URBAN ECOSYSTEMS – RESPONSE TO DISTURBANCES, RESILIENCE AND ECOLOGICAL MEMORY

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Man is now an urban species, because most of the mankind lives in cities. In cities, the only thing permanent is change. There are several agents of change in operation in cities, producing environmental disturbances at various temporal and spatial scales and regimes. This affects the living conditions of both man and other urban species. This study was an ecological stress tests how different urban habitats and species survived the actions of the agents of change.

The disturbances can be divided into pulse disturbances and press disturbances. In this study, air and water pollution were typical pulse disturbances. The ecosystems may have enough adaptive capacity to renew and remain in a stable state, but they may also shift to a new state. The ecosystems that maintain their stable state have high resilience, but others shift into a new, possibly undesirable domain (from the perspective of biodiversity conservation and ecosystem services).

The pulse of air pollution caused a temporary disappearance of urban epiphytic lichens in the city of Tampere (Finland). After ameliorating the air quality, the lichens returned, albeit in a reorganised combination of species. Thus, the ecosystem showed resilience as it was able to recover after the disturbance ended. Enough of external ecological memory was available and most of the lichens returned after the pollution episode was over.

Within a period of 100 years, water pollution and other disturbances of the urban lake of lidesjärvi (in Tampere) caused a shift from one stability domain (a clear-water state) to a new domain (turbid-water state). This domain shift presents a challenge for urban environmental management. A deadlock situation was created because the shift back to the desirable state would require excessive technical and economic resources. The upstream, non-polluted lake of Kaukajärvi in the same catchment area remained in a clear-water state with rich flora of elodeids and isoetids. The dynamic macrophyte species pool (1902–2008) of lidesjärvi consisted of 48 species, some of which disappeared temporarily and later returned. The shallow species-rich lakes in the region may occasionally experience species turnover; a species that disappears may recolonise later from other lakes.

The gradient paradigm provides a useful basis for studies in cities to quantify the intensity of urbanisation. In the present study, a 21 km long string of grid cells was established through the city of Tampere. The aim of the gradient study was to examine the distribution of native and alien plants along the gradient line and to find the most important variables, which determine the location and abundance of species along it.

The urban forest fragment under study (1.27 ha in the city of Tampere) had enough adaptive capacity to remain in
the same stability domain since it has been isolated 120 years ago. The urban pressure affected the forest in several cumulative ways and domain shift will occur in the foreseeable future. A special feature of boreal cities is the presence of remnants of seminatural habitats, mostly forests, close to central business districts. As a result, Nordic cities are resilient and show remarkably low extinction rates of plants.

The urban traffic corridors were compared with a river corridor on the municipal level. Despite their small area, the corridors are very rich in species. The corridor plants in the City of Vantaa represented 61 percent of the total number of species of the biogeographical province of Uusimaa. Disturbance regimes were the common denominator of the ecological profiles of traffic corridors and river corridors. In spite of the richness in species, urban corridors are not included in the networks of protected areas.

The Finnish cities showed a high degree of resilience in spite of the concomitant actions of several agents of change. This was a result of the urban structure of the Finnish cities. In Finland, fragments of original nature of different types are embedded in the urban structure.

Keywords: urban ecology, monitoring, disturbance, resilience, ecological memory
"Nothing puzzles me more than time and space, and yet nothing puzzles me less, for I never think about them."

Charles Lamb in a letter to Thomas Manning, January 2, 1810

LIST OF ORIGINAL PUBLICATIONS

I

II

III
Ranta, P., Viljanen, V. and Virtanen T. 2012: Spatiotemporal dynamics of plant occurrence in an urban forest fragment. – manuscript.

IV

V
Ranta, P. 2008: The importance of traffic corridors as urban habitats for plants in Finland. – Urban Ecosystems 11: 149–159.

Contributions

The following table shows the major contributions of authors to the original papers. The authors are referred to by their initials and the papers by roman numerals.

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1. INTRODUCTION

1.1. Urban ecology and the new paradigm in ecology

In ecology, time and space are intimately linked (Preston 1960, Haila 2002, Haila & Levins 1992). The present environmental crisis has created demand for ecologists to provide scientific advice on conservation matters. This advice should be time- and space-specific and be backed by ecological theories, which need to be exact and predictive (Haila 2002).

There has been a paradigm shift in ecology over the last decade; the previous equilibrium assumptions (balance of nature) have been rejected and are now described as myths (Haila 1990, Lomolino 2000, McDonnell 2011). The concept of a balance of nature comes from the ancient Greek philosophers. One of the most influential equilibrium theories in modern ecology has been the island biogeography theory of MacArthur and Wilson (1967). This theory has strongly influenced several fields of ecology since the 1960s, including conservation biology; for example, the idea that “reserves equal islands” surrounded by a “sea” of hostile environment to the species in the reserves (Gilpin & Diamond 1980).

As Haila (2002) pointed out, this statement of Gilpin & Diamond 1980 “can be read the other way around: whenever the preserves or fragments are not surrounded by an ‘inhospitable sea,’ the ‘empirical findings of island biogeographic theory are not pertinent”. For a fragment of green space, a city is hardly an inhospitable sea, but rich in species and novel habitats (Kowarik 2011).

The equilibrium assumptions have been replaced by a more dynamic “non-equilibrium” paradigm, which admits the idea of spatial and temporal variability driven by non-equilibrium processes in various scales. This approach emphasizes human activities as important agents of change (Pickett & McDonnell 1993). Another important feature, in addition to the stability proposed by the equilibrium assumptions, is resilience, an ecosystem’s ability to withstand disturbance without passing to a new stable state or stability domain (Holling 1973, Folke et al. 2004, Folke 2006, Walker et al. 2006).

The new non-equilibrium paradigm in ecology enhances the multidisciplinarity of urban ecology and allows the inclusion of humans as a component in urban ecology as well as in ecology in general (McDonnell 2011). Urban ecology may also be regarded as “data-intensive science” in which new and surprising patterns can be discovered using new data-driven approaches (Kelling et al. 2009).

Interactions between space and time provide the bases of this study. As Preston (1960) stated, “Since space and time are coexistent, it seems philosophically unlikely that cause is limited to
one and effect to the other. Indeed we are all aware that the effect, the change of species, is seen in time as well as in space”.

Urban ecology is a multidisciplinary field of research. It integrates both basic (that is, fundamental) and applied (that is, problem-oriented) natural and social science research to explore and elucidate the multiple dimensions of urban ecosystems (McDonnell 2011). Urban ecology may be divided into two components: ecology “in” the city and ecology “of” the city.

Modern cities can be seen as huge ecological test laboratories or unplanned experiments, the result of which are still poorly known. More information is needed regarding the basic ecological patterns and processes in cities (ecology “in” cities), and also about the ecology “of” cities (Niemelä et al. 2011). The ecology of cities includes the interactions between social and ecological systems in an urban framework. Cities must respond to the new and partly unknown challenges of global change (Grimm et al. 2008).

Meanwhile, a comprehensive theoretical framework of urban ecology is still in the making; a more “step-by-step” approach may be useful. It is not always possible to indicate where an individual study can “fit” into the theoretical framework. Specific, well-understood case studies may have more general relevance. These so-called “analogue models” may suggest important aspects and processes of urban ecology that deserve particular attention and may be generalised in other situations (Haila 2002). An analogue model may be regarded as real-life model of a theoretical idea (Haila and Dyke 2006). Later, the studies may be fitted into ecological theory, which will be “exact and predictive”. This is an especially useful and pragmatic approach in ever-changing cities.

Cities are rich complexes of human-induced and naturally occurring processes (Haila 1999, Niemelä 1999, Kowarik 2011, Niemelä et al. 2011). The urban habitat is the most rapidly expanding habitat around the world. Now that man has become an urban species, urban ecology has become a significant field of science (McDonnell 2011). In 1900, a mere 10 percent of the total world’s population was urban. Today, that figure exceeds 50 percent and is still increasing (Grimm et al. 2008, United Nations 2010). Man shares the urban environment with thousands of other species, which form a complex network of interactions (Clucas et al. 2011). Urbanisation is a major global trend and the survival of animal and plant species in urban conditions is a highly relevant question. The interactions are ecological, physical and social, and render the cities as socio-ecosystems in the sense of Grimm et al. (2008). As a result, the urban landscape is dynamic and highly heterogeneous, with interactions that are both spatial and temporal.

The spatially focused approach of patch dynamics is well suited to fragmented urban landscapes. In the city of Tampere, for example (pop. 220,000, area 127.4 km²), there are 3400 habitat patches (of homogenous land use) (Ranta & Rahkonen 2008, Ranta 2011).
An average of 2500 building permits is granted in Tampere each year, which usually creates increased fragmentation and disturbance.

Most of the studies on urban ecology have been made in the temperate zone. Compared to other cities around the world, the cities of the boreal zone are relatively small and young. The largest cities in the boreal zone in the eastern part of Fennoscandia are Petrozavodsk (pop. 270,000) (the capital of the Republic of Karelia (Russia)) and Tampere (pop. 220,000) in Finland.

The structure of boreal cities is relatively dispersed compared with more southern and older cities (Kasanko et al. 2006). Antipina (2003) described cities in Russian Karelia, in the boreal vegetation zone, as follows: “Karelian cities are unique in several respects: they are situated on the shores of lakes and rivers, surrounded by forests, and are ‘blended’ with the natural environment; and patches of natural (mainly forest, coastal and aquatic) vegetation are preserved within them. This favours maintenance of populations of entirely nonurban forest, bog, and coastal aboriginal plant species.” This description also applies to the Finnish cities only a few hundred kilometres to the west.

The unique structure of the cities in the boreal zone has several ecological consequences. For instance, native species are found abundantly in the centre of Finnish cities because patches of the surrounding matrix vegetation (usually coniferous forest) occur near the densely built business centres.

These structural features explain the favourable situation in the conservation of urban biodiversity in boreal cities. The cities of the boreal zone have resisted the loss of biodiversity better than their temperate counterparts (Ranta & Viljanen 2011, Hahs et al. 2009). In the management of urban forests, conservation and recreation prevail over timber production. This means that the proportion of old forest stands will increase in the forests of boreal cities (Gundersen et al. 2005).

### 1.2. Plants and disturbance

Disturbance is a key factor in urban landscapes. Expanding cities are in a constant state of change in their urban and exurban zones (Zipperer et al. 2000). The relationship between urban organisms and disturbance is not straightforward. Some species benefit from disturbance while others suffer from it; some species are well adapted to cities and others are not. The well-adapted species can be divided into synanthropic ones, which live exclusively with humans, and hemerobic ones, which prefer human influence. In relation to cities, vascular plants are traditionally classified as urbanophilous and urbanophobic species (Wittig et al. 1985, Wittig 1991, Sukopp et al. 1990).

Grime’s theory on plant strategies (the CSR triangle theory) is a wide-ranging theory in plant ecology (Grime 1979, Wilson and Lee, 2000). The three plant strategies are competitor (C), stress tolerator (S) and ruderal (R). The proportion of species with different strategies is likely to change within vegetation in
response to changing land use disturbance) (Hodgson, 1991). Plants with the same life strategy respond similarly to certain ecological conditions and will aggregate at a scale at which the ecological conditions are similar (Massant et al., 2009). Ruderals (R) are plant species that prosper in situations of high-intensity disturbance and low-intensity stress.

Another way to classify plant species is according to their tolerance to urban disturbances. Species can be grouped as urban exploiters, adapters and avoiders. The group determines the location of each species along the urban-rural gradient. Exploiters are most abundant in the city centre.

1.3. Resilience of urban ecosystems

In ecology, the term “resilience” is used in different contexts and has several meanings (Brand and Jax 2007). A review of definitions was published by Carpenter et al. (2001). The term “resilience” is also widely used in social sciences and business studies (e.g., Kotilainen & Eisto 2010).

The constant changes in urban areas test the ability of urban ecosystems to respond and maintain their stability, where stability is defined as the return of a system to equilibrium (Holling 1973). Resilience can be defined as the ability to absorb changes and return to the former equilibrium state or re-organise itself. Natural ecosystems systems may have a high capacity to absorb changes, but when certain limits are passed, the system can no longer return to its former state and must instead change to a different condition or system state. This new state may be undesirable from a human perspective but may nevertheless be highly resilient. This may lead to problems in practical management situations, where the objective is to reverse the undesirable state.

Recently, the system theoretical studies on socioecology have become more popular. The social and ecological systems are closely connected and studying them separately is not meaningful. Human activities affect all ecosystems so much that they must be taken into account both in research and policy making (Folke 2006).

The approach of the interaction of ecosystems and social systems is called “resilience thinking” (Walker & Salt 2006). The central concept in resilience thinking is socioecological systems. This refers to the comprehensive total system that evolved from the adaptation between natural ecosystems and the social systems of man, which tries to adapt to different spatiotemporal disturbances, both ecological and socio-economic (Scheffer et al. 2002).

A central idea in resilience thinking is the assumption that the socioecological systems are constantly changing (Walker & Salt 2006) and that their development is directed by poorly predictable disturbances.

Ecological memory is an essential part of resilience (Gunderson 2000). The more ecological memory an ecosystem has, the more resilient it will be. After
a disturbance, some of the legacies of the undisturbed ecosystem will persist and function as starting points for the reorganisation and recovery of the ecosystem (internal ecological memory). If these legacies are lost, mobile links from an undisturbed support area may help recolonise the disturbed site (external ecological memory) (Lundberg & Moberg 2002).

The external ecological memory is particularly important in urban conditions, where habitat loss is the rule and the ecosystems are more or less disturbed. The remaining fragments of undisturbed ecosystems may serve as pockets of ecological memory for future restoration.

1.4. The aim of the thesis

The aim of this thesis is to study how urban ecosystems respond to disturbances and maintain their resilience. More specifically, the study uses case studies to explore human-induced urban disturbances and disturbance regimes at various temporal and spatial scales (temporal studies I, II and III; spatial studies IV and V) and the ecological resilience in connection with these case studies. The response to urban disturbance is further analysed spatially by urban gradient analysis (IV) and, finally, the importance of disturbance dependent urban ecosystems for biodiversity on urban municipal level is evaluated.

Studies I–III hypothesise the disturbances can also be seen in urban ecosystems as pulse or press disturbances. The concept of ecological memory may be applied in cities and contributes to ecological resilience. Naturally, the three selected case studies represent only a small fraction of all ongoing urban processes and disturbances. The three case studies may also be seen as test cases of how well urban ecosystems resist disturbances and recover from them.

1.5. Temporal studies

It can be difficult to do anything in a city without it affecting biodiversity in some way. The agents of change usually overlap, both temporally and spatially. From the temporal point of view, some of the changes are episodic, but others are long-term.

These three case studies were selected because they coincide, both temporally and spatially. The fundamental agent of change is the same in cases I (epiphytic lichens and air pollution) and II (water pollution). The economic boom in Finland after World War II, and specifically the so-called “Korean conjuncture” of 1951–1952, favoured economically Finnish industries: paper, pulp, sawmill and metallurgic industries, all of which were represented in the city of Tampere, one of the main industrial cities in Finland (Hjerppe 1989). The increased industrial volume also meant an increase in pollution and garbage.

Environmental legislation at that time was poorly developed and pollution could continue uncontrolled for years, even decades. The pollution partly consisted of emissions to the urban atmosphere (sulphur dioxide). It was very harmful for the environment, materials and human health (I). Correspondingly,
the economic boom years affected numerous lakes, both large and small, in Finland. For example, Lake Iidesjärvi in Tampere was heavily polluted. Nutrients from untreated sewage, heavy metals and PCB accumulated in the bottom sediments of Lake Iidesjärvi.

Case study III (isolated urban forest fragment) is connected with the early industrialisation of Tampere. The arrival of the railway to Tampere in 1876 was important for the local industries as the Finnish railways were directly connected with the capital of the Russian empire, St. Petersburg. The new railway station was built in the village of Kyttälä, which still belonged to the rural municipality of Messukylä. After the annexation of Kyttälä village in 1877, the irregular working-class settlement of the village was demolished. Part of the annexed land was used to establish a new cemetery on the Kalevanharju esker in 1880. However, the increase in the urban population made it necessary to find a place for a new municipal cemetery. The new cemetery fragmented the uniform pine forest on the esker; much of the habitat was lost, but some remained as isolated forest fragments. One of these fragments is the Teerenpuisto urban forest (III).

1.5.1. Response of epiphytic lichens to air pollution in the city of Tampere, Finland (I).

Cities use many chemicals, such as herbicides, pesticides and fertilisers, while most factories and power plants produce various types of emissions. Very few of the chemicals have widespread effects on biodiversity. However, air pollutants may be responsible for extensive changes on biodiversity. A well-documented example is acid rain, which affected both forests and lakes across large parts of Europe (Kauppi et al. 1990). Case study I concerns urban air pollution. The Air Protection Act was introduced in Finland in 1995 and new national guidelines with limit values were issued in 1996 (Kukkonen et al. 1999). Nowadays, the quality of air is well monitored and regulated by different legal instruments. At the European Union level, the Commission to the Council and European Parliament decided to improve community environmental legislation, and prepared a Thematic Strategy on Air Pollution COM 446 (2005). On the national level, Finland’s air pollution control policies aim to maintain high air quality, in order to preserve healthy and pleasant residential environments and viable natural ecosystems (Suomen ympäristö 2002).

In the 1960s and 1970s, air pollution control was not a national priority, despite the damage to forests, human health and materials. One of the most damaging pollutants was SO₂, which originated mostly from energy production and industry (Statistics Finland 1996). The air pollution problem in the 1960s and 1970s was especially severe in industrial cities like Tampere.
The sensitiveness of lichens to air pollution was observed as early as the 1860s, when the Finnish lichenologist William Nylander was one of the first to conclude that luxuriant lichens indicate the purity of air (Nylander 1866). Lichens were recognised as being very sensitive to air pollution.

In the early 1900s, the decline of urban lichens was attributed to soot from coal burning. Much later, sulphur dioxide was recognised as the principal toxic agent. Lichens are well suited as biological indicators for monitoring environmental quality, for two main reasons. Firstly, lichens are sensitive to pollutants, which can be measured by their performance. Secondly, lichens have an exceptional ability to accumulate chemicals, which can be directly measured (Gries 1996, van Dobben et al. 2001, Conti & Cecchetti 2001).

Once the disappearance of lichens from cities had been recognised, systematic urban mapping studies began. Sernander (1926) recognised a “lichen desert” in the centre of Stockholm, with tree trunks bare of lichens. Outside the centre, poorly colonised trees belonged to the “struggle zone” and outside the city was the start of the “normal zone”. A similar study was conducted in Helsinki by Vaarna (1934) and later in Tampere (Sahrakorpi 1967).

By 1970, sulphur dioxide concentrations in the air could be compared with the lichen zones, also on a national scale (Hawksworth and Rose 1970). Lichen species could be ranked according to their sensitivity to sulphur dioxide. Some species, such as *Usnea* spp., *Lobaria pulmonaria* and *Ramalina* spp., are among the most sensitive, while *Lecanora conizaeoides*, *Hypogymnia physodes* and *Parmelia sulcata* resist higher sulphur dioxide concentrations.

As a response to severe air pollution (SO$_2$), epiphytic lichens disappeared...
completely from a wide area in the studied industrial city Tampere, and a “lichen desert” was formed (Ranta 1974). In the 1970s, the concentrations of SO$_2$ were very high by modern standards; on average, about six times higher than the present day limit value of 20 μg/m$^3$ (Air Quality Directive 2008/50/EY) and about five times higher than in Helsinki at the same time (Hosiaisluoma 2001).

Damage to forests combined with international pressure, forced Finland to adopt new strategies to reduce air pollution. These strategies were effective and emissions started to decline from the early 1970s onwards. This development continued so successfully that, by the end of century, the lowest detection limit of measuring instruments had been reached.

This development has also been noted in other European cities, such as London and Paris, where lichens started to recolonise the former lichen deserts (Rose & Hawksworth 1981, Hawksworth & McManus 1989, Showman 1981, Gilbert 1992, Seaward & Letrouit-Galinou 1991, van Dobben & de Bakker 1996), and also in Finland (Hosiaisluoma 2001). Lichens are highly versatile organisms that reflect both rising and falling levels of air pollution.

The rapid disappearance of SO$_2$ in Tampere created the opportunity to follow...
up the return of lichens to the former lichen desert. Despite several recolonisation studies around the world, the recolonisation process itself has not been followed up in detail. In Tampere, a monitoring system was established to follow up on the return of lichens between 1980 and 2000.

The aim of the present study is to monitor the recolonisation process over a period of 20 years, with air pollution as the principal agent of change.

1.5.2. Response of aquatic macrophytes on eutrofication in Lake Iidesjärvi (Tampere, Finland): from a rural lake to an urban problem (II)

In 1900, Lake Iidesjärvi in Tampere was situated in rural surroundings, at that time outside the administrative city limits. Encroaching urbanisation changed Lake Iidesjärvi from being largely in a rural area surrounded by cultivated fields, pastures and meadows, to an urban lake. Only during the last few decades has the lake been appreciated as valuable for conservation and recreation. Previously, it became damaged by waste waters, dumping of toxic waste, aggressive road construction, introduced species and the construction of new settlements close to the shore.

The damage created a deadlock situation: the rehabilitation of the lake has required measures that are too extensive and expensive to be realised. Therefore, the unsatisfactory situation continues for local inhabitants. The poor quality of the environment does not permit any possibilities for popular recreation apart from skiing and skating on the ice.

Lake Iidesjärvi can be considered as a local hotspot for biodiversity, as it contains aquatic plants, birds and insects (Ranta & Rahkonen 2008) with several rare and endangered species included. The focus of the present study is on changes in aquatic macrophytes during the 1900s.

The oldest information comes from 1902. Since then, the macrophytes have been regularly surveyed. In the case of Iidesjärvi, the agents of change that have had the greatest impact on the diversity of aquatic macrophytes are the eutroficating wastewaters, landfill on the shore (in operation 1929–1959), construction of a two-lane road across an ecologically valuable flooded meadow in 1975, and construction of new settlements on the shores. Some of these projects would hardly be possible now that Finland has joined the European Union and has to apply European environmental standards.

The sediment analysis reveals that Lake Iidesjärvi was highly productive lake before major human settlement in the area (Alhonen 1981, Vuorinen, Uusinokka & Alhonen 1983). Despite some efforts to improve the quality of the lake, severe blue-green algae blooms occur every year. The state of the lake reflects the past, and the internal loading of nutrients from the sediments keeps the water quality poor.

The aim of the present study is to evaluate the response of aquatic mac-
rophytes to the agents of change that have affected the lake over the last 100 years.

1.5.3. Urban forest fragment: resistance against urban pressure (III)

The fragmentation of forests is one of the main threats to biodiversity around the world (Haila 2002). Generally speaking, urban habitats, including forests, are fragmented because of expanding urban development (Godefroid & Koedam 2001). According to ecological theory, small urban forest remnants will have a rather ominous future, with a loss of species, invasion of aliens and other overwhelming agents of change, which can be summarised as “urban pressure” (Ode & Fry 2006, Hamberg et al. 2010). This urban pressure includes such agents as the invasion of alien species, trampling, dog walking, forest management practices, urban heat island and propagule pressure from surrounding urban habitats. The aim of the present study is to monitor the effects of all the concomitant agents of change in an urban forest fragment over a period of 20 years.

The study of urban forest fragments must consider several important factors, such as fragment size, shape, age and degree of disturbance (Ross et al. 2002). Size, shape and age are constants, while time is the variable. One central question concerns the fate of a small, isolated urban forest fragment and urban forests in general. To what extent will predictions of the ecological theory come true and how this can be applied in urban forestry? Species relaxation, relations between native and non-native species, eutrophication and edge effects could be monitored over 100 years after the forest patch was established by fragmentation.

The study area, the Teerenpuisto forest, is relatively well suited to this type of study because it has long forest continuity (hundreds of years) and it has escaped major disturbances like burning and clearing of agricultural land. Teerenpuisto was saved from modern urban development by the steepness of the esker slope. Disturbance level may be considered moderate, because the local neighbourhood is mostly detached houses. Human movement in the area has been channelled into a walkway at the edge of the forest. This case study can also be regarded as a spatial study because the spatial distribution inside the fragment is considered.

1.6. Spatial studies

Spatial and temporal heterogeneity in cities has both natural and human sources (Alberti 2005). Ecological studies have analysed the relationships between landscape structure and species distributions, movements and persistence. The degree of urbanisation affects both the composition and numbers of the species.

Urbanisation causes fragmentation and loss of natural habitats and puts pressure on the existing natural habitat patches. Some of the habitats are completely new, such as parks, gardens and wastelands. Human population density is negatively correlated with species richness, at least in stud-
ies conducted on a fine spatial scale, but it may be positively correlated in studies conducted on a more coarse spatial scale (Pautasso 2007). Urbanisation usually reduces species richness for most biotic communities. However, plants are an exception to this pattern: plant species richness often increases in cities more than in non-urban areas (Grimm et al. 2008). The native plant species usually decrease, but non-native species increase. This could be due to the importation of non-native plants for horticultural and landscaping purposes, which occurs at a rate that outpaces the extinction of native species (McKinney 2008).

The spatial part of this thesis includes two papers regarding rural-urban gradient and disturbance dependent ecosystems. The urban-rural gradient is a spatial representation of human influence and disturbance in a city (IV). Urban traffic corridors are the most widely distributed urban habitats and depend on regular human disturbance. Urban traffic corridors are artificially maintained in the early stages of succession. A city may also have natural corridors, such as river corridors. The disturbance of river corridors is caused by natural forces (floods, ice and flow of debris) (V).

1.6.1. Factors determining plant assemblages along a rural-urban gradient in the city of Tampere (IV)

Soon after the gradient paradigm was introduced in ecology, it was applied in urban ecology (Whittaker 1967, Austin 1987, McDonnell & Pickett 1990, McDonnell et al. 1997). It provides a useful basis for studies in spatially variable ecosystems in cities to quantify the intensity of urbanisation (McDonnell et al. 1997, Mörtberg 2009, Pickett et al. 2009). The gradient approach also includes humans and can be applied internationally in a standardised form (Niemelä et al. 2002, Niemelä & Kotze 2009). The gradient orders environmental variability in space, corresponding to the structure and function of ecological systems (McDonnell & Pickett 1990). The intensity or degree of environmental change determines how steep the gradient will be in ecosystem structure and function. The gradient analysis can be seen as an organising tool for research in urban ecology. Cities have numerous structural features that affect the spatial placement of species and communities. Environmental changes and the response of plants along the gradient provide a template for further research in urban ecology (McDonnell et al. 1997).

The aim of the present study is to examine the distribution of native and non-native plants along the urban gradient line and to find the most important variables that determine the location and abundance of species along it.

The gradient itself is a 21 km long string of grid cells that measure 500 m x 500 m. The cells are a part of a comprehensive mapping of the urban flora in the city of Tampere. The cells form a straight line from rural surroundings at the outer limit of the city (from the eastern rural municipality of Kangasala to the western town of Nokia through the central parts of Tampere). In fact, this
gradient is a forest-urban-forest gradient because the matrix ecosystem outside the city is boreal coniferous forest.

1.6.2. Disturbance dependent urban ecosystems: roadside and riverside green (V)

In urban ecology, corridors and patches are key elements of the landscape. According to its definition, a corridor is “a relatively narrow strip of a particular type that differs from the areas adjacent on both sides” and a patch is “surface area that differs from its surroundings in nature or appearance” (Turner et al. 2001). Corridors may be natural (like river corridors) or man-made (like roads, hedgerows, power lines, etc.). In ecology, corridors are particularly relevant because of their connectivity between otherwise isolated habitat patches. (Hobbs 1992). Corridors have been seen as tools that mitigate the negative impacts of fragmentation and maintain viable populations in fragmented ecosystems. This point of view is attractive as habitat fragmentation is regarded as one of the major threats to biological diversity. This assumption regarding the effectiveness and usefulness of conservation corridors (or wildlife corridors) has had, and continues to have, a profound effect on practical planning, where increased connectivity is seen as an unquestioned paradigm in conservation planning and reserve design (Hess & Fischer 2001).

However, both the functionality and usefulness of ecological corridors has been questioned because of the lack of supporting studies. A group of “conservation corridor sceptics” has emerged (Beier & Noss 1998), some of whom have stated that corridors may serve as conduits for pests, diseases, invasive species and unwanted predators. The discussion continues regarding suitable reserve design strategies (Minor & Lookingbill 2010, Moilanen et al. 2009).

Road corridors are probably the most widespread corridors in present-day industrial societies. In the United States, road corridors cover approximately 1 percent of the total land area, and 15–20 percent of the country is ecologically impacted by roads (Forman & Alexander 1998). The road corridors have several ecological functions: conduits, barriers, habitats, sources and sinks (Hess & Fischer 2001).

Road corridors serve several functions simultaneously. As for people, road corridors are conduits for animal and plants. The moving vehicles and the air turbulence they cause spread the propagules of several plants. This is largely the case for railways as well (Carpenter 1994), so road and rail corridors can be categorised as “traffic corridors”.

Traffic corridors also serve as habitats in which animals and plants can survive and reproduce. The value of traffic corridors for conservation has been well documented (e.g., Auestad et al. 2011, Tikka et al. 2000, 2001, Spellerbeg 1998, Forman et al. 2003, Vermeulen 1994 Vermeulen & Opdam 1995, Stottele 1995, Vägverket 1999). On the other hand, traffic corridors function effectively as conduits. Several plant species arrived in ports and were spread by railways to the interior of the country. In Finland, this has been documented

Corridors are often rich in species. In the United Kingdom, roadsides contained 870 species of vascular plants out of the county’s total flora of 2000 species (Way 1977).

The present study aims to treat traffic corridors as habitats and estimate their importance for the diversity of vascular plants on the municipal level. The cities of Vantaa, Kerava and Järvenpää were chosen because they are all floristically mapped. The results from traffic corridors can be compared with the comprehensive municipal mapping results. Most of the roads in Finland are managed by the municipalities, and municipal decisions affect the diversity of road corridors. All railways are managed by the state.

The City of Vantaa also has river corridors. The river Vantaa was comprehensively mapped and the results compared with other corridor types and with the city as a whole. The basic difference between the corridor types is the management: traffic corridors are regularly managed by man, but natural corridors by more or less regular natural forces, such as floods (Ranta, Kesulahti, Viljanen and Tanskanen 2012, unpublished manuscript).
2. METHODS AND RESULTS

2.1. Temporal studies

2.1.1. Response of epiphytic lichens to air pollution in the city of Tampere, Finland

A permanent monitoring system was established in 1980. It consists of (1) 25 study sites mainly in the area of the former lichen desert (Fig. 2), (2) six reference sites outside of the lichen desert and further away from the city centre, and (3) four sectors in the city centre for monitoring all the tree trunks in the most polluted area in the city centre (Fig.3) and 38 individual trees along the main street of Hämeenkatu.

All the permanent study sites were monitored in 1980, 1985, 1990 and 1995. Every site consists of five adjacent trees of the same species (Tilia x vulgaris). Tilia was selected because it is a very common ornamental tree along streets and in parks. Only trees with perimeters over 50 cm were included. Two of the 125 studied trees that were lost during the 15-year monitoring period were not included in the calculations. The same criteria were applied to the six reference sites as to other sites, including methods and monitoring years.

Fig. 3. The 25 permanent monitoring sites (1–25) and the four sectors (A–D) for monitoring the total number of colonised tree trunks.
The six reference sites are situated further away from the city centre (Härnälä, 3.5 km S from Central Square; Rahola, 6 km W; Pyynikki, 2 km SW; Linnainmaa, 6 km E; Haihara, 7 km SE and Koivistonkylä 3 km SSE).

The recolonisation process of lichens was monitored at four different levels: (1) total colonisable surface, (2) study site level, (3) individual tree level and (4) lichen species level. The total colonisable surface for epiphytic macrolichens is the sum of the surface areas of all tree trunks in the city. In the four monitoring sectors, the presence or absence of lichens on the tree trunks (from 0 cm to 200 cm) was noted. In the study sites, the cover values of lichen species were measured on each tree in cm² between 0 cm and 200 cm from the ground and later calculated as ‰ of the total available surface (200 cm x perimeter of the tree). The summed cover values and trunk surface areas were then calculated for the entire study site. At the individual tree level (the 38 trees along the main street), the surface of each tree was divided into four zones: upper sides of branches, upper trunk, rough surfaces and lower trunk. Colonisation of these zones was recorded at every tree. The upper sides of branches were observed from the windows and roofs of buildings or with binoculars from the ground. The trees were studied in a similar way in 1980, 1985, 1990 and 1995. At the species level, the appearance of each species in study sites was noted, together with the changes of frequency and cover value during the monitoring period.

Before the high sulphur dioxide concentrations started to fall in the early 1970s, a lichen desert of 5 square kilometres was formed in the centre of the city of Tampere (Ranta 1974) (Fig. 2).

The zone of damaged lichens was much wider, about 30 square kilometres. The recolonisation of lichens had already started before the monitoring sites were established, and eight species were observed in 1980. The number of species increased steadily: 11 in 1985, 19 in 1990, 21 in 1995 and 22 in 2000. Over the same period, the total cover of lichens increased from 0.06 percent to 10.9 percent. The mean number of species increased 10-fold, but the increase on total cover was almost 180 times higher. The numbers of species increased linearly, but cover increased exponentially.

Fig. 4. Increase of the mean number of species and cover of lichens on monitoring sites.
In addition to the quantitative increase, qualitative differences could be observed. The recolonising lichens could be divided in “early colonisers” and “late colonisers”. Among the first colonisers were Hypogymnia physodes, Hypocenomyce scalaris and Vulpicida pinastri. Ramalina farinacea, Usnea spp. and Bryoria spp. and Evernia prunastri belong among the latest colonisers.

Despite the rapid recovery, there was still a considerable difference in species richness and total cover of lichens between the 25 study sites in the city centre and the six reference sites. In 2000, the study sites had roughly half the species number and the total lichen cover compared with the reference sites. The mean number of species in the reference sites increased from 6.8 in 1980 to 13.8 in 2000. The mean cover increased from 7.8 percent in 1980 to 19.6 percent in 2000. In both cases, the relative increase was much lower than in the central monitoring sites. This was due to the higher number of species to begin with, as only the most sensitive species were missing from the reference sites in 1980.

Despite the rapid fall of SO₂ concentrations, the recolonisation had barely started by 1980 when the monitoring started. There was a lag period of 10 years before the rapid recolonisation started. The recolonisation process did not show a spatial pattern, but lichens also appeared in the middle of the former lichen desert.

Although lichens reappeared rapidly in the former lichen desert, both lichen flora and vegetation are still impoverished compared to the reference sites. By 2000, the reference sites had twice as many species than the city sites and twice the average lichen cover.

Even in the near total absence of SO₂, lichen recovery seems to take several decades.

2.1.2. Response of aquatic macrophytes on eutrophication in Lake lidesjärvi (Tampere, Finland): from a rural lake to an urban problem (II)

As an urban, species-rich lake, lidesjärvi has been the object of biological observations and research throughout most of the 20th century. The material is widely scattered and only partly published. In the beginning, plants and insects were collected irregularly for private and public collections. During the latter part of the century, the local scientific societies (botany, entomology and ornithology) collected a lot of information about lidesjärvi. The results have mostly been published in the local journals and leaflets of these societies. Regular environmental monitoring by municipal and other authorities started at the middle of the 20th century. The main objective for monitoring was the quality and hygienic state of the water, although heavy metal concentrations in fish were also investigated. Relevant information has been found in many non-biological sources, such as the archives of local museums, collections of historical photographs, local newspapers and magazines.

Systematic botanical research started with floristic inventories in the 1930s
(Lehtonen, 1933). Later on, botanical studies focused on the influence of different environmental variables like pH and nutrients (Perttula 1954, Järnefelt 1956, Toivonen & Ranta 1976). The frequency and abundance of plants were estimated in the same way as in earlier studies. Species included in this study were vascular aquatic plants, as defined by Linkola (1933). Aquatic macrophytes were divided to growth forms according to Toivonen and Huttunen (1995).

The comprehensive macrophyte pool of lidesjärvi consists of 48 species. Twenty-two of these were present in all surveys from 1902 to 2008, so they can be considered permanent species.

The number of species in each indicator value class is as follows: eutrophy (12), meso-eutrophy (14), indifferent (11), oligo-mesotrophy (6) and oligotrophy (0). Nine of the species can be regarded as dominant on the basis of their frequencies and abundances. The dominant species belong to the highest frequency and abundant classes (Toivonen & Ranta 1976). The changes of the dominant species can be explained by the hypereutrophy and the introduction of an alien species, the muskrat (Ondatra zibethicus). The now-disappeared Schoenoplectus lacustris and Equisetum fluviatile are favourite foods of the muskrat and E. fluviatile suffers from overeutrofication (Ranta & Toivonen 2009). The decrease of elodeids can be connected with the increasing turbidity of the water. The present hypertrophic state of the lake explains the yearly algal blooms in the lake, which greatly reduce the ecosystem services that the lake might otherwise provide.

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<tbody>
<tr>
<td>Schoenoplectus lacustris</td>
<td>7/7</td>
<td>7/7</td>
<td>7/4</td>
<td>%</td>
<td>-/-</td>
<td>-/-</td>
<td>-/-</td>
</tr>
<tr>
<td>Equisetum fluviatile</td>
<td>7/7</td>
<td>6/5</td>
<td>4/4</td>
<td>3/6</td>
<td>2/1</td>
<td>2/1</td>
<td>2/2</td>
</tr>
<tr>
<td>Phragmites australis</td>
<td>5/4</td>
<td>6/5</td>
<td>7/5</td>
<td>7/6</td>
<td>7/6</td>
<td>6/6</td>
<td>6/6</td>
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<tr>
<td>Typha latifolia</td>
<td>-/-</td>
<td>-/-</td>
<td>4/2</td>
<td>4/5</td>
<td>5/5</td>
<td>5/6</td>
<td>5/6</td>
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<td>7/4</td>
<td>7/7</td>
<td>7/5</td>
<td>7/6</td>
<td>6/7</td>
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<td>6/5</td>
<td>7/3</td>
<td>3/3</td>
<td>4/2</td>
<td>3/5</td>
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<td>7/7</td>
<td>7/7</td>
<td>7/3</td>
<td>4/3</td>
<td>-/-</td>
<td>-/-</td>
<td>3/6</td>
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<tr>
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<td>7/5</td>
<td>5/2</td>
<td>6/6</td>
<td>%</td>
<td>6/5</td>
<td>6/4</td>
</tr>
<tr>
<td>Potamogeton praelongus</td>
<td>7/7</td>
<td>6/5</td>
<td>4/2</td>
<td>2/4</td>
<td>3/2</td>
<td>2/1</td>
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Table 1. Dominant macrophyte species in lidesjärvi in different surveys. The first number represents frequency and the second number indicates abundance (Ranta & Toivonen 2009).
A special feature of the macrophyte flora in lidesjärvi is the existence of so-called “lagoons”. They are separate water bodies from the main basin of the lake and have a very different water quality. The lagoons are springs on a sandy bottom that have clear water. Algal blooms do not enter the lagoon and they are a suitable environment for elodeids. Some rare elodeids, such as *Potamogeton compressus* and *Callitriche hamulata*, occur only in these lagoons. If the water quality of the lake should ever improve, these species of the lagoons could invade the main basin (external ecological memory). However, the internal loading from the bottom sediments will not permit any improvement of water quality if the sediments are not removed or isolated.

The number of observed macrophytes was at its highest in the survey of 1947 (74 percent out of the species pool) and lowest in 1991 (58 percent). On the basis of macrophytes, the state of the lake was at its worst in 1991, when practically all elodeids had disappeared from the main basin.

The changes in the macrophyte community from 1933 to 1947 (14 years) and from 1947 to 1975 (28 years) were comparable, but the change from 1975 to 2003 (28 years) appears to have been more dramatic (Table 2).

Lake lidesjärvi shows the classic relationships between disturbance, ecological structure, invasions and extinctions. The anthropogenic disturbance (mainly water pollution) exceeded the resilience of the lake. The macrophyte communities changed and, at the same time, the yearly algal blooms (hypertrophy) destroyed the living possibilities of most isoetids and elodeids. These changes led to the invasion of both vascular plants and an alien mammal species – the muskrat (*Ondatra zibethicus*). The muskrat consumed the favourite food plants *Schoenoplectus lacustris* and *Equisetum fluviatile* to extinction. New plants invaded the vacant habitats (Fig. 5).

<table>
<thead>
<tr>
<th>years between surveys</th>
<th>D.I.</th>
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<tbody>
<tr>
<td>1933–1947</td>
<td>13.8%</td>
</tr>
<tr>
<td>1947–1975</td>
<td>11.1%</td>
</tr>
<tr>
<td>1975–2003</td>
<td>25.3%</td>
</tr>
<tr>
<td>1933–1975</td>
<td>14.7%</td>
</tr>
<tr>
<td>1947–2003</td>
<td>29.5%</td>
</tr>
<tr>
<td>1933–2003</td>
<td>31.3%</td>
</tr>
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</table>

Table 2. Floristic change: dissimilarity index (D.I.) between surveys T1 and T2 = \( \frac{nT2 + dT2}{tT1 + tT2} \). \( nT2 \) = new species in the T2 survey, \( dT2 \) = disappeared species in the T2 survey, \( tT1 \) = number of species in the T1 survey, \( tT2 \) = number of species in the T2 survey.

Fig. 5 The collapse of Lake lidesjärvi followed this classic model (from Allen, Forys & Holling 2010).
2.1.3. Vegetation of an urban forest remnant after 120 years of fragmentation (III)

The vegetation data for the present study was collected from every 5 x 5 m grid cell within the forest. A comprehensive systematic grid was used to map the plants. The number of grid cells is 508 and the size of each cell is 5m x 5m. The total mapping area is 1.27 ha.

Fig. 6. Map of the study area.

Each cell was surveyed twice, in 1980 (100 years after fragmentation) and again in 2000 (120 years after fragmentation). The presence/absence of each plant species was noted. No individuals were counted. Two data sets were formed and the presence of all vascular plant species was recorded. Seasonal variations are of little importance in the sub-xeric forest and one yearly survey (carried out in June and July) is sufficient to gain a comprehensive picture of the flora. Sub-xeric forest does not have the clear spring aspect of a more herb-rich forest (Reunikainen et al. 2001).

Firstly, the plants were distinguished into two categories with respect to their immigration status, which was either native (indigenous, 61.9 percent of all species in 1980 and 56.7 percent in 2000) or non-native (aliens, 42.5 per-
During the 20-year period, the number of native and alien species remained remarkably stable. The total number of native species increased from 57 to 68 (1980-2000). Aliens increased from 83 to 89 during the same period. The total species richness increased from 134 to 157.

The average cover (the number of grid cells with corresponding species present) of native species increased in the same period from 13.7 to 14.4, and the aliens from 2.0 to 4.2. Despite the generally modest increase in alien occurrence, some individual species increased considerably; for example, *Pinus cembra* increased from 27 cells to 231 cells and *Sorbus intermedia* from 77 to 234 cells. At the same time, some original species of the pre-fragmented forest decreased; for example, *Calluna vulgaris* from 50 to 9 cells (-82 percent), *Arctostaphylos uva-ursi* from 36 to 8 cells (-72 percent) and *Trientalis europaea* from 75 to 7 (-91 percent). The native species that increased most were typically trees and bushes: *Prunus padus* (+200 percent) and *Ribes alpinum* (+231 percent). The spatial distribution of aliens did not change to a statistically significant degree over the study period. Although the number of aliens increased evenly throughout the study area, their share is still very low (Figs. 7 and 8).
Fig. 7. Distribution pattern of native species in 1980 and 2000. The natives concentrated in 1980 in the central part of the forest, but were more evenly distributed in 2000.

Fig. 8. The distribution pattern of alien species in 1980 and 2000.

Nitrogen and light indicators

Several qualitative differences were also detected. Between 1980 and 2000, the sum of indicator values (according to Ellenberg 1991) for nitrogen (average per cell) increased from 40.1 per cell to 52.8. After 1980, the number of nitrogen indicators decreased significantly in the central part of the area, in relation to the edge, because the nitrogen input was not directed towards the central zone (Fig. 9).

Fig. 9. The nitrogen indicators were concentrated along the pathway and the edges.

In 2000, the nitrogen indicator species dominated near the pathway and at the southern slope of the area. The greater the distance to the edge, the lower the number of nitrogen indicator species. The absolute number of nitrogen indicator species had a positive and statistically significant correlation with the distance to the edge (-0.272).
CSR strategies

The eutrofication of the study area favours competitors (C-strategists) and impairs stress tolerators (S-strategists), but has little effect on ruderal strategists (R-strategists). Between 1980 and 2000, the average value of C-strategists per grid cell increased from 3.2 to 3.9 (Fig. 10).

Between 1980 and 2000, the average number of S-strategists per cell decreased from 5.5 to 4.9 (Fig. 11). Generally speaking, the greater the distance to the edge, the higher the number of S-strategists. The S-strategists had a positive and statistically significant correlation with both the distance to the edge (0.498) and to pathways (0.227). The two variables accounted for 31 percent of the variability of the S-strategists in the regression model.
The spatial distribution of R-strategists did not change to a statistically significant degree during the study period. R-strategists showed high numbers near the edge and had a negative and statistically significant correlation with the distance to the edge (-0.514). The two independent variables accounted for 27 percent of the variability of the number of R-strategists in the regression model.

2.2. Spatial studies

2.2.1. Vascular plants along an urban-rural gradient in the city of Tampere, Finland (IV).

The material collected for this study is derived from the comprehensive floristic mapping of the city of Tampere (Ranta and Rahkonen 2008). The city was divided into 596 quadrates of 500 m x 500 m. Observations of 1239 plant species (409 of which were natives) were made in the original citywide mapping. There were 200,000 observations in total. The transect consisted of 42 mapping cells of the citywide material (Fig. 12).

Three different methods were used to study the relationships between urbanisation and spatial patterns of species richness. The first involved studying the variation in species along the urban-rural gradient with the help of graphic diagrams.

Secondly, in order to capture the effects of urbanisation on the native and non-native species and their numbers and percentage, a multiple regression analysis was conducted. On the basis of the reviewed literature, four variables were selected to identify urban and rural features (see Table 1): (1) Percentage of forest land; (2) percentage of detached houses; (3) distance to the city centre (the cell that represents the city centre shows the highest number of retail and commercial services, the central business district of the city of Tampere); and (4) population (log transformation was performed on population because of its non-normal distribution). The predictor variables did not correlate highly with each other (the highest correlation between independent variables was .764 between the distance to the city centre and the percentage of forest land).

Thirdly, in order to examine the relationships between plant species and the urban structure in more detail, the variables were studied in relation to the proportion of forest land with a simple linear regression analysis. In addition, the nonlinear relationships between the variables were analysed using a quadratic model.

A total of 8267 plant observations (presence of species in 500×500 cell) were made along the entire transect (an average of 197 observations per quadrate). The share of natives on the transect is 44 percent. The group of non-natives consists of archaeophytes (24.6 percent), ornamentals (6.9 percent), garden escapes (9.7 percent) and neophytes (14.2 percent) (Figs. 14 and 15).
Fig. 13. The urban-rural transect (500m × 500m) and human population density in the city of Tampere.

Fig. 14. Proportion of forest land along the transect.
The percentage of non-natives exceeds the percentage of natives in 26 quadrates. The highest difference between the percentage of native plant species and aliens is approximately 70 percent (Fig. 15).

Fig. 15. Absolute number of native and alien plant species along the transect.

Fig. 16. The percentage distribution of native and alien plant species along the transect.
In the regression model, the variables account for approximately 30 percent of the total variability in the number of species among the quadrates (see Tables 2 and 3). Compared to other variables, the total number of species has the lowest coefficient of determination; this is because the total number of species includes a large variety of species. The total number of species has a statistically significant correlation with the percentage of detached houses. This high correlation suggests high species richness in semi-urban areas.

| Total number of species | 0.266* | 193.2 | 2.11 | -0.033 |
| Absolute number of natives | 0.597*** | 52.3 | 2.33 | -0.021 |
| % of native species | 0.719*** | 27.2 | 0.656 | -0.001 |
| Absolute number of alien species | 0.469*** | 139.3 | -0.167 | -0.013 |
| % of alien species | 0.710 | 72.1 | -0.631 | 0.001 |

Table 5. Simple quadratic regression model (independent variable: proportion of forest land): coefficients of determination (R²), constants, unstandardised regression coefficients.

Fig. 17. Relationships between proportion of forest land and total numbers of all (A), native (B) and alien plant species (C).
The absolute number of natives has a positive and highly statistically significant correlation with the percentage of detached houses and the distance to the city centre and significant correlation with the percentage of forest land. The absolute number of natives correlates negatively with population. The total number of natives shows the highest coefficient of determination with distance to the city centre. Increased distance indicates more forests or other habitats that are suitable for native species, such as natural lakes and shores, brooks, bogs, rocky outcrops and meadows. Although the natives are basically forest species, the distance from the city centre explains the number of natives better than the share of forested land. These habitats are not abundant near the most densely populated and built-up parts of the city.

The number of natives increases continuously with the proportion of forest land. The linear and quadratic models both show a highly statistically significant relation to the proportion of forest land (Table 2). However, the quadratic response is stronger, with the curve peaking at 50 percent of forest land. At the very rural ends of the gradient, the number of natives represents the undisturbed and monotonous nature of coniferous forests. The absolute number of natives is similar in the rural and suburban areas. Suburban settlement does not necessarily correspond to lower numbers of native species in Finnish conditions. In Finnish suburbia, buildings are like small isolated spots in the wide forest and they have little effect on general vegetation. In the city centre, however, there is very little forest or any type of vegetation and, consequently, relatively few native species.

The percentage of natives has a highly statistically significant relationship to the distance from the city centre and the percentage of forest land, and a negative relation to population. The percentage of natives follows the proportion of forest land continuously, which reflects the importance of the forests to the natives (Fig. 16 and Table 2). When the proportion of forest land is lower than approximately 30 percent, the aliens take over. Landscaping of these areas has brought ornamentals and other alien plant species to the area.

The four selected variables account for as much as 88 percent of the variability of the percentage of the alien plant species (Table 2). The percentage of alien species has a highly significant negative relation to the distance from the city centre and the percentage of forest land. The percentage of aliens has a highly significant positive relation to the population.

The alien species dominate in the most urban quadrates (low in forests), but the share of alien species drops as forests increase (Fig. 16). The decrease in the share of forest land results in a linear increase in the share of alien species. The proportions of natives and aliens are inversely related to the proportion of forest. The absolute number of non-natives drops in the very city centre, but the percentage of non-natives does not (Figs 14 and 15). In the most urban areas, only a few habitats are available
for any plants, but the non-natives are not replaced with the natives either.

2.2.2. Disturbance dependent urban ecosystems: roadside and riverside green (V)

Study V consists of two parts: (1) comparison of traffic corridor species (species of road corridors and railway corridors) with the whole urban floras in cities of Vantaa, Kerava and Järvenpää (Fig. 17), and (2) comparison of urban corridors (both traffic and river corridors) with the entire urban flora at the municipal level in the city of Vantaa.

The material of traffic corridors is derived from the comprehensive study of the urban flora in the city of Vantaa (Ranta & Siitonen 1996). An update of the survey was published in 2002 (Metsätö Y 2002). The cities of Kerava and Järvenpää were mapped during the 1990s. The survey of the urban flora was made using the same methods in all cities: systematic mapping by grid cells of 1 km² (Fig. 19). The frequency and abundance of each plant observed in all grid cells was recorded with a habitat code. A system of 34 different habitat codes was used. Five of the codes were different types of traffic corridors (roads and railways). If the plant was observed in a traffic corridor, a corresponding code was used. If the plant was observed in different environment, one or several of the remaining 29 codes were selected. A single plant species could receive several codes according to the different habitats where it was growing (Figs. 18 and 19, Tables 6 and 7).

Fig. 18. The study area: cities of Vantaa, Kerava and Järvenpää in southern Finland with the main railway line.
Table 6. Main results of the floristic mapping of the cities of Vantaa, Kerava and Järvenpää with traffic corridors.

<table>
<thead>
<tr>
<th>City/municipality</th>
<th>Vantaa</th>
<th>Kerava</th>
<th>Järvenpää</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area (km²)</td>
<td>243</td>
<td>30.9</td>
<td>37</td>
</tr>
<tr>
<td>No. of grid cells</td>
<td>246</td>
<td>126</td>
<td>172</td>
</tr>
<tr>
<td>Total no. of species</td>
<td>704</td>
<td>771</td>
<td>712</td>
</tr>
<tr>
<td>No. of species in traffic corridors</td>
<td>485</td>
<td>516</td>
<td>501</td>
</tr>
<tr>
<td>No. of species not in traffic corridors</td>
<td>219</td>
<td>255</td>
<td>211</td>
</tr>
<tr>
<td>% of species in traffic corridors</td>
<td>68.9</td>
<td>66.9</td>
<td>70.4</td>
</tr>
</tbody>
</table>

The River Vantaa was mapped separately. The river was divided into one-kilometre long mapping units (1 km * 25 m). There are 27 of these mapping units inside the city of Vantaa, between 12 and 34 km from the river mouth (the other shore of the river partly belongs to Helsinki, the other to Vantaa). The right and left banks of the river were mapped separately. All plant observations along the river were attached with one of 11 river habitat codes and the estimated abundance and frequency values. The codes indicate the position of a plant in the river corridor (for example, in the water, on the shore below flood level or in the riverside forest). The mapping of river corridor plants along the River Vantaa was completed in 2002.

The total number of corridor species (traffic corridors and river corridors) in Vantaa is 540, which represents 76.1 percent of Vantaa’s total flora. The flora of the biogeographical province of Uusimaa consists of 880 species (Lahti et al. 1988), 61 percent of which have occurrences in corridors of Vantaa. The total estimated area of all corridors in Vantaa is approximately 653.4 ha (2.7 percent of the city area of 240.4 km²).

A general description of the city of Vantaa and its traffic corridors is presented in Article V. The River Vantaa is 99 km long and disembogues in the Gulf of Finland in the Baltic Sea. It stretches 37 km within the city of Vantaa (Fig. 18).

The total number of river corridor plant records in the study area (species x 1 km unit x habitat code) was 6650. A total of 339 species were observed in the river corridor inside the city of Vantaa (508 species along the entire 99 km-long corridor. The estimated total area of the corridors will be 189 ha (river corridors) and 464.4 ha (traffic corridors). The corridors are among the smallest habitat types in the city.

A comparison of the frequency distributions between corridor plants and non-corridor plants produces a clear difference. Corridor plants show bimodal
Fig. 19. Map of the study area: city of Vantaa with the River Vantaa, main highways and railways.

Fig. 20. The grid cells in the comprehensive urban floristic mapping. Each of the 246 cells is 1 km x 1 km. The white area in the middle of the city is the Helsinki-Vantaa airport (not mapped). Numbers indicate coordinates in the used coordinate system. Similar grid cell systems were used in the cities of Kerava and Järvenpää.
Table 7. Ecological profiles of the different species groups in Vantaa. RC = river corridor, TC = traffic corridors and NC = non-corridor (Ranta 2008). Variables: total habitat codes are the sum of habitat codes attached to each species in the citywide material. Total cells: the sum of the cells (1 km) where the species has been observed in the citywide mapping.

<table>
<thead>
<tr>
<th></th>
<th>RC</th>
<th>TC</th>
<th>NC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of species</td>
<td>339</td>
<td>485</td>
<td>164</td>
</tr>
<tr>
<td>% of all species</td>
<td>47.7</td>
<td>68.9</td>
<td>23.1</td>
</tr>
<tr>
<td>Total number of habitat codes</td>
<td>71.841</td>
<td>73.476</td>
<td>1682</td>
</tr>
<tr>
<td>No. of grid cells in citywide mapping</td>
<td>47.978</td>
<td>49.671</td>
<td>1511</td>
</tr>
<tr>
<td>Habitat codes/species observations</td>
<td>1.5</td>
<td>1.5</td>
<td>1.1</td>
</tr>
</tbody>
</table>

U-shaped frequency curves (Fig. 20 and 21), while non-corridor plants show a unimodal L-shaped frequency curve (Fig. 22).

A total of 540 species of vascular plants (76.1 percent of all the plants in Vantaa) have occurrences in corridors. By way of comparison, only 262 species have occurrences in herb-rich forests, the most productive and species-rich forest type in Finland (Ranta and Siitonen 1996). Corridor species represent a
dominant share of the available species pool of the city.

There are 800 established vascular plant species in the biogeographical province of Uusimaa (Lahti et al. 1988), 61 percent of these species occur in the corridors of the city of Vantaa. Three hundred and thirty species have occurrences both in traffic and river corridors.

Plant strategies have been defined as “groupings of similar or analogous genetic characteristics, which recur widely among species or populations and cause them to exhibit similarities in ecology” (Grime 2002). Plants with the same life strategy have a similar response to certain ecological conditions and will aggregate at a scale at which the ecological conditions are similar (Massant et al. 2009) (Table 7).

<table>
<thead>
<tr>
<th>Strategy</th>
<th>TC</th>
<th>RC</th>
<th>NC</th>
<th>Whole Vantaa</th>
</tr>
</thead>
<tbody>
<tr>
<td>C</td>
<td>16.8</td>
<td>18.5</td>
<td>12.4</td>
<td>17.2</td>
</tr>
<tr>
<td>S</td>
<td>14.7</td>
<td>15.7</td>
<td>29.2</td>
<td>18.0</td>
</tr>
<tr>
<td>SR</td>
<td>5.0</td>
<td>4.4</td>
<td>8.9</td>
<td>7.1</td>
</tr>
<tr>
<td>SC</td>
<td>10.7</td>
<td>12.4</td>
<td>8.8</td>
<td>10.2</td>
</tr>
<tr>
<td>R</td>
<td>19.7</td>
<td>17.1</td>
<td>16.8</td>
<td>17.5</td>
</tr>
<tr>
<td>CSR</td>
<td>16.4</td>
<td>13.0</td>
<td>14.6</td>
<td>13.2</td>
</tr>
<tr>
<td>CS</td>
<td>2.0</td>
<td>1.7</td>
<td>4.4</td>
<td>3.1</td>
</tr>
<tr>
<td>CR</td>
<td>14.9</td>
<td>16.7</td>
<td>5.8</td>
<td>13.8</td>
</tr>
<tr>
<td>N</td>
<td>457</td>
<td>183</td>
<td>329</td>
<td>272</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>C</th>
<th>S</th>
<th>R</th>
</tr>
</thead>
<tbody>
<tr>
<td>RC</td>
<td>329</td>
<td>3.7</td>
<td>3.1</td>
</tr>
<tr>
<td>TC</td>
<td>457</td>
<td>3.5</td>
<td>3.0</td>
</tr>
<tr>
<td>NC</td>
<td>137</td>
<td>2.8</td>
<td>4.3</td>
</tr>
<tr>
<td>Whole Vantaa</td>
<td>647</td>
<td>3.2</td>
<td>3.9</td>
</tr>
</tbody>
</table>

**Table 8.** Plant strategy types of different species groups (river corridors, traffic corridors and not in corridors) and all species in Vantaa. Percentages of all species. Strategy types as follows: C = competitor, S = stress-tolerator, SR = stress-tolerant ruderal, SC = stress-tolerant competitor, R = ruderal, CSR = CSR strategist, CR = competitive ruderal. Intermediate strategy types, such as CS and CR, were interpreted as in Hermy et al. (1999). Please note that there are a few species with no strategy type included in the used database.

**Table 9.** Mean strategy profiles of species included in corridor groups and the whole Vantaa.
3. DISCUSSION

3.1. Conservation of urban biodiversity in Finland – a success story?

Urbanisation is a significant factor in both current and predicted species extinctions, the consequences of which remain poorly known (Goddard et al. 2008, McDonald et al. 2008). In the study area, however, urbanisation is not a significant factor in the extinction of urban plants. The several agents of change and stressors have altered the species composition at different temporal and spatial scales, but the losses in the form of extinctions are minimal. In Helsinki, the list of extinct species in the 1900s consisted of 37 species out of 1070, of which 30 are natives (Kurtto pers.com., Kurtto & Helynranta 1998, Vähä-Piikkiö et al. 2006). Species of wetlands and seashores are well represented (23 out of 37).

According to the municipality of Tampere, 30 species of vascular plants (out of 1225) became extinct during the 1900s (Korte & Kosonen 2003) (Table 10.) A closer look at the list reveals that relatively few of the species are natives (8) or archaeophytes (10), while 12 are neohytes. There are several specialised weeds of expired cultivated plants on the list, such as flax (*Linum*) and rye (*Secale cereale*). Some species, such as corn cockle (*Agrostemma githago*), arrived in connection with grain imports. Several of the species have not been observed in the city proper, but in the rural parts of the city, the formerly independent municipalities of Aitolahki and Teisko.

The species on the list are mostly plants of cultural habitats (23/30), four species (4/30) of mires, swamps and shores (*Geranium palustre, Malaxis monophyllos, Pedicularis sceptrum-carolinum* and *Viola uliginosa*), two species (2/30) of dry meadows (*Botrychium lanceolatum* and *Gentianella amarella*) and one (1/30) of lakes (*Utricularia stygia*).

Extinction lists are remarkably short in the cities of Helsinki and Tampere, despite the rapid increase in the urban population over 100 years (Helsinki grew from 79,000 in 1900 to 550,000 in 2000, while Tampere grew from 36,000 to 210,000 in the same period) (Statistics Finland 2011). An increase in population means an increase of buildings, roads and other infrastructure. Several rural municipalities or parts of them have been annexed to Helsinki and Tampere (city proper) over 100 years, but these annexed areas are also now densely urbanised. There are no particular “safe havens” for plants, although the urban structure in the Finnish cities is clearly favourable for the conservation of plants (Antipina 2003).

The most extinction-prone species in any environment are rare ones, which
Table 9. Vascular plants that have disappeared from the City of Tampere (Korte and Kosonen 2002). NAT = native, ARC = archaeophyte, NEO = neophyte (Hämet-Ahti et al. 1998). IUCN categories, according to Rassi et al. (2010).

<table>
<thead>
<tr>
<th>Species name</th>
<th>NAT</th>
<th>ARC</th>
<th>NEO</th>
<th>IUCN category</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agrostemma githago</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alchemilla filicaulis ssp. vestita</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Allium igeraceum</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Androsace septentrionalis</td>
<td></td>
<td>x</td>
<td></td>
<td>EN</td>
</tr>
<tr>
<td>Asperugo procumbens</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Botrychium matricariifolium</td>
<td></td>
<td>x</td>
<td></td>
<td>EN</td>
</tr>
<tr>
<td>Bromus secalinus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Camelina alyssum ssp. alyssum</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Camelina alyssum ssp. integerrima</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carex praecox</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cuscuta epilinum</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cynoglossum officinale</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Draba nemorosa</td>
<td></td>
<td>x</td>
<td></td>
<td>EN</td>
</tr>
<tr>
<td>Dracocephalum triflorum</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Galium odoratum</td>
<td></td>
<td>x</td>
<td></td>
<td>NT</td>
</tr>
<tr>
<td>Gentianella amarella</td>
<td></td>
<td>x</td>
<td></td>
<td>EN</td>
</tr>
<tr>
<td>Geranium palustre</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juncus tenuis</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lithospermum arvense</td>
<td></td>
<td>x</td>
<td></td>
<td>EN</td>
</tr>
<tr>
<td>Lolium remotum</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Malaxis monophylllos</td>
<td></td>
<td>x</td>
<td></td>
<td>EN</td>
</tr>
<tr>
<td>Medicago sativa ssp. falcata</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Odontites vernus</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pedicularis sceptrum-carolinum</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plantago media</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Potentilla recta</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Satureja vulgaris</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thalictrum simplex</td>
<td></td>
<td>x</td>
<td></td>
<td>VU</td>
</tr>
<tr>
<td>Utricularia stygia</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Viola uliginosa</td>
<td></td>
<td>x</td>
<td></td>
<td>EN</td>
</tr>
</tbody>
</table>

are usually habitat specialists with narrow geographical distributions and patchy distributions (Volkov et al. 2003). These narrow specialists occur only in limited areas, where their preferred habitat is available. Many of the species that have disappeared from Finnish cities are specialists in one way or another. Populations are usually small and may disappear for stochastic reasons.

The present urban floras may be seen partly as legacies from the past agrarian areas, which later were transformed to cities. Modern cities may carry a large extinction debt. Finnish cities like Tampere, Helsinki and Vantaa have largely expanded on agricultural land. The species of the former agricultural areas may still constitute a considerable part of the present urban floras. The long-term survival of these species in a city may be doubtful (Hahs et al. 2010).
Urban extinction is usually caused by the construction of urban infrastructure to meet human needs (Williams et al. 2009). Some habitat types, such as wetlands and bogs, are clearly incompatible with the needs of urban people. Most bogs and similar habitats in Finnish cities have been drained and transformed, which explains the extinctions of several wetland species.

Some generalisations can be made on the basis of the implemented urban floristic surveys in Finland. If an urban environment is geologically, historically and culturally diverse, there should be ecological niches for several kinds of plants, including specialists. One way to test the diversity of a city is to calculate the minimum number of grid cells that include all the native plant species (or any other group of origin). In the city of Vantaa, for example, only 38 grid cells (1 km²) out of 246 (15.5 percent) contain all the native species. In Tampere, 88 grid cells (0.25 km²) out of 598 (14.7 percent) contain all the native plant species (Ranta and Siitonen 1996, Ranta et al. 1997, Ranta 2012).

On the other hand, in the urban archipelago (207 islands) outside the city of Helsinki, the number of species could be predicted by knowing only the size of the island (Ranta et al. 1999). This reflects the Finnish nature, including urban nature, which could be considered somewhat monotonous. The dominant ecosystem is the boreal coniferous forest. This reflects the prevalent Precambrian bedrock, young acid soils and the low variability of the topography (peneplain relief). Edaphic anomalies are known to diversify floras (such as so called serpentine species), but such anomalies are rare in Finnish cities (Williams et al. 2009). The history of mankind also has a substantial influence on the flora. For example, the period when Finland was united with the Russian empire (1809–1917) left a considerable legacy in the present flora of Finland. Such historical crossroads and periods of international exchange are rare in Finland.

The latest assessment of threatened species in Finland does not directly mention urbanisation as a threat factor (Rassi et al. 2010). However, factors like disturbance and traffic, mechanical wear, construction and other random factors may be indirectly connected with urbanisation.

Other studied agents of change (air and water pollution) have not caused regional extinctions of species. The air pollution episode was a meso-scale event, but the lichens returned after the amelioration of air quality, albeit in reorganised communities. In the case on lidesjärvi, a few species disappeared from the lake over 100 years, but not from the whole city or region. New arrivals offset the losses. The macrophyte species composition is influenced by the total available species pool of the region, within approximately 25 km of lidesjärvi (Toivonen & Huttunen 1995). This interchange of species increases resilience. According to Toivonen and Huttunen (1995), Lake lidesjärvi is part of the group of five regional hypertrophic lakes, which also includes Lake Kirk-
kojärvi, from where the new species *Potamogeton crispus* invaded Iidesjärvi in 2000.

Small urban woodlands may be seen as conservation hot-spots and as a good choice for promoting biodiversity conservation in towns (Croci et al. 2008). The studied urban forest fragment of Teerenpuisto seems to confirm this. After 120 years of fragmentation, the forest still maintains populations of rare and endangered species of both vascular plants and insects, such as the endangered *Hadena albimacula* (on *Silene nutans*) (Tampereen kaupunki 2008, 2009). None of the vascular plants of the forest disappeared in the 20-year period. “Woodlands seem to be a good choice for promoting biodiversity in towns” (Croci et al. 2008).

3.2. Resilience of urban ecosystems

Ecological resilience may be defined as the amount of disturbance that an ecosystem can withstand without changing its self-organised processes and structures (defined as alternative stable states) (Gunderson 2000). Ecological resilience is generated by a diverse but overlapping function within a scale and by apparently redundant species that operate at different scales. Scale can be defined as a range of spatial and temporal frequencies (Peterson et al. 1998).

A heuristic of a ball and cup has been developed to describe the different types of resilience (Gunderson 2000, Scheffer et al. 1993). At equilibrium, the ball remains at the bottom of the cup, while disturbances shake the cup and move the ball to another position in the cup. If the disturbance is strong enough, the ball may roll over to a new cup, a new alternative state.

Resilience building should be part of the agendas of urban spatial planning and design. Ecological land use complementation is suggested as a method to synergistically support biodiversity. So far, however, the urban development seems to have generated some of the greatest local extinction rates of species and eradicated a large proportion of native flora and fauna (Colding 2007). In Finland, however, cities have lost only a very small proportion of their plant species during the timescale of 100–150 years.

The three cases on temporal changes of biodiversity (papers I-III) and the two spatial studies (IV and V) are viewed below from the perspective of resilience.

3.2.1. Lichens and air pollution (I)

Air pollution in Tampere was a meso-scale event, both temporarily and spatially. However, a new alternative state was not reached because the epiphytic lichens returned after the improvement of air quality and, further away from the city, lichens survived the pollution, albeit in a deteriorated state. The epiphytic lichen community was reorganised because the lichens formed a different kind of vegetation after their return. The case is an example of external memory; the lichens survived outside of the city and returned from there to the former lichen desert.
3.2.2. Lake lidjesjärvi: a century of change – from a rural lake to an urban problem (II)

In the same catchment area as Lake lidjesjärvi, but upstream, is Lake Kaukajärvi. It has remained in a clear-water state (Bäck et al. 1988), provides several important ecosystem services, such as fishing and swimming, and has a rich aquatic flora. Downstream, Lake lidjesjärvi is in a turbid water state due to 100 years of pollution. The quality of water was probably not as clear as that of Kaukajärvi, but historical records mentioned lidjesjärvi as being suitable for recreation, fishing and swimming in the early 1900s. Water was used directly as drinking water (Keskitalo-Tanskanen 1998). After a long history of pollution, lidjesjärvi has lost most of its ecosystem services; frequent algal blooms in the hypertrophic lake prevent the penetration of light, while the fish have high concentrations of heavy metals and pesticides that reflect the condition of the sediments. Internal loading from nutrient-rich sediments is largely responsible for maintaining the high productivity. Nature observation remains the main ecosystem service of Lake lidjesjärvi.

In conclusion, the lake has collapsed into an undesirable state from a human point of view. The present management alternatives are:
(a) Restore it to a desirable state
(b) Allow it to return to a desirable state by itself
(c) Adapt to the changed system because the changes are irreversible.

Restoration may be theoretically possible, but would require huge resources that clearly exceed the possibilities of the municipality. Adaptation is the only viable option (Tampereen kaupunki 2009).

3.2.3. Urban forest fragment of Teerenpuisto: resisting urban pressure (III)

In Teerenpuisto, the incipient transition from one state to another can already be observed and will take place in relative near future. The invasion of alien species, increase of nitrogen and management practices (like temporary removal of thick coppice of Sorbus aucuparia) accelerate the change of the forest. In the period since fragmentation, habitat loss and isolation in 1880, the transition has barely started. The transition will occur when the dominant tree species, Pinus sylvestris, is replaced by Pinus cembra, Acer platanoides and Quercus robur, and this will have a profound effect on the species composition of the forest. Currently, the litter consists mostly of pine needles, but in the future there will be more deciduous trees and foliar litter. The forest canopy influences nutrient cycling in the soil, which affects the species composition in the field layer (Prescott, 2002). However, the area will remain as forest, although it will no longer be a sub-xeric esker forest.

The ecosystem services (recreation, biodiversity conservation, part of traditional cityscape) of Teerenpuisto forest have not changed and will remain unchanged after the transition to a new state. Teerenpuisto forest contains a lot of internal memory and it will be useful as a source of external memory for other urban areas.
3.2.4. Urban gradient (IV)

When boreal forests are considered, the five following factors are considered especially important for biodiversity: fire disturbance, deciduous trees, gap disturbance, long forest continuity and coarse woody debris (Esseen et al. 1997). None of these is particularly relevant in cities.

The observed resilience in Finnish cities has a clearly different foundation. The main explanatory factor is the typical structure of cities in the boreal zone. As Antipina (2003) stated, the urban structure is the key to resilience. The land use combinations of Finnish (and boreal) cities clearly promote biodiversity and maintain resilience (Golding 2007).

3.2.5. Disturbance dependent urban ecosystems: roadside and riverside green (V)

The corridors may connect different urban habitat patches with each other, which itself is a factor that increases resilience. Species must move from one habitat patch to another if they are to obtain enough resources (Pope et al., 2000, Melles et al. 2003).

The corridors also serve important functions as habitats and could contribute significantly to the urban biodiversity if they were taken into account in urban planning. Over 50 km of the River Vantaa will be included “accidentally” in the NATURA 2000 system because of the presence of a single endangered species, a protected River mussel Unio crassus. However, the river corridor would also be taken into account on the basis of other merits, as it is one of the most diverse urban ecosystems.

It seems as though now is not quite the time to identify traffic corridors as being worthy of biodiversity protection. This only occurs when an endangered species uses the road corridor as habitat. There is a clear need for a paradigm change in urban biodiversity conservation to achieve this.
4. IMPLICATIONS FOR URBAN PLANNING AND BIODIVERSITY CONSERVATION

4.1. Biodiversity conservation targets after 2010

The EU and the international community as a whole failed to reach the 2010 biodiversity targets. New targets were set for 2020 (Nagoya biodiversity targets) to stem the worst loss of biodiversity. These so-called “Aichi targets” are supposed to reduce the loss of natural habitats by at least half and expand the nature reserves to 17 percent of the world’s land area (Ortiz 2011). Among the Aichi biodiversity targets are several strategic goals, which intend to address the underlying causes of biodiversity loss, reduce the pressure on biodiversity and improve the status of biodiversity by safeguarding ecosystems, species and genetic diversity (Rands et al. 2010).

4.2. Institutional crisis of biodiversity conservation

At the EU level, the current policies appear to be insufficient to reverse the ongoing losses (Spangenberg et al. 2012). The United Nations’ establishment of the Intergovernmental Platform for Biodiversity and Ecosystem services represents a substantial but very recent strengthening of biodiversity governance (Vadrot 2011, Larigauderie & Mooney 2010). In spite of these improvements, there have been some difficulties in implementing the Convention of Biological Diversity (CBD) to stop the biodiversity loss. The reasons for these difficulties can be summarised as an “institutional crisis” (Vadrot 2011). The necessary legal instruments to implement the convention do exist and have existed for some time. The problem is clearly in governance (Warleigh-Lack 2010, Farinha-Marques et al. 2011).

4.3. The role of urban biodiversity

Urban biodiversity can play an important role in the implementation of the CBD’s future targets (Müller & Werner 2010, Pierce et al. 2011). In the urban context, however, the old planning paradigm is insufficient and even counterproductive because it is too rigid and static (Ernstson et al. 2010). A transition in urban governance is needed to face an uncertain future and build new capacity to absorb upcoming shocks. Resilience in cities is orientated towards sustaining local-to-regional ecosystem services. In general, essential parts of the resilience theory are highly relevant in cities (Batty 2008). Integrating resilience thinking and optimisation for urban biodiversity conservation can be seen as an important step forward. While resilience thinking emphasises the non-linearity of changes and the interdependency of social and ecological systems, optimisation is an outcome-orientated tool that contributes to the rationality and transparency of conservation decisions (Fisher et al. 2009). Recently, these two policy-relevant approaches have started to converge and

4.4. Paradigm change in urban planning

The present paradigm in urban planning can be described as rigid, inflexible and static. Although this paradigm was once progressive and useful, temporal renewal is necessary. Otherwise, the old paradigm will become a chain that prevents any future development. This is an impending danger in present urban planning and conservation.

Some of the main differences between the old and the new, emerging paradigm can be summarised as follows (Table 10).

In Europe, the present (old) paradigm is mainly based on legislation, particularly European Union legislation that has since been incorporated into national legislation. A conflict is emerging between the application of the main directives, such as the Habitat directive, and more general principles of conservation, such as the CBD.

In practice, when something like an environmental impact assessment is being conducted, only the status-species are taken into account. This is clearly not the way to protect biodiversity. Meanwhile, this legal loophole remains open; there is no need for conservation authorities to do anything more than just follows the legislation. The institutional inertia makes the presentation of creative alternatives unlikely. In the field of practical urban ecology, there appears to be puzzling lack of interest.

<table>
<thead>
<tr>
<th>Old paradigm</th>
<th>New paradigm</th>
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<tr>
<td>Static</td>
<td>Dynamic</td>
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<tr>
<td>Unidirectional</td>
<td>Interactive</td>
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<td>Sectorial</td>
<td>Holistic</td>
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<td>Goal-oriented</td>
<td>Process-oriented</td>
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<td>Public against private</td>
<td>Cooperation public-private</td>
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<td>Based on technical issues</td>
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<td>Government as provider</td>
<td>Private initiative</td>
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<tr>
<td>Centralised</td>
<td>Decentralised</td>
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Table 10. Some differences between the old and the new emerging paradigm in urban planning and conservation. Modified based on Cassano (2004).
in seeking new and innovative solutions, despite the fact that the academic field of urban ecology produces new approaches and innovations. Somehow, this is true for ecology in general. The lack of information and knowledge is not the problem, but the institutional inertia of present governance does not favour innovative new approaches.

The lack of alternatives is also reflected in urban conservation through protected areas. Among the new types of protected area that have been proposed are “ecological fallows”, which certainly could be useful for urban conservation (Bengtsson et al. 2003), but there are no examples yet of how to implement the idea.

The present urban structure in the boreal zone is favourable for biodiversity conservation. This feature may be threatened by the current trend of infill development. While infill development may provide some ecological advantages, there is a risk of serious losses in biodiversity and a weakened resilience capacity of urban nature.

Scenarios such as the air pollution episode of the 1970s and the collapse of Lake Iidesjärvi are no longer possible. In this respect, the European legislation with explicit limit values is an essential improvement. National regulatory protection also improved conservation in urban areas. Unfortunately, biodiversity conservation appears to still be in the shadow of other global challenges, such as climate change. Implementation deficits are proposed as a cause of the gap between policy goals and outcomes (Jordan 1999). Maintaining resilient cities is essential in order to meet any impending global change and major stochastic changes. On the other hand, slow variables may also push systems over a threshold (Ernstson 2010).

One of the new innovative ideas is the application of the no-net-loss (NNL) approach to urban ecology, which helps achieve biodiversity-neutral or even biodiversity-positive development projects.

Several practical mitigation techniques have been proposed (Sadler et al. 2011), mostly to manage site-specific problems. The main problem with improving and maintaining biodiversity in cities is that the cities have not been built with biodiversity conservation in mind. Conservation projects have to adapt themselves in the existing urban structures, both physically and ideologically.

Some positive developments can be noted. For example, the “Erfurt Declaration” of 2008 is a good starting point for raising awareness about protecting the unique urban contribution to global biodiversity (Müller & Werner 2010). However, are urban ecologist able to provide the demanded “exact and predictive” advice on conservation matters (Haila 2002) or will the urban environmental management be a classic case of a “wicked problem” (Gaston 2010)? The answer may be in the uniqueness of urban problems. There may not be a comprehensive theory to back the advice; pragmatism may be the only solution.
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