Characterisation and typification of urban ecosystem types

A test of the NiN system

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Master of Science thesis
Department of Biosciences
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UNIVERSITY OF OSLO

June 2019

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Printed: Reprosentralen, University of Oslo

Abstract

The urban landscape includes a variety of habitat types, from strongly modified to semi-natural and natural ecosystems. This study uses a comprehensive approach to document natural variation in urban ecosystem types, as described by the classification system “Nature in Norway” (NiN), with the aim to identify gradients of species composition and environmental gradients that might explain these.

This study was conducted in the urban landscape of Oslo, Norway. Species composition was studied in 201 10 x 10 m plots, in which nature types were mapped to the scale 1:500 and vascular plant species recorded for each mapping unit. The plots were located in 12 500 x 500 m blocks, which were placed in three zones that differed in level of urbanisation, representing an urban-rural gradient from the city centre to the surrounding forest. To identify the main gradients of species compositions, the data was analysed using multiple parallel ordinations with DCA and GNMDS. To identify the main local complex environmental gradients that might explain the gradients of species composition, correlation between ordination axes and environmental variables were analysed.

The results showed that there were few correlations between gradients of species composition and environmental variables, and only for a select few strongly modified nature types. This suggests that there are other processes which structure the species composition of these types. However, dominating grain size to a large degree explained distinct species compositions in two T35 minor types. Comparison between the strongly modified types and a natural system (T4) showed that there is a much stronger relation between species composition and environmental factors in the natural system, which may indicate that the higher intensity and frequency of disturbance in strongly modified systems continuously disrupt natural ecological processes.

In regards to the NiN-system, this study shows that the different major types have distinct species compositions, although they were not clearly explained by any of the included environmental variables. Regarding minor type partitioning, the results confirm the NiN-hypothesis of T35 partitioning based on the LCE dominating grain size (S1). To determine the cause of the observed difference in strength of gradient structure, and to identify environmental factors that structure the species composition in strongly modified types and the NiN-partitioning of these, further research is required.

Acknowledgements

First and foremost, I want to thank my absolutely fantastic supervisors, Olav Skarpaas and Rune Halvorsen, for not only giving me the opportunity to work on this project, but also the guidance and encouragement to help me see it through. Being a part of the great and inclusive environment at the GEco research group by the Natural History Museum has been a truly wonderful experience. Thank you all for assistance and feedback, and especially Anne-Barbi Nilsen for providing invaluable QGIS expertise.

Thank you to the people at NINA and Urban EEA, for sharing your knowledge and experience, especially Anders Often, Harald Bratli and Egil Bendiksen, who did the field work in 2017 and have been immensely helpful to me and this project.

Thank you to Ariane, field work companion and skilled cityscape pathfinder, for making the long days we had in the field seem not very long at all, and without whom I would (literally) be lost. Many thanks to Tøyen-Triangelet, Ida and Eirin, for providing cookies, fruit, never-ending support, and a great many laughs, and my other friends and fellow students at Student Room B-335 Lid's Hus, for being a truly amazing bunch of people. Thank you also to my awesome gang of friends, Andrine, Fredrik, Håkon and Pawel. I have thoroughly enjoyed every moment since we first started studying biology together, here's hoping for many more adventures to come!

Thank you so much to my lovely family, especially my brothers Daniel and Adam, and Mormor, for always being so supportive and taking such an enthusiastic interest in what I do.

Above all, thank you to my dad Fred Ove and mum Sigrun, the most wonderful and supportive parents anyone could ever hope for. Thank you for always believing in me, most especially when I did not believe in myself.

Table of contents

1 Introduction 1

2 Materials and methods 15

2.1 Study area 15

2.2 Study design and sampling 15

2.2.1 Study design 15

2.2.2 Block characteristics 17

2.2.3 Mapping of nature types 22

2.2.4 Recording of species data 23

2.2.5 Post field work data processing 24

2.3 Explanatory variables 24

2.4 Statistical analyses 27

3 Results 30

3.1 Ecosystems and species observations 30

3.2 Environmental variables 32

3.3 Ordinations 34

3.4 Environmental interpretation 42

3.4.1 Full data set 42

3.4.2 Strongly modified types 45

3.4.3 T35 – Artificial ground on mineral deposits 45

3.4.4 T37 – Synthetic soft substrate 45

3.4.5 T43 – Road verge, embankment, lawn, and park 45

3.4.6 T4 – Forest 48

3.4.7 Species richness 50

4 Discussion 53

4.1 Interpretation of ordinations 53

4.1.1 Full data set 53

4.1.2 Strongly modified types 54

4.1.3 T35 – Artificial ground on mineral deposits 54

4.1.4 T37 – Synthetic soft substrate 55

4.1.5 T43 – Road verge, embankment, lawn, and park 55

4.1.6 T4 – Forest 56

4.2 Key ecological processes 56

4.3 Implication for NiN 58

4.4 Future studies 58

4.5 Conclusions 59

References 61

Appendix 1 66

Appendix 2 68

Appendix 3 73

Appendix 4 74

1 Introduction

Terrestrial ecosystems are now to a large extent influenced by anthropogenic land use (Ellis, 2010). Currently, the percentage of ice-free land on earth in direct use for agriculture and urban settlements, and land not used for this but embedded within such biomes is about 77 % (Ellis, 2010). Global population growth and consequent expansion of urban areas has affected community assemblages and habitat availability (Seto *et al*., 2012). A common urbanisation pattern is a gradient from developed urban centre, which radiates in diminishing development towards suburban and rural areas (Dickinson, 1966). Because of this pattern, the urban landscape includes a variety of habitat types, from modified, semi-natural to natural ecosystems. There is evidence that the urban landscape can sustain high biodiversity (Ellis, 2010), and also include rare and threatened species (Shepherd 1994). The structure of variation in species composition in urban ecosystems and the causes for this variation is not very well studied.

One of the most important structuring processes that explain variation in species composition is disturbance. Disturbance is defined as an event that causes some level of destruction of living organisms by reduction of biomass in an area (Grime, 1979), or abrupt change in the structure of ecosystems or communities (White, 1979). Because the extent and intensity are so different between them, anthropogenic disturbance is generally distinguished from natural disturbance (Hobbs & Huenneke, 1992). Examples of natural disturbance are events such as snow avalanches and sand and mudslides, fire, storms (White, 1979). Anthropogenic disturbance can be divided into two types: land management and other anthropogenic disturbance (Halvorsen *et al.*, 2016). Land management is defined as a regular human-caused activity that maintains specific nature types through disturbance, often in a way that advances agricultural production, but can also include e.g. mowing and fertilisation of lawns and road verges (Halvorsen *et al.*, 2016). The intensity of land management is a local environment gradient that to a large degree decides the species composition, and is as such separated from other anthropogenic disturbance, which is comprised of all other anthropogenic disturbance not included in the definition of land management (Halvorsen *et al.*, 2016).

Disturbance may facilitate succession, the more or less consistent change in the species composition over time as a result of extinction debt contingent on disturbance. However, succession may be less important for systems characterised by strong intensity of disturbance, because such systems are continuously in an early succession stage and may therefore show little variation along a successional gradient (Halvorsen *et al.*, 2016). Competitive replacement during succession may not occur until disturbances cease to operate (White, 1979). Different types and duration of disturbance may result in different species compositions. However, the knowledge of how the species composition varies between areas affected by different kinds of disturbance is currently insufficient.

"Nature in Norway" (NiN) is a system for typification and description of the variation in nature in Norway (Halvorsen *et al*. 2016). NiN was commissioned by Artsdatabanken; the first version was launched in 2009 and version 2.0 was launched in 2015. NiN divides nature into types, i.e. more or less homogeneous parts of nature with respect to defined characterising properties, at three hierarchical levels of biodiversity: landscapes, ecosystems and microhabitats (Noss, 1990). The theoretical foundation for the system is the gradient analytic perspective (Whittaker, 1967), the understanding that species respond (usually unimodally) to continuous variation along underlying environmental complex-gradients. Three main points are outlined by Halvorsen (2012): 1) The species composition responds to environmental factors acting collectively as complex-gradients, not to each environmental factor separately; 2) a few major complex-gradients normally explain most of the variation in species composition within an ecosystem that can be explained environmentally; 3) species have a restricted tolerance for, and therefore occur within a limited interval along each major complex-gradient.

At the ecosystem level of the NiN system, the key characterising property is species composition. Local environmental variation that in turn lead to variation in the species composition is systemised into nature types, where each type can be described as a uniform type of ecosystem that encompasses all living organisms occurring together in a given location and the environmental conditions that affect them. The nature types are organised hierarchically in major type groups, major types and minor types. Within major type groups, ecosystems that are contingent on or characterised by different ecological structuring processes are separated into major types. Major types are determined by the most important structuring processes for local variation in species composition, such as geophysical and biotic processes, which are represented by local complex environmental variables (LCEs). LCEs are composed of several single environmental variables that co-vary and affect the species composition on a long-term scale. Examples include KA – lime-richness and UF – risk of severe drought. Major types are characterised by a set of dominant LCEs that differ from the dominant LCEs of other types. Each major type is further divided into minor types based on the substitution of species along the most important gradients of variation for the major type, so that each segment, measured in units of species compositional turnover, contains an equal amount of compositional variation. The typification system is adapted to mapping to scales ranging from 1:500 to 1:20 000, which involves aggregation of minor types to mapping units (Bryn & Halvorsen, 2016). The NiN description system contains variables for describing variation not included in the typification system. It is divided into nine categories of sources of variation, which are described by semi-standardised variables (Halvorsen & Bratli, 2018).

In NiN, there are three kinds of major types: Strongly modified, semi-natural, and natural major types, which are grouped based on the intensity of anthropogenic disturbance impacting the system (Halvorsen *et al.*, 2016). Strongly modified systems are ecosystems that are characterised by a high intensity of anthropogenic disturbance. These ecosystems are no longer intact, their ecological structure and functions are modified, and natural ecological processes are disrupted. Strongly modified systems are often the result of high-intensity anthropogenic disturbance, which in NiN is defined as anthropogenic disturbance that result in immediate biomass reduction and that usually open the area for primary succession (Halvorsen *et al.*, 2016). Semi-natural systems are exposed to intermediate anthropogenic disturbance so that the system is altered but remains an intact ecosystem. Natural systems are ecosystems that have not been significantly altered because of anthropogenic disturbance (Halvorsen *et al.*, 2016). The heterogeneous urban landscape will include all these systems; while strongly modified types will dominate in the city centre, semi-natural and natural systems also occur intermittently, and will dominate in rural areas. In the NiN system there are 11 strongly modified major types. Examples of major types that will be emphasised in this thesis are T35 – *Artificial ground on mineral deposits*, T37 – *Waste deposit, spoil heap, plastic and other synthetic soft substrate*, and T43 – *Road verge, embankment, lawn, park and similar artificial land*. In terms of area, these are the most important strongly modified major types in the NiN system. NiN article 3 (Halvorsen, 2016) describes the type partitioning at the ecosystem level, including T35, T37 and T43:

T35 includes land where a new cover of deposited unconsolidated material that consists of soil, gravel, sand, silt or clay has been supplied through high-intensity anthropogenic disturbance. This causes biomass reduction and exposes ground to primary, rapid succession that is largely area-specific, and colonisation by ruderal species is typical for this nature type (Bratli *et al*., 2017). Proposed LCEs characterising T35 is dominating grain size (S1, *dominerende kornstørrelse*), which is the basis for partitioning for this type. T35 is partitioned into four minor types: *soil-covered ground* (T35-1), *gravel-covered ground* (T35-2), *sand-covered ground* (T35-3), *and silt- and clay-covered ground* (T35-4). However, the extent of variation due to random events is presumed to be large (Halvorsen, 2016). Additional tentative LCE is lime-richness (KA, *kalkinnhold*), with two major-type specific segments (Halvorsen, 2016).

T37 includes land that has, through high-intensity anthropogenic disturbance, acquired a new cover of strongly modified or synthetic soft substrates, such as plastic and asphalt. This causes biomass reduction and facilitates rapid succession that is mostly area-specific, typically characterised by ruderal and disturbance tolerant species (Bratli *et al*., 2017). The basis for partitioning in T37 is a major type specific LCE (HS, *hovedtypespesifikk inndeling*), which is used because the variation in species composition within the major type is not known. T37 is therefore partitioned into 3 minor types based on disturbance and substrate characteristics: *Spoil heap and chemical waste deposit* (T37-1), *inorganic moderate soft synthetic substrate* (T37-2), and *household and other organic waste deposit* (T37-3) (Halvorsen, 2016). Examples of minor type T37-2 include asphalt, loose concrete etc., which is particularly common in the urban landscape. T37-2 generally consists of substrates that are inhospitable to plants, yet plants (generally weeds) manage to establish themselves in cracks, and gaps between the curb and pavement.

T43 includes land that is strongly modified and characterised by intensive management (e.g. regularly sown, mowed, fertilised etc., but the ground itself is not processed in any way, such as by ploughing etc.). The land is cultivated, but not used in agricultural production, and includes lawns, parks and road verges, which are characterised by sown, planted, and ruderal species (Bratli *et al*., 2017). T43 is not partitioned into minor types. However, the LCEs land management intensity (HI, *hevdintensitet*), lime richness (KA, *kalkinnhold*), and water saturation (VM, *vannmetning*) are tentatively included as subordinate LCEs, i.e. LCEs that contribute to observable, but not significant difference in species composition. These are only thought to be of importance after cessation of management for a considerable time, which allows species differentiation to occur as a response to the environmental conditions (Halvorsen, 2016). Between instances where the land is managed, it may accumulate species; however intensely managed T43 will have limited number of native species.

There are several studies related to biodiversity in urban ecosystems (e.g. Cornelis & Hermy, 2004; Yang *et al.*, 2019 (lawns) and Bonthoux *et al.*, 2019 (built areas)), however there are few studies using multivariate analyses to investigate the species composition in urban ecosystems. More research of the ecology of urban ecosystems, e.g. to what extent the structuring processes, such as anthropogenic disturbance, land management and other environmental gradients, give rise to distinct ecosystem types, is required. The knowledge that NiN, which is the classification system used in all publicly financed mapping projects, is based on is insufficient when it comes to the strongly modified types. This basic ecological knowledge is also important for several applications from local area management to ecosystem monitoring and accounting.

This thesis is connected to the Urban EEA (Experimental Ecosystem Accounting) research project, which is led by the Norwegian Institute for Nature Research (NINA) and funded by the Research Council of Norway. The purpose of the project is to study urban ecosystems in the Oslo region, both green infrastructure and natural areas with proximity to the city. This research will contribute to the experimental ecosystem accounting put forth by the UN (SEEA, 2013), and on ecosystem services and biodiversity in the context of sustainable development. This thesis aims to provide important input to the Urban EEA research project and international development of ecosystem accounting schemes by defining and testing basic ecological units within the NiN system.

Aims

This thesis aims to document the variation in species composition in the major types of strongly modified systems, to test the NiN-hypotheses about these types. Specifically, the thesis aims to answer the following questions:

1. Which gradients of species composition exist in urban ecosystems?
2. Which environmental gradients can explain these species composition gradients?
3. Are the proposed types (i.e. type hypotheses) in NiN 2.1 about the partitioning of minor types and major types supported by empirical data? (With a focus on major types T35, T37 and T43)

2 Materials and methods

2.1 Study area

The study area was located in Oslo, south east Norway. The city is situated at the northernmost end of the Oslo fjord, surrounded by forested ridges. Oslo is interesting as a case because of the strong gradient from natural to urban areas and high levels of bio- and geodiversity. This allows testing of several urban ecosystem types, based on a broad range of species. The study sites were located across the city in an urban-rural gradient, from the city centre to the forest, mainly towards Østmarka (Figure 2.1). Oslo as a county covers a large area. Only around one third of the total area consists of built up land like infrastructure, and residential and industrial areas (27.4 %), while the remaining area is largely covered by forest (61.6 %) (SSB, 2019). Oslo is the most populous city in Norway, with 670,000 - 675,000 inhabitants during the study period; a high population growth rate has led to a corresponding urban expansion (Nore *et al.*, 2014) that may threaten semi-natural systems. The larger degree of human intervention in cities is related to the proportion of alien species that manage to establish (Hendrichsen *et al*., 2014), and so Oslo is dynamic in terms of species composition.

The study area lies in the boreonemoral vegetation zone (Moen, 1998). The annual mean temperature in Oslo is around 6°C, based on measurements from Blindern-Oslo, 1937 – 1990 (Aune, 1993). It is milder in Oslo than in continental areas of similar latitudes, because of oceanic influences. 2018, when the field work was carried out, saw an exceptionally warm summer due to the 2018 European heat wave. In July 27th 2018, the temperature in Oslo rose to 34.6°C, the warmest recorded since 1937. The annual precipitation is 763 mm (Førland, 1993). Oslo is located in the middle of the Oslo Rift, a graben that formed during the Permian period, and is surrounded by Precambrian basement (Bjørlykke, 1974). The bedrock in Oslo is made up of lower Palaeozoic marine shales and limestone in the city centre and southwest towards Asker and Bærum, while Permian igneous rocks are found to the north and west (Bjørlykke, 1974).

2.2 Study design and sampling

2.2.1 Study design

A stratified sampling design by Urban EEA was used in this study, which was based on mapping of land covers in urban environments using Sentinel 2 satellite imagery, with a particular focus on the classification on green spaces.

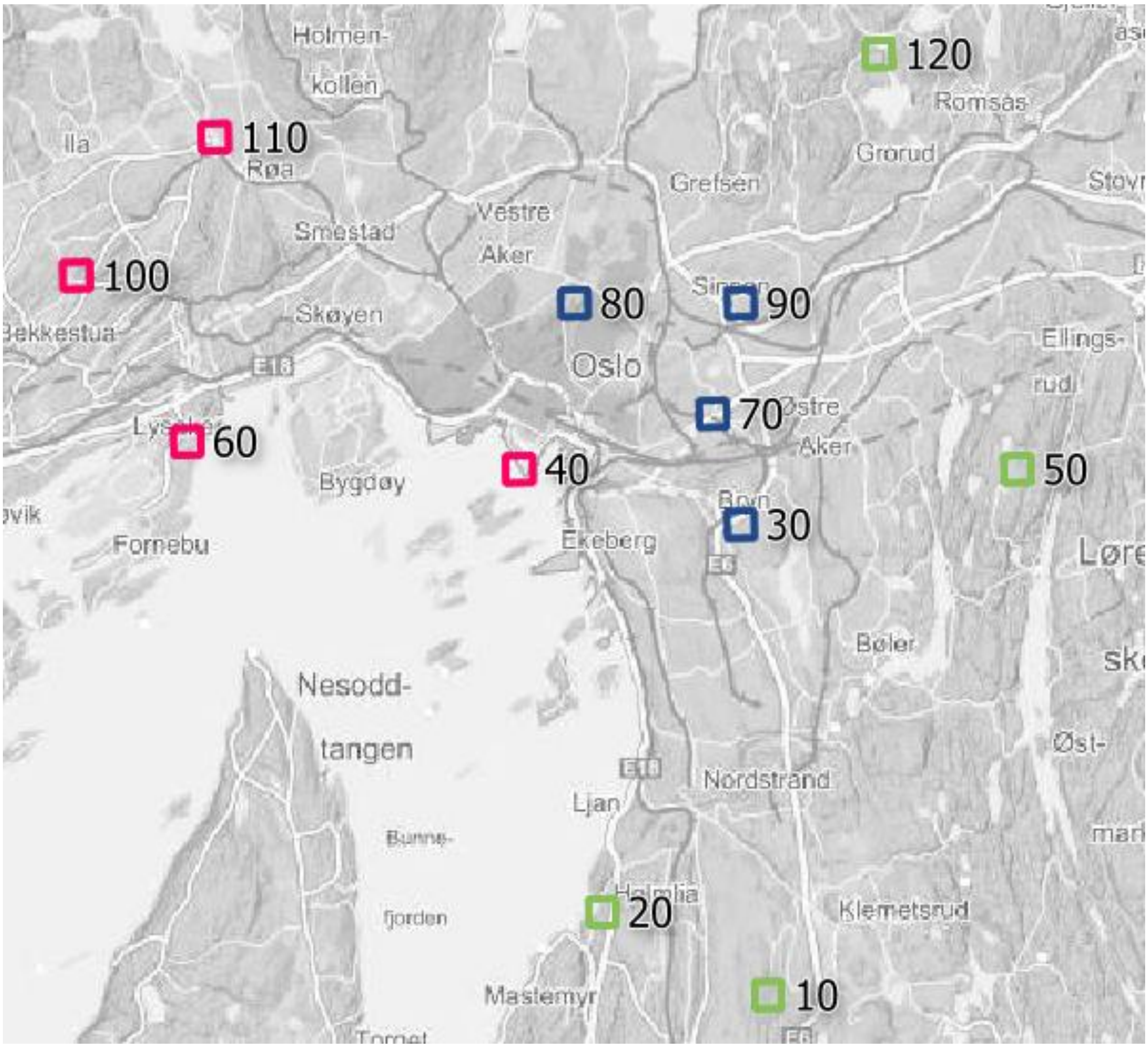


Figure 2.1 Map of the study areas, showing the locations of the 12 500 x 500 m sampling blocks in Oslo. Prepared with QGIS 3.2.0 (QGIS Development Team, 2018), background map retrieved from Geonorge.no.

12 sampling blocks were randomly selected from a 500 x 500 m grid (retrieved from Statistics Norway, http://www.ssb.no/natur-og-miljo/geodata) from three zones featuring varying levels of urbanisation that represent an urban-rural gradient. This stratification was based on the area of impermeable surface, calculated from the Sentinel 2 land cover map.

The thresholds used for stratification were as follows:

1. 0 – 76393.7 m^2 -> Low
2. 76393.7 – 152787.3 m^2 -> Medium
3. 152787.3 – 229181 m^2 -> High

There were 6 land cover classes of interest: agricultural edge, built-up, calcareous grassland (on calcareous bedrock), grassland (on other bedrock), tree canopy and water edge (Table 2.1). This area-classification was derived from Sentinel 2 satellite maps using the decision tree-based ensemble learning method for classification *random forest* (Nowell, 2016). Ten by ten m plots, corresponding to Sentinel 2 pixels, were randomly selected from the 12 sampling blocks. Where possible, ten plots in each land cover class were chosen from each block. This resulted in a total of 444 plots. Field work was conducted by NINA staff in 2017 in 201 of the total sampling plots; these 201 plots were the focus in the 2018 field work.

2.2.2 Block characteristics

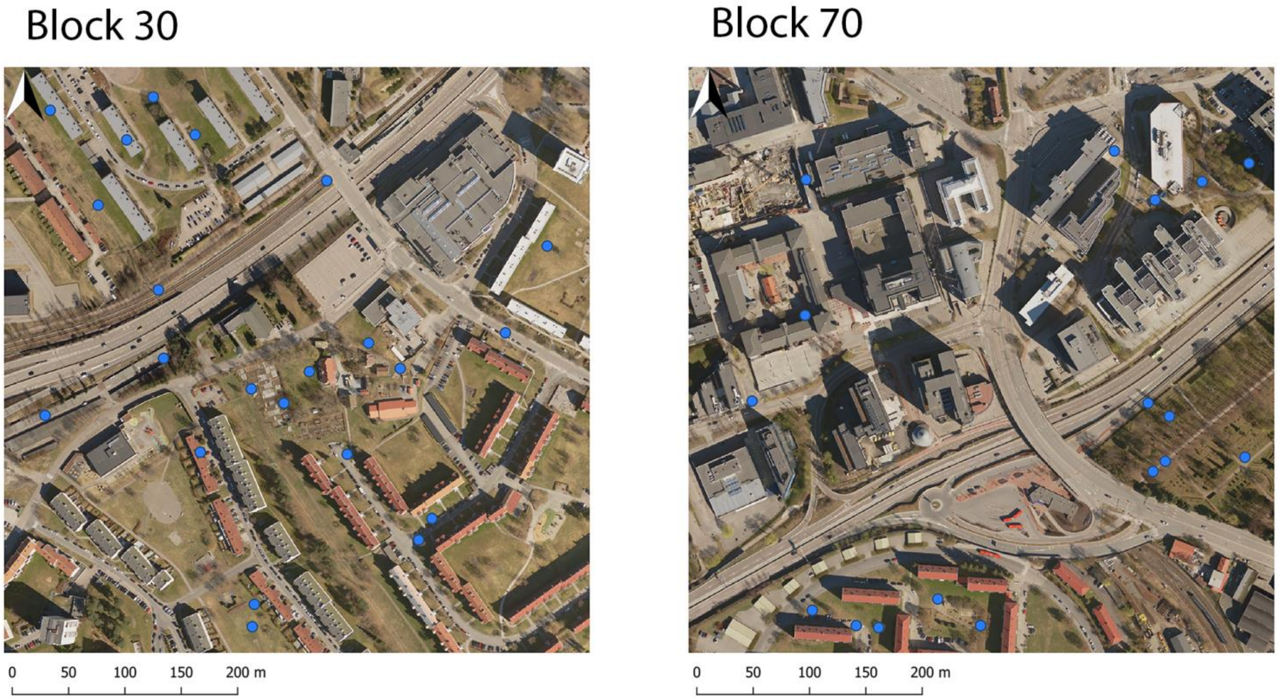
An overview of the blocks is presented in Table 2.2. The three strata of sample blocks showed variation in the degree of urbanisation. Blocks of high levels of urbanisation (Figure 2.2) were largely represented by built-up in all four blocks of this stratum. Blocks of medium levels of built-up (Figure 2.3) were located in mainly suburban areas, with the exception of block 40, where the land cover was predominantly built-up. However, due to water covering a large part of the block area, it was classified as having medium levels of built-up. Blocks of low levels of built-up (Figure 2.4) were located in predominantly forested areas. However, all plots in block 10 and nearly half of plots in block 20 were placed in strongly modified systems.

Table 2.1 Description of the 6 land cover classes (from Nowell, 2016).

Land cover class	Description
Agricultural edge	Areas within a 10 m buffer of agriculture pixels
Built-up	Impermeable surfaces (including buildings, roads etc.)
Calcareous grass	Grass on calcareous bedrock
Grass	Grass on all bedrock, except calcareous bedrock
Tree Canopy	Tree canopy cover
Water edge	Areas within a 10 m buffer of water pixels

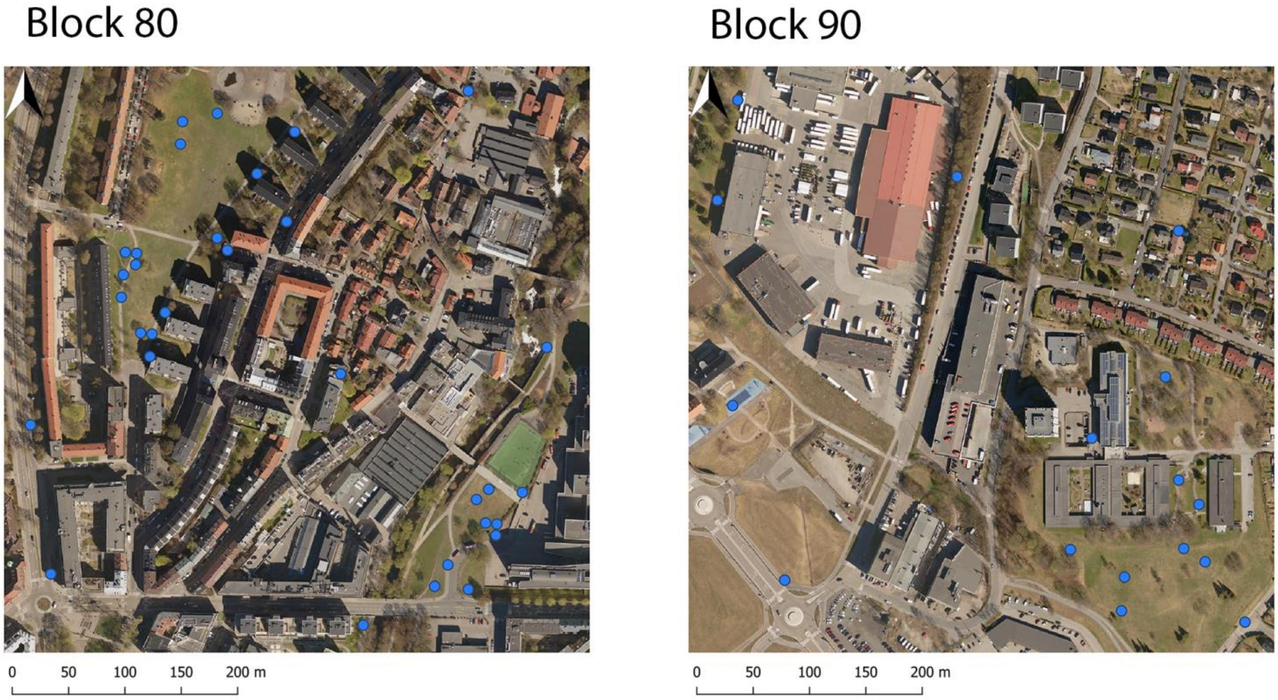
Table 2.2 Overview of blocks, with number of plots across the 6 land cover classes.

Block location	Block number	Built-up level	Agri. edge	Built-up	Calc. grass	Grass	Tree Canopy	Water edge	Total plot number
Bjørndal	10	Low	5	5	0	6	0	0	16
Hvervenbukta	20	Low	0	6	0	7	6	6	25
Manglerud	30	High	2	8	0	8	4	0	22
Vippetangen	40	Medium	0	5	0	5	2	3	15
Haukåsen	50	Low	0	0	0	0	5	0	5
Fornebu	60	Medium	4	6	5	0	5	0	20
Helsfyr	70	High	0	6	3	2	5	1	17
Iladalen	80	High	4	7	5	9	7	0	32
Økern	90	High	0	5	0	7	4	0	16
Bekkestua	100	Medium	5	3	0	6	1	0	15
Røa	110	Medium	1	2	0	2	5	1	11
Svartkulp	120	Low	0	0	0	0	3	4	7
			21	53	13	52	47	15	201



Block 30

Block 70



Block 80

Block 90

Figure 2.2 Map of sampling plots within blocks with high levels of built-up; block 30, 70, 80 and 90. Figures prepared with QGIS 3.2.0 (QGIS Development Team, 2018). Orthophotographs retrieved from norgeibilder.no (accessed in May/June 2018).

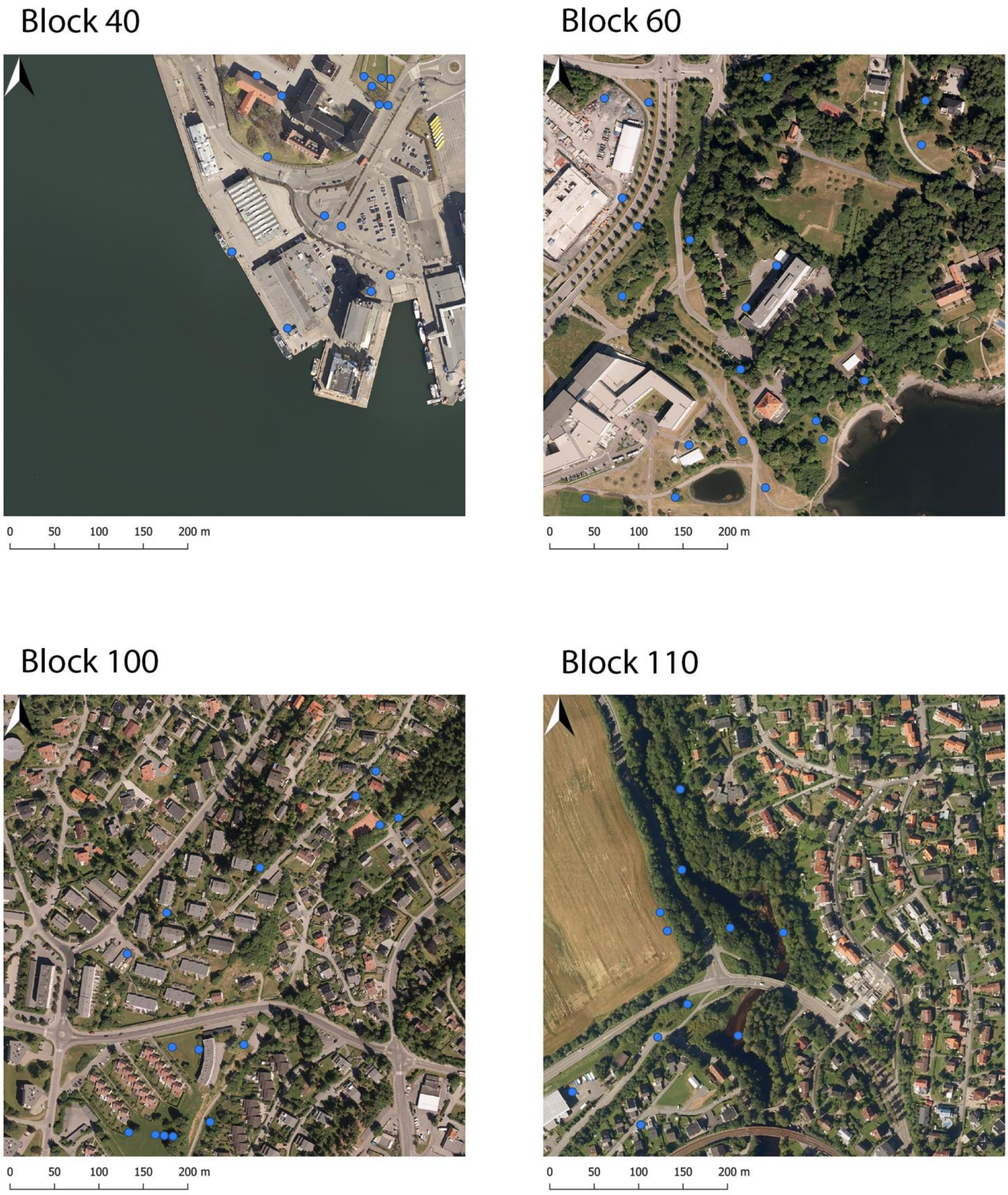


Figure 2.3 Map of sampling plots within blocks with medium levels of built-up; block 40, 60, 100 and 110. Figures prepared with QGIS 3.2.0 (QGIS Development Team, 2018). Orthophotographs retrieved from norgeibilder.no (accessed in May/June 2018).

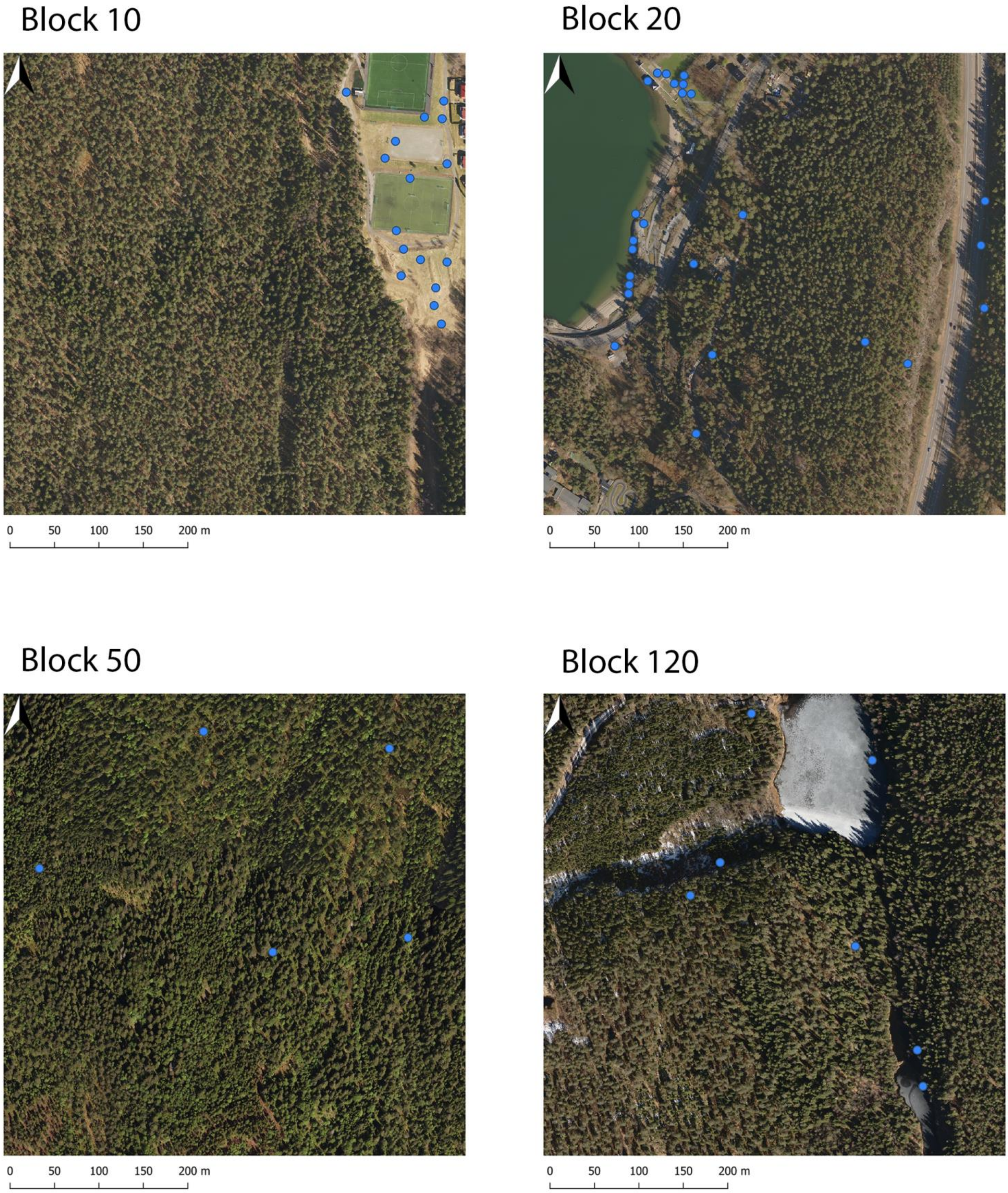


Figure 2.4 Map of sampling plots within blocks with low levels of built-up; block 10, 20, 50 and 120. Figures prepared with QGIS 3.2.0 (QGIS Development Team, 2018). Orthophotographs retrieved from norgeibilder.no (accessed in May/June 2018).

2.2.3 Mapping of nature types

The field work was carried out from the 11th of July to the 29th of August 2018. The field work consisted of nature type mapping and assigning species registrations to the resulting nature type polygons. The data were recorded in a QGIS 3.2.0 project (QGIS Development Team, 2018) prepared with species lists from 2017 and the NiN mapping application, using a Getac-toughpad (Getac F110, Windows 10 Pro 64 bits). Nature type polygons were digitised with orthophotographs as background. The orthophotography projects (Bærum 2014 (12.5 cm), Oslo Østlandet 2016 (25 cm) and Oslo 2017 (8 cm)) were collected from www.norgeibilder.no (accessed in May/June 2018), resolution was prioritised over recency. Plots were located using orthophotographs and GPS integrated in the Getac toughpad.

The NiN mapping instructions (Bryn & Halvorsen, 2016) were used. The sampling plots were mapped to scale 1:500, which is the most precise in the NiN system. The minimum size of area of polygons to this scale is 1 m^2, which allowed within-plot nature type variation to be recorded. For 1:500 the mapping units correspond to the minor types in NiN, so aggregation of nature types into mapping units was not necessary, as they are already given. An example of a 10 x 10 m plot with orthophotography and digitised minor types is shown in Figure 2.5.

The majority of strongly modified types lack both shrub and tree layers, and in these cases, the ground is visible in orthophotographs. Most polygons will have clear borders to surrounding polygons, because strongly modified systems are the results of planned physical alteration of the landscape (Bratli *et al.*, 2017). Therefore, the majority of polygons were digitised in QGIS preceding field work, as advised by the NiN mapping guidelines (Bryn & Halvorsen, 2016):

- Pre-field work delineation was performed if:
  - The units were separated by clear borders in orthophotographs
  - The borders between units were distinct
  - The ecological reasons for the borders between units were understood
- Pre-field work nature type classification was performed if:
  - The unit belonged to strongly modified types
  - The unit belonged to mapping units that are defined through the absence of species
  - The unit belonged to mapping units that are easily recognisable by its object shape, structure or texture in orthophotographs

Both polygon delineation and nature type classification were controlled in the field and corrected where necessary. To ensure correct typification, uncertain nature type classifications were corrected post-field work using historical orthophotographs and expert help (Bratli & Halvorsen, pers. comm., September 17, 2018).

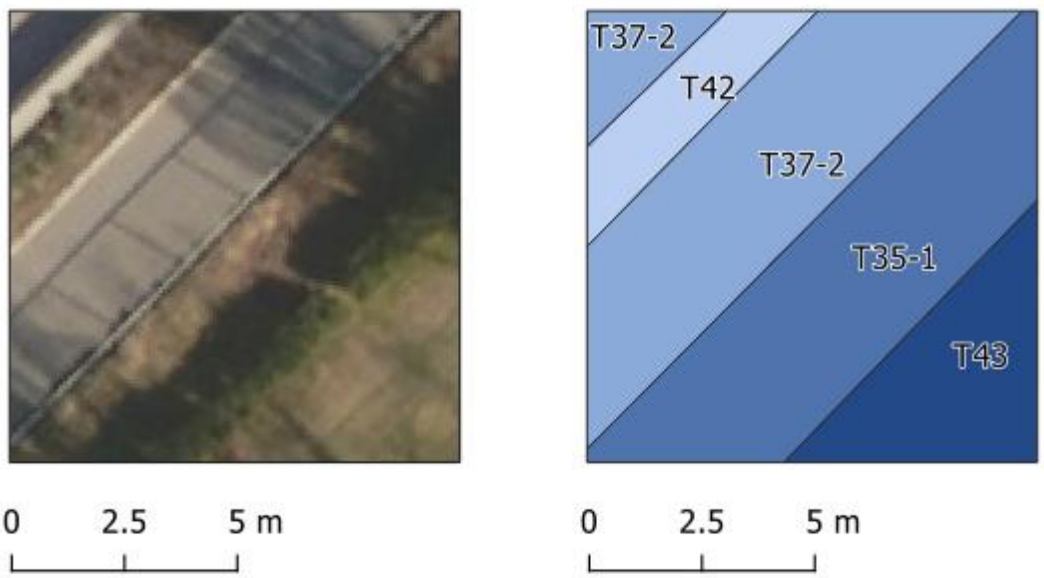


Figure 2.5 Example of a 10 x 10 m plot (plot 199, block 70), showing orthophotography and digitised polygons in QGIS.

Table 2.3 A8 scale (modified from Bryn & Halvorsen, 2016) and translation from the 2017 approximate abundance scale.

A8								
Levels	7	6	5	4	3	2	1	0
Fraction	> 3/4	1/2 – 3/4	1/4 – 1/2	1/8 – 1/4	1/16 – 1/8	1/32 – 1/16	0 – 1/32	0
Percentage	> 75	25 – 50	25 – 50	12.5 – 25	6.25 – 12,5	3.125 – 6.25	0 – 3.125	0
Approx. scale								
Levels	Dominant	Dominant	Common	Common	Rare	Rare	Random	0

2.2.4 Recording of species data

The species data were recorded over two years. In 2017 all vascular plant species and their respective abundances within *each plot* were registered by NINA staff in the summer and autumn (Often, Bendiksen and Bratli, unpublished data), using the following five-grade abundance scale shown in table 2.3: dominant, common, occurring, rare, and random, for 201 of the total plots.

In 2018, species data were digitised in the field in QGIS, using the 2017 species lists as assistance. Species abundances were recorded for *each polygon in each plot* using the A8 scale from the description system in NiN (Bryn & Halvorsen, 2016), presented in table 2.3. The cover for all vascular plant species was registered in each polygon, recorded as visually estimated percent cover of each species. Species nomenclature follows the Norwegian Biodiversity Information Centre (www.artsdatabanken.no).

2.2.5 Post-field work data processing

The approximate abundance scale from 2017 was translated to the A8 scale (Table 2.3). Because of the 2018 summer drought, some polygons presented difficulties regarding species identification and accurate estimation of abundances. Therefore, in some cases certain species registered in 2017 were missing in 2018. This concerns mainly graminoids and species that were rare in the plot. In cases where nature type affiliation of a species registered in 2017 was unclear (several different nature types in one plot), the registration was removed entirely before analysis. In cases where polygons were severely affected by drought (vegetation predominantly dead), the species abundances of species registered in 2018 were adjusted up to the 2017-abundances. This concerned 11 polygons, all T43-affiliated.

2.3 Explanatory variables

The explanatory variables were collected from a range of sources and assigned to the same 10 x 10 m grid as the sampling plots (the Sentinel grid, see above), with values corresponding to the coordinates for the midpoint of each plot, except Ellenberg Indicator Values, which were calculated for each polygon. Overview of environmental variables is presented in Table 2.4, and values for the environmental variables are exemplified in Appendix 4. Because the polygon number was so high, direct measurements of environmental variables were not possible, except in the case of T35-affiliated polygons, where the dominating grain size of the polygon was represented by the minor type classification.

Digital elevation model (DEM)

The digital elevation model was retrieved from Kartverket (by A.-B. Nilsen, through Geonorge: www.geonorge.no). The following variables were derived from this source:

- Aspect
- Elevation
- Topographic position index (TPI)
- Topographic wetness index (TWI)

TWI-values were extracted using SAGA (Conrad *et al.*, 2015), and values for the remaining DEM variables were extracted using R (R Core Team, 2018). TPI is calculated as the difference of the centre pixel to the mean of its surrounding pixels, and expresses the degree to which the site is convex or concave. TWI is a function of slope and upstream contributing area (Beven & Kirkby, 1979).

Aspect favourability was calculated from aspect, on a 0 – 180° scale, following the approach of Dargie (1984) and Økland & Eilertsen (1993). SSW (202.5°) was set as the most favourable aspect for plants, and NNE (22.5°) set as the least favourable, and new values (a) were calculated as such:

a < 22.5°	-> 22.5° – a
202.5° > a > 22.5°	-> a – 22.5°
a > 202.5	-> 382.5 – a

Climate data

In this study, surface temperature was used instead of air temperature because it varies more locally and is to a larger degree influenced by urban structures. Land surface temperature was estimated for Oslo, 2015, using Landsat8 imagery; the raster map (Blumentrath, 2016) was retrieved from (http://urban.nina.no/layers/geonode%3Alc81980182015183lgn00_lst_const_lc).

Geological data

Geological bedrock and soil maps retrieved from Geological Survey of Norway (NGU) (by A.-B. Nilsen, through Geonorge: www.geonorge.no). The following variables originated from this source:

- Limestone
- Substrate

Limestone is a binary factor variable of presence-absence of lime-rich bedrock (prepared by O. Skarpaas), based on the presence of the term limestone (“kalk”) in the description field (“tegnforkl”) of bedrock types in the geological bedrock map. Substrate is a factor variable, reclassified from 14 to 4 levels of substrate type (“løsmasser”; reclassified by O. Skarpaas): 1) bare rock; 2) soil (sediments and glacial deposits); 3) weathered rock; 4) land fill (anthropogenic soil).

Ellenberg’s Indicator Values

Ellenberg’s indicator values were included as surrogate environmental variables (Ellenberg *et al.*, 2001). Ellenberg's Indicator Values were derived from occurrences of Central European plant species in relation to 7 environmental gradients. 4 EIV of interest were used: L - Light, F

- soil moisture, R - soil reaction/pH, and N - soil nitrogen, which indicate that species prefer open, moist, basic and nitrogen-rich sites, respectively (Hill *et al.*, 1999). The values are on the scale 1-9, except F which is on the scale 1-12. The values were retrieved from JUICE (*www.sci.muni.cz/botany/juice/?idm=10)*. For a small number of recorded species indicator values were not available, in most cases these were escaped non-native species. The EIV for each polygon were calculated using weighted averaging calibration, with species abundance of each polygon as the weight. The weighted averaging formula described by ter Braak & Barendregt (1986) was used:

$$\hat{x}wa = \frac{\sum_k Y_k\, u_k}{\sum_k Y_k} \quad ,$$

where Y_k is the abundance of the k^{th} species (k = 1, 2, 3, ...), and u_k is the species' indicator value.

The use of EIVs is advantageous in generating hypotheses about species-environment relationships when direct measures are unavailable. However, they do also come with certain limitations, which will be taken into account in the ecological interpretation. These are as follows: 1) EIVs are derived from subjective judgements, not systematic measurements (Økland, 1990); 2) Species may shift in their response to environmental factors towards the margin of their geographical distributions (Diekmann & Lawesson, 1999); 3) EIVs are calibrated for Central Europe and as such may be geographically biased (e.g. Wamelink *et al.*, 2002) and inappropriate for use in Norway. (However, see study from Sweden by Hedwall *et al*., 2019); 4) Species respond to environmental factors acting collectively as complex-gradients, and indicator values based on single parameter cannot fully account for this complexity (Schaffers & Sýkora, 2000); 5) Using EIVs in ecological interpretation entails circular reasoning: the EIVs are derived from species composition of sites where the environmental data is known, and are then used to estimate species-environment relationships; 6) It is unclear which environmental factors the EIV variables actually represent; for example, N is in practice an indicator of general soil fertility as opposed to nitrogen availability (Hill & Carey, 1997; Myklestad, 2004).

Table 2.4 Overview of explanatory variables.

Variable	Abbreviation	Description	Range	Mean
Aspect	Aspect	*Aspect favourability, 0° – 180°*	0.7° – 179.3°	112.9°
Elevation	Elevation	*Height above sea level*	0 – 344.8 m	74.2 m
Limestone	Limestone	*Presence/ absence of lime-rich bedrock*	Binary	0.6
Slope	Slope	*Angle of the terrain around the pixel*	0 – 0.7	0.1
Substrate	Substrate	*Factor variable, substrates*	4 levels	-
Surface temperature	SurfaceTemp	*Annual mean surface temperature*	21.7 – 39.2° C	32.5° C
Topographic Position index	TPI	*Difference of centre pixel to the mean of surrounding pixels*	–2.8 – 2.1	–0.1
Topographic Wetness Index	TWI	*Function of slope and upstream contributing area*	–1.3 – 16.7	7.5
Light (EIV)	L	*Indication of preference for open sites*	4.5 – 8.2	6.9
Moisture (EIV)	F	*Indication of preference for moist sites*	2 – 8	5.1
Reaction (EIV)	R	*Indication of preference for basic sites*	1.7 – 9	6.0
Nitrogen (EIV)	N	*Indication preference for nitrogen-rich sites*	1 – 9	5.9

2.4 Statistical analyses

R Version 3.4.3 (R Core Team, 2018) was used for all statistical analyses. The R Package vegan version 2.5-3 (Oksanen *et al.*, 2018) was used for all multivariate analyses.

Correlations between environmental variables were calculated using Kendall's rank correlation coefficient τ (Kendall, 1938). Kendall's τ is non-parametric and takes only the variable ranks into account. The Kruskal-Wallis test (Kruskal & Wallis, 1952) was used for comparing pairs of continuous variables and factor variables. Due to the nested composition of the data, the assumption of statistical independence of polygons is uncertain, and correlation coefficients are only interpreted as indication of correspondence (as advised by Økland, 2007).

To identify main gradients of species composition, the data was analysed using ordination methods. The multiple parallel ordinations procedure (MPO; van Son & Halvorsen, 2014) was used, performing detrended correspondence analysis (DCA; Hill & Gauch, 1980) and global non-metric multidimensional scaling (GNMDS; Kruskal, 1964) in parallel, because obtaining similar results by different ordination methods may to a larger extent confirm that the main gradient structure has been identified. In GNMDS, plots are placed along species composition gradients based on the floristic dissimilarity, while in DCA plots are placed on the basis of differences in abundance of species with different estimated optima.

DCA was run with the *decorana* function with default arguments; four rescaling cycles with 26 segments in each rescaling. The DCA axes were scaled in S.D. units. GNMDS was run using the Bray-Curtis dissimilarity measure, comparing dissimilarities to the distance matrix. Unreliable distances were replaced with new geodesic distances, calculated with stepacross (Williamson, 1978); threshold values were set to $\varepsilon = 0.8$ (or 0.9, depending on the subset). The number of starting configurations was 100, maximum number of iterations was set to 2000, and stress reduction ratio (convergence criteria) was set to $1 \cdot 10^{-7}$. The GNMDS solutions were accepted when reached from at least two different starting configurations, comparing best and next best stress values. The GNMDS axes were rotated to principal components through varimax rotation, and were scaled in half-change units. Two-dimensional GNMDS were obtained for all subsets. Pairwise comparison of DCA and GNMDS axes was made using Kendall's rank correlation coefficient τ to decide if axes confirm each other in the parallel ordinations. Correlations between axes of different ordinations with a tau value of $\tau > 0.4$ were considered corresponding, as suggested by Liu *et al*. (2008).

The two ordination methods were applied to 5 subsets in addition to the full data set, which included all the natural and the strongly modified nature types. The data were divided based on nature type affiliation, to analyse structure within and between major types. In addition to the full data set ordinations of the following subsets were obtained:

1. Strongly modified types (SMT): comprised of all strongly modified major types in the data, 305 polygons
2. T35, 60 polygons
3. T37, 70 polygons (all were affiliated with minor type T37-2)
4. T43, 157 polygons
5. T4, 19 polygons

The subset of the natural system T4 was included despite a low number of polygons to compare results with those of a nature type with known structure.

Empty and incomplete polygons were removed before the analyses. Two sets of strong outliers, plots situated at isolated points along an axis (Gauch & Gauch, 1982), in preliminary DCA ordinations were identified. The first set of outliers were the two L4-affiliated polygons (2-2 and 51-2, with 3 and 4 species, respectively) in the full data set, which belonged to a different major type group (limnic seabed systems) than the rest of the polygons (terrestrial systems).The other set of outliers (17-1 and 64-1, with 5 and 16 species, respectively) were T35-affiliated polygons situated in natural areas, and as such contained mainly forest and riverside associated species. These polygons were omitted from all subsets in which they occurred, and ordinations were then run on the remaining polygons.

To identify the main local complex environmental gradients that explain the gradients of species composition, correlation between ordination axes (plot scores) and continuous explanatory variables were calculated using Kendall's rank correlation coefficient τ. The Kruskal-Wallis test was used for testing the relationship between axes and factor variables. Biplots were made with the *envfit* procedure in R, plotting plot positions from the ordinations and environmental variables as vectors, to identify the direction of maximum increase of the environmental variable in the ordinations. To give a more detailed picture of the variation of each environmental variable, isoline diagrams were made with the *ordisurf* procedure in R, fitting smooth surfaces to the environmental variables, which were then plotted to the ordination diagrams. Isoline diagrams were made for the environmental variables with a Kendall's correlation coefficient of $\tau > 0.3$ with one of the relevant axes. The number of species recorded in each polygon was also included as a derived biotic variable, to identify species richness patterns along ordination axes.

3 Results

3.1 Ecosystems and species observations

The total number of polygons was 454 (before outlier removal). The complete data set consisted of 27 basic types across 14 major types. An overview of nature types can be found in Appendix 1. The most common nature type in the data set was T43 (Road verge, embankment, lawn, and park) with 165 polygons, followed by T37 (T37-2, inorganic soft synthetic substrate) and T35 (Artificial ground on mineral deposits), with 128 and 69 polygons, respectively (Table 3.1). No semi-natural systems were represented in this data. Note that this summation of the data set is not an area-representative estimate for the study area.

In the full data set, a total 393 species of vascular plants were registered. An excerpt of the species-plot matrix is presented in Appendix 3. The species that occurred the most frequently were *Taraxacum officinale agg.* and *Plantago major* (232 and 223 occurrences, respectively), followed by *Trifolium repens*, *Achillea millefolium*, *Poa annua*, *Festuca rubra*, *Polygonum aviculare*, *Agrostis capillaris*, *Scorzoneroides autumnalis*, and *Lolium perenne*. The mean and total species richness for each nature type are given in Table 3.1. Despite a much lower number of total polygons, major type T35 had nearly the same amount of total species as T43, the most common major type, and nearly the same mean species number. T35-1 alone had a mean species number of 26.6, while the mean for T35-2 was only 5.8. T37, the second-most common nature type in the data, had an average of only 3.7 species per polygons; 55 of the total 128 T37-affiliated polygons had no species. The highest mean species number were T2 and T40 with 41 and 29 respectively, however both were represented by only 1 polygon.

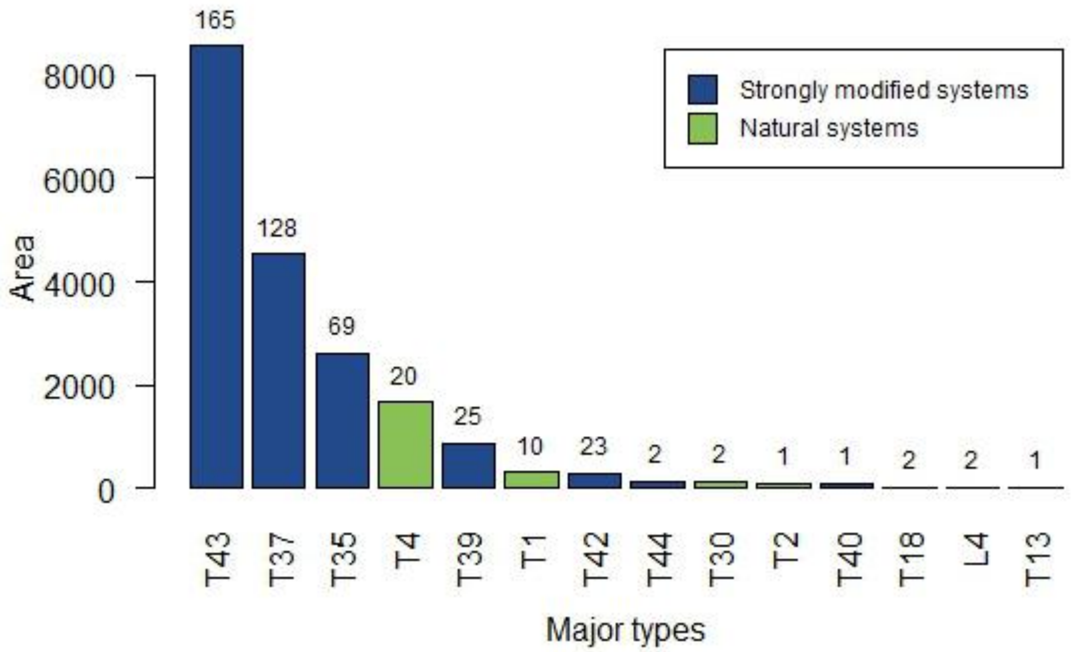


Figure 3.1 Area size (in m^2) of each major type in the data set. The number above each bar is the number of polygons for the major type (before outlier removal). Nature type code abbreviations are in accordance with Table 3.2. This is not an area-representative estimate for the study area.

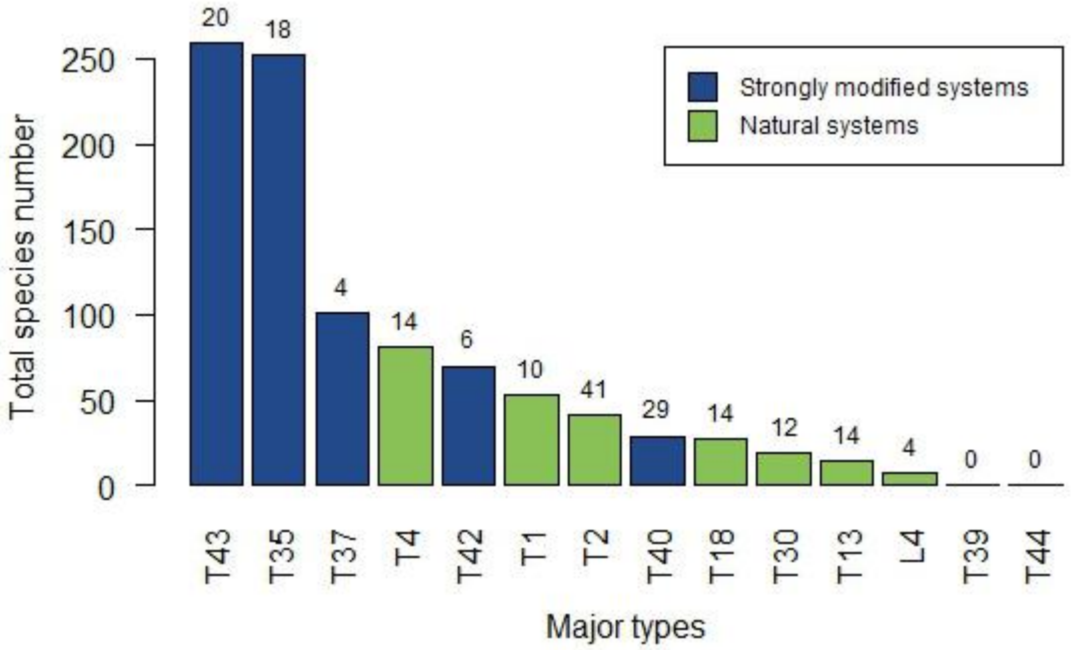


Figure 3.2 The bars show the total number of unique species recorded in each major type. The number above each bar is the mean species number for the major type. Nature type code abbreviations are in accordance with Table 3.1. This is not an area-representative estimate for the study area.

Table 3.1 Overview of nature type and species observations.

Type code	Nature type	Total Area (m^2)	Mean polygon area (m^2)	Number of polygons	Total number of species	Mean number of species
L4	*Helophyte-dominated freshwater swamp*	30.3	15.1	2	7	3.5
T1	*Bare rock*	306.7	30.7	10	53	10.5
T2	*Open shallow-soiled ground*	100.0	100.0	1	41	41
T4	*Forest*	1670.9	83.5	20	81	14.3
T13	*Open scree*	19.8	19.9	1	14	14
T18	*Open alluvial system*	31.9	15.9	2	27	13.5
T30	*Alluvial forest*	127.6	63.8	2	19	12.5
T35	*Artificial ground on mineral*	2611.6	37.8	69	252	17.8
T35-1	*Artificial or highly modified soil-covered ground*	-	46.9	-	-	26.6
T35-2	*Artificial or highly modified gravel-covered ground*	-	21.4	-	-	5.8
T37	*Waste deposit, spoil heap, plastic and other synthetic soft*	4530.5	35.4	128	101	3.7
T39	*Extraction site, quarries, buildings and other synthetic*	874.2	35.0	25	0	0
T40	*Artificial land cultivated as semi-natural grassland*	90.8	90.8	1	29	29
T42	*Flowerbeds and other regularly cultivated, planted area with bare soil*	304.6	13.2	23	70	5.8
T43	*Road verge, embankment, lawn, park and similar artificial land*	8566.9	51.9	165	259	20.3
T44	*Arable field*	147.0	73.5	2	0	0

3.2 Environmental variables

Pairwise comparison of continuous environmental variables revealed some moderate correlations (Table 3.2). N and R were found to have a moderately strong positive correlation ($\tau = 0.49$), whereas the following pairs of variables had weak correlations with coefficients ranging between 0.2 and 0.3: Slope and Surface Temperature, Elevation and F, and L and F. Otherwise there were very weak to no correlation between the remaining variables. The Kruskal Wallis test showed that both Limestone and Substrate was related to Elevation, Slope, SurfaceTemp and N, and that in addition, Substrate was also related to L and R (Table 3.3).

Table 3.2 Correlation matrix with pairwise comparison of continuous variables. The lower triangle displays Kendall's τ; the upper diagonal displays corresponding p-values. p-values < 0.05 in bold. Abbreviations of environmental variable names are in accordance with Table 2.4.

	Aspect	Elevation	Slope	SurfaceTemp	TPI	TWI	L	F	R	N
Aspect		0.3391	0.8516	0.4396	0.6816	0.0426	0.0842	0.5648	0.1397	**0.0004**
Elevation	–0.0309		0.2142	0.6021	**0.0028**	0.3134	**<0.0001**	**<0.0001**	**0.0010**	0.1063
Slope	–0.0061	0.0402		**<0.0001**	0.8276	0.3739	**<0.0001**	0.9322	**0.0250**	0.0967
SurfaceTemp	0.0250	0.0169	**–0.2629**		**0.0037**	**0.0159**	**<0.0001**	0.8268	**<0.0001**	**0.0032**
TPI	–0.0133	**0.0969**	–0.0070	**0.0939**		**0.0002**	0.5153	0.0845	0.1294	0.1033
TWI	0.0663	0.0330	–0.0290	**0.0788**	**–0.1217**		0.2940	0.2665	0.3994	0.1220
L	0.0635	**–0.1556**	**–0.1642**	**0.1520**	–0.0239	0.0390		**<0.0001**	**0.0025**	0.5761
F	–0.0211	**0.2215**	–0.0031	–0.0080	–0.0633	0.0412	**–0.2536**		0.4143	**<0.0001**
R	0.0565	**–0.1265**	**–0.0858**	**0.1635**	–0.0581	–0.0326	**0.1163**	0.0313		**<0.0001**
N	**0.1286**	–0.0591	–0.0607	**0.1078**	–0.0596	–0.0571	0.0206	0.1704	**0.4977**	

Table 3.3 Kruskal-Wallis test, comparing pairs of continuous variables and factor variables. p-values < 0.05 in bold. Abbreviations of environmental variable names are in accordance with Table 2.4.

	Aspect		Elevation		Slope		SurfaceTem		TPI		TWI		L		F		R		N	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Limestone	0.0	0.895	7.6	**0.0060**	53.0	**<0.0001**	28.8	**<0.0001**	1.8	0.1820	1.7	0.1957	0.6	0.4539	0.0	0.8614	2.7	0.0975	11.2	**0.0008**
Substrate	18.5	0.0003	82.6	**<0.0001**	78.0	**<0.0001**	71.0	**<0.0001**	0.9	0.8217	5.3	0.1516	18.3	**0.0004**	15.9	0.0012	55.3	**<0.0001**	71.4	**<0.0001**

3.3 Ordinations

Some corresponding ordination axes were identified with Kendall's rank correlation coefficient τ between axes of DCA and GNMDS ordinations (Table 3.4). In all six subsets, GNMDS axes corresponded to at least one DCA axis; however the ranking of axes differed. Regarding the full data set, GNMDS1 and DCA2 were negatively correlated (τ = –0.43), while GNMDS1 and GNMDS2 obtained a near equal negative correlation coefficient with DCA1 (τ = –0.38). In the ordination of SMT, the first axes of each method were most strongly correlated with the subsequent axes of the other method, so that DCA axis 1 correlated with GNMDS axis 2, and DCA axis 2 correlated with GNMDS axis 1. For subset T35, DCA1 and GNMDS1 had a moderately strong correlation (τ = 0.53), while the other axis pairs were only weakly correlated. In the T37 ordination, GNMDS2 were moderately strongly correlated with both DCA1 and DCA2 (τ = 0.53 and –0.49, respectively), while GNMDS1 were not correlated and as such not confirmed by either DCA axes. For subset T43, the first and second axes of the two methods corresponded, with moderately strong correlations (τ = 0.49 and 0.51, respectively).

Table 3.4 Pairwise correlation coefficients (Kendall's τ) between axes obtained by the two different methods for all subsets. p-values < 0.05 in bold, τ > 0.4 in bold.

	DCA1		**DCA2**	
	τ	p	τ	P
Full				
GNMDS1	–0.381	**<0.0001**	**–0.430**	**<0.0001**
GNMDS2	–0.382	**<0.0001**	0.053	0.1113
SMT				
GNMDS1	–0.258	**<0.0001**	**0.573**	**<0.0001**
GNMDS2	**0.483**	**<0.0001**	0.133	**0.0006**
T35				
GNMDS1	**0.531**	**<0.0001**	0.166	0.0608
GNMDS2	0.287	**0.0012**	–0.225	**0.0111**
T37				
GNMDS1	0.033	0.685	–0.092	0.2603
GNMDS2	**0.530**	**<0.0001**	**–0.492**	**<0.0001**
T43				
GNMDS1	**0.487**	**<0.0001**	–0.291	**<0.0001**
GNMDS2	0.038	0.4850	**0.511**	**<0.0001**
T4				
GNMDS1	**0.906**	**<0.0001**	–0.205	0.2378
GNMDS2	–0.146	0.4063	**0.731**	**<0.0001**

Table 3.5 Gradient lengths of axes for all subsets, estimated in S.D. units for DCA, and in half-change units for GNMDS.

	Full	SMT	T35	T37	T43	T4
DCA1	5.6673	5.1512	4.8421	7.1813	3.4325	3.4229
DCA2	5.3775	4.9700	3.7539	4.3850	2.9784	2.5793
GNMDS1	5.1619	3.7944	3.1589	3.8580	2.3359	2.6871
GNMDS2	5.9821	4.4733	2.5716	3.8853	2.1948	1.6015

Table 3.6 Eigenvalues for all DCA axes.

	Full	SMT	T35	T37	T43	T4
DCA1	0.6395	0.3962	0.4760	0.5511	0.2344	0.5183
DCA2	0.3731	0.2889	0.3408	0.4647	0.2494	0.2786

The correlations between axes in the full data set and all the subsets of strongly modified types were at most moderately strong, with correlation coefficients ranging between 0.4 - 0.6. However, the correlations between axes for subset T4 were very strong between the first axes ($\tau > 0.9$), and strong between subsequent axes ($\tau > 0.7$).

The gradient lengths of all ordinations are presented in Table 3.5. The first axes were longer than the subsequent axes in all cases except the GNMDS for the full data set (GNMDS1: 5.1619 < GNMDS2: 5.9821), subset SMT (GNMDS1: 3.7944 < GNMDS2: 4.4733), and subset T37 (GNMDS1: 3.8580 < GNMDS2: 3.8853).

Regarding the full data set, the DCA ordination showed a pronounced tongue-distortion, where the plots were compressed along the second axis towards the left end of the first axis, and spread out towards the right end (Figure 3.3). The GNMDS showed two distinct clusters: T37-2 (inorganic soft synthetic substrate) and T43 (lawns and parks), which were separated along the first axis. T42 (flowerbeds), T35-1(soil-covered ground), and T1 (bare rock) to some extent overlapped with T37. T35-2 (soil-covered ground) overlapped to some extent with T43 but was more spread out and gained more extreme plot score along axis 2. T4 (forest), T30 (alluvial forest), T2 (open shallow-soiled ground), and one T18-plot (open alluvial system) formed a somewhat isolated group that obtained the more extreme negative values along GNMDS axis 2, with the exception of one outlying T4-plot which obtained the highest positive plot score along GNMDS2.

In the DCA ordination of the subset of strongly modified types (SMT), T43 and T37 were separated along DCA axis 2. The GNMDS of the SMT subset separated nature types along GNMDS axis 1, where T43 and T35-2 mainly obtained negative plot scores and T37 and T35-2 mostly obtained positive plot scores. T42 was very spread out in the ordination, but mainly obtained positive plot scores along GNMDS1.

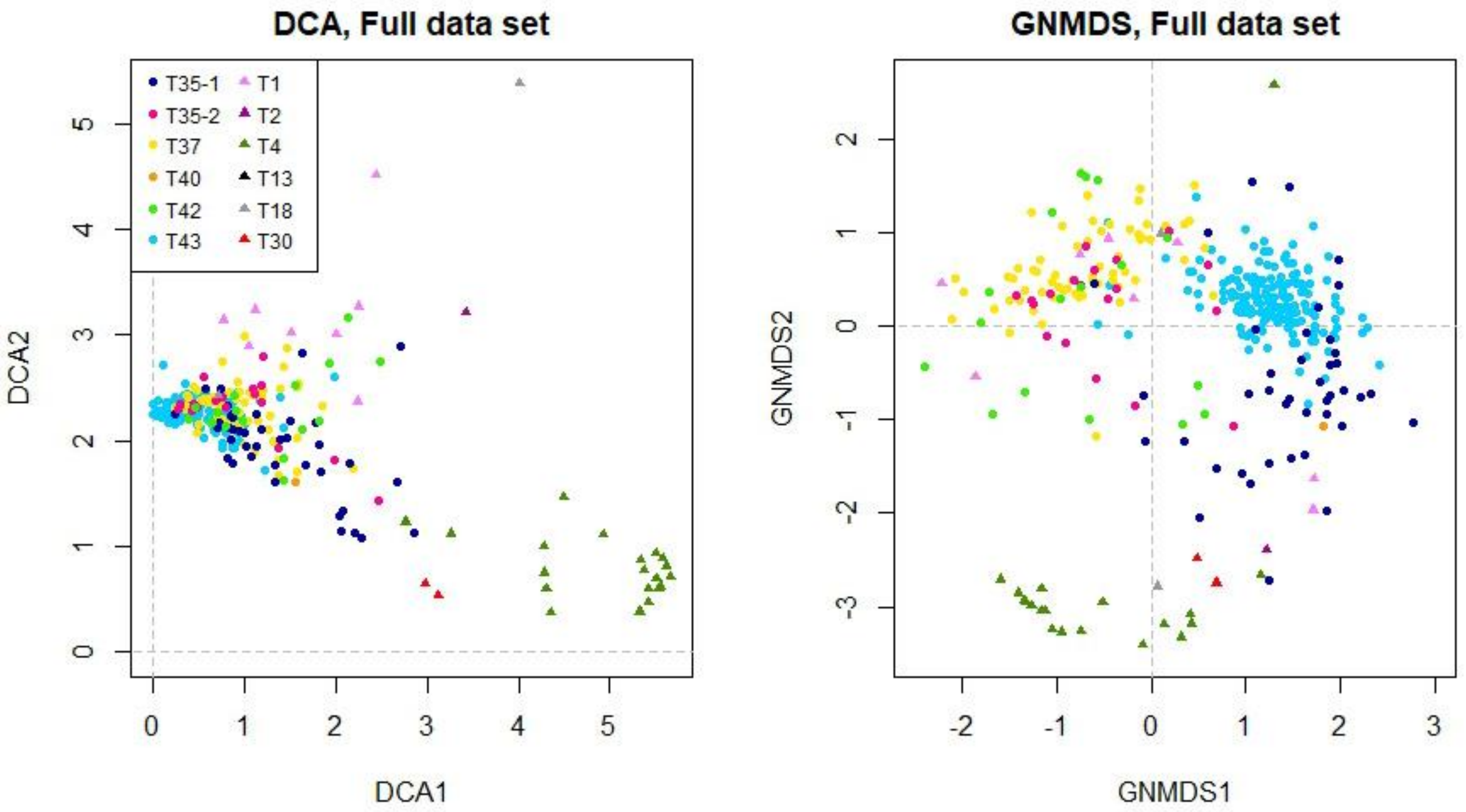


Figure 3.3 DCA and GNMDS ordinations of the full dataset. The strongly modified systems are represented by circles and natural systems by triangles. Each colour represents one nature type, as shown in the legend. Nature type code abbreviations are in accordance with Table 3.1. Both axes in each ordination are on the same scale, illustrating gradient lengths.

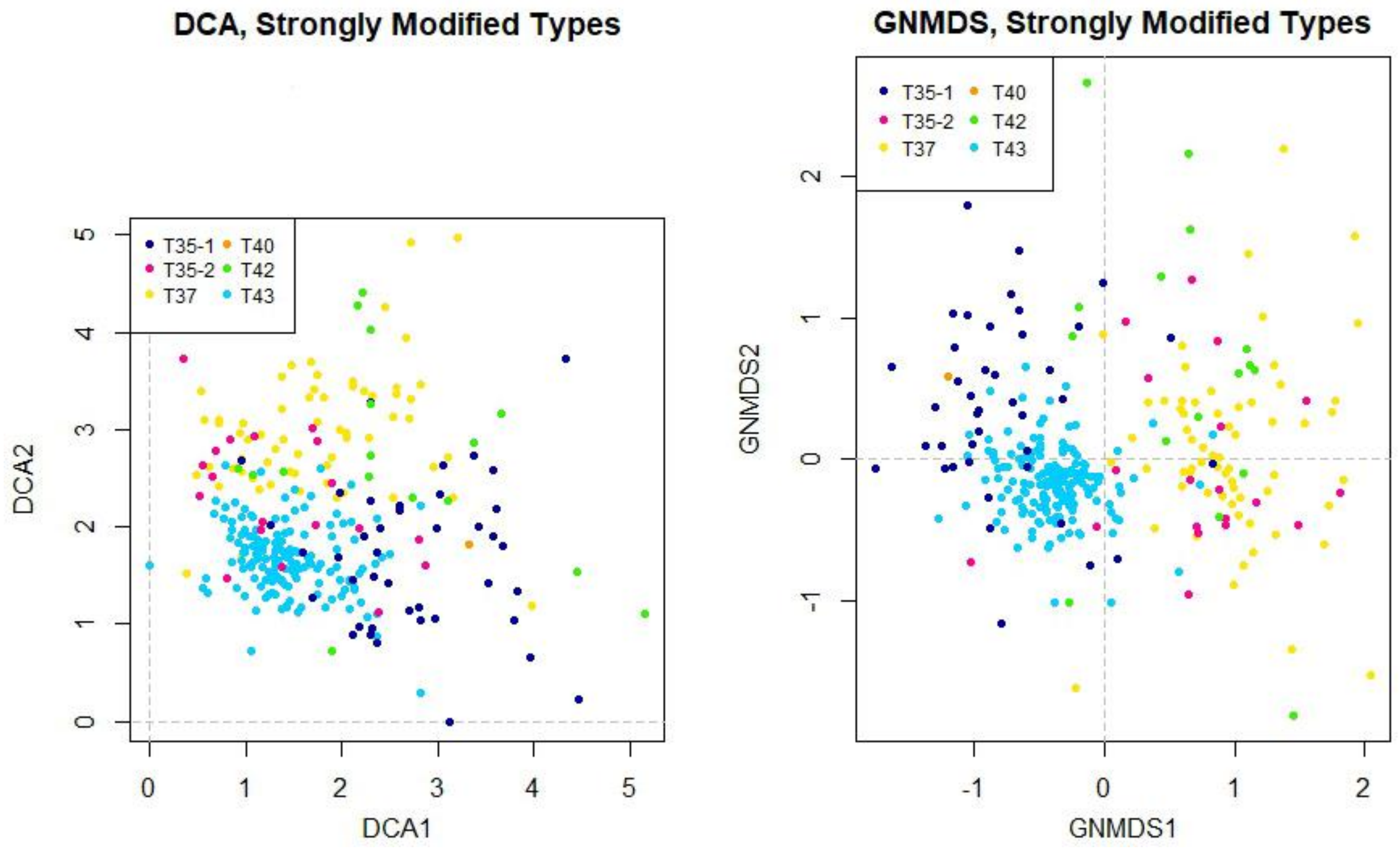


Figure 3.4 DCA and GNMDS ordinations of the SMT subset, including all strongly modified types in the data. Each colour represents one nature type, as shown in the legend. Nature type code abbreviations are in accordance with Table 3.1. Both axes in each ordination are on the same scale, illustrating gradient lengths.

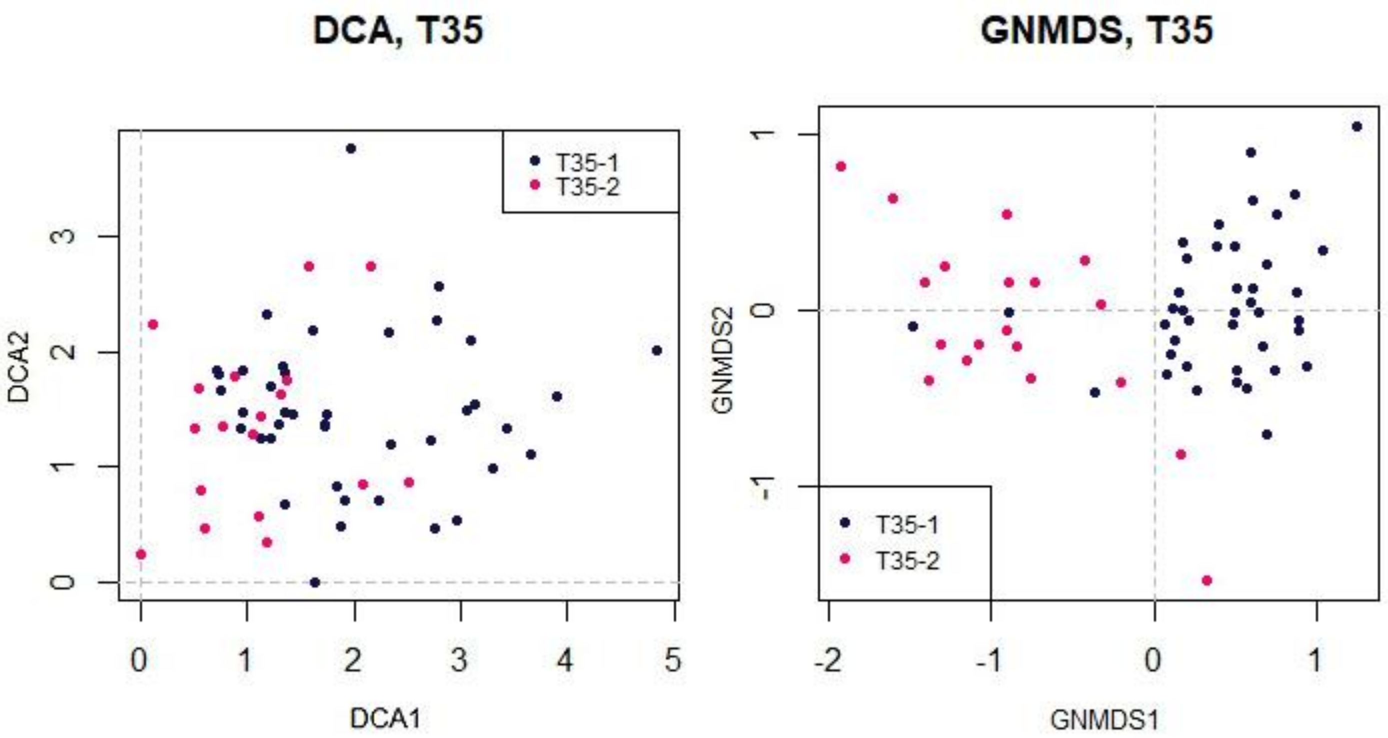


Figure 3.5 DCA and GNMDS ordinations of the T35 subset. Each colour represents a T35 minor type, as shown in the legend. Both axes in each ordination are on the same scale, illustrating gradient lengths.

For the ordinations of the T35 subset, the DCA showed an overlap of minor types T35-1 (soil-covered ground) and T35-2 (gravel-covered ground), but the group of T35-2 mostly occurred towards the left in the ordination (Figure 3.5). The GNMDS ordination separated plots from the two basic types along the first axis: with five exceptions, T35–1 plots obtained negative scores and T35–2 plots obtained positive scores. The cluster of T35–1-plots was more spread out along GNMDS axis 1 than plots from T35–2. GNMDS axis 2 mainly separated one outlying T35–2-plot from the rest of the plots.

In the ordinations of subset T37, a double-sided tongue-effect appeared in the DCA (Figure 3.6). In the GNMDS, the plots were clustered together at the centre, scattering towards the periphery.

The DCA ordination of subset T43 showed a homogenous core group of plots (Figure 3.6). DCA1 separated one outlying plot (plot 301, which was the most species rich plot in the dataset with 58 unique species. See Appendix 2 for ordinations with plot numbers). In the GNMDS, the main assembly of plots was clustered at the centre of the ordination, becoming less dense toward the periphery.

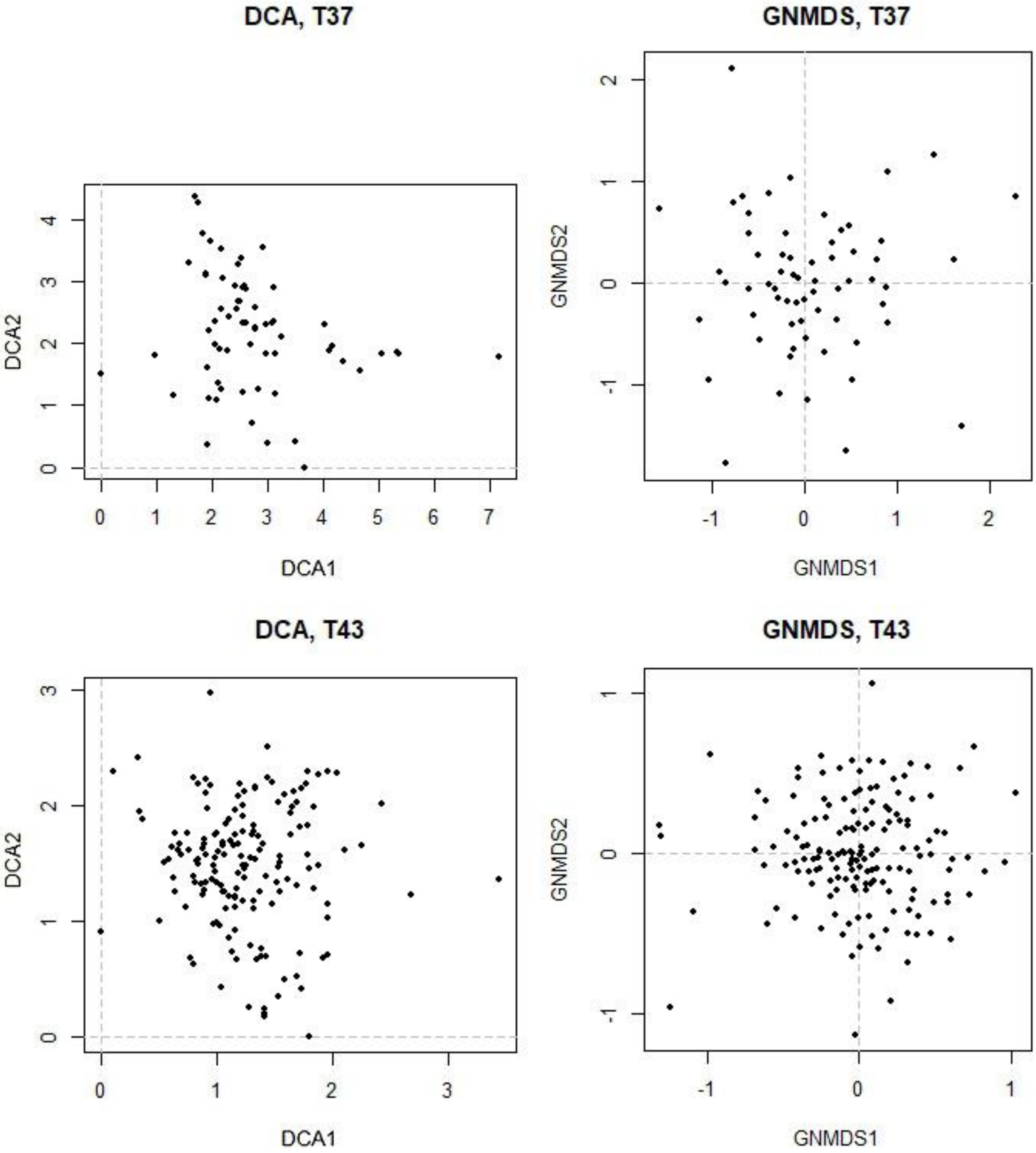


Figure 3.6 DCA and GNMDS ordinations of the T37 subset (upper) and the T43 subset (lower). T37 is only represented by minor type T37-2, while T43 is not partitioned into minor types. Both axes in each ordination are on the same scale, illustrating gradient lengths.

Both ordinations of the T4 subset captured the same overall structure (Figure 3.7). The ordinations separated lime-poor polygons (KA segment 1) and polygons that were to some degree lime-rich (KA segments 2 and 3) along the first axes. The second axes do not clearly separate the UF segments, except to some degree the polygons that are lime-poor (KA segment 1).

Due to a tongue effect appearing in some DCA ordinations, GNMDS generally performed better and thus emphasis was put on GNMDS for environmental interpretation.

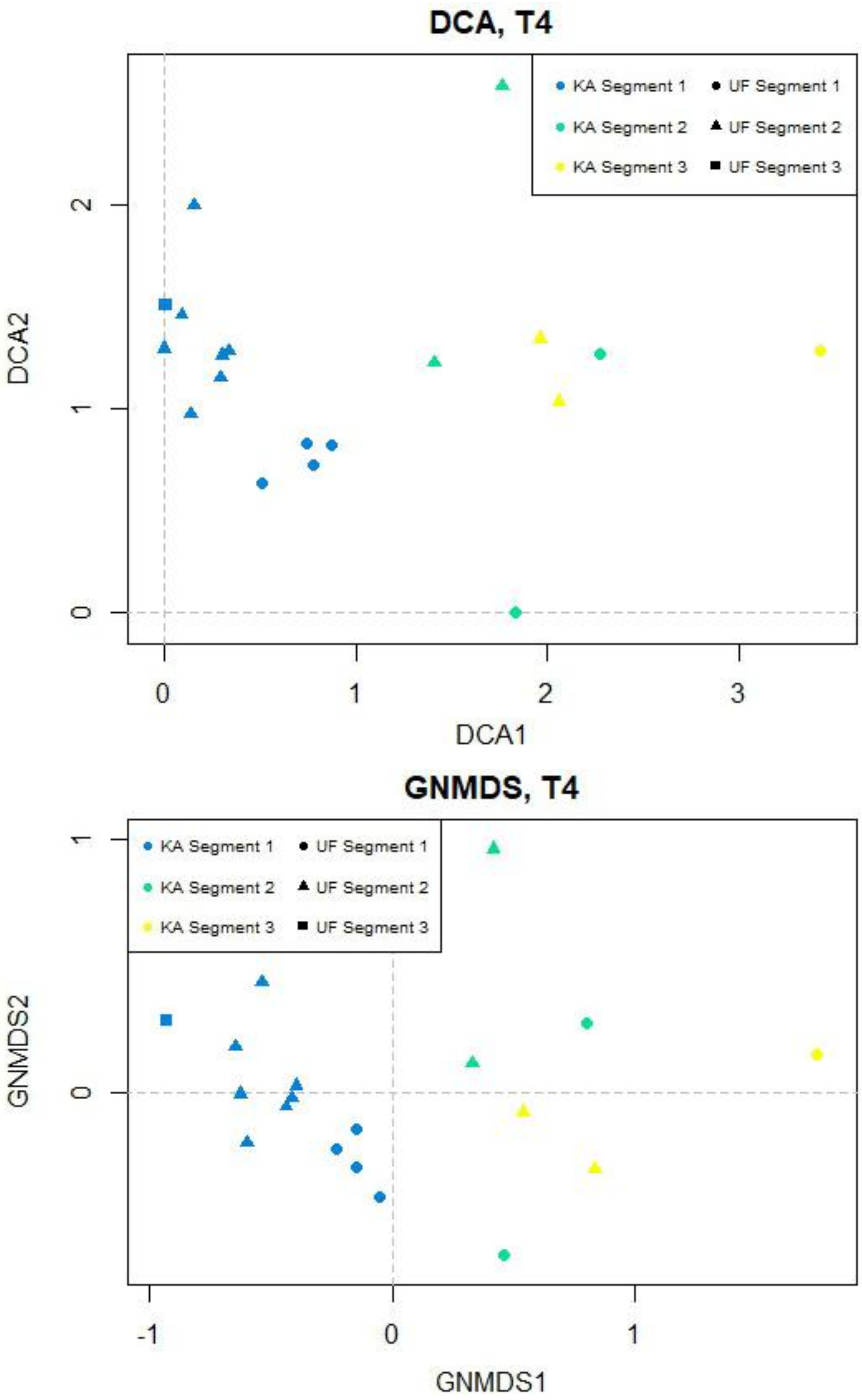


Figure 3.7 DCA and GNMDS ordinations of the T4 subset. Each colour represents a segment along the LCE lime richness (KA), and each symbol represents a segment along the LCE risk of severe drought (UF), as shown in the legend. Both axes in each ordination are on the same scale, illustrating gradient lengths.

3.4 Environmental interpretation

Correlation coefficients between environmental variables and GNMDS axes are presented in Table 3.7, and results of the Kruskal-Wallis test of the relationship between GNMDS axes and factor variables are shown in Table 3.8 (Tables for the DCA ordinations can be found in Appendix 2).

3.4.1 Full data set

Regarding the full data set, GNMDS1 was weakly positively correlated with F ($\tau = 0.22$), and GNMDS2 was positively correlated with L ($\tau = 0.35$), as well as related to the factor variable Substrate (Table 3.8). Otherwise there were only very weak to no correlations between environmental variables and ordinations axes.

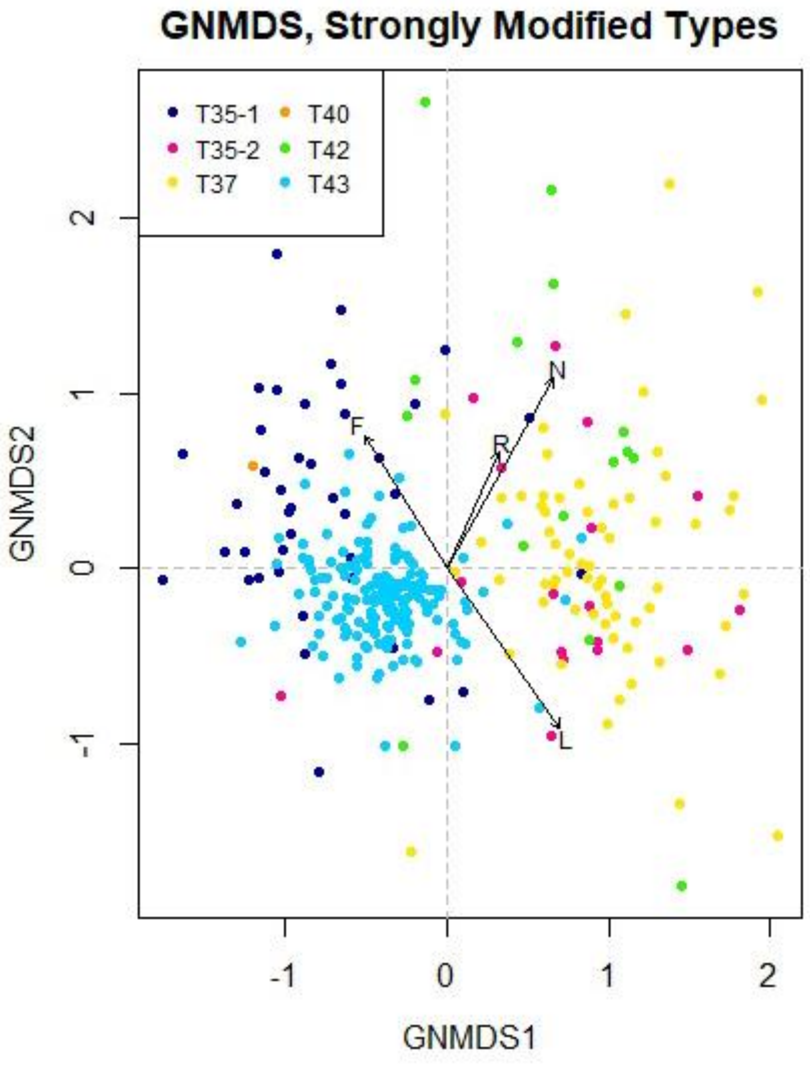


Figure 3.8 Biplot of plot positions for the GNMDS ordination of the SMT subset and explanatory variable vectors. The vectors point in the direction of maximum increase of each environmental variable. Only a selection of the most important variables is included ($\tau > 0.2$).

Table 3.7 Correlation coefficients (Kendall's τ) between environmental variables and plots scores along GNMDS axes of all subsets. p-values < 0.05 in bold, τ > 0.3 in bold.

	Aspect		**Elevation**		**Slope**		**SurfaceTemp**		**TPI**		**TWI**		**L**		**F**		**R**		**N**	
	τ	p	τ	p	τ	p	τ	p	τ	p	τ	p	τ	p	τ	p	τ	p	τ	p
Full																				
GNMDS1	0.0226	0.4882	0.0341	0.2957	0.0346	0.2893	0.0191	0.5586	–0.0222	0.4964	0.0062	0.8514	–0.1837	**<0.0001**	0.2216	**<0.0001**	–0.0354	0.3537	–0.1611	**<0.0001**
GNMDS2	0.1147	**0.0004**	–0.1774	**<0.0001**	–0.1597	**<0.0001**	0.1339	**<0.0001**	0.0892	**0.0062**	–0.0484	0.1419	**0.3495**	**<0.0001**	–0.1341	**0.0002**	0.1672	**<0.0001**	0.1856	**<0.0001**
SMT																				
GNMDS1	0.0463	0.2288	–0.1573	**<0.0001**	–0.0829	**0.0311**	0.0350	0.3639	0.0265	0.4913	–0.0562	0.1479	**0.3160**	**<0.0001**	–0.2387	**<0.0001**	0.1412	**0.0005**	0.2995	**<0.0001**
GNMDS2	–0.0313	0.4159	0.0547	0.1558	0.1268	**0.0010**	0.0416	0.2797	–0.0454	0.2378	0.0128	0.7421	–0.2776	**<0.0001**	0.2045	**<0.0001**	0.2618	**<0.0001**	**0.3249**	**<0.0001**
T35																				
GNMDS1	–0.0703	0.4289	0.1611	0.0700	0.2167	**0.0148**	–0.0250	0.7789	–0.0125	0.8884	0.0577	0.5190	**–0.5865**	**<0.0001**	0.2935	**0.0010**	–0.0504	0.5858	–0.0679	0.4440
GNMDS2	0.0284	0.7497	–0.1010	0.2561	–0.0318	0.7209	0.0976	0.2725	0.0136	0.8783	0.0371	0.6782	–0.2053	**0.0209**	0.0598	0.5025	0.2588	**0.0052**	**0.4290**	**<0.0001**
T37																				
GNMDS1	–0.0765	0.3508	0.0158	0.8472	–0.0805	0.3253	0.1684	**0.0400**	0.0968	0.2374	–0.0147	0.8590	–0.2375	**0.0053**	0.2345	**0.0054**	–0.0430	0.6679	0.0373	0.6542
GNMDS2	0.0179	0.8274	0.0012	0.9879	0.0029	0.9717	–0.0274	0.7379	–0.0598	0.4653	–0.0862	0.2958	–0.0563	0.5077	0.0302	0.7206	**0.4084**	**<0.0001**	**0.4198**	**<0.0001**
T43																				
GNMDS1	–0.0795	0.1401	0.1539	**0.0043**	–0.0675	0.2105	0.1542	0.0043	0.0467	0.3861	–0.0645	0.2359	–0.2582	**<0.0001**	0.1262	**0.0193**	0.1552	**0.0040**	–0.1319	**0.0144**
GNMDS2	–0.0252	0.6401	0.1255	**0.0200**	0.0819	0.1287	0.0029	0.9564	–0.0302	0.5754	0.0500	0.3587	–0.1668	**0.0020**	0.2142	**<0.0001**	0.0802	0.1368	0.1664	**0.0020**
T4																				
GNMDS1	–0.0117	0.9442	–0.2111	0.2076	0.07038	0.6744	–0.0352	0.8336	**–0.4765**	**0.0046**	0.2163	0.2050	**–0.5439**	**0.0008**	0.2229	0.1834	**0.8563**	**<0.0001**	**0.8246**	**<0.0001**
GNMDS2	0.0235	0.8886	**–0.4575**	**0.0063**	–0.0117	0.9442	**0.4223**	**0.0117**	0.1359	0.4204	0.2283	0.1809	**0.5088**	**0.0019**	–0.0235	0.8886	–0.1056	0.5286	–0.1813	0.2983

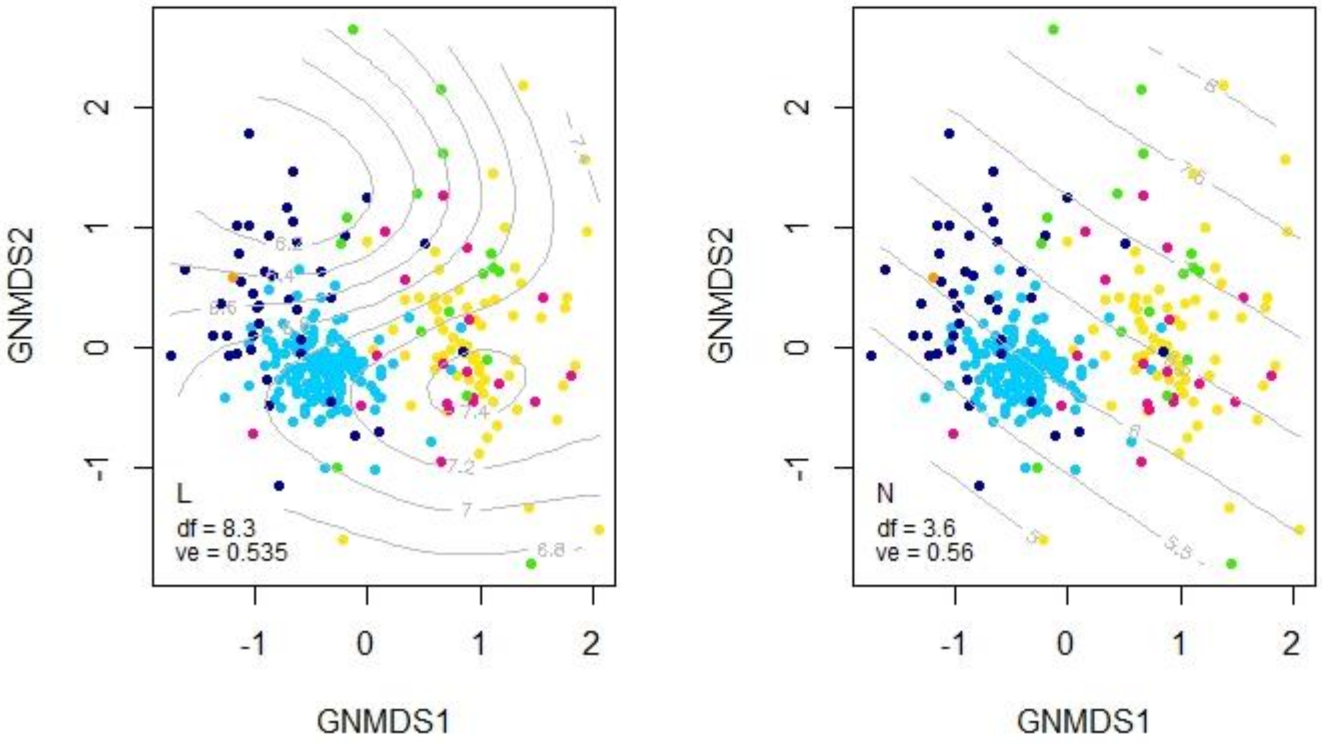


Figure 3.9 Isoline diagrams fitted to the GNMDS ordination of the SMT subset, df = degrees of freedom, ve = fraction of variation explained. Left: isoline for L, higher values indicate preference for open sites. Right: Isoline of N, higher values indicate preference for nitrogen-rich sites.

Table 3.8 Kruskal-Wallis test of the relationship between GNMDS axes of all subsets and factor variables (Limestone: degree of freedom = 1, Substrate: degrees of freedom = 3). p-values < 0.05 in bold

	Full				**SMT**				**T35**			
	GNMDS1		GNMDS2		GNMDS1		GNMDS2		GNMDS1		GNMDS2	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Limestone	0.4	0.5205	0.0	0.8363	0.0	0.9492	0.6	0.4582	1.4	0.2302	1.6	0.2065
Substrate	5.5	0.1374	52.0	**<0.0001**	8.3	**0.0403**	2.5	0.4664	1.1	0.7729	8.2	**0.0413**
Grain size	-	-	-	-	-	-	-	-	29.5	**<0.0001**	0.2	0.6167
	T37				**T43**				**T4**			
	GNMDS1		GNMDS2		GNMDS1		GNMDS2		GNMDS1		GNMDS2	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Limestone	1.1	0.2931	0.0	0.9298	14.3	**0.0002**	0.0	0.8453	0.5	0.4990	1.2	0.2719
Substrate	23	0.3200	0.6	0.7488	5.6	0.1311	10.4	**0.0154**	3.1	0.2112	0.6	0.7582

3.4.2 Strongly modified types

For the SMT subset, GNMDS1 was correlated with L (0.32), F (–0.24), and N (0.29). GNMDS2 was most strongly correlated with N (0.32), as well as correlated with L (–0.28), F (0.20), and R (0.26). Figure 3.8 shows a biplot of the SMT GNMDS plot positions and vectors representing the maximum increase for a selection of important explanatory variables. The vectors for L and F pointed in more or less opposite directions, while R and N pointed "northeast", near-orthogonal to L and F. Isolines for the most important variables, L and N, are shown in Figure 3.9.

3.4.3 T35 – Artificial ground on mineral deposits

For subset T35, GNMDS1 was related with grain size (Table 3.8), and was most strongly correlated with L (τ = –0.59), indicating more open plots to the right in the ordination; and was also weakly correlated with slope (τ = 0.21) and F (τ = 0.29). GNMDS2 was correlated with L (τ = –0.21), R (τ = 0.26) and N (τ = 0.43). These were included as vectors in the T35 GNMDS biplot (Figure 3.10). The vectors for N and R pointed upwards in the biplot, indicating more nitrogen-rich, basic plots were placed towards the upper parts of the ordination. However, as both GNMDS1 and GNMDS2 were correlated with L, biplot vector pointed "southwest". Isolines for the most important variables, L and N, are shown in Figure 3.11. However, N does not show a particularly large range in values in this ordination (5.2 – 6.8).

3.4.4 T37 – Synthetic soft substrate

In the ordination of the T37 subset, GNMDS1 was weakly negatively correlated with L (τ = –0.24), and weakly positively correlated with F (τ = 0.23), however GNMDS1 was not confirmed by any DCA axes. GNMDS2 had a moderately strong positive correlation with R (τ = 0.41) and N (τ = 0.42) (which were themselves correlated). In the T37 biplot (Fig. 3.12), the vectors for N and R pointed upwards, indicating values for nitrogen and basic sites were in the upper parts of the ordination, while the vector for L pointed leftwards, indicating plots that were more open. Isolines for the most important variables, R and N, are shown in Figure 3.13.

3.4.5 T43 – Road verge, embankment, lawn, and park

For the GNMDS ordination of T43, no strong correlations between axes and environmental variables were identified, only weak correlations between GNMDS axis 1 and L (τ = 0.26), and GNMDS2 and F (τ = 0.21). For the factor variables, GNMDS1 was related to Limestone, and GNMDS2 related to Substrate (Table 3.8).

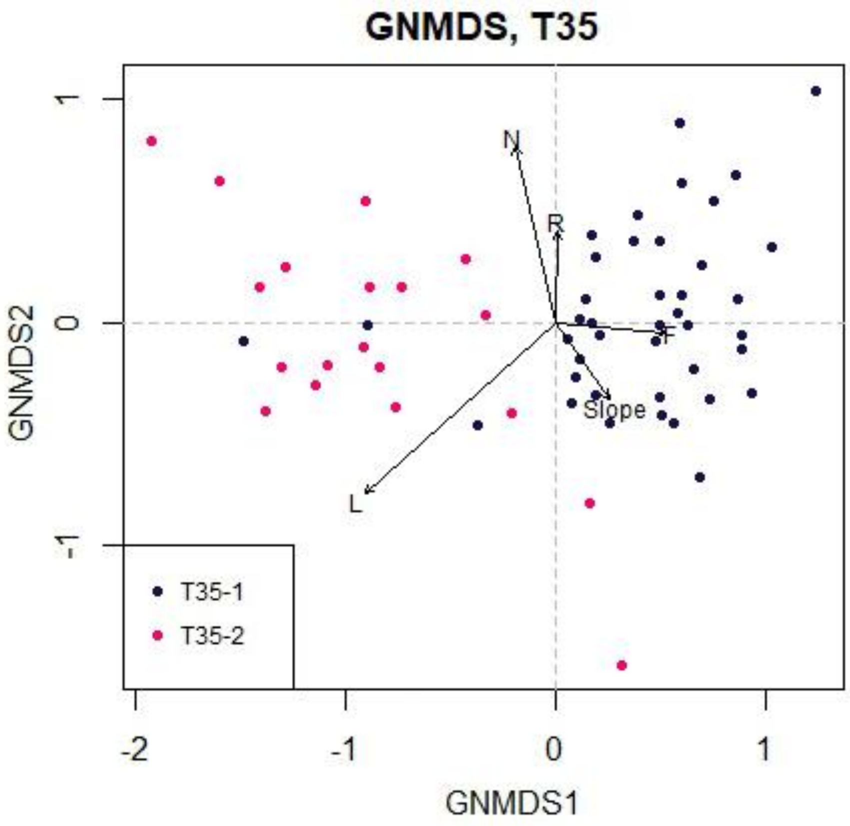


Figure 3.10 Biplot of plot positions for the GNMDS ordination of the T35 subset and explanatory variable vectors. The vectors point in the direction of maximum increase of each environmental variable. Only a selection of the most important variables is included (τ > 0.2).

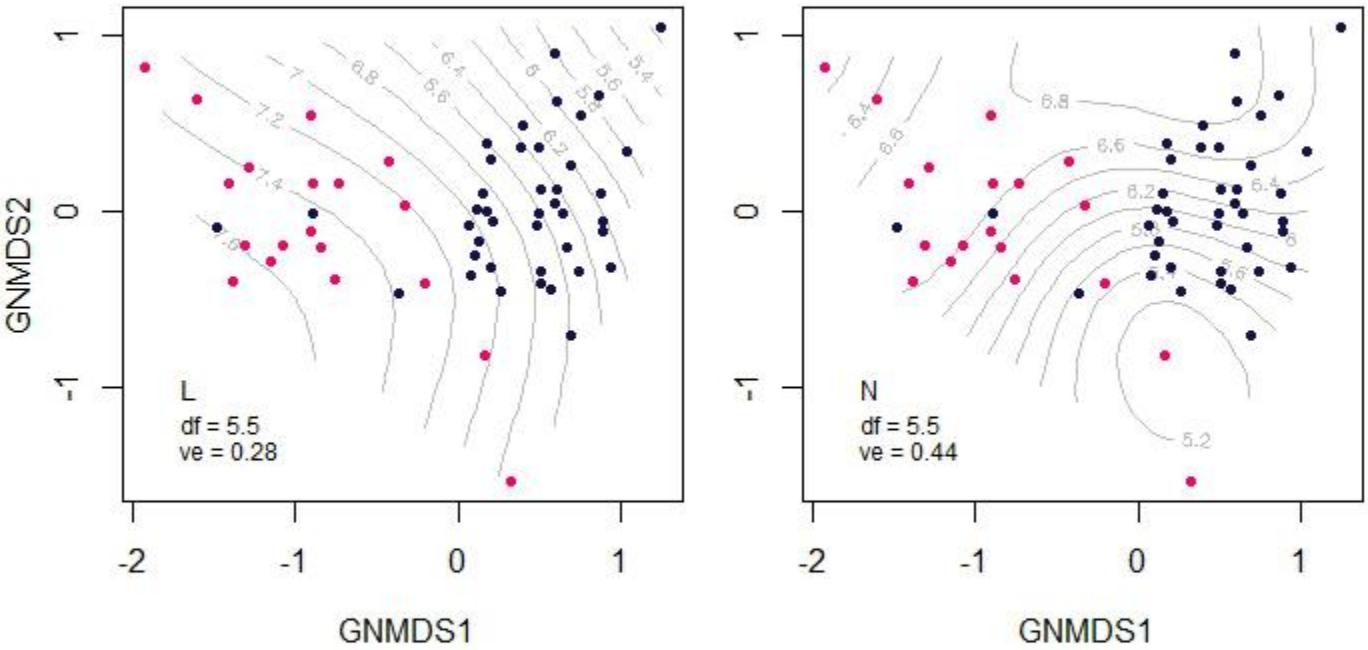


Figure 3.11 Isoline diagrams fitted to the T35 GNMDS, df = degrees of freedom, ve = fraction of variation explained. Left: isoline for L, higher values indicate preference for open sites. Right: isoline values for N, higher values indicate preference for nitrogen-rich sites.

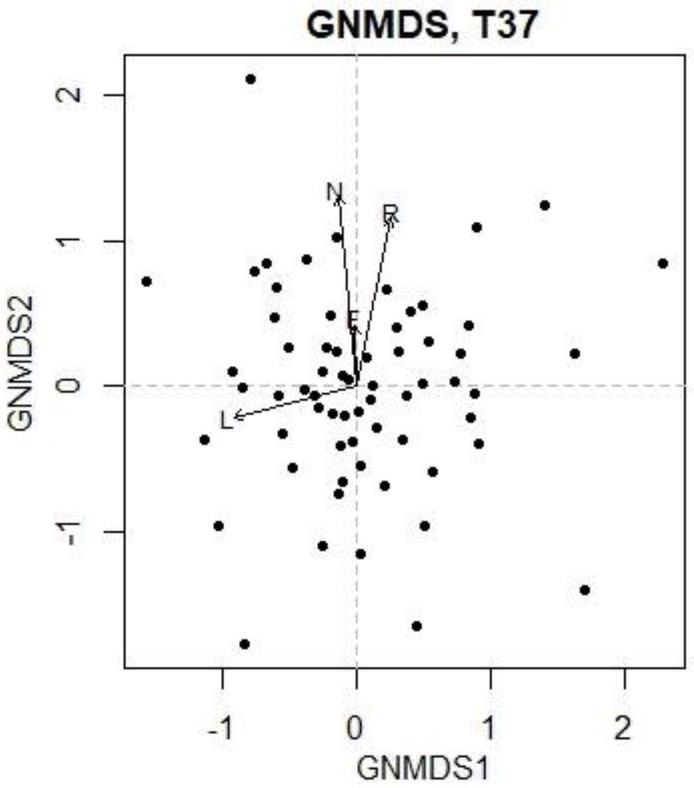


Figure 3.12 Biplot of plot positions for the GNMDS ordination of the T37 subset and explanatory variable vectors. The vectors point in the direction of maximum increase of each environmental variable. Only a selection of the most important variables is included (τ > 0.2).

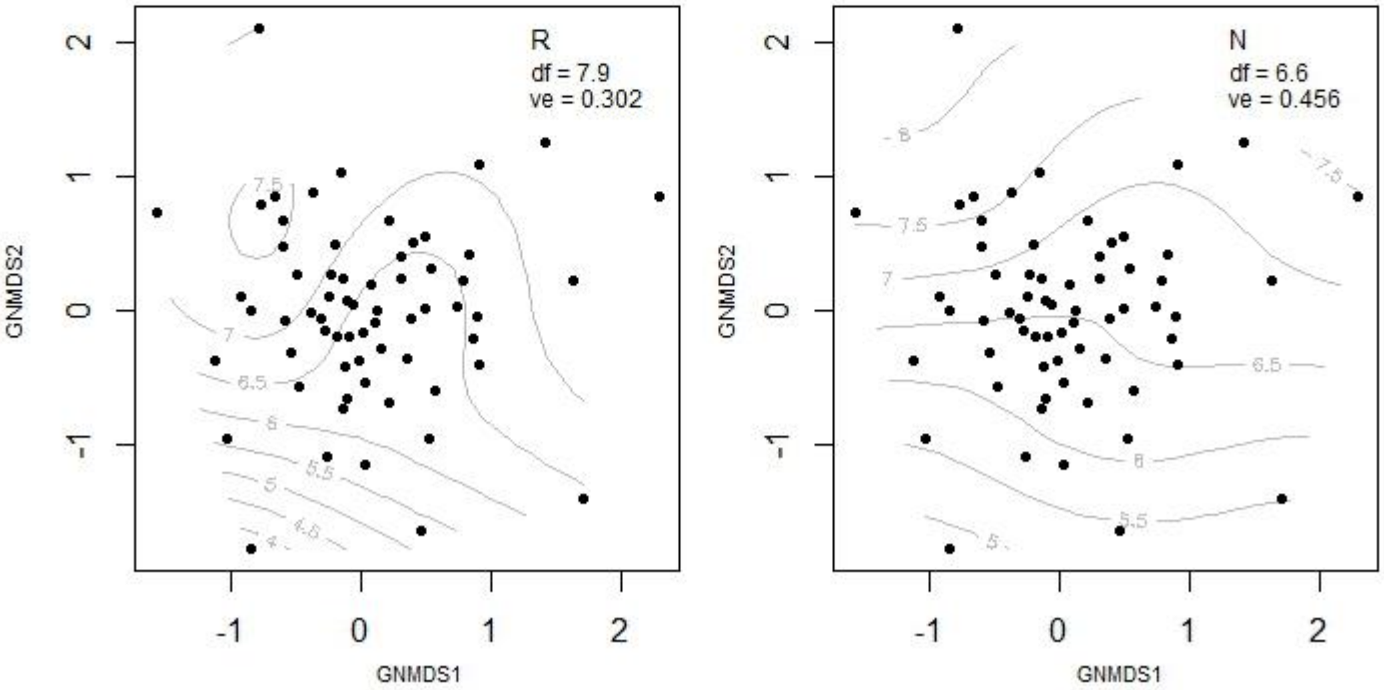


Figure 3.13 Isoline diagrams fitted to the GNMDS ordination of the T37 subset, df = degrees of freedom, ve = fraction of variation explained. Left: Isoline for R. Higher values indicate prefernce for basic sites. Right: Isoline values for N, higher values indicate preference for nitrogen-rich sites.

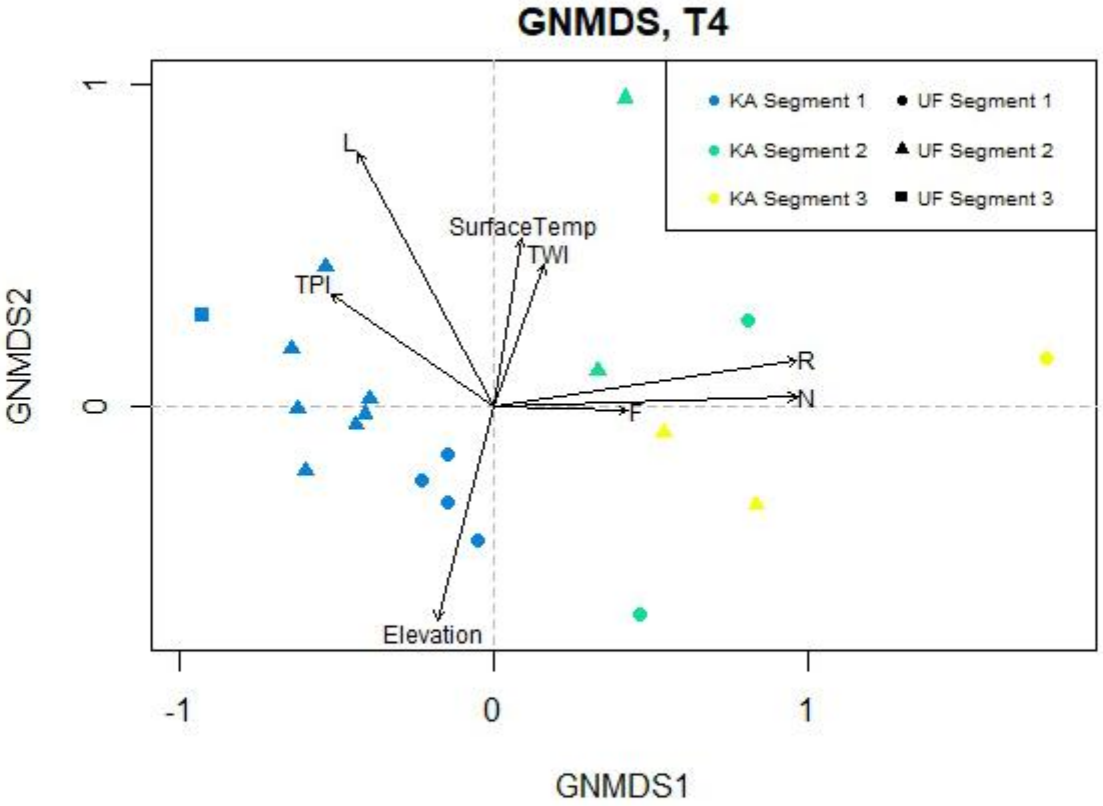


Figure 3.14 Biplot of plot positions for the GNMDS ordination of the T4 subset and explanatory variable vectors. The vectors point in the direction of maximum increase of each environmental variable. Only a selection of the most important variables is included (τ > 0.2).

3.4.6 T4 – Forest

Several environmental variables were correlated with GNMDS axes of subset T4. GNMDS1 had a strong positive correlation with R and N (τ > 0.8 for both variables), and a moderately strong negative correlation with TPI and L (τ = –0.47 and –0.54, respectively). Otherwise there were weak positive correlations with TWI (0.21) and F (0.22), and weak negative correlation with elevation (τ = –0.21). GNMDS2 was negatively correlated with Elevation (τ = –0.46), and positively correlated to SurfaceTemp (τ = 0.42) and L (τ = 0.50). In the T4 biplot, the vectors for R and N (and F) pointed left in the diagram, indicating more basic and nitrogen-rich plots (Figure 3.14). The vector for elevation pointed downward, while SurfaceTemp and TWI pointed upwards in the opposite direction. L and TPI pointed "northwest". Isolines made for 6 of the most important environmental variables are shown in Figure 3.

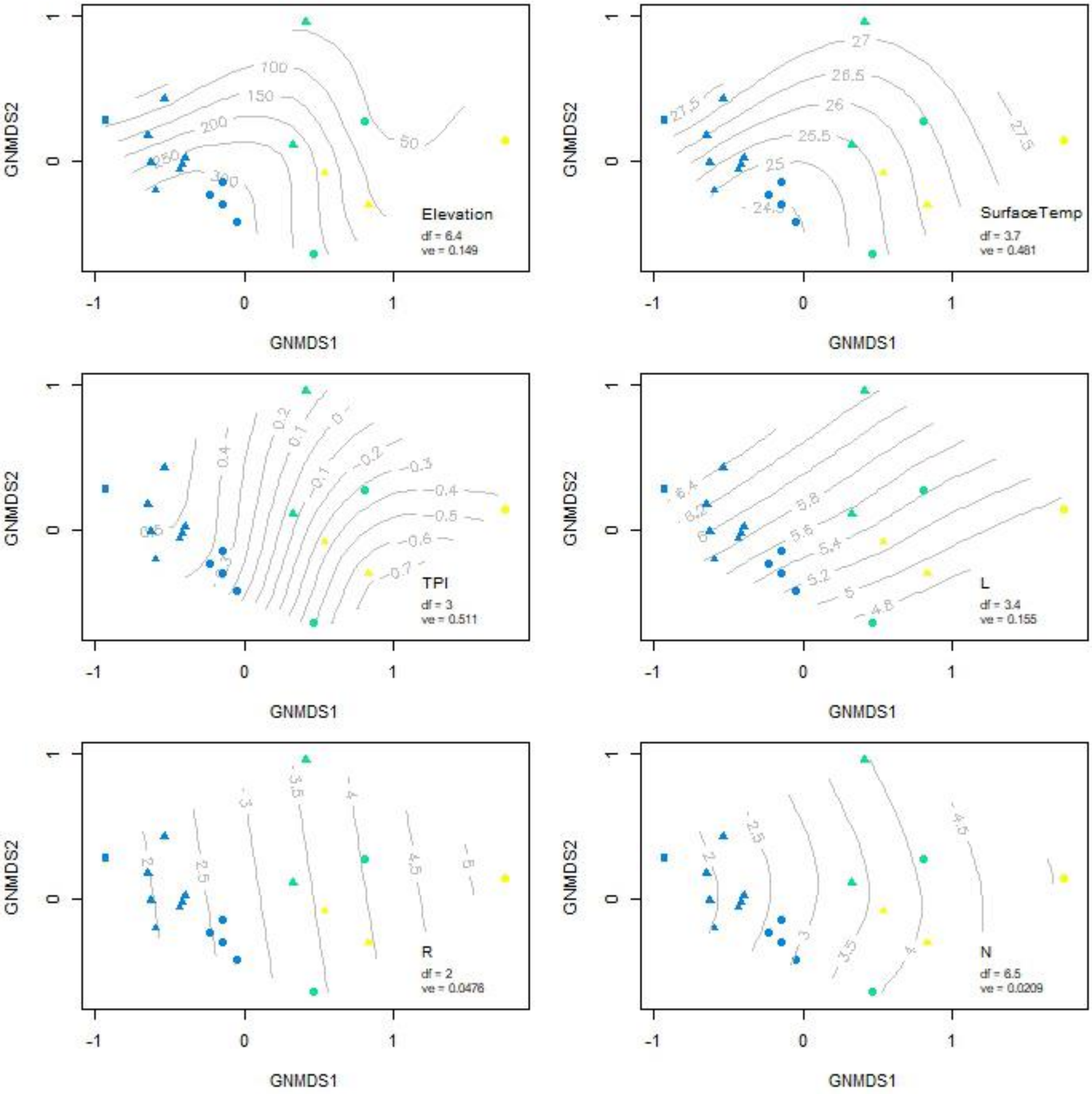


Figure 3.15 Isoline diagrams fitted to the GNMDS ordination of the T4 subset, df = degrees of freedom, ve = fraction of variation explained. Upper left: Isoline for elevation. Upper right: Isoline for surface temperature. Middle left: Isoline for TPI, positive values represent sites that are higher than their surroundings, negative values represent sites that are lower than their surroundings. Middle right: Isoline for L, higher values indicate preference for open sites. Lower left: Isoline for R, higher values indicate preference for basic sites. Lower right: Isoline for N, higher values indicate preference for nitrogen-rich sites.

3.4.7 Species richness

The number of vascular plants in the polygons was positively correlated with GNMDS axis 1 in all subsets, except for the SMT subset which had a negative correlation. The correlation with GNMDS1 was strong for the full data set, T37, and T4 (τ ranging between 0.7 – 0.8), and moderately strong for T35 and T43 (τ = 0.423 and 0.569, respectively). Kendall's rank correlation coefficients for the species number variable and GNMDS axes for all subsets are shown in Table 3.9, and isoline diagrams for the species number variable for all subsets are presented in Figures 3.16 and 3.17.

Table 3.9 Kendall's rank correlation coefficients for the species number variable and GNMDS axes for all subsets.

	Species richness			
	GNMDS1		**GNMDS2**	
	τ	p	τ	p
Full	**0.8013**	**<0.0001**	0.0060	0.8582
SMT	**–0.6828**	**<0.0001**	0.1320	**<0.0001**
T35	**0.4231**	**<0.0001**	–0.0325	0.7160
T37	**0.7152**	**<0.0001**	–0.0300	0.7214
T43	**0.5689**	**<0.0001**	–0.0296	0.5884
T4	**0.7561**	**<0.0001**	–0.0298	0.8606

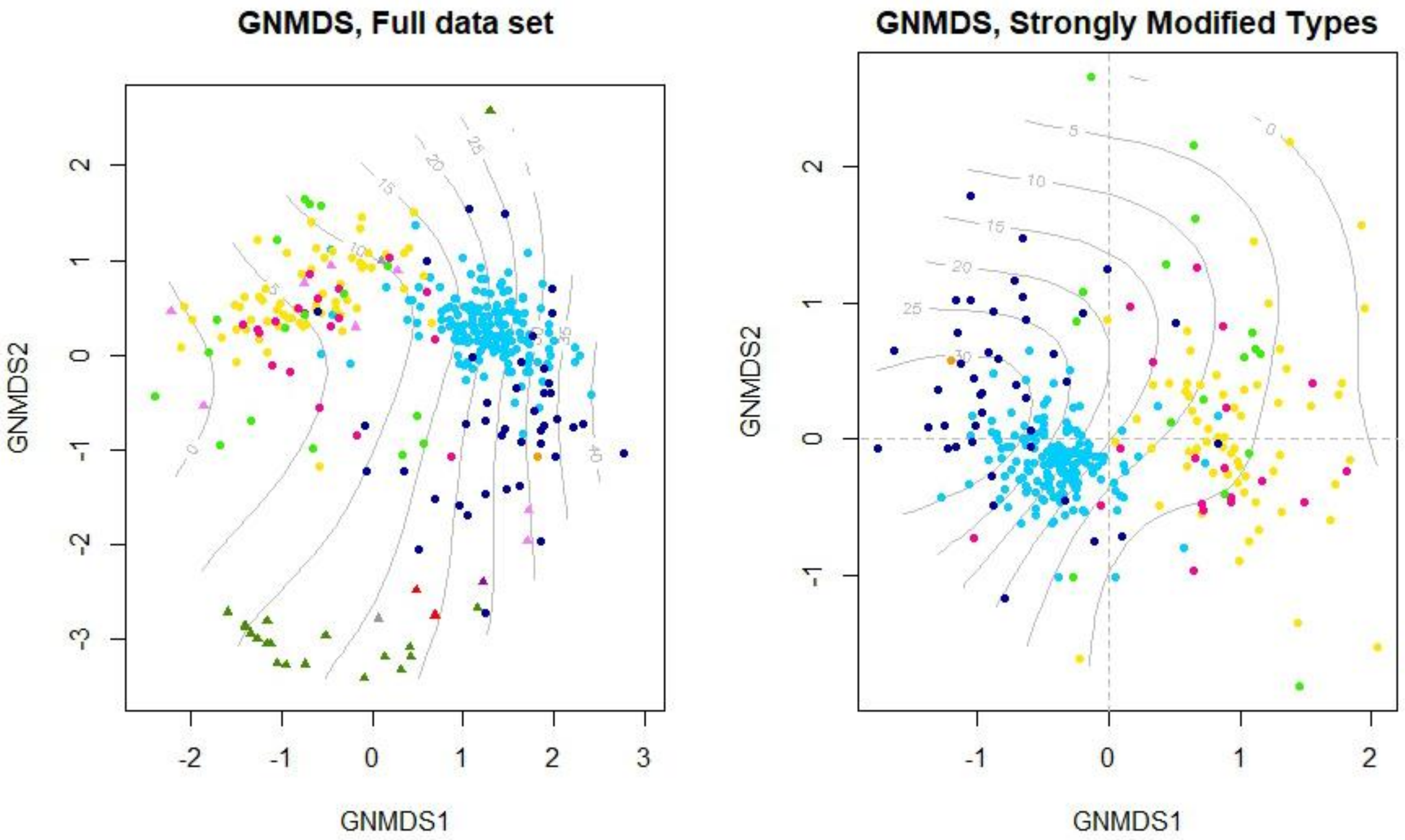
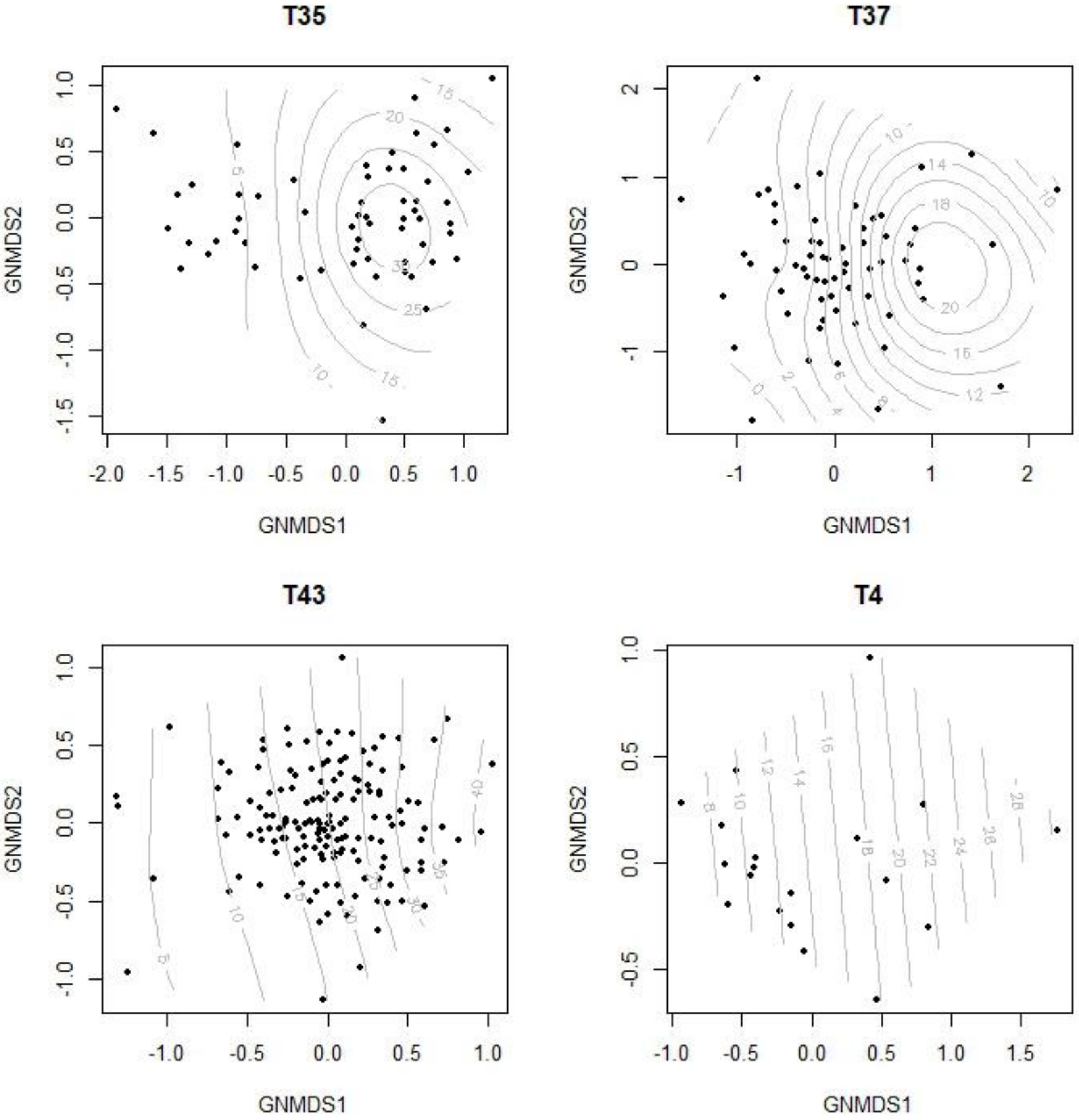


Figure 3.16 Isoline diagrams for the species number variable fitted to the GNMDS ordinations of the full data set and the SMT subset.


T35

T37

T43

T4

Figure 3.17 Isoline diagrams for the species number variable fitted to the GNMDS ordinations of the T35, T37, T43, and T4 subsets.

Discussion

This is one the first studies to investigate the structure of urban ecosystem types by means of coenoclines, gradients in species composition, obtained as corresponding ordination axes. The results showed large consistent difference in species composition between natural and strongly modified systems. In contrast to the natural forest types (T4) there were relatively weak gradient structures and correlations between environmental variables and ordination axes in the strongly modified types. The gradients in species composition in strongly modified types were most clearly related to Ellenberg's Indicator Values, in particular L and N (and R), which were common across several subsets. The main gradient seems to be related to Light (L): the coenocline moves from species with a preference of more open areas (T37, T35-2) to species that prefer to grow in semi-shade (T4), with T35-1 and T43 falling in between. In addition, dominating grain size correlated with this gradient, and appears as strongly related to T35 minor types. The second gradient is related to soil fertility (N and R), in SMT, T35 and T37, which also appeared very strongly in the T4 subset ordination.

These results regarding species composition and environmental gradients have important implications for the partitioning of variation into ecosystem types. In the following, these findings will be discussed in greater detail, expanding on low gradient structure in the strongly modified types and concluding with implications for the NiN system and future research in this area.

4.1 Interpretation of ordinations

4.1.1 Full data set

The full data ordination showed a large consistent difference in species composition between natural and strongly modified systems (Fig. 3.3). Similar results, with coenoclines moving from natural to urban ecosystem types have also been found by Tonteri & Haila (1990) in a study from Helsinki. The coenoclines in the full ordination are not strongly related to any of the included environmental variables, the second gradient is only weakly related to L, which expresses a gradient moving from shaded (forest types) to more open areas (strongly modified types). As several major types are included in the ordination, and major types being characterised by a dominant set of LCEs that should differ from those of other types, set of correlating environmental gradients is not necessarily expected.

4.1.2 Strongly modified types

The overall pattern in ordination of the strongly modified types was similar to the full data ordination (Figure 3.3 and 3.4), with both ordinations showing the same clustering patterns of major types. The ordinations showed that the strongly modified major types (T35-1, T42 and T43) are characterised by distinct species compositions. Furthermore, the ordinations show that the type T37(-2) is distinct from the others by having a different and more species-poor species composition. A similar pattern was found by Godefroid & Koedam (2007), in that species composition to a large degree as explained by a high density of built-up, and was also affected by different anthropogenic substrates. Fig. 3.8 and table 3.6 show that the distinct species compositions of major types only to some degree are related to variation in environmental conditions. L, F, and N were related to both coenoclines, and the second coenocline was also weakly related to R. These results coincides to some degree with the findings of Tonteri & Haila (1990), who identified a gradient of dry and open to moist and shaded sites within urban types studied in Helsinki.

4.1.3 T35 – Artificial ground on mineral deposits

Regarding the major type T35, there was a very clear species compositional gradient explained by dominating grain size (represented by minor types) and environmental factors that are correlated with grain size. This coenocline moved from T35-2 (gravel-covered ground) towards T35-1 (soil-covered ground. Preference for open areas (L) decreased along this coenocline, while preference for moist areas (F) increased towards T35-2. The main coenocline was also associated with variation in species richness; T35-1 had on average 26.6 species, while T35-2 had only 5.8 species on average. The second coenocline was related to N (and R), which indicates soil fertility may be an important factor for this type. These results coincide with a study by Prach *et al*. (2014), who found that substrate was important in early succession (sand, peat, soul, clay), although this may have been largely due to difference in soil nutrients rather than soil texture. Řehounková & Prach (2006) found that the soil texture (expressed as proportion of silt and gravel) influenced the vegetation pattern in early successional stages in a study of abandoned sand-gravel pits. However, in later stages site moisture was the most important structuring process when more stable ecosystems were reached. It is hypothesised in Nin that T35 will develop towards T4 if succession is able to proceed, in which case complex gradients related to risk of severe drought and lime-richness will structure the species composition (Halvorsen, 2016). However, higher frequency of anthropogenic disturbance in cities (Rebele, 1994) means that T35 is often kept in early successional stages.

4.1.4 T37 – Synthetic soft substrate

The ordinations of major type T37 showed a very homogenous plot distribution, with some few satellites (Figure 3.6). As this subset is only represented by one of its three minor types, little variation in species composition is expected. The first coenocline was associated a preference for open areas and with variation in species richness (although this gradient was not confirmed by the DCA ordination of this subset). Overall this type was very species poor compared to the other types, which is a result of the substrate being inhospitable to plants.

The second coenocline was related to N and R, moving from polygons indicated to have low soil fertility/ reaction, to polygons indicated to have high soil fertility/ reaction. A similar study by Melander *et al*. (2009), found that town zone, distance to roads and adjacent vegetation explained some of the variation in composition of weeds on pavement. Weed occurrence was higher in industrial town zones (related to land management, sweeping/weeding etc. not as prioritised in industrial areas). A study on biodiversity of pavements (Bonthoux *et al*., 2019 found a similar pattern: higher species richness was related to industrial areas and to some degree the presence of adjacent vegetation. These findings suggest that there might be relevant structuring process that had not been included for this type.

4.1.5 T43 – Road verge, embankment, lawn, and park

The ordination of T43 showed that there is little variation in species composition, and very short gradients. The main vegetation cover in T43 usually originates from sown and planted species, which may contribute to the homogeneity in species composition for this major type. Several species common in the T43 subset are frequently used in Norwegian seed mixes, such as *Poa annua*, *Festuca rubra*, *Lolium perenne*, *Agrostis capillaris* and *Poa pratensis*, which were all were present in more than half of T43-affiliated polygons; *P. annua* and *F. rubra* occurred in more than 70 percent of T43-affiliated polygons.

The coenoclines are not strongly related to any environmental variables; however the main coenocline (GNMDS1) was associated with species richness. The coenocline moves from species-poor to species-rich (with the range of 5 to 40 average species). This may indicate that sites at right end have had a longer time since establishment or has been affected by lower intensity of land management, which have allowed species accumulation in these polygons, as is hypothesised in NiN (Halvorsen, 2016). Unfortunately, this study did not have any available data on either time since establishment or different types and intensity of land management. However, previous studies of ecosystems similar to T43 (mainly on lawns and parks) have found that land management have a significant effect on this type of ecosystem, either on species composition or biodiversity. Stewart *et al.* (2010) did similar study on urban lawns, and found a main gradient in land management that was related to frequency of fertilisation, mowing, herbicide use, irrigation and clipping removal. Bertoncini *et al.*

(2012) found similar results; use of fertilisers affected the species composition, and pesticide and fertiliser use had a negative effect on diversity. Other studies on biodiversity also found that frequency of mowing affected species diversity, while Yang *et al*. (2019) found that species diversity was also associated with adjacent green spaces and lawn age, which indicate that there is a potential of species accumulation in T43. These studies suggest that relevant explanatory variables for this nature type may not have been included in this study. No variables that could have been related to the subordinate LCEs water saturation (VM; TWI and F) or lime-richness (KA; N and R) were strongly related to either T43 coenoclines.

4.1.6 T4 – Forest

The ordinations of T4 shows there are much stronger gradient structure in the forest than in strongly modified systems, which is also clearer in ecological interpretation. The first coenocline was related to TPI, L, N and R, while the second coenocline was related to Elevation, SurfaceTemp and L. Generalised species lists for T4 has been analysed in NiN, which showed that the nature type is structured by two main LCEs, risk of severe drought (UF) and lime-richness (KA) (Halvorsen, 2015). The samples in this study do not cover all realised minor types for T4. Both UF and KA have 4 segments each (Halvorsen, 2016), however in these data only the three first segments of both LCEs are represented, and there are no combinations of both high UF and KA. Even so, the ordination identifies a main coenocline from low to higher soil fertility and reaction, indicated by the very strong correlations between GNMDS1, and N and R, which to a large degree also correspond with the KA segment classifications. The second coenocline identified by the ordination do not correspond as well with the NiN partitioning, however this can be explained by the incomplete sampling space and low number of polygons in this subset. A comprehensive study of species composition of boreal coniferous forests (Økland & Eilertsen, 1993), found that the gradient structure was strong, with strongly corresponding DCA and NMDS axes.

4.2 Key ecological processes

The most important structuring processes that explained some of the variation in species composition was related to the preference for open sites (L), which appeared in all subsets. The second most important gradient was related to soil fertility and pH (N and R), which appeared in the strongly modified types, T35, T37. It also to a large degree explained variation in species composition for T4. The results showed a much stronger relation between species composition and environmental factors in natural ecosystems (represented by T4) than in strongly modified systems. In addition, correspondence between different ordination methods showed a marked difference in the strength of gradient structure between the two types of systems; there is a much stronger gradient structure in natural ecosystems.

The low structure in strongly modified types may have been due to methods used in the study, either study design and sampling or the ordination methods used. For instance DCA is strongly affected by the scale of species abundances (van Son & Halvorsen, 2014) and sample plot size (Økland *et al*., 1990). While the majority of T4-polygons cover the whole sample plot (average polygon size was 83.5 m^2), the strongly modified types frequently occur in mosaics together (e.g. as shown in Figure 2.5) and as a result have smaller polygon sizes on average (Table 3.1). Sample plot size has been found to affect gradient structure in that smaller sample plots lead to weaker gradient structure and species relationships (Økland *et al*., 1990). It is possible that the varying sample polygon sizes have contributed to the differences in gradient structure across types.

While these results could be explained by the data set or methods, the strong structure in T4 indicate that this may rather be a quality of strongly modified types, in that there is a larger degree of stochasticity in the species compositions. But which ecological processes might explain the difference in stochasticity? Rebele (1994) outlines several different features of urban ecosystems compared to natural ecosystems, mainly related to anthropogenic disturbance and introduction of species from other regions. The intensity of disturbance exacted on the different ecosystems may an important factor in explaining the lack of gradient strength, as the frequency of disturbance is higher in urban ecosystems and therefore early and mid-successional stages are more common in these areas (Rebele, 1994). Disturbance may reset the system, which opens up for stochasticity in colonisation. The more frequent and intense the disturbance is, the more often the system is reset (White, 1979), which may lead to more random species composition. Disturbance may facilitate high species richness as per the intermediate disturbance hypothesis (Connell, 1978), as well as encourage invasion by non-native plant species (Hobbs, 1989). Stochasticity may be due to introduced species, as they can create noise in the data, which may explain the observed lower gradient structure in strongly modified types. Invasion is another key feature of urban ecosystems, as invasion by alien species is more common in urban ecosystems compared to natural ecosystems (Trepl, 1995). Invasion and establishment by alien species have been found to correlate with human intervention (Hendrichsen *et al*., 2014). A study in Berlin found that the proportion of invading species was 50 % in the city centre, and only 28 % in the city outskirts (Sukopp *et al*. 1979). In Norway, 61 % of escaped and 39 % of stowaway species have managed to establish (Hendrichsen *et al*., 2014). However, not all introduced species manage to survive, which means that local extinctions may maintain variation in species composition (Rebele 1994) and contribute to stochasticity in urban ecosystems. While not delved into in this study, there seems to be a difference in the amount of alien species between natural and strongly modified systems, which should be studied further.

4.3 Implications for NiN

Regarding the major types, the results showed a difference in species composition between the strongly modified types that was particularly clear between T37 and T43. The partitioning of strongly modified major types in NiN is mainly based on substrates and physical history (Halvorsen, 2016), and while coenoclines are not clearly related to any of the included environmental variables, this study shows that these partitions result in distinct species compositions.

Although not all minor types proposed for T35 is included in the data set, the result would suggest that the data support the proposed partitioning of T35-1 and T35-2 in the NiN system, based on the LCE dominating grain size (S1). The second gradient in this subset, related to N and R, may indicate that the tentatively included LCE lime-richness (KA) has some importance in structuring species composition in this type. Comparison with T4 results suggests that Ellenberg's N and R may be a good indicator of the local-complex variable lime-richness, however the relation between the coenocline and N and R was much lower in T35, than in T4.

As T37 is only represented by one basic type, it is not possible to elucidate how much variation in species composition there is within this major type. However, the little variation and short gradients suggest no further partitioning.

In regards to T43, no strong correlations with environmental variables are identified. Findings by several other studies suggest that land management may structure the species composition in this type. While they have found that different types of land management affect species composition and diversity for ecosystems corresponding with T43, this variation in species composition might not constitute a significant amount of species compositional turnover along the gradients. However, based on this study alone, the little variation along gradients of species composition means that HI, VM and KA should still only be regarded as subordinate LCEs for this major type. The little variation in species composition and the short gradient length would suggest no partitioning of T43 into minor types.

4.4 Future studies

Further research needed to identify gradients in species composition and ecoclines in urban ecosystems, and to further test the partitioning of strongly modified types in the NiN-system. In order to accomplish this, more data is needed. For instance:

- Data covering the full array of strongly modified types
- Standardised plot sample sizes
- Additional relevant environmental variables, in particular those related to management regimes, anthropogenic disturbance, and direct measurements of soil qualities
- More detailed environmental variables
- Different species groups (vascular plants are not relevant for e.g. T39)

Ellenberg's indicator Values, while not strict ecological interpretation, has been useful in generating hypotheses about important ecoclines in urban ecosystems. The results indicate potential ecoclines that should be investigated further by use of direct measurements of environmental variables.

To determine to what extent introduced species contribute to the observed lack of structure in the strongly modified types in this data, it would be interesting to analyse the data set and look at native and introduced species in types with differing intensity of anthropogenic disturbance by group species by native/invasive, and look at the distribution of these species in the nature types and ordination diagrams.

4.5 Conclusions

Major coenoclines identified through ordination methods showed large consistent difference in species composition between major types of natural and strongly modified ecosystems types. Furthermore, the ordinations show that the strongly modified major types (T35, T42 and T43) are characterised by distinct species compositions, and that T37 differ from the others by having a more species-poor species composition.

Environmental variables only explained some of the variation in species composition in strongly modified systems; the two main gradients that appeared were related to indicators of preference for open (L) and nitrogen-rich (N) sites, which may indicate that ecological processes associated with openness and soil nutrients to some extent are important in structuring urban ecosystems. In addition, grain size, correlating with L, to a large degree explained distinct species compositions in two T35 minor types. Comparison between strongly modified systems and a natural system showed that there is a much stronger relation between species composition and environmental factors in the natural system than in strongly modified systems, which may suggest that there may be other important processes affecting strongly modified types that were not included in this study. In addition, correspondence between different ordination methods showed a difference in the strength of gradient structure between the two types of systems; there is a much stronger gradient structure in natural ecosystems. This may be explained by the higher intensity and frequency of disturbance that continuously disrupt natural ecological processes in the strongly modified systems.

In regards to the NiN-system, this study shows that the different major types have distinct species compositions, although they were not clearly explained by any of the included environmental variables. Regarding minor type partitioning, the results confirm the NiN-hypothesis of T35 partitioning based on the LCE dominating grain size (S1). To determine the cause of the observed difference in gradient structure, and to identify environmental factors that structure the species composition in strongly modified types and NiN partitioning of these, further research is required.

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Appendix

Appendix 1.

Table A.1 Code explanations and translations of NiN-terminology used in this thesis.

Code	**English**	**Norwegian**
LCE	**Local complex environmental variables**	**Lokale komplekse miljøvariabler**
HI	Management intensity / Land	Hevdintensitet
HS	Major type specific partitioning	Hovedtypespesifikk inndeling
KA	Lime richness	Kalkinnhold
S1	Dominating grain size	Dominerende kornstørrelse
SP	Land-use regime	Beite-/slåttepreg
UF	Risk of severe drought	Uttørkningsfare
VM	Water saturation	Vannmetning
	Major type groups	**Hovedtypegrupper**
L	Limnic seabed systems	Ferskvannsbunnsystemer
T	Terrestrial systems	Fastmarkssystemer
	Major types	**Hovedtyper**
L4	Helophyte-dominated freshwater swamp	Helofytt-ferskvannssump
T1	Bare rock	Nakent berg
T2	Open shallow-soiled ground	Åpen grunnlendt mark
T4	Forest (non-wetland)	Fastmarksskogsmark
T13	Open scree	Rasmark
T18	Open alluvial system	Åpen flomfastmark
T30	Alluvial forest	Flomskogsmark
T35	Artificial ground on mineral deposits	Sterkt endret fastmark med løsmassedekke
T37	Waste deposit, spoil heap, plastic and other synthetic soft substrate	Ny fastmark på sterkt modifiserte og syntetiske substrater, rask suksesjon
T39	Extraction site, quarries, buildings and other synthetic hard substrate	Sterkt endret og ny fastmark i langsom suksesjon
T40	Artificial land cultivated as semi-natural grassland	Sterkt endret fastmark med preg av semi-naturlig eng
T42	Flowerbeds and other regularly cultivated, planted area with bare soil	Sterkt endret, hyppig bearbeidet fastmark med intensivt hevdpreg
T43	Road verge, embankment, lawn, park and similar artificial land	Sterkt endret, varig fastmark med intensivt hevdpreg
T44	Arable field	Åker
	Minor types	**Grunntyper**
T4-1	Lime-poor submesic forest	Blåbærskog
T4-2	Intermediate lime-rich submesic forest	Svak lågurtskog

T4-3	Lime-rich submesic forest	lågurtskog
T4-5	Lime-poor submesic to subxeric forest	Bærlyngskog
T4-6	Intermediate lime-rich submesic to subxeric forest	Svak bærlyng-lågurtskog
T4-7	Lime-rich submesic to subxeric forest	Bærlyng-lågurtskog
T4-9	Lime-poor subxeric forest	Lyngskog
T35-1	Artificial or highly modified soil-covered ground	Sterkt endret fastmark med dekke av jord og andre mer eller mindre usorterte masser
T35-2	Artificial or highly modified gravel-covered ground	Sterkt endret fastmark med grusdekke
T35-3	Artificial or highly modified sand-covered ground	Sterkt endret fastmark med sanddekke
T35-4	Artificial or highly modified silt- and clay-covered ground	Sterkt endret fastmark med dekke av silt og leire
T37-1	Spoil heap and chemical waste deposit	Ny fastmark på substrat med avvikende kjemisk sammensetning
T37-2	Inorganic moderate soft synthetic substrate	Ny fastmark på sterkt modifisert eller syntetisk, overveiende uorganisk substrat
T37-3	Household and other organic waste deposit	Ny fastmark på sterkt modifisert eller syntetisk, overveiende organisk substrat
T39-3	Open-cast mine, quarry, road cut and other artificial hard substrate in pioneer phase	Blottlagt fast fjell i pionérfase
T39-7	Synthetic hard substrate in pioneer phase	Sterkt modifisert eller syntetisk, overveiende uorganisk fast substrat i pionérfase

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Appendix 2.

Additional ordination diagrams and correlation tables.

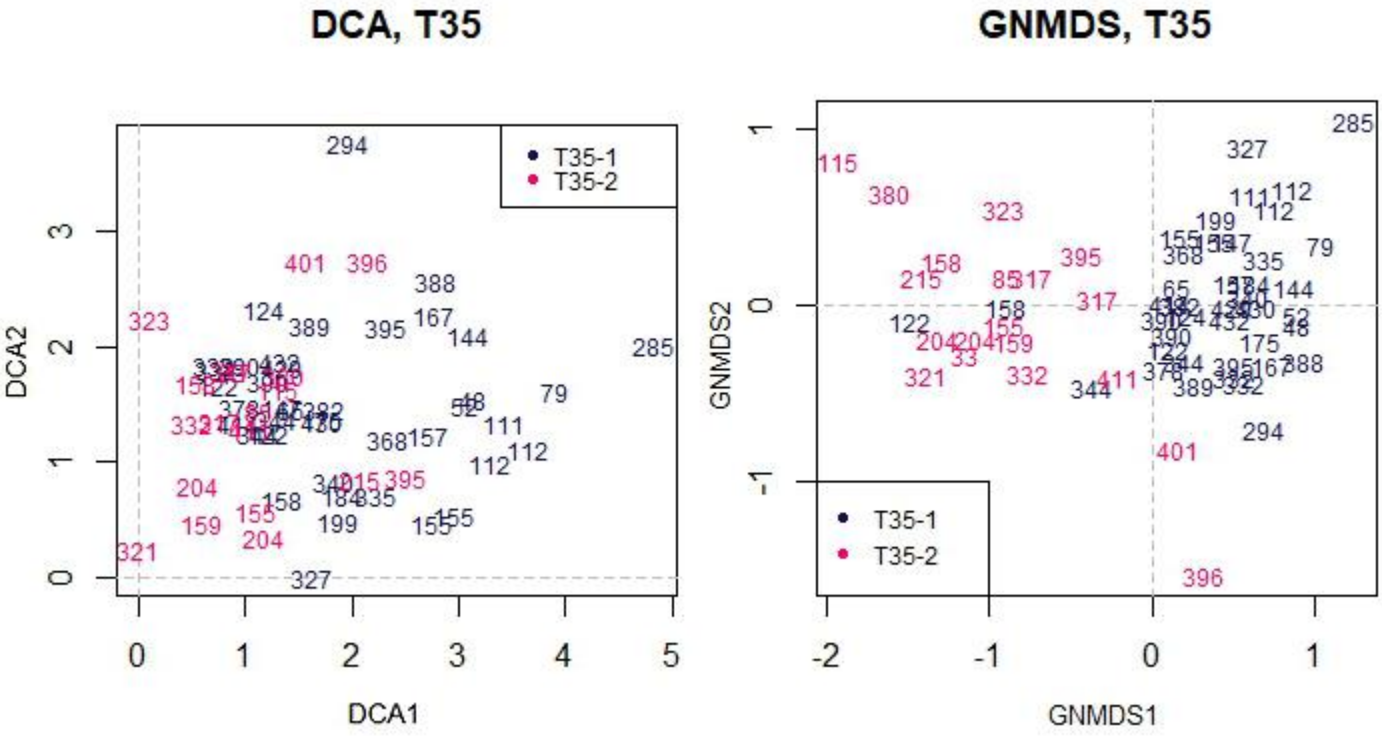


Figure A.1 DCA and GNMDS ordinations of the T35 subset, displaying plot numbers. Each colour represents a T35 minor type, as shown in the legend.

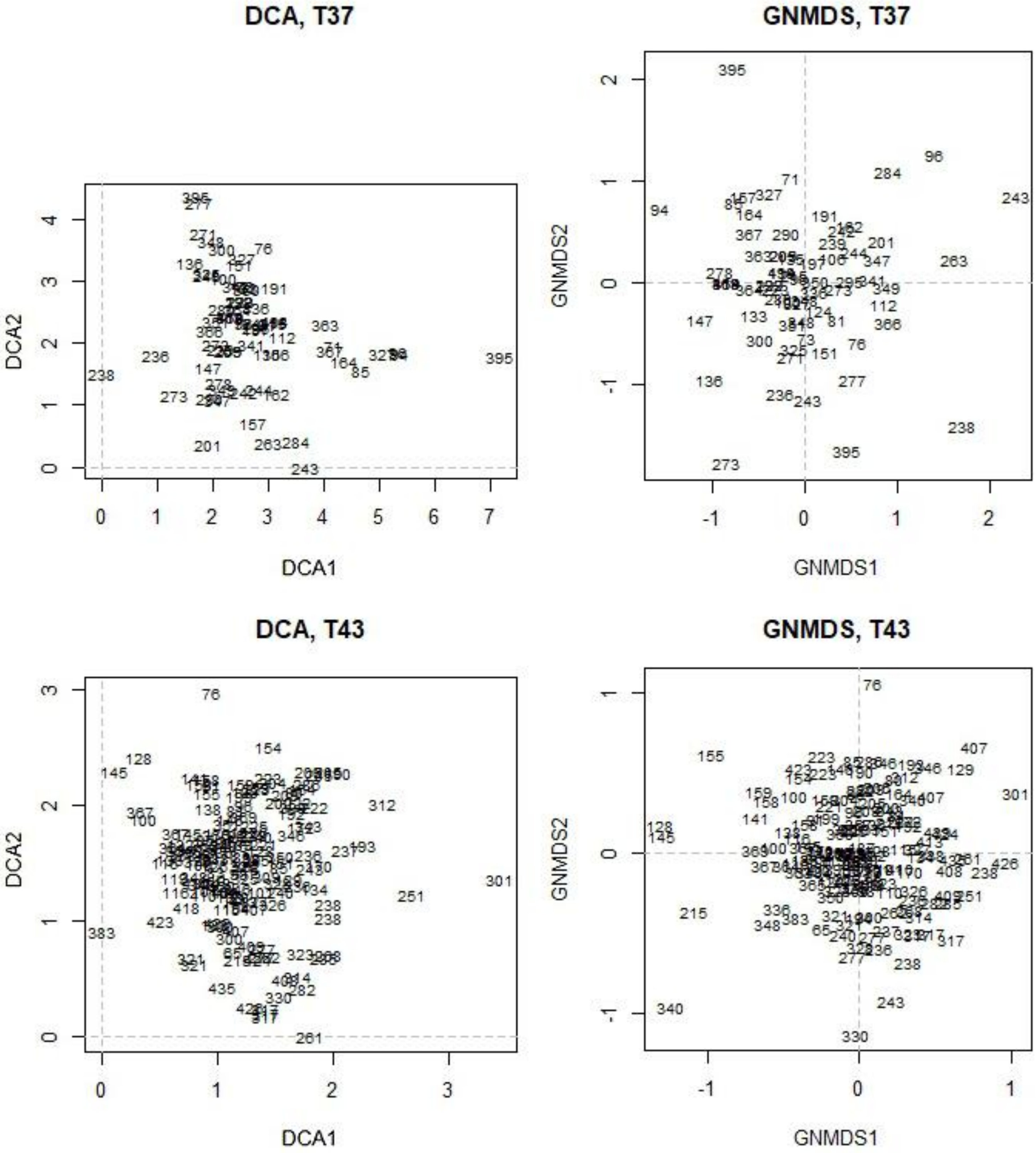
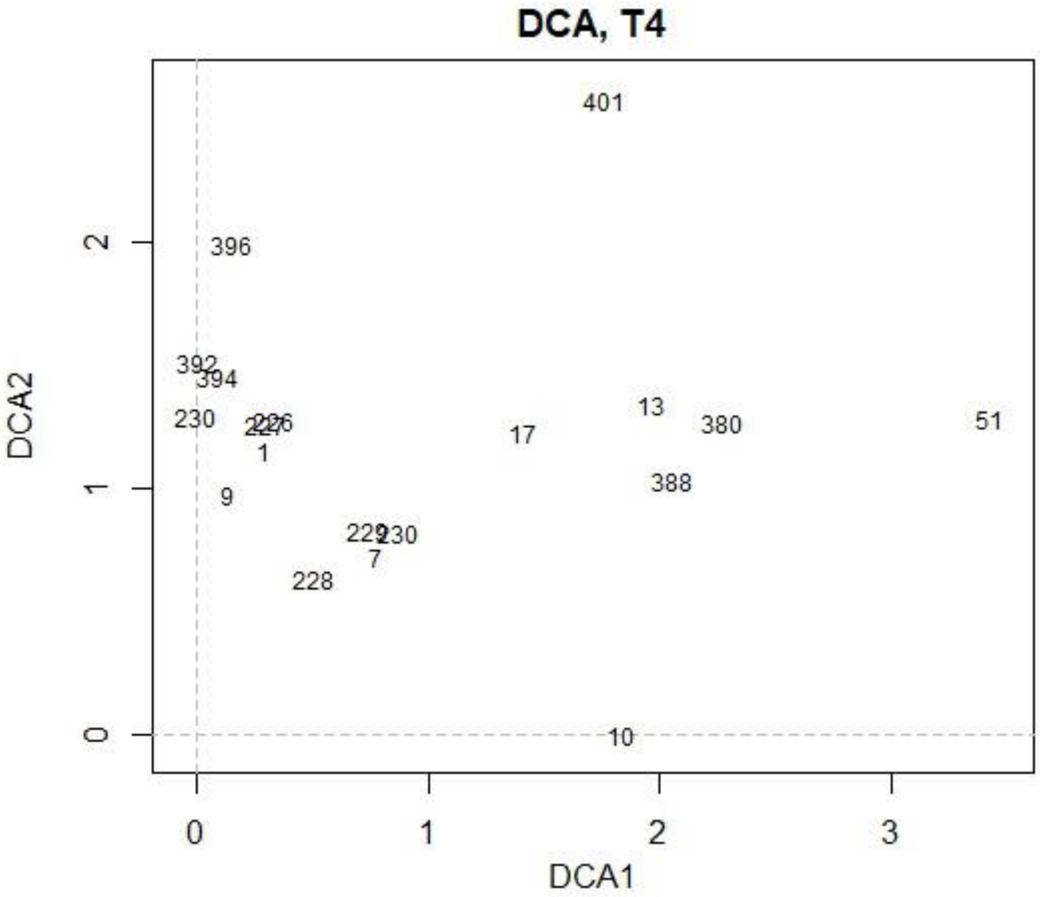


Figure A.2 DCA and GNMDS ordinations of the T37 subset (upper) and the T43 subset (lower), displaying plot numbers.



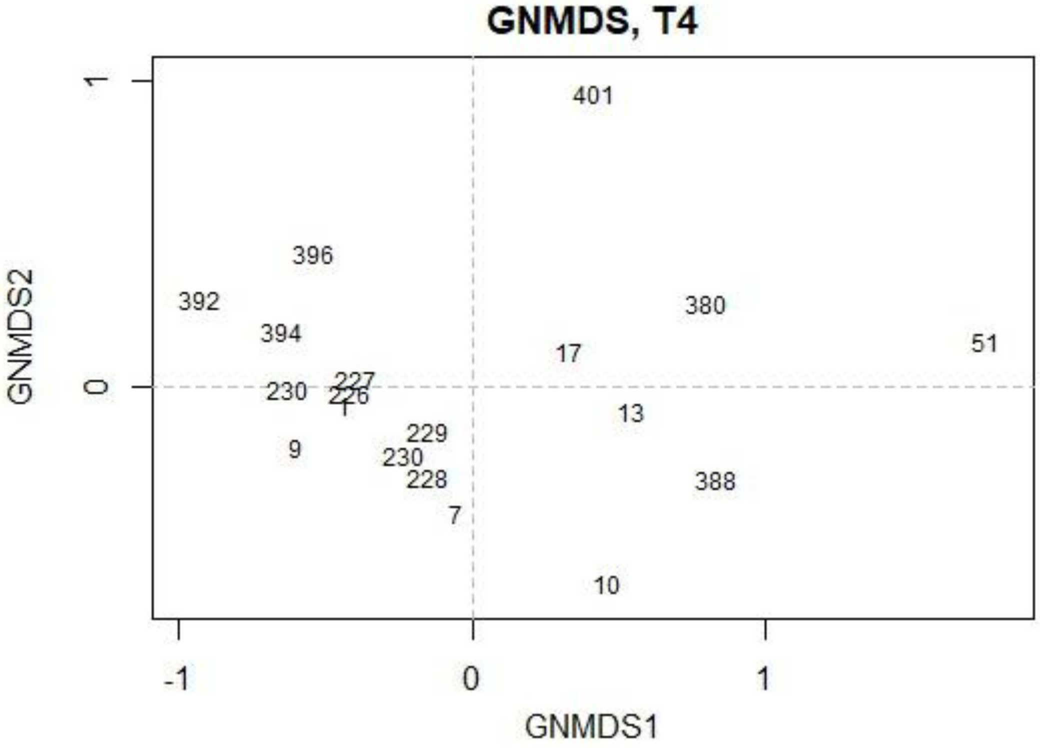


Figure A.3 DCA and GNMDS ordinations of the T4 subset, displaying plot numbers.

Table A.2 Correlation coefficients (Kendall's τ) between environmental variables and plots scores along DCA axes of all subsets. p-values < 0.05 in bold, τ > 0.3 in bold.

	Aspect		**Elevation**		**Slope**		**SurfaceTemp**		**TPI**		**TWI**		**L**		**F**		**R**		**N**	
	τ	p	τ	p	τ	p	τ	p	τ	p	τ	p	τ	p	τ	p	τ	p	τ	p
Full																				
DCA1	-0.1044	**0.0015**	0.0803	0.0147	0.1094	**0.0009**	–0.0779	**0.0178**	–0.0455	0.1662	0.0376	0.2571	–0.2774	**<0.0001**	0.0265	0.4692	–0.0005	0.9900	–0.0657	0.0718
DCA2	0.0501	0.1272	–0.1192	**0.0003**	–0.1388	**<0.0001**	0.1219	**0.0002**	0.0127	0.6999	0.0377	0.2557	**0.4705**	**<0.0001**	–0.2394	**<0.0001**	0.0297	0.4373	–0.0021	0.9535
SMT																				
DCA1	–0.0405	0.2931	0.0364	0.3452	0.0941	0.0145	0.0635	0.0995	–0.0671	0.0812	0.0292	0.4524	**–0.3948**	**<0.0001**	0.2718	**<0.0001**	0.2072	**<0.0001**	0.1254	**0.0011**
DCA2	0.0505	0.1892	–0.1046	**0.0066**	–0.0491	0.2016	0.0983	**0.0107**	0.0424	0.2713	–0.0739	0.0573	0.1090	**0.0049**	–0.2053	**<0.0001**	0.1853	**<0.0001**	**0.3545**	**<0.0001**
T35																				
DCA1	–0.0340	0.7019	0.0182	0.8382	0.2689	**0.0025**	–0.1850	**0.0375**	–0.0397	0.6552	0.0691	0.4398	**–0.5990**	**<0.0001**	0.2320	**0.0093**	0.0334	0.7182	0.0894	0.3135
DCA2	–0.1395	0.1165	–0.1078	0.2254	0.1883	**0.0342**	–0.1146	0.1975	0.0476	0.5920	–0.2050	**0.0219**	–0.1112	0.2111	–0.0986	0.2692	–0.1946	**0.0356**	**–0.4143**	**<0.0001**
T37																				
DCA1	–0.0262	0.7493	0.1228	0.1346	0.1533	0.0613	–0.0208	0.7998	–0.0083	0.9192	–0.0804	0.3298	–0.0893	0.2944	0.1829	**0.0303**	**0.4421**	**<0.0001**	**0.5358**	**<0.0001**
DCA2	0.0046	0.9555	0.1919	**0.0194**	0.0976	0.2334	–0.1148	0.1616	–0.0424	0.6050	0.1608	0.0513	0.0502	0.5555	0.0060	0.9430	–0.1743	0.0816	–0.1664	**0.0460**
T43																				
DCA1	–0.1098	**0.0416**	–0.0109	0.8400	–0.1203	**0.0256**	0.1934	**0.0003**	–0.0025	0.9625	–0.0801	0.1413	–0.1907	**0.0004**	0.0039	0.9419	0.1821	**0.0007**	–0.1962	**0.0003**
DCA2	0.0095	0.8602	–0.0522	0.3336	0.0128	0.8116	–0.0156	0.7730	–0.0135	0.8022	0.0213	0.6950	–0.1072	**0.0467**	0.0147	0.7847	–0.0391	0.4681	0.1208	**0.0251**
T4																				
DCA1	–0.0117	0.9442	–0.2346	0.1614	0.0704	0.6744	–0.0352	0.8336	**–0.4529**	**0.0070**	0.2163	0.2050	**–0.4737**	**0.0041**	0.2698	0.1073	**0.8094**	**<0.0001**	**0.8246**	**<0.0001**
DCA2	–0.0117	0.9442	**–0.4223**	**0.0117**	0.0938	0.5754	**0.3636**	**0.0300**	0.0765	0.6488	0.2043	0.2313	**0.5906**	**0.0002**	0.0352	0.8336	–0.0938	0.5754	–0.1939	0.2669

Table A.3 Kruskal-Wallis test of the relationship between DCA axes of all subsets and factor variables (Limestone: degree of freedom = 1, Substrate: degrees of freedom = 3). p-values < 0.05 in bold

	Full				**SMT**				**T35**			
	DCA1		DCA2		DCA1		DCA2		DCA1		DCA2	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Limestone	5.7	0.0173	0.2	0.6652	2.6	0.1050	0.7	0.4148	0.6	0.4315	0.5	0.4994
Substrate	58.5	**<0.0001**	9.1	**0.0280**	12.7	**0.0054**	13.8	0.0032	4.0	0.2636	6.8	0.0803
Grain size	-	-	-	-	-	-	-	-	13.9	0.0002	0.4	0.5096

	T37				**T43**				**T4**			
	DCA1		DCA2		DCA1		DCA2		DCA1		DCA2	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p	χ^2	p
Limestone	1.1	0.2904	0.8	0.3595	8.5	**0.0035**	2.9	0.0868	0.7	0.3980	1.0	0.3105
Substrate	3.8	0.1488	6.3	**0.0459**	8.4	**0.0386**	16.8	**0.0008**	3.1	0.2112	0.4	0.8137

Appendix 3.

Example from the species- plot matrix. Because of the large size of the data matrix, only an excerpt is included to illustrate the data structure. The full data matrices are available through the author.

Table A.4 Excerpt from the species-plot matrix, showing the percent cover (levels in accordance with Table 2.3) of a selection of species in the full data set and nature type classifications of the polygons.

Polygon number	**423-1**	**423-2**	**423-3**	**424-1**	**424-2**	**426**	**429**	**430**	**432**	**435**	**439**
Nature type classification	T43	T37-2	T37-2	T43	T37-2	T43	T35-1	T35-1	T35-1	T43	T43
Achillea millefolium	1	0	0	3	0	4	3	0	4	3	2
Aegopodium podagraria	0	0	0	0	0	0	5	0	4	0	0
Agrostis capillaris	3	0	0	4	0	4	2	0	3	3	2
Alchemilla micans	0	0	0	2	0	1	2	0	2	1	1
Anthriscus sylvestris	0	0	0	2	0	4	3	0	4	1	1
Artemisia vulgaris	0	0	0	1	0	1	1	2	1	1	0
Bunias orientalis	0	0	0	0	0	1	4	2	2	0	0
Capsella bursa-pastoris	0	0	0	0	0	0	0	0	0	1	0
Cerastium fontanum ssp. vulgare	0	0	0	0	0	0	0	0	0	0	1
Cirsium arvense	0	0	0	2	0	2	2	1	1	1	0
Dactylis glomerata	0	0	0	4	0	4	3	2	4	1	3
Elytrigia repens	0	0	0	0	0	0	3	0	2	0	5
Festuca rubra	0	0	0	4	0	0	1	4	0	3	0
Fragaria vesca	0	0	0	0	0	0	0	0	1	0	1
Galium album	0	0	0	2	0	2	3	3	2	2	1
Geum urbanum	0	0	0	1	0	0	1	2	1	0	1
Glechoma hederacea	0	0	0	2	0	0	0	0	0	0	2
Lepidotheca suaveolens	0	0	0	0	0	0	0	0	0	0	1
Lolium perenne	0	0	0	0	0	0	2	0	0	0	0
Plantago major	2	0	0	2	0	1	1	0	0	1	1
Poa annua	3	0	0	1	0	0	0	0	0	0	1
Poa pratensis ssp. angustifolia	0	0	0	4	0	0	0	0	0	0	0
Poa pratensis ssp. irrigata	0	0	0	0	0	0	0	0	0	0	0
Poa pratensis ssp. pratensis	0	0	0	0	0	0	0	2	3	0	4
Polygonum aviculare	1	0	0	0	0	0	0	0	0	0	1
Prunella vulgaris	0	0	0	1	0	0	0	0	0	0	0
Ranunculus repens	1	0	0	2	0	0	1	1	1	2	2
Rubus idaeus	0	0	0	0	0	0	0	2	0	0	0
Rumex longifolius	0	0	0	1	0	0	0	2	1	0	2
Scorzoneroides autumnalis	4	0	0	1	0	1	1	0	1	2	2
Stellaria graminea	0	0	0	1	0	0	0	0	0	0	1
Stellaria media	0	0	0	0	0	0	0	0	0	0	0
Taraxacum officinale agg.	1	0	0	3	0	2	2	1	3	3	3
Trifolium pratense	1	0	0	4	0	5	3	2	3	2	2
Trifolium repens	3	0	0	2	0	0	0	1	1	4	3

Appendix 4.

Example from the environmental variable matrix. Because of the large size of the data matrix, only an excerpt is included to illustrate the data structure. The full data matrices are available through the author.

Table A.5 Excerpt from the environmental variable matrix. Abbreviations of environmental variable names are in accordance with table 2.4. The coordinates are in projection UTM32.

Polygon	Block ID	X-coord.	Y-coord.	Aspect	Elevation	Limestone	Slope	Substrate	SurfaceTemp	TPI	TWI	L	F	R	N
423-1	10	602795	6632885	79,76484	156,3	0	0,058775	2	33,42736	-0,15	7,215297	7,125	5,756757	5,533333	5,631579
423-2	10	602795	6632885	79,76484	156,3	0	0,058775	2	33,42736	-0,15	7,215297	NA	NA	NA	NA
423-3	10	602795	6632885	79,76484	156,3	0	0,058775	2	33,42736	-0,15	7,215297	NA	NA	NA	NA
424-1	10	602805	6632865	70,10271	155,8	0	0,055002	2	33,68258	0,050003	10,02512	7,142857	5,569444	6,419355	5,681818
424-2	10	602805	6632865	70,10271	155,8	0	0,055002	2	33,68258	0,050003	10,02512	NA	NA	NA	NA
426	10	602825	6632855	68,77312	154,6	0	0,056204	2	33,67515	-0,025	11,1487	7,254237	5,254902	6,473684	5,72549
429	10	602855	6632855	130,9347	153,7	0	0,016769	2	32,14034	-0,0625	8,126691	7,061538	5,114754	6,945946	6,083333
430	10	602805	6632835	53,4638	155,8	0	0,061768	2	32,31229	-0,06249	7,624956	6,780822	5,405797	6,531915	5,926471
432	10	602845	6632825	42,1539	153,9	0	0,026274	2	31,00774	-9,5E-06	-1,25724	6,916667	5,19697	6,428571	5,734375
435	10	602845	6632805	19,48748	154,2	0	0,033621	2	28,49151	-0,075	11,0021	7,25	5,526316	6,416667	5,784314
439	10	602855	6632785	8,463242	154,6	0	0,014577	2	28,49151	0,062504	2,596319	6,913043	5,492063	6,36	6,129032