics = 2

File : C:\DOCUME~1\THORIN~1\MYDOCU~1\Hovedfag\Canoco\snail.dta
Title : SNAIL DENSITIES X100 (CANOCO FULL FORMAT)
Format : (I5,1X,14F5.0,2(/6X,(14F5.0)))
No. of couplets of species number and abundance per line : 0

No samples omitted
Number of samples 132
Number of species 30
Number of occurrences 1040

No transformation of species data
No species-weights specified
No sample-weights specified
downweighting of rare species

Final species weights applied (weight*downweight)
.526 .629 .897 .351 .144 .355 .836 .848 1.000 .467 .764 1.000 .699 .960 .103 .144 1.000 .164 1.000 .599
1.000 1.000 .884 .303 .132 .072 .126 1.000 1.000 .652

Axes are rescaled

No. of active samples: 132
No. of passive samples: 0
No. of active species: 30
Total inertia in species data=
Sum of all eigenvalues of CA = 1.22115

**** Summary ****

Axes		1	2	3	4	Total inertia
Eigenvalues	:	.367	.156	.086	.043	1.221
Lengths of gradient	:	2.797	2.811	2.062	1.710	
Cumulative percentage variance of species data	:	30.0	42.8	49.9	53.4	

Sum of all unconstrained eigenvalues 1.221
[Mon Oct 20 13:52:22 2003] CANOCO call succeeded

Program CANOCO Version 4.0 April 1998 - written by Cajo J.F. Ter Braak
Copyright (c) 1988-1998 Centre for Biometry Wageningen, CPRO-DLO
Box 100, 6700 AC Wageningen, the Netherlands.
CANOCO performs (partial) (detrended) (canonical) correspondence analysis,
principal components analysis and redundancy analysis.
CANOCO is an extension of Cornell Ecology program DECORANA (Hill,1979)

For explanation of the input/output see the manual or
Ter Braak, C.J.F. (1995) Ordination. Chapter 5 in:
Data Analysis in Community and Landscape Ecology
(Jongman, R.H.G., Ter Braak, C.J.F. and Van Tongeren, O.F.R., Eds)
Cambridge University Press, Cambridge, UK, 91-173 pp.

*** Type of analysis ***

Model	Gradient analysis		
	indirect	direct	hybrid
linear	1=PCA	2= RDA	3
unimodal	4= CA	5= CCA	6
„	7=DCA	8=DCCA	9
	10=non-standard analysis		

Type analysis number
Answer = 5

*** Data files ***
Species data : C:\DOCUME~1\THORIN~1\MYDOCU~1\Hovedfag\Canoco\snail.dta
Covariable data :
Environmental data : C:\DOCUME~1\THORIN~1\MYDOCU~1\Hovedfag\Canoco\envvar.dta
Initialization file:

Forward selection of envi. variables = 3
Scaling of ordination scores = 2
Diagnostics = 3

File : C:\DOCUME~1\THORIN~1\MYDOCU~1\Hovedfag\Canoco\snail.dta
Title : SNAIL DENSITIES X100 (CANOCO FULL FORMAT)
Format : (I5,1X,14F5.0,2(/6X,(14F5.0)))
No. of couplets of species number and abundance per line : 0

No samples omitted
Number of samples 132
Number of species 30
Number of occurrences 1040

File : C:\DOCUME~1\THORIN~1\MYDOCU~1\Hovedfag\Canoco\envvar.dta
Title : Environmental variables, some log-transformed
Format : (I5,1X,10F7.2,1(/6X,(10F7.2)))
No. of environmental variables : 12

No interaction terms defined
No transformation of species data
No species-weights specified
No sample-weights specified
downweighting of rare species

Final species weights applied (weight*downweight)
.526 .629 .897 .351 .144 .355 .836 .848 1.000 .467 .764 1.000 .699 .960 .103 .144 1.000 .164 1.000 .599
1.000 1.000 .884 .303 .132 .072 .126 1.000 1.000 .652

No rescaling
No detrending

No. of active samples: 132
No. of passive samples: 0
No. of active species: 30

Total inertia in species data=
Sum of all eigenvalues of CA = 1.22115

****** Check on influence in covariable/environment data ******
The following sample(s) have extreme values

Sample	Environmental variable	Influence	Covariable influence	+ Environment space influence
1				6.5x
1	1	9.7x		
1	6	7.5x		
1	8	6.1x		

1	10	7.4x		
1				4.9x
5			4.5x	
5	2	10.9x		
5	6	5.3x		
5				3.6x
8			7.5x	
8	1	11.2x		
8	2	5.0x		
8	5	5.3x		
8	6	8.6x		
8	7	51.1x		
8	8	7.0x		
8	10	8.5x		
8				5.3x
9			4.4x	
9	2	10.5x		
9	4	6.1x		
9	11	10.7x		
9				5.1x
20			3.2x	
20	7	16.1x		
28	7	8.6x		
28				3.1x
46			3.1x	
50				4.1x
58			7.9x	
58	1	11.9x		
58	2	5.3x		
58	4	5.8x		
58	5	5.6x		
58	6	9.4x		
58	10	9.0x		
58	12	39.9x		
58				5.3x
65				3.0x
67			5.2x	
67	4	8.8x		
67	6	7.4x		
67	10	5.9x		
67	12	22.6x		
67				4.1x
68	5	20.5x		
68				5.1x
69	11	7.4x		
69				3.9x
98	9	7.4x		
103			4.7x	
103	10	5.1x		
105	5	6.6x		
107	9	38.4x		
107				4.2x
112	9	8.2x		
116	9	20.7x		
116				3.5x
121			3.4x	
121	2	12.5x		
121	8	8.0x		
121				5.0x
127	7	5.2x		

****** End of check ******

**** Start of forward selection of variables ****

*** Unrestricted permutation ***

Seeds: 6699 4054

N	Name	Extra fit
9	ANTPERC	.02
11	MOSSWET	.02
7	POLLARD	.04
3	GORGE	.05
2	ASPECT	.06
4	LOGCLIFF	.06
5	MIRE	.07
8	TOPOPOS	.08
6	LOGSCREE	.17
1	H40	.18

10 VEGIND .21
12 MOSSDRY .26
Environmental variable 12 tested
Number of permutations= 9999

*** Permutation under reduced model ***

P-value .0001 (variable 12; F-ratio= 35.58; number of permutations= 9999)

Environmental variable 12 added to model
Variance explained by the variables selected: .26
" " " all variables : .50

N	Name	Extra fit
9	ANTPERC	.01
2	ASPECT	.01
11	MOSSWET	.02
7	POLLARD	.03
8	TOPOPOS	.03
4	LOGCLIFF	.03
5	MIRE	.04
3	GORGE	.04
6	LOGSCREE	.04
1	H40	.05
10	VEGIND	.05

Environmental variable 10 tested
Number of permutations= 9999

*** Permutation under reduced model ***

P-value .0001 (variable 10; F-ratio= 7.72; number of permutations= 9999)

Environmental variable 10 added to model
Variance explained by the variables selected: .32
" " " all variables : .50

N	Name	Extra fit
9	ANTPERC	.00
1	H40	.01
2	ASPECT	.01
11	MOSSWET	.01
6	LOGSCREE	.02
8	TOPOPOS	.02
3	GORGE	.02
7	POLLARD	.02
5	MIRE	.03
4	LOGCLIFF	.04

Environmental variable 4 tested
Number of permutations= 9999

*** Permutation under reduced model ***

P-value .0001 (variable 4; F-ratio= 5.41; number of permutations= 9999)

Environmental variable 4 added to model
Variance explained by the variables selected: .35
" " " all variables : .50

N	Name	Extra fit
9	ANTPERC	.00
11	MOSSWET	.01
1	H40	.01
6	LOGSCREE	.02
2	ASPECT	.02
8	TOPOPOS	.02
7	POLLARD	.02
3	GORGE	.02
5	MIRE	.03

Environmental variable 5 tested
Number of permutations= 9999

*** Permutation under reduced model ***

P-value .0036 (variable 5; F-ratio= 4.83; number of permutations= 9999)

Environmental variable 5 added to model

Variance explained by the variables selected: .39
" " " all variables : .50
N Name Extra fit

9 ANTPERC .00
11 MOSSWET .01
8 TOPOPOS .01
2 ASPECT .02
1 H40 .01
6 LOGSCREE .02
7 POLLARD .02
3 GORGE .02
Environmental variable 3 tested
Number of permutations= 9999

*** Permutation under reduced model ***

P-value .0030 (variable 3; F-ratio= 3.17; number of permutations= 9999)

Environmental variable 3 added to model
Variance explained by the variables selected: .41
" " " all variables : .50

N Name Extra fit

9 ANTPERC .00
11 MOSSWET .01
8 TOPOPOS .01
2 ASPECT .01
6 LOGSCREE .02
1 H40 .01
7 POLLARD .02
Environmental variable 7 tested
Number of permutations= 9999

*** Permutation under reduced model ***

P-value .0166 (variable 7; F-ratio= 3.17; number of permutations= 9999)

Environmental variable 7 added to model
Variance explained by the variables selected: .43
" " " all variables : .50

N Name Extra fit

9 ANTPERC .00
11 MOSSWET .01
8 TOPOPOS .01
2 ASPECT .01
6 LOGSCREE .01
1 H40 .02
Environmental variable 1 tested
Number of permutations= 9999

*** Permutation under reduced model ***

P-value .0146 (variable 1; F-ratio= 2.44; number of permutations= 9999)

Environmental variable 1 added to model
Variance explained by the variables selected: .44
" " " all variables : .50

N Name Extra fit

9 ANTPERC .01
11 MOSSWET .01
8 TOPOPOS .01
6 LOGSCREE .01
2 ASPECT .01
Environmental variable 2 tested
Number of permutations= 9999

*** Permutation under reduced model ***

P-value .0181 (variable 2; F-ratio= 2.36; number of permutations= 9999)

Environmental variable 2 added to model
Variance explained by the variables selected: .46
" " " all variables : .50

N Name Extra fit

9 ANTPERC .01
11 MOSSWET .01
8 TOPOPOS .01
6 LOGSCREE .01
Environmental variable 6 tested
Number of permutations= 9999

*** Permutation under reduced model ***

P-value .0280 (variable 6; F-ratio= 2.41; number of permutations= 9999)

Environmental variable 6 added to model
Variance explained by the variables selected: .47
" " " all variables : .50

N Name Extra fit

9 ANTPERC .01
11 MOSSWET .01
8 TOPOPOS .01
Environmental variable 8 tested
Number of permutations= 9999

*** Permutation under reduced model ***

P-value .0235 (variable 8; F-ratio= 2.22; number of permutations= 9999)

Environmental variable 8 added to model
Variance explained by the variables selected: .48
" " " all variables : .50

N Name Extra fit

9 ANTPERC .00
11 MOSSWET .01
Environmental variable 11 tested
Number of permutations= 9999

*** Permutation under reduced model ***

P-value .1245 (variable 11; F-ratio= 1.49; number of permutations= 9999)

Environmental variable 9 tested
Number of permutations= 9999

*** Permutation under reduced model ***

P-value .6860 (variable 9; F-ratio= .63; number of permutations= 9999)

Environmental variable 11 omitted
Environmental variable 9 omitted
1
**** Weighted correlation matrix (weight = sample total) ****

	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENVI AX1	ENVI AX2	ENVI AX3	ENVI AX4
SPEC AX1	1.0000							
SPEC AX2	.0870	1.0000						
SPEC AX3	.1312	.2073	1.0000					
SPEC AX4	-.0811	.0554	-.0491	1.0000				
ENVI AX1	.9110	.0000	.0000	.0000	1.0000			
ENVI AX2	.0000	.5912	.0000	.0000	.0000	1.0000		
ENVI AX3	.0000	.0000	.6456	.0000	.0000	.0000	1.0000	
ENVI AX4	.0000	.0000	.0000	.6218	.0000	.0000	.0000	1.0000
H40	.6887	-.1265	.2218	.1569	.7560	-.2140	.3436	.2524
ASPECT	.3752	-.0389	.0819	-.1251	.4118	-.0658	.1268	-.2012
GORGE	.2636	-.1724	.3064	.3686	.2893	-.2916	.4747	.5928
LOGCLIFF	.3148	-.3261	-.2665	.1563	.3456	-.5516	-.4128	.2513
MIRE	-.3212	.3704	-.1181	.2603	-.3526	.6265	-.1829	.4186
LOGSCREE	.6713	-.1548	.1233	.0914	.7369	-.2619	.1910	.1471
POLLARD	.1934	-.0199	.4803	.0265	.2124	-.0336	.7440	.0427
TOPOPOS	.4183	-.1505	.0789	.4126	.4592	-.2545	.1222	.6635
VEGIND	.7425	-.1178	.1797	.1768	.8151	-.1992	.2783	.2843
MOSSDRY	.8495	.0503	-.1544	-.0388	.9326	.0851	-.2392	-.0624
	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENVI AX1	ENVI AX2	ENVI AX3	ENVI AX4

H40	1.0000			
ASPECT	.1441	1.0000		
GORGE	.4237	.3350	1.0000	
LOGCLIFF	.3008	.2265	.3366	1.0000

MIRE	-.2642	-.0805	-.1667	-.2589	1.0000					
LOGSCREE	.8460	.1053	.4243	.4320	-.5007	1.0000				
POLLARD	.4469	.2409	.5421	.1373	-.2770	.4665	1.0000			
TOPOPOS	.6298	.2001	.6041	.4854	-.1055	.5749	.3786	1.0000		
VEGIND	.8977	.1810	.5244	.4034	-.3823	.8861	.4776	.6631	1.0000	
MOSSDRY	.5867	.3372	.1134	.4174	-.2697	.5854	.0836	.3502	.6177	1.0000
	H40	ASPECT	GORGE	LOGCLIFF	MIRE	LOGSCREE	POLLARD	TOPOPOS	VEGIND	MOSSDR

Y

N	name	(weighted) mean	stand. dev.	inflation factor
1	SPEC AX1	.0000	1.0977	
2	SPEC AX2	.0000	1.6916	
3	SPEC AX3	.0000	1.5490	
4	SPEC AX4	.0000	1.6082	
5	ENVI AX1	.0000	1.0000	
6	ENVI AX2	.0000	1.0000	
7	ENVI AX3	.0000	1.0000	
8	ENVI AX4	.0000	1.0000	
1	H40	10.6763	4.6044	6.7602
2	ASPECT	5.7951	2.0245	1.4724
3	GORGE	.3596	.4799	2.3708
4	LOGCLIFF	1.5116	1.1389	1.6797
5	MIRE	9.2040	14.2054	1.6186
6	LOGSCREE	1.3133	1.4913	6.8279
7	POLLARD	.4028	.9421	1.7952
8	TOPOPOS	4.3282	1.7867	2.5912
10	VEGIND	2.9628	1.8237	9.2051
12	MOSSDRY	1.5911	2.5967	2.5811

**** Summary ****

Axes	1	2	3	4	Total inertia
Eigenvalues :	.298	.058	.042	.032	1.221
Species-env correlations :	.911	.591	.646	.622	
Cumulative percentage variance					
of species data :	24.4	29.2	32.6	35.2	
of species-env relation:	61.5	73.6	82.2	88.8	
Sum of all unconstrained eigenvalues					1.221
Sum of all canonical eigenvalues					.484

[Thu Aug 28 18:23:32 2003] CANOCO call succeeded
[Thu Aug 28 18:23:43 2003] Running CanoDraw
[Thu Aug 28 18:23:43 2003] CanoDraw call succeeded
[Thu Aug 28 18:23:57 2003] CON file [C:\Documents and Settings\Thor Inge\My Documents\Hovedfag\Canoco\CCA.con] saved

6.5 SAMPLE VOLUMES

Appendix 6.5. Number of samples and total volume in liters of samples from all sampled squares. Where only 3 or 4 samples (12 squares) were analysed, the volumes have been standardized to 6 samples.

Squares	Samples	Volume
1	6	9,3
2	6	11,2
3	6	13,4
4	6	8,3
5	6	8,4
6	6	11,1
7	6	15,5
8	6	12,3
9	6	10,5
10	6	14,8
11	6	12,6
12	6	11,2
13	6	19,2
14	6	17,7
15	6	14,7
16	6	15,4
17	6	14
18	6	14,7
19	6	15,3
20	6	12,7
21	6	13,1
22	6	13,1
23	6	14,4
24	6	14,7
25	6	11,9
26	6	15,2
27	6	15,8
28	6	13,2
29	6	15,6
30	6	11,8
31	6	16,6
32	6	13,4
33	6	16,7
34	6	18,9
35	6	17,3
36	6	18,4
37	6	15,1
38	6	12,8
39	6	11,9
40	6	15,1
41	6	13,9
42	6	11,5
43	6	11,9
44	6	9,2

Squares	Samples	Volume
45	6	18,5
47	6	17,8
48	6	14,6
49	6	16,8
50	6	17,3
51	6	11,9
52	6	16,9
53	6	16
54	6	17,3
55	6	14,7
58	6	18,1
59	6	12,3
60	6	16,4
61	6	13,7
62	6	16,3
63	6	15,1
64	6	13,2
65	3	17,8
68	6	10,9
69	6	11,9
70	6	18,2
71	6	15,3
72	6	14
73	6	11
74	6	11,8
75	6	14,5
76	6	17,8
77	6	15,8
78	6	14,3
79	6	10,9
80	6	11
81	6	14,2
82	6	16,1
83	6	15,6
84	6	16
85	4	18,9
86	6	19,2
87	6	16,9
89	6	10,8
90	6	8,8
91	6	16,6
92	6	15,1
93	6	16,4
94	6	13,4
95	6	17,5

Squares	Samples	Volume
96	6	14,8
98	6	15,8
102	6	11,8
103	3	13,8
104	6	18
105	6	14,2
106	3	12
107	6	16,2
108	6	15,7
109	6	14,4
112	6	11,8
113	6	15,5
114	6	13,2
115	6	12,3
116	3	11,2
117	6	14,2
118	6	16,3
119	6	16,7
122	6	12,1
123	3	12,8
124	3	18
125	6	10,2
127	6	16,8
128	6	17,6
129	6	14,2
130	6	10,9
131	6	15,3
132	6	14,4
133	3	12,4
134	3	8
135	6	16,2
136	3	13,2
137	3	16
138	3	12,2
139	3	13
140	6	13,8
141	3	9,4
142	6	11,1
143	6	11,8
144	3	11,2
145	6	11,1
146	6	10,9
147	6	14,5

6.6 TREE SPECIES AND ABBREVIATIONS

Appendix 6.6. Tree species included as covariables in the multivariate analyses.

ID	SPECIES	ABBREVIATION	ENG. NAME	NORW. NAME
1	*Alnus glutinosa*	ALNUGLUT	Common alder	Svartor
2	*Alnus incana*	ALNUINCA	Grey alder	Gråor
3	*Betula pubescens*	BETUPUBE	Birch	Bjørk
4	*Corylus avellana*	CORYAVEL	Hazel	Hassel
5	*Fraxinus exelsior*	FRAXEXCE	Common ash	Ask
6	*Ilex aquifolium*	ILEXAQUI	Holly	Kristorn
7	*Juniperus communis*	JUNICOMU	Juniper	Einer
8	*Lonicera periclymenum*	LONIPERI	Honeysuckle	Vivendel
9	*Picea abies*	PICEABIE	Norway spruce	Gran
10	*Pinus sylvestris*	PINUSYLV	Pine	Furu
11	*Populus tremula*	POPUTREM	Aspen	Osp
12	*Prunus padus*	PRUNPADU	Bird cherry	Hegg
13	*Quercus sp.*	QUERSPEC	Oak	Eik
14	*Rhamnus frangula*	RHAMFRAN	Alder buckthorn	Trollhegg
15	*Salix aurita*	SALIAURI	Eared willow	Ørevier
16	*Salix caprea*	SALICAPR	Goat willow	Selje
17	*Sorbus aucuparia*	SORBAUCU	Rowan	Rogn
18	*Sorbus hybrida*	SORBHYBR	Oakleaf mountain ash	Rognasal
19	*Taxus baccata*	TAXUBACC	Yew	Barlind
20	*Tilia cordata*	TILICORD	Small-leaved lime	Lind
21	*Ulmus glabra*	ULMUGLAB	Wych elm	Alm
22	*Viburnum opulus*	VIBUOPUL	Guelder rose	Krossved

6.7 CANOCO SETTINGS

Appendix 6.7. The following settings were used for the analyses in Canoco.

DCA (Detrended correspondence analysis):

- No samples omitted
- Detrending by segments
- No species-weight specified
- No sample-weights specified
- No transformation of species data
- Downweighting of rare species

CCA (Canonical correspondence analysis):

- No samples omitted
- No interaction terms defined
- No transformation of species data
- No species-weight specified
- No sample-weights specified
- Downweighting of rare species
- No rescaling
- No detrending
- Forward selection of environmental variables
- Number of permutations: 9999

6.8 BRIEF SPECIES DESCRIPTIONS

Appendix 6.8. List of the collected snail species and their habitat requirements.

	Scientific Name	Description
1	*Acanthinula aculeata*	Deciduous woods, hedgerows, scrub. In leaf litter and under fallen timber. Occationally in open habitats.
2	*Aegopinella nitidula*	Common in a wide variety of moist places; deciduous woods, hedgerows, herbage, among rocks; often in humanly disturbed places.
3	*Aegopinella pura*	Moderately moist places; charachtristic of ground litter in deciduous forests.
4	*Arianta arbostorum*	Widespread, meadows, herbage, woods and hedgerows, always in damp places, and very restricted in areas with dry climate and good drainage. Also alpine.
5	*Balea perversa*	Characteristic of dry places among rocks and on old stone walls; less common on trees, only very occationally found in ground litter. Also alpine.
6	*Carychium minimum*	Wet places, marshes and very moist woods. Common, but abscent from northern Scandinavia and Iceland
7	*Carychium tridentatum*	Deciduous woods, damp grasslands, well-vegetated places. Usually in drier habiats than *C. minimum*.
8	*Cepaea hortensis*	Very varied, deciduous woods, grasslands, hedges and dunes. Also alpine.
9	*Clausilia bidentata*	Moderately moist places, among rocks, old walls, deciduouswoods, hedgebanks, rare above 1000m.
10	*Cochlicopa lubrica*	Moderately damp places of all kinds; marshes, grasslands, deciduous woods.
11	*Cochlodina laminata*	Shaded places in deciduous woods and scrub under ground litter; in wet weather often climbing trunks.
12	*Columella aspera*	Coniferous and deciduous woodland, poor acid grasslands; often found in drier, less calcareous habitats than *C. edentula*.
13	*Columella edentula*	Marshes, deciduous woods, grasslands; moderately damp and calcareous places, typically lowland.
14	*Discus rotundatus*	Moist sheltered places of all kinds. Woods, under ground litter and stones, in damp herbage, often among rubbish in gardens.
15	*Discus ruderatus*	Mainly coniferous woods, especially under bark and logs, also marshes and moist grassland.

16	*Ena obscura*	Deciduous woods, hedgerows, walls, shaded rocky places; climbing bare surfaces in wet weather.
17	*Euconulus fulvus*	Widespread in coniferous and deciduous forests, grasslands, marshes, usually in fairly moist places.
18	*Lauria cylindracea*	Deciduous woods, rocks, grasslands; not usually in very wet places. Often abundant under ivy on calcareous stone walls.
19	*Nesovitrea hammonis*	Damp to moderately dry places of all kinds; marshes, coniferous and deciduous woods, grassland, often in poor acidic places.
20	*Nesovitrea petronella*	Similar to *N. hammonis*, but most common in woods, especially boreal forests.
21	*Oxychilus alliarius*	Woods, fields, rocks, occationally in greenhouses and gardens. Tolerant of poor acidic places, such as coniferous plantations.
22	*Punctum pygmaeum*	A wide variety of moderately moist and well vegetated places, especially common in leaf litter in forests. Also in marshes. Tolerates acidic conditions.
23	*Spermodea lamellata*	Old native deciduous woods and undisturbed pine forests, in leaf litter and under fallen timber.
24	*Vertigo lilljeborgi*	Saturated decaying vegetation in marshes and alder fens at the margins of rivers and lakes, usually in places subject to flooding.
25	*Vertigo pusilla*	Rather dry places; rocks, stone walls, ground litter in open deciduous woodland, hedge-banks, occasionally in sand-dunes.
26	*Vertigo pygmaea*	Characteristic of dry calcareous grassy places; also sand-dunes; occationally in marshes. Not in woods, except occationally in dry calcareous cliffs.
27	*Vertigo ronnebyensis*	Coniferous and deciduous woodland, under ground litter and moss; often among *Vaccinium* on poor non-calcarous soils. Moderately hydrophile, and with an eastern distribution in Norway.
28	*Vertigo substriata*	Damp places; mainly deciduous woods, marshes, lake margins; in upland areas often in poor marshy grassland.
29	*Vitrea contracta*	Mainly in deciduous woodland, sometimes in grassland. Common among rocks and screes.
30	*Vitrina pellucida*	Common in a wide veriety of moderately damp places; deciduous woods, grasslands, among rocks; often abundant in he grassy hollows of coastal sand-dunes. Most often found in the litter in the autumn, more subterran in the rest of the season.

6.9 PICTURES FROM THE STUDY AREA

Appendix 6.9. Pictures from different squares, illustrating the heterogenity and other aspects of the study site.

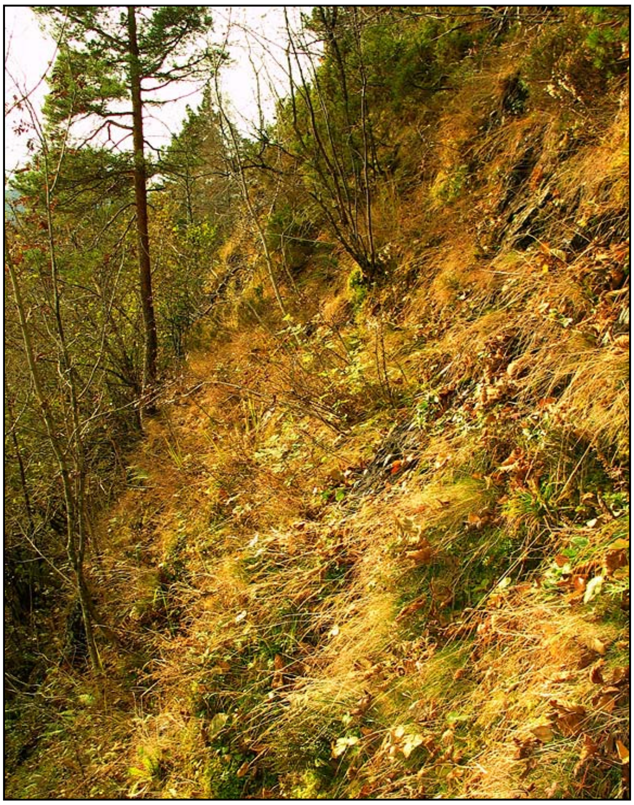
Picture 1 - Square 41:
This is a picture taken in one of the poorest squares, where only four species were found. The vegetation is typical for areas with little accessible nutrients, dominated by heath and a few slender pine trees.

Picture 2 - Square 61:
In contrast to picture 1, this is a picture from one of the richest squares. At least 22 species of snails occurs here, indicating a very favourable environment for snails. Several species of deciduous trees grow here, and there is a mixture of scree, mosses and a thick layer of litter.

Picture 3 - Square 83:
A eutropic mire, inhabited only by a few species. Nearly 70% of the individuals found in this square belong to the species *Carychium minimum* and *Vertigo lilljeborgi*. Mires are habitats that represent a potential risk of drowning for the snails.

Picture 4 - Square 61:
Pollarding was used as a method to increase the amount of leaves and twigs on deciduous trees.

Picture 5 - Square 72:
Many of the squares contained more than one type of vegetation. This picture shows the change from eutropic mire, via deciduous forest to pine forest.



Picture 6 - Square 7:
A cliff with rich vegetation and good exposure to sunlight. The bedrock has a high content of calcium, and the species richness is high.

Picture 7 - Square 17:
Not all cliffs are associated with high species richness, in this square only two species were found. The vegetation and the naked cliffs indicate poor conditions for snails.