

# **Managing forest and meadow habitats for the enhancement of urban biodiversity**

**– messages from carabid beetles and vascular plants**

**Stephen Venn**

**Department of Biosciences,  
P.O. Box 65 (Viikinkaari 2),  
FI-00014 University of Helsinki  
FINLAND**

Helsinki 2013

**Academic dissertation**

**to be presented, with the permission of the Faculty of Biological and  
Environmental Sciences of the University of Helsinki, for public criticism  
in Auditorium 1041, Biocentre 2, Viikinkaari 5, Helsinki, on 9<sup>th</sup> August  
2013 at 12 p.m.**

## Contributions

The following table shows the contributions of authors to the original articles. The authors are referred to by their first initials, and the articles by their roman numerals.

|                 | I              | II         | III                            | IV         | V          |
|-----------------|----------------|------------|--------------------------------|------------|------------|
| Original idea   | DK, SV, JN, JS | JN         | JN, DK,                        | SM, SV     | SV         |
| Design          | DK, SV, JN, JS | JN, DK, SV | JN, DK, LP, IS, JS, DH, EM     | SM, SF, SV | TL, SV     |
| Methods         |                | JN, DK, SV | JN, DK, LP, IS, JS, DH, EM     | SM, SF,    | TL, SV,    |
| Data collection | DK, SV, JN, JS | DK, SV     | DK, IS, DH, EM, SV             | SF         | TL, SV     |
| Analyses        | -              | SV, JK     | IS, DH, EM, SV                 | SM         | TL, SV, DK |
| Writing         | DK, SV, JN, JS | SV, DK, JN | JN, DK, LP, IS, JS, DH, EM, SV | SM, SF, SV | SV, DK, JN |

DK = D. Johan Kotze, JN = Jari Niemelä, JS = John Spence, LP = Lyubomir Penev, IS = Ivailo Stoyanov, DH = Dustin Hartley, EM = Enrique Montes de Oca, SM = Sirkku Manninen, SF = Sonja Forss, SV = Stephen Venn

Supervised by

Professor Jari Niemelä,  
University of Helsinki,  
Finland.

Reviewed by

Professor Kari Heliövaara,  
University of Helsinki,  
Finland.

Senior Researcher Gabor Lövei (Ph.D.),  
Aarhus University,  
Denmark.

Examined by

Senior Lecturer Alvin Helden (Ph.D.),  
Anglia Ruskin University,  
UK.

ISBN 978-952-10-9049-3 (paperback)

ISBN 978-952-10-9050-9 (PDF)

Unigrafia  
Helsinki 2013

If all mankind were to disappear, the world would regenerate back to the rich state of equilibrium that existed ten thousand years ago. If insects were to vanish, the environment would collapse into chaos.

~Edward O. Wilson



# INDEX

## LIST OF ORIGINAL ARTICLES

### Abstract

|   |    |
|---|----|
| 1. Introduction.....  | 8  |
| 1.1 Urban Ecology.....  | 8  |
| 1.2 The Gradient approach .....   | 10 |
| 1.3 Urbanization gradients - Geographically arranged and non-geographically arranged gradients..... | 12 |
| 1.4 Stress and disturbance in urban ecosystems.....   | 12 |
| 1.5 Effects of stress on biological communities in urban landscapes.....                            | 15 |
| 1.6 Comparisons between habitats.....   | 18 |
| 1.7 Carabid beetles as study organisms .....  | 19 |
| 1.8 Objectives of the thesis .....  | 22 |
| Hypotheses .....  | 22 |
| 2. Materials and Methods .....  | 24 |
| 3. Results.....   | 28 |
| 3.1 Results of paper I.....   | 28 |
| 3.2 Results of paper II.....  | 28 |
| 3.3 Results of Paper III.....   | 30 |
| 3.4 Results of paper IV.....  | 31 |
| 3.5 Results of paper V.....   | 31 |
| 4. Discussion .....   | 32 |
| 4.1 Hypotheses revisited.....   | 35 |
| 4.2 Conclusions and recommendations for enhancing biodiversity in urban habitats .....              | 41 |
| Acknowledgements .....  | 44 |
| References .....  | 45 |

## LIST OF ORIGINAL ARTICLES

- I. Kotze, J., Venn, S., Niemelä, J. & Spence, J. 2011 Effects of urbanization on the ecology and evolution of arthropods. In: J. Niemelä, J. Breuste, T. Elmqvist, G. Guntenspergen, P. James and N. McIntyre (eds.) *Urban Ecology: Patterns, processes and applications* Oxford University Press, Oxford, UK pp. 159-166, with the kind permission of Oxford University Press.
- II. Venn, S.J., Kotze, D.J. & Niemelä, J. 2003 Urbanization effects on carabid diversity in boreal forests. *European Journal of Entomology* **100**: 73-80 with the kind permission of the Biology Centre, Institute of Entomology, Czech Academy of Sciences.
- III. Niemelä, J., Kotze, D.J, Venn, S., Penev, L., Stoyanov, I., Spence, J. Hartley, D. & Montes de Oca, E. 2002 Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison. *Landscape Ecology* **17**: 387-401, figures 1-3, with kind permission from Springer Science and Business Media.
- IV. Manninen, S., Forss, S. & Venn, S.J. 2010 Management mitigates the impact of urbanization on meadow vegetation. *Urban Ecosystems* **13**: 461-481, figures 1-5, with kind permission from Springer Science and Business Media.
- V. Venn, S.J., Kotze, D.J., Lassila, T. & Niemelä J.K. 2013 Urban dry meadows provide valuable habitat for granivorous and xerophilic carabid beetles. *Journal of Insect Conservation* **17**(4): 747-764, figures 1-5, (Springer Science+Business Media Dordrecht 2013), with kind permission from Springer Science and Business Media.

## Abstract

In this thesis I use carabid beetles (*Coleoptera, Carabidae*) and vascular plants to investigate the ecological effects of urbanization on forested and dry meadow habitats in the city of Helsinki, Finland. I also investigate factors that affect species diversity and the occurrence of rare and sensitive species in particular, in order to draft recommendations for habitat management for the enhancement of urban biodiversity. Urbanization gradient analyses are conducted using multivariate ordination analyses to elucidate assemblage level responses, ANOVA is applied to determine the assemblage level response of spruce forest carabid assemblages and GLMM is used to model individual species responses. The results suggest that, in contrast to Gray's suggestion, Preston's log-normal does not accurately describe the species distributions of carabid beetles in the studied habitats but rather they follow the predictions of Fisher's log series and Hubbell's unified neutral theory. I conclude that fragmentation, isolation and homogenization are the main problems regarding maintenance of urban biodiversity, and that biodiversity strategies should focus on the conservation of stenotopic species. In particular, habitats and ecologically important microhabitat conditions should be retained in as large and contiguous a form as possible. For instance, spruce forest habitats need to be managed to maintain shady, cool and moist conditions and dry meadows should be mown late in the season and the cut vegetation removed. Additionally, supplementation of habitat networks should be implemented, by habitat restoration and habitat creation, such as the construction of dry meadows on landfills and noise abatement banks.

**Key words:** Carabid beetles, disturbance, forests, gradient, meadows, stress, urban ecology

# 1. Introduction

This thesis considers the carabid beetle (Plate 1) communities of two biotopes that are predominant in cities of the boreal region, such as Helsinki. These are spruce forest (Plate 2) and dry meadows (Plate 3). My primary objective is to derive recommendations for the management of semi-natural habitats in urban regions for the maintenance and enhancement of biodiversity. Thus the fields of study for this thesis are Urban Ecology and Conservation Biology. Urban ecology has been defined by McDonnell (2010) as follows: “*Urban ecology integrates both basic (i.e. fundamental) and applied (problem oriented) natural and social science research to explore and elucidate the multiple dimensions of urban ecosystems.*” Conservation biology in turn has been defined by Hunter and Gibbs (2007) as “*the applied science of maintaining the earth’s biological diversity.*” Soulé and Wilcox (1980) emphasized that conservation biology is also about influencing the conservation of biodiversity as opposed to simply documenting its fate by described conservation biology as “*a mission-oriented discipline comprising both pure and applied science*” which Soulé (1985) later refined by adding that conservation biology is a “*crisis-oriented*” or “*crisis-driven*” field of science. In this thesis there is ecological research of the plant and carabid beetle assemblages of the studied habitats and data on environmental factors associated with urbanization, to allow the elucidation of some dimensions of the studied urban ecosystems.

## 1.1 Urban Ecology

The study of the ecology of urban habitats received little attention prior to the latter part of the twentieth century (Grimm 2000, McDonnell 2010) and only really began with vegetational studies by such researchers such as Sukopp, Wittiger and Gilbert, after pioneering studies in the city of Berlin by Scholz (1960). During the early decades of ecological science, in the late 18<sup>th</sup> and much of the 19<sup>th</sup> century, the equilibrium paradigm, which suggests that nature is in equilibrium, and returns to a state of stability subsequently to disturbance events (Marsh 1864, Simberloff 1982), ecological studies were invariably focussed on natural areas, as far as possible from the influence of the actions of man (McDonnell 2010). As a consequence of this, very little information is available on the ecology of urban habitats prior to the late 20<sup>th</sup> century (Pickett & McDonnell 1993) and humans came to be viewed as observers of, rather than participants in, ecological processes (Rees 1997, Sukopp 1998). Critical appraisal of the equilibrium paradigm during the 1990s led to the emergence of the contradictory non-equilibrium paradigm, whereby ecosystems are seen to depend on functions and processes (Pickett *et al.* 1992) rather than on a course towards an equilibrium status. This paradigm shift in the discipline of ecology has facilitated the



development of environmental science, with its basis in the multidisciplinary study of practical problems and urban ecology, which focuses on the ecosystems of urban regions (McDonnell 2010). A direct consequence of the advent of the non-equilibrium paradigm is the recognition of humans as components of ecosystems, and interest in studying the responses of ecosystems to human activities increased (Alberti 2008, McDonnell 2010).

New inertia for the study of urban ecosystems has arisen from human population growth and the ever increasing proportion of the human population living in cities (UNFPA 2007), which has resulted in urbanization affecting an ever increasing proportion of the earth's surface and consequent decline in the proportion of undisturbed habitats. It has been suggested that there is now no ecosystem on earth which is unaffected by humans (Vitousek *et al.* 1997, Berkes & Folke 1998). It is estimated that more than 50% of the world's population now lives in cities and it is projected that the urban population of 3.6 billion in 2011 will increase to 6.3 billion by 2050 (UN 2011). It has also been estimated that the amount of urban land cover is increasing at twice the rate the urban population is expanding (Seto *et al.* 2011).

In recent decades, faunistic and ecological studies have been carried out to study the responses of various taxa to urbanization, such as those of Czechowski and Pisarski (1981) in Poland and Klausnitzer (1993) in Germany, for example. This has led to the recognition of species with an affinity for urban habitats, which have been termed synanthropic (Nuorteva 1963, 1971). Klausnitzer (1993) focused on carabid beetles as an indicator group for studies on the ecological effects of urbanization, conducted in Leipzig. Niemelä subsequently initiated the Globenet project (Papers II & III), which used forest carabid assemblages to elucidate global patterns of ecological responses to urbanization. Results of the Globenet project have been reviewed by Niemelä and Kotze (2009) and Magura *et al.* (2010).

Subsequent to these studies, there has been much work on the ecology of urban regions, and the environmental factors affecting urban ecosystems. A good review of early studies is provided by Gilbert (1989) and more recently a number of volumes have been published containing syntheses of urban ecological research, including those by Alberti (2008), Gaston (2010), Marzluff *et al.* (2008) and Niemelä *et al.* (2011). There is general consensus on the characteristics of urban habitats, such as highly fragmented habitat patches, mosaics with patches of harsh and inhospitable habitats, frequent disturbance events, early successional stages, high levels of nutrients, pollution and altered climatic conditions (Gilbert 1989, Niemelä 1999, Niemelä *et al.* 2011). This has led to attempts to develop a theory of urban ecology to account for the influences of urbanization on species assemblages (McDonnell & Hahs 2008). On a broad scale, this has been thwarted by the fact that, in contrast to the homogeneity of land-use in agriculture and forestry, patterns of urbanization are

highly variable. In practice, attempts to define some habitats as urban and contrast these with “natural” habitats, is beset by the problem that throughout most of the ecologically studiable habitats in the world, remarkably few approach naturalness in terms of being unaffected by humans. This distinction between natural habitats (those unaffected by humans) and anthropogenically modified habitats brings us also to the question of whether humans are part of the ecosystem we are studying or an extrinsic factor affecting it. If we take the latter viewpoint, then it would also be necessary to consider the status of some other species that radically modify habitats. Urban habitats are clearly characterized by intensive modification of the landscape and habitats by human activity, so the ecosystem approach, in which the human population is an integral part of the urban ecosystem, is highly applicable to the study of urban ecology.

There has also been a growing trend in urban ecology towards studies of ecological processes at the level of the whole city (see Alberti 2008, Hahs *et al.* 2009) and the distinction between studies of ‘ecology in cities’ and ‘ecology of cities,’ the former concentrating on species responses to urban phenomena and the latter to processes involving the city as an entity and the environments and humans which are involved in those processes (Pickett *et al.* 2001).

A major element of the study of ecology in cities has been the use of environmental gradients to investigate species and assemblage responses to urban phenomena or more generally to urbanization, often by means of urbanization indicators. The gradient paradigm provides the basis of the empirical studies of this thesis (Papers II, III, IV and V).

## **1.2 The Gradient approach**

The use of gradients in ecological studies was pioneered by Robert Whittaker (1967), who conducted an exhaustive series of field studies on plant communities along gradients of a variety of environmental variables, to look for patterns in species and community responses. The results of these studies clearly showed that the response for plant species to the tested variables was a unimodal Gaussian curve, with a peak response at the optimal level of the variable, which then tails off as the level of the variable increases or decreases (Whittaker 1967).

Ecological application of the gradient approach has subsequently diverged into direct gradients, in which “*a species’ abundance is described as a function of measured environmental variables*” and indirect gradients, in which “*community samples are displayed along axes of variation in composition that can subsequently be interpreted*”

*in terms of environmental gradients*" (ter Braak & Prentice 1988). If there is more than one factor that possibly varies along the gradient and potentially affects the occurrence probability of the species being considered, then the gradient is said to be complex as opposed to simple gradients, in which the species response is considered to be elicited by a single environmental variable (ter Braak 1994). In complex gradients, it is often impossible to ascertain with certainty which factor is responsible for the observed response. In practice, it is highly unlikely that we can be 100% certain that a particular gradient is simple, so it is probably wisest to assume that most gradients are complex. Direct gradients are gradients in which we take measurements of both the environmental gradient and the species response, which enables us to generate a calibrated curve that can subsequently be used for estimating species responses to particular levels of the environmental variable. In indirect gradients, we try to derive a curve that describes the relationship between species and environmental factors but is not calibrated and not suitable for making quantitative estimations of response (ter Braak 1995).

Another important conclusion that can be drawn from Whittaker's studies is that we cannot always assume that the response of a species to an environmental gradient is independent of other species that occur along that gradient. This influence can be clearly appreciated when interspecific interactions, such as competition, occur along the studied gradient. Some rhododendron species, for example, produce a unimodal response but competitively exclude most other plant species, so that other species growing along the same gradient consequently exhibit a bimodal response, with a trough coinciding with the peak of the strong competitor species and peaks to either side. This obviously implies that, even within the taxon of vascular plants, there is a range of possible species interactions that could produce deviations from the simple Gaussian curve response. (Whittaker 1967)

Sessile taxa, such as vascular plants, are clearly an ideal group for gradient studies, as individuals are bound to a fixed point in the substratum and are absolutely subject to the level of the tested factors at that point. However, it is also desirable to study the results of higher taxa to environmental gradients and consider such questions as whether they are responding directly to the studied gradient or indirectly to the response of a lower taxon. With taxa that are large, motile and relatively scarce at the geographical scale of the study in question, this might be impractical, however taxa which are more speciose and move over a more confined area, such as arthropods, have proven suitable for gradient studies (Paper III, Blair 2004, Niemelä & Kotze 2009).

Whilst Whittaker's original work was based on direct linear gradients, studies of more complex gradients have led to a broadening of the ecological gradient paradigm and

its application to such phenomena as urbanization (Paper III, McDonnell *et al.* 1997, Niemelä & Kotze 2009).

### **1.3 Urbanization gradients - Geographically arranged and non-geographically arranged gradients**

Whittaker's (1967) gradient studies focused on responses of plant species to environmental variables, which tend to undergo gradual changes through the studied environment. One of the challenges with applying this approach to urbanization gradients is that urban areas comprise of mosaics of often highly contrasting habitat types and thus many environmental factors undergo abrupt and discontinuous (Niemelä 1999), rather than smooth and linear, changes. This challenge has been addressed in different ways in different studies. One approach is to use a sufficiently large geographic scale, e.g. at the whole city level, with a gradient extending from the city centre to the surrounding peri-urban or rural region, and sampling a selected taxon from a standard habitat type at regular intervals along the gradient. This approach has been employed in a comprehensive series of studies by McDonnell *et al.* (1993, 1997) in New York and the international Globenet project (Papers I, II & III, Niemelä & Kotze 2009, Magura *et al.* 2010), for instance. An alternative approach has been to construct a gradient that is independent of geographical location, but arranged into a gradient on the basis of levels of a measurable or estimable variable, such as vegetation cover (Blair 2004, Vallet *et al.* 2008). Whilst both of these approaches have their advantages and disadvantages, and ardent critics and supporters, each is suitable for the investigation of certain ecological problems. In this thesis, the geographically organized gradient approach has been applied to studies of carabid assemblages of forest habitats (Plate 2) in the Globenet project (Papers II & III) and the non-geographically arranged gradient in the study of carabid assemblages and vegetation of dry grasslands (Papers IV & V). In each case, the gradient approach applied revealed an urbanization effect and can therefore be considered successful. It is likely that there would be a high degree of correlation if the two approaches were applied to the same study.

### **1.4 Stress and disturbance in urban ecosystems**

The terms stress and disturbance describe additional factors that influence the species communities of urban habitats in particular. For plant communities, Grime (1977) defined stress as "*conditions that restrict production, e.g., shortages of light, water, or mineral nutrients and suboptimal temperatures*" and disturbance as "*the partial or total destruction of the plant biomass*" that "*arises from the activities of herbivores, pathogens, man (trampling, mowing, and ploughing)*" as well as "*from*

*phenomena such as wind damage, frost, desiccation, soil erosion and fire*". They can be distinguished from each other in that stress refers to a factor which continuously affects a community or habitat, and disturbance refers to a factor which occurs as a periodic event. Disturbance is likely to result in loss of individuals and species, and causes a temporary change in conditions, followed by a period of recovery towards the conditions that were prevalent prior to the disturbance. Stress refers to factors that are generally continuously present in a community and restrict the growth of some species, often as a consequence of which the growth of other species may be enhanced, for example, by reducing the growth of competitors. Grime suggested already in 1974 that stress represents a potential means of enhancing species diversity by reducing the growth of dominant species and providing opportunities for poorly competitive species (Grime 1974).

Application of the phenomena stress and disturbance to higher taxa necessitates modification of their definitions, and thus disturbance is defined by Krebs (2001) as "*any discrete event that disrupts community structure and changes available resources, substrate availability or the physical environment.*" From the perspective of biodiversity, disturbance events restrict the populations of some species in a community (predominantly abundant or dominant species) and provide an opportunity for other species to become established or expand (Sousa 1984, Pickett *et al.* 1989, Wootton 1998). This concept of disturbance effects has emerged from the development of the non-equilibrium model of community organization, in which it is recognized that species communities are not proceeding towards an ideal stable state but that some species communities are dependent on patch dynamics and the influence of disturbance events which interrupt the course towards such a stable condition (Krebs 2001). Disturbance processes often have a successional response, characterized by 1) the disturbance event, 2) gradual recovery and return to pre-disturbance conditions and 3) subsequent disturbance event. In urban regions, it has been suggested that the influence of stress and disturbance is at least partially the cause of reductions in the evenness of assemblages (Paper I) and dominance by tolerant species, including introduced species (Niemelä & Kotze 2009). This may seem to contradict the suggestion of Grime that stress can enhance biodiversity by controlling the growth of dominant plant species, though this can probably be explained referring to the Intermediate Disturbance Hypothesis (IDH) (Connell 1978). Connell suggested that assemblages with low levels of disturbance have relatively low levels of diversity, because of the limited amount of resources and niches available. Moderate levels of disturbance increase the availability of resources and niches and facilitate colonization by opportunistic species, whilst retaining most of the original assemblage and thus lead to enhanced species diversity. When the level of disturbance becomes excessive, then the original species are lost and the diversity gradually declines (Connell 1978). Thus in terms of Connell's paper, the level of disturbance represented by management of meadow vegetation would be equivalent

to an intermediate level of disturbance and therefore beneficial in terms of species diversity, and that represented by carabid communities of highly stressed urban habitats would equate with high levels of disturbance, that result in loss of species from the original assemblage and reduction in species diversity. It was also pointed out in Connell's (1978) paper that many species are well adapted to natural anthropogenic disturbance regimes, though the impact of anthropogenic disturbances tend to be more dramatic, which is also likely to be the case with many urban habitats and their assemblages. IDH has been found to apply reasonably well to studies of individual taxa at low trophic levels, though generally not to taxa at higher trophic levels (Wootton 1998). Wootton (1998) also found that in taxa with effective dispersal, outside immigration produced results that differed from the predictions of IDH.

Clearly many forms of habitat management also constitute disturbance or stress. For semi-natural grassland habitats – which also occur in urban landscapes - it has long been recognized that management regimes involving the periodic removal of vegetation enhance the growth of forbs, which are otherwise unable to compete with more vigorous plant species (Paper IV, Luoto *et al.* 2003). Thus the growth of dominant vascular plant species is reduced and that of sub-dominant species enhanced. Consequently, insect taxa that are dependent on these forbs also benefit from such management, even though they may sustain losses of numbers as a direct response of such management (Pöyry *et al.* 2004). This procedure can also be considered as a strategy for addressing eutrophication (Paper IV). Traditional management, by grazing with livestock or mowing for fodder, removes nutrients from such grassland habitats. In grassland habitats that are not managed, eutrophic plants dominate the field layer vegetation and increase soil nutrient levels, thus generating conditions that are unsuitable for plants of nutrient poor conditions (Paper IV). Therefore, in the absence of appropriate management, grassland habitats revert to eutrophic swards from which suitable conditions for many declining plant species are absent.

As the decline in such management strategies for agricultural purposes (Luoto *et al.* 2003) has caused declines of many insect and vascular plant species, the resumption of such management of suitable habitats is the optimal strategy for addressing the issue. However, as the cessation of management of meadow habitats in Finland has affected more than 1.5 million hectares, of which much has been converted to other forms of land-use (Luoto *et al.* 2003), the task of redressing this loss is insurmountable, though it is essential for us to develop measures for providing and maintaining suitable habitat for these communities. However, in municipal regions it is often possible to budget resources for habitat maintenance for the express purpose of enhancing biodiversity (Paper V).

Contrastingly, in the case of boreal spruce forests (Plate 2) (which are widespread in cities of the boreal region), it is generally considered that the late successional stage is the most important for biodiversity (Niemelä *et al.* 1996). The reason for this is that many of the most threatened species, i.e. the scarcest and most stenotopic species, are dependent on this stage. Additionally this is the successional stage that has declined most due to intensive land-use changes during the 20<sup>th</sup> century (Rassi *et al.* 2010). For obvious reasons, such forests have also declined in urban areas.

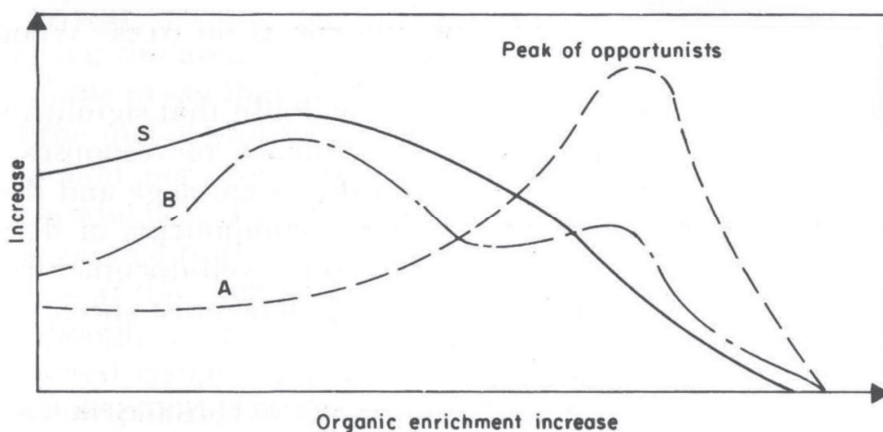
The contrast between forest (Plate 2) and grassland (Plate 3) habitats regarding disturbance and from a conservation perspective is interesting. Whilst maintenance of biodiversity in grassland habitats requires the application of management regimes that interrupt the successional process at an early stage and prevent progress towards subsequent successional stages (e.g. Paper IV, Balmer & Erhardt 2000), management regimes that interrupt the succession of boreal spruce forests are generally considered as harmful to biodiversity. Storm damage and fire, however, are forms of disturbance that are generally considered to enhance forest biodiversity, by increasing heterogeneity and creating niches and resources that are required by a considerable number of specialized species in a variety of taxa (Angelstam & Kuuluvainen 2004).

### **1.5 Effects of stress on biological communities in urban landscapes**

Stress constitutes a factor that regulates growth (of plant species in Grime's original context) rather than an event from which affected taxa gradually recover. The biological effect of stress is to directly reduce the growth of individuals and populations of some species or taxa, as a consequence of which other species might experience improved growing conditions as an indirect response. Such stress factors could be temperature or growth retarding chemicals. Many such factors have negative effects on some taxa and positive on others. Clearly, along a temperature gradient there will be a point when there is high species richness, around a temperature that is ambient to most of the community (Whittaker 1969). As we proceed in either direction from this point, the number of species will fall, as less tolerant species disappear and tolerant species remain. Thus increasing or decreasing temperature constitutes a stress for those species that are not tolerant and benefits those species that are tolerant.

Gilbert (1987) observed that dog urea is toxic for many plant species but enhances the growth of a small number of species that are tolerant, such as stinging nettle *Urtica dioica* and ground elder *Aegopodium podagraria*. Pearson and Rosenberg (1987, reviewed by Gray 1989) studied the effects of stress in the form of organic

solvents in seawater on benthic plankton communities adjacent to North Sea oil rigs and a number of studies have subsequently tried to apply this model to studies of carabid beetle assemblages along urbanization gradients (Magura *et al.* 2004, Niemelä & Kotze 2009, Magura *et al.* 2010), considering urbanization gradients as equivalent to stressor gradients. Pearson and Rosenberg (1987) estimated changes in biomass, species richness and abundance along a solvent gradient (Fig. 1). For species richness, they found an initial slight increase in species number and rapid increase in biomass, due to an increase in abundant opportunist species. This model, however, does not allow for the influence of extinction debt (Hanski & Ovaskainen 2002), according to which, after an unfavourable change in conditions in a habitat, affected species do not disappear immediately but rather there remains for some time a cohort of species for which the habitat is no longer suitable. These species gradually decline and eventually become extirpated. A proportion of the species present at this part of the gradient will probably constitute such an extinction debt, and which are in decline due to unfavourable changes in conditions.

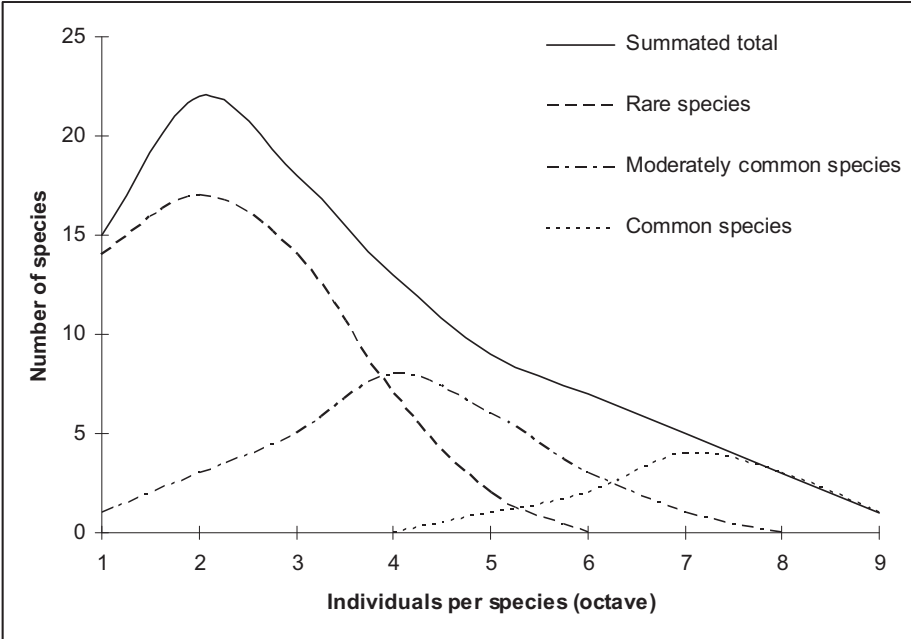


**Fig. 1** Generalized model of the effects of organic enrichment on species (S), abundance (A) and biomass (B), reproduced with permission of the publisher from Gray 1989.

Gray (1987) had previously proposed the multi-group model for the assemblage composition of undisturbed communities (Fig. 2), based on Preston's (1948, 1962) log-normal distribution. His model suggests that the log-normal distribution of ecological communities is based on three underlying Gaussian curves, 1) rare species, of which there are a large number in octaves with few individuals, resulting in a Gaussian curve with a high peak, a low mean and a broad amplitude 2) moderately common species, of which there are fewer species, an intermediate mean and a broad amplitude and 3) very common species, of which there are only few species, with a greater mean and a broad amplitude. The combination of these three curves should, according to Gray, produce the characteristic log-normal curve,



as a Gaussian curve skewed towards the right. The curve should not intersect the y-axis but commence from the y-value corresponding to the number of species represented by single observations, as there should be no value for the zero octave. In this thesis I consider how this distribution applies to carabid assemblages of urban habitats.



**Fig. 2** Multi-group model, based on Preston's (1948, 1962) log-normal distribution and proposed by Gray (1987). Number of species is plotted along the y-axis and individuals per species along the x-axis, where the first octave represents the number of species represented by single individuals, and the second by species represented by two individuals, etc. The summated curve is the sum of the underlying curves for rare species, moderately common species and common species. Adapted from Gray 1987.

The studies of both Whittaker (1969) and Pearson and Rosenberg (1987) have shown that the response of species richness to factors affecting population growth is generally non-linear. The response of individual species is to increase in number of individuals towards their optima and decline at a rate determined by their tolerance. By plotting responses of individual species in communities to gradients of a variety of factors affecting plant growth, Whittaker also showed that the tolerance ranges of different species vary considerably and that interspecific effects, such as competition, can also strongly affect the response patterns. Whittaker only considered plant taxa, so the possible influence of other taxa, such as herbivores, which might also respond to the same gradients, was not considered. In this thesis I study the responses of carabid beetles to urbanization gradients and consider whether their response to the

urban gradient is comparable to the gradient responses suggested for plants and plankton. I will do this by evaluating the responses of species richness and activity density (Paper III) and of individual species (Paper V) to the urbanization gradient. Whilst it is logical that plant species exhibit Gaussian responses to gradients of required factors, such as light, moisture, etc., with their median at the optimal value, responses to stressors are likely to be more complicated for motile taxa, such as carabid beetles along complex gradients, such as the urbanization gradient.

## **1.6 Comparisons between habitats**

The species assemblages of similar habitats can objectively be compared with a reasonable degree of confidence using any of a number of diversity indices for this purpose, subject to their fulfilling the criterion of similarity (Magurran 2004). When attempting to make any comparisons between assemblages from dissimilar habitats with very different levels of trophic and structural complexity, such as the forests and grasslands of this thesis, then it is highly challenging to go beyond the assertion that one contains more species than the other. Forests in the boreal region undergo an extremely long successional process (Angelstam & Kuuluvainen 2004). If ecological value is estimated according to the resources present, the difficulty of replacing them if they were lost and the presence of conservationally important scarce and vulnerable species which utilize those resources, then forest habitats should generally be considered highly valuable. In comparison, grasslands represent very low levels of structural complexity, contain little in the way of irreplaceable or slowly developed resources and constitute an early stage in the same woodland succession. However, in practise, all but a very small minority of such forests in southern Finland consist of relatively young forests with very low provision of such ecologically important resources as continua of decaying wood (Rassi *et al.* 2010).

A total of 16% of Finland's threatened and near threatened vascular plant species are associated with forests and 28% are associated with cultural habitats, such as meadows. It has been suggested that the overgrowth of meadows and other open habitats is the key threat for threatened plant species in Finland (e.g. Kalliovirta *et al.* 2010). For the Coleoptera, 22% of the total of 3416 species recorded from Finland are threatened and, of these, 37% are primarily associated with forests and 31% primarily with cultural habitats (Hyvärinen *et al.* 2010). Regarding the focal species of this thesis, however, there are only few threatened carabid beetle species associated with forest habitats and a considerable number associated with cultural habitats. To illustrate the true conservation value of forest habitats, it would be necessary to include a study of saproxylic taxa, which are not within the scope of this thesis.

## 1.7 Carabid beetles as study organisms

Carabid beetles (Plate 1), also commonly referred to as ground beetles (Coleoptera, Carabidae), are a family of insects that are predominantly epigeic in the temperate region, and are generally described as fast moving and voracious predators (e.g. Chinery 1993). The Finnish carabid fauna contains approximately 330 species (Chinery 1988, p. 292). The carabid fauna of Northern Europe in particular has been very well studied over a long period and the literature contains precise information on species traits and habitat preferences (Thiele 1977, Lindroth 1985, 1986, 1992, Lövei & Sunderland 1996, Luff 2007). This makes them highly appropriate for studies of the ecological effects of environmental phenomena, though caution is required when applying the results of such studies to other taxa.

Classifications of carabid beetles usually divide species into forest and open-habitat species. Other categorizations include habitat amplitude (e.g., eurytopic/synanthropic), moisture preference (hygrophilic/mesic/xerophilic), mode of feeding (predator/herbivore) and length of flight wings (macropterous/brachypterous/apterous) (e.g. Lindroth 1985, 1986, 1992). Whilst the latter of these is based on measurable physiological and anatomical features (presence/absence of wings, wing length and presence/absence of functional flight muscles), most of these traits include elements of subjectivity. Categorization into predatory or herbivory feeding types has been determined on the basis of mandibular anatomy (Forsythe 1982, Paarman *et al.* 2006) though the reliability of using anatomical features to determine feeding mode has been called into question by research on actual feeding preferences, which has revealed that the majority of species are in practice omnivorous (Saska 2008). Also the open habitat study presented in this thesis shows that many carabids that are commonly associated with forest habitats, such as *Pterostichus melanarius*, *P. niger* and *Trechus secalis*, are also among the most predominant species in open habitats (Paper V). These categorizations are still very useful aids in the interpretation of empirical data collected in ecological field studies using carabid beetles and constitute an essential element of this thesis, though contemporary research results should also be used to periodically revise species classifications in order to improve their applicability.

Carabid beetles of the Fennoscandian region have been categorized into forest species and open habitat species (Lindroth 1985, 1986, 1992). Regarding open habitat species in Northern Europe, a number of studies have looked at the carabid assemblages of agricultural habitats (Kinnunen *et al.* 2001, Holland 2002, Saska *et al.* 2007), and urban green space (Šustek 1992, Klausnitzer 1993), though studies on conservationally important meadow habitats have focused more on such taxa as vascular plants (Luoto *et al.* 2003), butterflies (Kuussaari *et al.* 2007) and bees (Oertli *et al.* 2005).

According to the red data book (Rassi *et al.* 2010) there are 47 vascular plant and 284 coleopteran species associated with forest habitats, and 90 vascular plant and 223 coleopteran species associated with cultural habitats. For both forest and agricultural habitats, considerable species data collection has been performed already. Ongoing urban expansion, however, has led to the increasing presence of such habitats in urban regions. Such habitats often have a similar history to rural sites but are influenced by a different set of environmental variables, including stresses and disturbances in a variety of forms. Furthermore, these habitats are often not subject to economic productivity requirements and therefore provide an opportunity to be managed primarily for the purpose of biodiversity maintenance or enhancement. However, as most ecological research has been conducted outside urban regions, there is a need for careful study of the effects of 1) the environmental factors that are characteristic of urban habitats and 2) the refinement of management strategies.

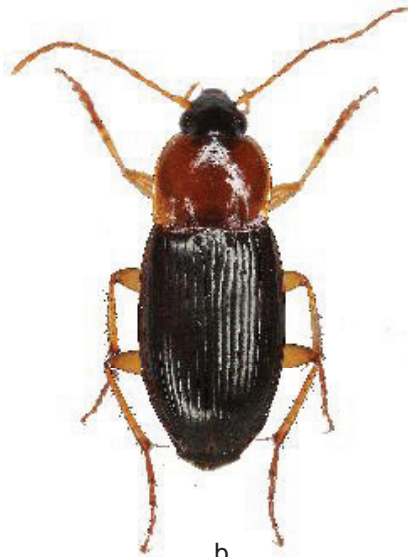
Whilst the value of pollinating insect communities is well appreciated, there is clearly a need to improve our understanding of the ecosystem functions and services provided by such taxa as grassland carabids. Working with spiders, Schmitz (2009) has shown that predators of phytophagous insects have an effect on plant diversity and basic ecosystem functions, such as element cycling and productivity. A large proportion of the carabid assemblages of open grassland, particularly in the predominant genera *Harpalus* and *Amara* (39% of the catch in this study), comprise of granivorous species (Luff *et al.* 1989). Granivorous and omnivorous carabid species have been shown by Bohan *et al.* (2011) to have a significant effect on the soil seed bank, and they also determined that the provision of this function was dependent on the availability of seeds. Thus we can deduce that declines in diverse semi-natural grassland habitats and their animal assemblages will reduce their capacity to control abundant plant species, which in turn will lead to further simplification and homogenization of grassland plant assemblages. This also suggests that biodiversity is a prerequisite to the provision of control ecosystem services in particular, and that loss of biodiversity will become self-perpetuating.

Data used for the analysis of carabid beetles in my thesis comprise carabid species richness, activity density and individual species catches, which were all obtained by pitfall sampling. The data therefore represent samples of the assemblages of the studied sites and habitats. I acknowledge that there will be differences in the sampling efficiency between different habitats and different species, as has been established by Digweed *et al.* (1995). In order to avoid some of the pitfalls associated with analyzing pitfall data, I acknowledge that the catches for different species correspond to their activity density (Greenslade 1964, Lövei & Sunderland 1996,

Plate 1



a



b



c



d

**Plate 1** Carabid beetle species of dry grassland habitats a) *Harpalus luteicornis* (x7.5), b) *Calathus melanocephalus* (x8), c) *Ophonus schaubergerianus* (x8) and d) *Amara nitida* (x8). Photographs copyright Kari Heliövaara 2013.

Thomas *et al.* 1998), which is dependent on both the abundance of the species at a site and its vulnerability to pitfall trapping. This vulnerability will include a simple statistical component based on the actual abundance of that species at the site, its activity or motility and its behaviour (Thiele 1977, Thomas *et al.* 1998). The behavioural component includes the suggested ability of some small-sized species in particular to retract from the edge of the trap without falling in (Thiele 1977) and the fact that specific foraging behaviours, for instance, also influences whether a species will be inclined to enter a pitfall trap or not. To address these potential issues, pitfall trapping regimes were standardized as much as possible. In particular, the traps were set and removed at as close to the same time as possible, generally over a two to three day period. Precise marking of traps was employed to minimize trap losses. Multivariate ordination analyses were employed to make compositional comparisons between assemblages which are robust to the influence of quantitative differences between the activity densities of different species (ter Braak 1995, Oksanen 2007).

## **1.8 Objectives of the thesis**

The objective of this thesis is to determine the responses of carabid beetles and vascular plants to the environmental factors affecting forest and meadow habitats in urban environments, and thereby determine the potential of these habitats for the enhancement of urban biodiversity. In the thesis, I apply the gradient method to investigate the effects of urbanization on communities of carabid beetles. Whilst carabid beetles are relatively motile (Den Boer 1971), I assume that the carabid assemblages of different habitats are relatively stable, though they also undergo seasonal and annual variation in response to demographic and extraneous factors, such as climate. I also assume that the activity densities of particular species within these communities will be influenced by gradients of various environmental variables, such as human population density, soil sealing, roads and soil chemistry. However, their response is likely to be more complex than that of vascular plants, as carabids are 1) mobile and 2) their occurrence is subject to the influence of both higher and lower trophic levels.

## **Hypotheses**

1. Urbanization will have a generally negative effect on species richness. Already in 1983 Klausnitzer (1993) reported that whilst there can be small downtown islands with high species richness, there is generally a decrease in the

number of species on gradients from the rural surroundings into cities. Suggested reasons include decreasing habitat diversity and more hard surfaces.

2. There will be a distinct effect of urbanization on species diversity. Whilst Connell (1978) has suggested that diversity should be highest at intermediate levels of disturbance, Gray (1989) predicted that species diversity should decrease from a higher level in rural to a lower level in urban areas, and Klausnitzer (1993) reports a number of studies which support this suggestion for carabid beetles, other coleopteran taxa and even birds.
3. Eurytopic species will increase with increasing urbanization and stenotopic species will decrease. Gray (1989) predicted that opportunistic species should be dominant in urban areas. Also Klausnitzer (1993) found a greater proportion of eurytopic carabid species in urban areas compared to outlying areas.
4. Large-sized carabid species will decrease with increasing urbanization. Klausnitzer and Richter (1993) report that small-sized carabids were predominant at the urban end of an urbanization gradient in Leipzig, Germany and that a similar trend has also been reported for a number of other invertebrate taxa, as well as birds. Also Gray (1989) has suggested that body size should decrease with increasing disturbance.
5. Flightless carabid species will decrease with increasing urbanization. Thiele (1977), Desender (1989) and Niemelä and Spence (1991) have all reported that young carabid populations contain higher proportions of macropterous species than longer established populations, and Klausnitzer (1993) suggested that there should accordingly be less flightless species in urban regions because most of the populations there should be younger, due to the frequency of disturbance events in urban regions.
6. I expect there to be some rare and scarce species in urban habitats. Schwerk (2000) found that some highly disturbed urban habitats can contain rare and threatened species, though the species in question are generally thermophilic and the habitats quite specific. Also Eversham *et al.* (1996) and Koivula *et al.* (2005) have reported that highly disturbed urban habitats can accommodate even stenotopic, rare and threatened species of carabid.
7. The carabid assemblages of forest and grassland habitats will follow a log-normal distribution in urban habitats, as has been suggested for assemblages of disturbed habitats by Gray (1987).

## 2. Materials and Methods

Study sites were selected in forest (Plate 2) and meadow (Plate 3) habitats across the metropolitan region of Helsinki (Fig. 3). The forest sites consisted of 12 spruce dominated forests of *Vaccinium myrtillus* type (Cajander 1949) along an urbanization gradient extending from Central Helsinki to northern Espoo (Paper II). In Paper III, the results of the study presented in Paper II are compared with the results of application of the same study design in two other countries, Sofia, Bulgaria and Edmonton, Canada. The grassland sites consisted of 18 meadows (Paper IV) containing forbs indicative of *Festuca ovina* grassland (Plate 3a) or dry meadow on bedrock (Plate 3b) (Påhlsson 1998) for the vegetation study (Paper IV). Twelve sites of these grassland types or prevalent matrix grasslands were used for the study of carabid assemblages of dry meadows (Paper V).

Vascular plants were surveyed by means of 5-15 (depending on the size of the site) 1 m x 1 m quadrats, from which all species were listed and their percentage cover estimated. Carabid beetles were sampled using ten pitfall traps arranged along linear transects in the forest study (Papers II and III) and five traps arranged in a square with four traps in the corners and the fifth at the centre at a minimum of 5 m apart per treatment in the meadow sites (Paper V), due to restrictions imposed by the small size of some sites.

Ordination plots have been used to reveal the responses of both vascular plant and carabid beetle species to environmental variables. Assemblage level responses to urbanization level and environmental factors were analyzed using diversity indices in both habitat types. General effects on carabid species richness and activity density were assessed using nested ANOVA in the forest study (Paper II) and in the grassland study (paper IV), individual species responses were modelled using generalized linear mixed modelling (GLMM). In both of these studies, the carabid species were categorized into groups according to such traits as wing morphology, habitat association, moisture preference and habitat specificity to facilitate analysis of trait responses to the tested variables.



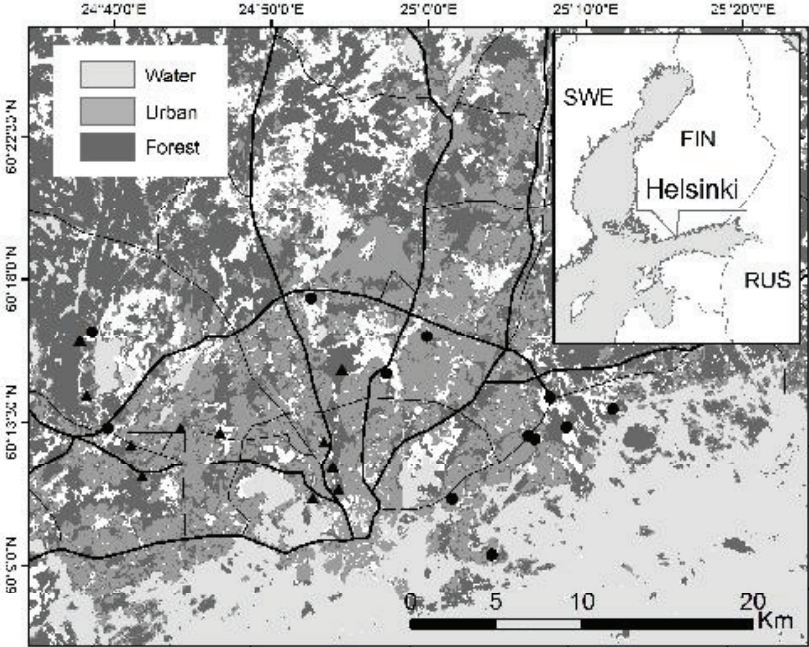


**Plate 2** Globenet forest study sites a) rural (Pirttimäki) and b) urban (Laakso). Both contain deadwood and heterogeneous tree structure, though more urban sites were more open and suffered more from erosion of the field layer.



**Plate 3** Dry meadow habitats in Helsinki, a) sheep's fescue dry meadow type (Herttoniemi) and b) dry meadow on bedrock (Suomenlinna). The Herttoniemi site is managed by the Helsinki Civil Works department using traditional methods to mow the hay and dry it on stakes. Dry meadows on bedrock do not require management.

Graphs of the numbers of individuals per carabid species against number of carabid species were plotted for both the forest and grassland urbanization classes, to allow comparison with the multi-group model proposed by Gray (see Fig. 2 above) for species composition in undisturbed communities.



**Fig. 3** Map of the study area. Forest study sites are represented by triangles, and meadow sites by circles.

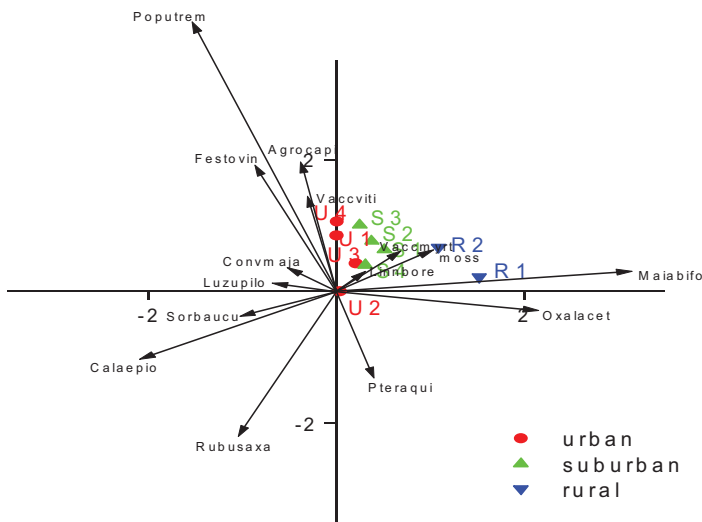
## 3. Results

### 3.1 Results of paper I

This paper presents a review of 65 papers on the effects of urbanization on arthropods. The fragmentation and isolation of urban habitats constitute a major challenge for insects inhabiting urban regions. Urbanization gradients constitute an appropriate tool for studies into the ecological responses of insect to urbanization. In addition to the carabid gradient studies reviewed in this thesis, similar results of declining species richness with increasing urbanization have also been shown for other taxa, such as gall inhabiting moths. Whilst such studies of the assemblages of patches of indigenous habitats in urban areas indicate general declines in numerous taxa, a number of typically urban habitats, such as ruderal habitats, domestic gardens, parks and roadside verges can provide valuable niches for some arthropod taxa, and even support some stenotopic and uncommon species.

### 3.2 Results of paper II

This paper investigated carabid beetle and vascular plant assemblages in spruce forest habitats (Plate 2) along an urbanization gradient in Helsinki. A total of 2203 individuals of 25 carabid species were collected in this study. The most abundant species, *Calathus micropterus*, was equally abundant across urbanization classes, though the three next most abundant species, *Pterostichus melanarius*, *P. oblongopunctatus* and *P. niger*, favoured rural forests (Plate 2a). This suggests that of the most abundant species, only *C. micropterus* is not sensitive to urbanization, though the three next most abundant carabids of spruce forests in this region were intolerant of even low levels of urbanization.



**Fig. 4** DCA of vegetation data from *Myrtillus vaccinium* type spruce forests along an urbanization gradient in Helsinki. The sites can be seen to cluster according to urbanization intensity and separate along the first ordination axis (see Paper II for details).

The ordination plot for the spruce forest habitats demonstrated a linear vegetational gradient according to urbanization level (Fig. 4), though the carabid ordination (fig. 2 in Paper II) showed a more complex response, with separation in three different directions according to the three levels of urbanization tested. This seems to suggest that the response at lower trophic levels, in this case vascular plants, is simpler and easier to interpret, and thus a useful aid to the interpretation of the more complex responses of higher taxa. The carabid ordination shows that flight-capable species which were able to utilize open habitat (e.g. *Amara brunnea*, *Leistus ferrugineus*) were predominant in urban and suburban forests. Flightless species were more predominant in rural and suburban sites, as their dispersal between more isolated urban forest (Plate 2b) patches would be handicapped. Flight ability and ability to use open habitat are characteristic of generalist and opportunistic species (fig. 2 in Paper II).

An effect of urbanization on the number of carabid individuals was demonstrated ( $p = 0.061$ ) and the effect on species richness was highly significant ( $p = 0.007$ ) (table 1 in Paper II). There was also an effect of urbanization on diversity as indicated by the Brillouin diversity index, which increased along the gradient from urban through suburban to rural, though it was not statistically significant when tested with a Kruskal-Wallis Anova ( $p = 0.138$ ). Results of this study suggested that the main

driver behind the loss of forest specialist species from urban forests (Plate 2b) and the incursion of open habitat species is the loss of the cool, dark and moist microclimatic conditions. This could be further studied by taking a set of forest sites along a similar gradient and purposefully selecting sites with such a dark, cool and moist microclimate, and monitoring the conditions using data loggers. However, whilst such sites occur even in urban regions, they are so scarce and isolated that the likelihood of their containing specialist forest species and in similar numbers to those in rural forest sites would be low.

### **3.3 Results of Paper III**

This paper investigated the carabid assemblages of forest habitats (Plate 2) along an urbanization gradient in the cities of Sofia (Bulgaria), Edmonton (Canada) and Helsinki (Finland). There was considerable difference in the catches from the three cities investigated: 7035 individuals of 71 species (Sofia), 15 543 individuals of 41 species (Edmonton) and 2203 individuals of 25 species (Helsinki). The results from Edmonton were strongly affected by three introduced European species, which constituted 76.6% of the total catch. Of these, *Pterostichus melanarius* was particularly abundant, comprising 66.3% of the catch. There was relatively low complementarity between the urbanization classes in Helsinki, and the cluster analyses of the results showed strong clustering of assemblages according to urbanization level. However, Sofia and Edmonton had higher complementarity and less clear clustering of urbanization classes (fig. 1 in Paper III). The exotic species in Edmonton were more abundant in the more urban sites in comparison to rural. There was a significant increase in species richness from urban to rural sites in both Edmonton and Helsinki, though not in Sofia. Also in both Edmonton and Helsinki, there was dominance by opportunistic species, whereas in the urban sites in Sofia, the dominant species was a stenotopic forest specialist, *Aptinus bombardae*. Dominance structures were investigated using rank-abundance plots. For Edmonton and Helsinki these showed lower dominance in the rural and suburban sites than urban, however, no such pattern was detected in the Sofia results. Finally, in support of Gray's (1989) suggestion that body size should decrease with increasing disturbance, there was a significant trend of increasing body size from urban to suburban and rural sites in both Sofia and Helsinki, though not in Edmonton.

### **3.4 Results of paper IV**

This paper investigated the vascular plant assemblages of dry meadow habitats under three levels of management by mowing and three levels of urbanization. A total of 252 vascular plant species were recorded from the 18 meadow sites, of which 209 were forbs. Of the forbs, three species, *Achillea millefolium*, *Anthriscus sylvestris* and *Stellaria gramina* occurred in all of the sites. Seventy species were only recorded from one site. A species-area effect was supported by the correlation between the total number of plant species and site area ( $r^2 = 0.371$ ,  $p = 0.007$ ), though this seemed to level out at a site area of ca. 0.25 ha. The PCA ordination (fig. 5 and table 4 in Paper IV) revealed that high soil pH and low concentrations of the nutrients  $\text{NO}_3^-$ ,  $\text{N}$  and  $\text{N}_{\text{tot}}$  and K, were important determinants of the proportion of nitrophobic plants. Regular meadow management was associated with reduced nutrient levels and also enhanced the ratio of nitrophobic:nitrophilic plants. Management of the meadows (Plate 3a) by mowing resulted in an increase in the number of plant species, an increase in their Shannon-Wiener diversity and an increase in the proportion of nitrophobic plant species, though the Shannon-Wiener values were considerably lower than those reported from comparable habitats in rural regions. Soil chemistry and vegetation analyses confirmed that a considerable number of factors varied with position along the urbanization gradient. These included most of the nutrients and metals tested, as well as the ratio of nitrophilic:nitrophobic plants species. There were significant correlations between human population density, length of roads within a 1 km buffer zone and the amount of open habitat within the buffer zone, so it was not possible to distinguish whether these results were due to disturbance effects or due to the effects of isolation and poor connectivity. Detectable vegetation responses to urbanization included a decrease in nitrophobic plant species. The nitrophobic species include the most stenotopic species and those that are most sensitive to stress. Whilst many such species require management to maintain suitably low levels of soil nutrients and control dominant species, they are also vulnerable.

### **3.5 Results of paper V**

This paper investigated the carabid beetle assemblages of three dry meadow habitats (Plate 3) under three levels of urbanization. A total of 3428 carabid beetles of 78 species were collected in this study. The three most abundant carabid species were *Pterostichus melanarius*, *P. niger* and *Trechus secalis*. The most abundant xerophilic granivorous (XG) carabid species favoured managed dry meadow habitats (Plate 3a) and the scarce XG species favoured the harsher dry rocky meadow habitats (Plate 3b) ( $p < 0.001$ ) and also favoured urban ( $p = 0.003$ ) environments.

Three out of four abundant xerophilic predators favoured dry rocky habitats, and urban and suburban over rural. Hygrophilic species favoured matrix grassland habitat and rural environments, apart from *P. cupreus*, which favoured urban. Granivorous species, such as *Harpalus luteicornis* (Plate 1a), were generally more prevalent in dry meadows and rocky dry meadows (figs. 2 and 3 and table 3 in Paper V). All the studied grassland habitats were dominated by open habitat or open woodland species. A GNMDS ordination revealed that urbanization influenced carabid species composition, though habitat did not. Unmanaged grassland habitats contained a higher proportion of predatory carabid species, whereas managed dry meadows and the sparsely vegetated meadow types contained higher proportions of granivorous species. Carabid species were most influenced by vegetation height, asphalt surfaces adjacent, rubbish and open habitat adjacent. *A. montivaga*, *A. famelica* and *A. familiaris* were least sensitive to asphalt. *C. erratus*, *C. melanocephalus* (Plate 1b) and *Bembidion properans* were associated with open habitat adjacent (fig. 5 and table 4 in Paper V).

There was a significant effect of habitat on diversity and evenness (matrix < managed < rocky), whereas the effect of urbanization was not significant, though there was a trend of increasing diversity and increasing evenness from rural through suburban to urban (table 5 in Paper V). There was also a significant effect of area on the numbers of xerophilic ( $p = 0.002$ ), eurytopic ( $p = 0.038$ ) and open habitat ( $p = 0.046$ ) species, with larger open habitats containing significantly more species.

## 4. Discussion

Paper I of this thesis presents a synthesis on the effects of urbanization on arthropods. In particular, isolation and the high proportion of edge that result from intense fragmentation of urban habitats result in the loss of many species (Connor *et al.* 2002). Large-sized forest carabid species are particularly sensitive to habitat fragmentation (Sadler *et al.* 2006). However, it has also been shown that, for carabid beetles, urbanization can have a stronger effect on species richness than loss of habitat (Weller & Ganzhorn 2004). Also the homogenization of urban assemblages is an acknowledged problem, whereby stenotopic species are lost and assemblages from diverse habitats become more similar to each other, and become more dominated by highly dispersive and eurytopic species (Šustek 1987, Kotze & O'Hara 2003). A number of studies have shown the importance of high dispersal capacity for persistence in urban areas (Small *et al.* 2006, Sharma & Amritphale 2007). Urbanization gradient studies have revealed that there tends to be a general increase in carabid species richness with decreasing levels of urbanization (Niemelä & Kotze 2009), which was more distinct when focusing on forest species (Magura *et al.* 2010).



Whilst the assemblages of rural habitats, such as forests, do not thrive in urban regions, cities contain a number of varyingly unique habitats, some of which can support diverse assemblages. Ruderal habitats in particular can support rare and threatened species of carabid, particularly those that are thermophilic (Schwerk 2000). Such ruderal habitats also tend to retain their ecological value without requirements for specific management regimes, which further enhances their potential role in the enhancement of urban biodiversity (Angold *et al.* 2006, Hartley *et al.* 2007). Also domestic gardens can account for a large part of the surface area of a city (Smith *et al.* 2006), and contribute to habitat heterogeneity and thereby enhance arthropod diversity (Tallamy 2009). It appears that the provision of key ecosystem services by arthropods, such as biological control and pollination, are incentives for gardeners to implement measures to support diverse arthropod assemblages (Symondson *et al.* 2003, Matteson *et al.* 2008).

Paper II presents a study of carabid assemblages of spruce forest sites (Plate 2) along an urbanization gradient in Helsinki, which was conducted as part of the Globenet project. Urbanization had a negative effect on overall species richness, number of individuals, and on all of the abundantly collected species apart from *Calathus micropterus*. There were also more flightless and forest habitat species in the rural forests (Plate 2a) and more open habitat and flight capable species in the urban and suburban forests, as has also been reported by Czechowski (1982) for woodland areas in Warsaw. These findings thereby support the suggestions from Paper I that species richness declines with increasing urbanization, as does the number of stenotopic species. Also the reduction in the proportion of species with poor dispersal ability with increasing urbanization is supported. A review of 105 studies of urbanization gradients of a variety of taxa in a variety of habitats by McKinney (2008) showed that there is generally a reduction in species richness in areas with intense urbanization. He suggested that the main reason for such a decline is simply a species-area response due to fragmentation and loss of habitat, together with an additional component from the degradation of remaining habitat. In Paper II sites were selected such that there was no correlation between site size and urbanization category. However, on a larger scale, a relationship between forest area and urbanization is to be expected. In addition, the amount of forest habitat with microhabitat conditions suitable for stenotopic forest species is likely to also decrease with increasing urbanization, as urban forests (Plate 2b) tend to be predominantly managed for recreational activities. McKinney (2002) suggested that the best way to address the problem of declining species diversity in intensely urban areas would be to preserve “*as much remnant natural habitat as possible,*” and avoiding the unnecessary removal of vegetation during construction. In the case of boreal forests, this would require the conservation of stands with suitable microhabitat conditions.

Paper III presents and compares three studies from the Globenet project, including the Helsinki study that was the subject of Paper II. The results suggest that it is possible to make some generalizations about the responses of carabid assemblages to urbanization, such as assemblage complementarity within urbanization classes, decreasing species richness with increasing level of urbanization, increased dominance by opportunist species in urban habitats, stronger dominance pattern in more urban habitats and increasing body size with decreasing level of urbanization. However, these effects are far from universal, and other regional conditions and extraneous factors, such as the influence of introduced species in Canada, also account for much variation in the results.

Paper IV presents a study of the vegetation of dry meadow habitats (Plate 3) along an urbanization gradient and under different management regimes. Previous studies have shown that management by mowing or grazing is essential to avoid eutrophication and overgrowth (Pykälä 2005) though it is also well known that deposition from traffic emissions leads to elevated levels of nitrogen in urban habitats (Suding *et al.* 2005, Truscott *et al.* 2005), leading to doubts about the potential benefits of mowing urban meadows to reduce nutrient levels. The results of this study show, however, that mowing of urban meadows does lead to reductions in soil nutrient levels and increased proportions of nitrophobic plant species. There was also a corresponding increase in plant species diversity, though the Shannon-Wiener diversity index values and species richness levels remained considerably lower than those reported from more rural parts of the region (Pykälä 2003). A significant species-area effect ( $p = 0.007$ ) was discernible (fig. 1 in Paper IV), though this trend levelled off at approximately 0.25 ha, suggesting that habitat size restricts species richness in sites smaller than 0.25 ha. This could therefore be recommended as a minimum size for dry meadow habitats from the perspective of vegetation, though it is likely that the threshold would be greater for species of higher taxa. This paper suggests that conservation of dry meadow habitats and the implementation of appropriate management strategies is a useful means of supporting meadow plant species, though the comparison with the results of Pykälä (2003) makes it clear that such sites located in rural regions probably have greater potential for enhancing biodiversity. However, in addition to vascular plants, dry meadow habitats have particular significance for numerous insect taxa, and indeed 54.4% of Finland's threatened species are associated with dry meadow habitats (Rassi *et al.* 2010). Many of these insect taxa are involved in the provision of important ecosystem services, such as pollination and biological control (Tscharntke *et al.* 2005). Therefore it would also be important to know what kind of potential urban dry meadow habitats have for contributing to the maintenance of meadow diversity beyond their vascular plant assemblages.

Paper V presents a study of carabid assemblages of managed and unmanaged dry meadow habitats (Plate 3) and matrix grasslands along an urbanization gradient in Helsinki. The fauna comprised mostly carabid species of open habitats and open woodland, though the three most abundant species, *Pterostichus melanarius*, *P. niger* and *Trechus secalis*, are also abundant in coniferous forests, suggesting that they are eurytopic species of both open and forested habitats. Of these, *T. secalis* was absent from the dry rocky meadow habitats (Plate 3b), which have the most exposed and harsh conditions, suggesting that it has a narrower spectrum of suitable habitats than the two *Pterostichus* species. Of the Xerophilic Granivorous (XG) species of this study, the most abundant species favoured managed dry meadows (Plate 3a), though the pooled less abundant species in this group favoured the harsher dry rocky meadows (Plate 3b). This suggests that these less abundant XG species are predominantly stenotopic species, adapted to the more extreme conditions of these habitats. A study of the urban greenery of Warsaw indicated that there is a large number of xerophilic species, with a relatively broad habitat spectrum, inhabiting roadside green in particular (Czechowski 1982). At the other end of the moisture affinity spectrum, the hygrophilic species favoured the lush matrix habitats, which presumably had cooler, moister and shadier conditions in comparison to the two dry meadow habitat categories. This is consistent with the findings of Czechowski (1982), who reported that hygrophilic carabid species were predominant in the urban greenery of Warsaw. The ordination figure (fig. 5a of Paper V) showed that there was an effect of urbanization, with clustering of sites according to level of urbanization, though no clearly discernible effect of habitat type. This suggests that urbanization intensity affects carabid assemblage composition, whereas habitat did not. This does not however mean that the influence of habitat is inconsequential, as habitat type did affect both species diversity and evenness, (table 5 in Paper V), as there was a trend of increasing diversity and decreasing evenness from matrix through managed to dry rocky meadow habitat ( $p = 0.055$ ), whereas the trend for urbanization level was insignificant.

#### **4.1 Hypotheses revisited**

Hypothesis 1 – that urbanization will have a generally negative effect on species richness – is supported by the study of spruce forest carabids in Finland and for Canada if the introduced species are excluded (Paper III). For Bulgaria both urban and suburban sites were less species rich than rural. The meadow carabids (Paper V) also had lowest species richness in the urban habitats. Even for plants, whilst Tonteri and Haila (1990) have shown that the urban region of Helsinki has a higher level of plant species density than comparable areas outside the city, Paper IV demonstrated that for dry meadow habitats in Helsinki, there was a trend of lower plant species richness in the urban class, though no significant difference between

suburban and rural. This decrease in species richness with increasing urbanization level is in keeping with results of the review by McKinney (2008).

Hypothesis 2 stated that there will be a distinct effect of urbanization on species diversity. Species diversity decreased for carabid beetles of spruce forest habitats (Plate 2) in Helsinki with increasing urbanization (Paper II), which is in keeping with the prediction of Gray (1989). For the meadow carabid assemblages, there was a non-significant trend of increasing species richness with increasing urbanization (Paper V). For meadow plants, there was no effect of urbanization on diversity, though the Shannon-Wiener diversity values obtained for these urban habitats were considerably lower than those reported for similar meadows in rural parts of the region (Linusson *et al.* 1998, Pykälä 2003). The review of McKinney (2002) suggested that a considerable number of urbanization gradient studies reported higher species richness in suburban areas, which they mostly attributed to the IDH (Connell 1978). Frankie and Ehler (1978) have suggested that the reason could be the high habitat heterogeneity of suburban areas and McKinney additionally suggests that suburban areas tend to be well provisioned with important resources, such as water and nutrients, consistent with the IDH.

Hypothesis 3 stated that eurytopic species will increase with increasing urbanization and stenotopic species will decrease. The most stenotopic forest species in the Helsinki spruce forest study (Paper II), *Platynus mannerheimii* and *Trechus rubens*, were recorded only from rural sites and eurytopic species such as *Leistus ferrugineus* and *Patrobis atrorufus* were more predominant in urban sites. The exotic and eurytopic European species that were predominant in the Canadian study (Paper III) were much more abundant in urban habitats. The only stenotopic old-forest specialist detected in the Helsinki study, *Platynus mannerheimii*, was found from only one of the rural sites, although potentially suitable habitat conditions were recorded from some of the studied urban forest sites (Plate 2b). In this case, there are a number of factors that make the occurrence of *P. mannerheimii* in urban spruce forest sites unlikely. Firstly the species is scarce and probably exists as a metapopulation, thus requiring 1) a network of suitable habitat patches and 2) the potential to disperse between these discrete patches (Hanski 1999). Thus such isolated patches within a high contrast mosaic of habitats, which are typical of urban regions (Niemelä 1999) are unlikely to contain such stenotopic forest species (Niemelä *et al.* 1987). However, whilst in Canada and Bulgaria stenotopic forest species were also predominantly recorded from rural sites, one stenotopic forest species, *Aptinus bombardae*, was also found from suburban sites, suggesting that it is possible to maintain populations of some stenotopic forest species in urban areas if suitable habitat conditions can be retained.

In the Bulgarian study, whilst the stenotopic forest carabid *Aptinus bombarda* was dominant in suburban sites, most of the stenotopic forest species were predominantly recorded from the rural region. In the meadow vegetation study, we can consider the nitrophilic species to be the most eurytopic and nitrophobic species to be generally stenotopic, and these indeed correlated with urbanization level positively and negatively respectively.

In Hypothesis 4, I argued that large-sized carabid species will decrease with increasing urbanization. Both the Finnish and Bulgarian forest studies (Paper III) supported this hypothesis for forest carabid assemblages, though there was no significant effect in the Canadian data. In the meadow habitats (Paper V), the effect of disturbance represented by habitat management on carabid body size was considered, rather than that of urbanization. This was because the authors considered that for grassland carabids, mowing would constitute a stronger disturbance than urbanization. In that case, small-sized species were most abundant in the unmanaged and lush grassland matrix habitats than the two dry meadow habitats, contradicting our expectations. There were, however, more large-sized species in the dry rocky meadow habitats (Plate 3b), which can be considered the least disturbed of the three habitats, as they have scanty vegetation and require no management. This is in keeping with the findings of Blake *et al.* (1994), who found that body size was strongly correlated with management intensity in a study of 50 grassland sites in northern England. In the same study, data from 39 woodland sites found no correlations with carabid body size; however habitat disturbance was not included in their forest study. Thus the results of both forest and meadow studies support the hypothesis that large-sized species decline in more disturbed habitats, in keeping with the prediction of Gray (1989) and the findings for carabids by Klausnitzer and Richter (1993) and Šustek (1987). Eyre (1994) also identified a set of 12 small-sized grassland carabid species that were tolerant of disturbance and a set of 13 large species that were intolerant. Blake *et al.* (1994) considered that the most probable explanation for this phenomenon was that larger species tend to have a longer developmental period, during which they would require stable provision of resources, which would not be available in intensively managed grasslands.

Hypothesis 5 postulated that flightless carabid species will decrease with increasing urbanization. Flight capable species were dominant in urban and suburban sites in the Helsinki spruce forest study (Paper II), whereas flightless species were restricted to the rural and suburban habitats, which supports this hypothesis. The meadow study (Paper V) contained only very few brachypterous species, as open habitats are generally dominated by flight capable species. This leaves an open question as to whether the reason is evolutionary, in that flight has been evolutionarily selected for in species of open habitats, or phylogenetic, with macroptery simply being prevalent in such speciose open habitat genera as *Harpalus* and *Amara*. The phylogenetic

explanation is supported by the fact that both of these genera also include species that are associated with forests, *Harpalus quadripunctatus* and *Amara brunnea*, which are both macropterous, though these genera also include brachypterous species that are associated with open habitats. In the meadow study, wing morphology was studied for habitat types rather than urbanization level, and the highest level of macroptery was found from the rocky (Plate 3b) and managed dry meadows (Plate 3a) compared to the matrix grassland. This was considered to result from the fact that these two habitats are more isolated, whereas the matrix grassland is more contiguous, and flight capacity is more valuable to species of isolated habitats to facilitate dispersal. Den Boer (1970, 1971) has suggested that populations at high risk of extinction should be expected to invest more in dispersal. In this instance, the small size and isolation of these habitats, compared to the more abundant and contiguous matrix grasslands, can be considered to constitute a higher risk of extinction. It was recommended by den Boer (1970) to ensure the provision of large and heterogeneous areas of natural habitats to support populations of species with poor dispersal capacity, and to supplement those by maintaining networks of semi-natural habitats, such as roadside verges and hedgerows to facilitate dispersal. In fact, den Boer considered the maintenance of species with poor dispersal capacity as a major challenge for conservation planning (den Boer 1970).

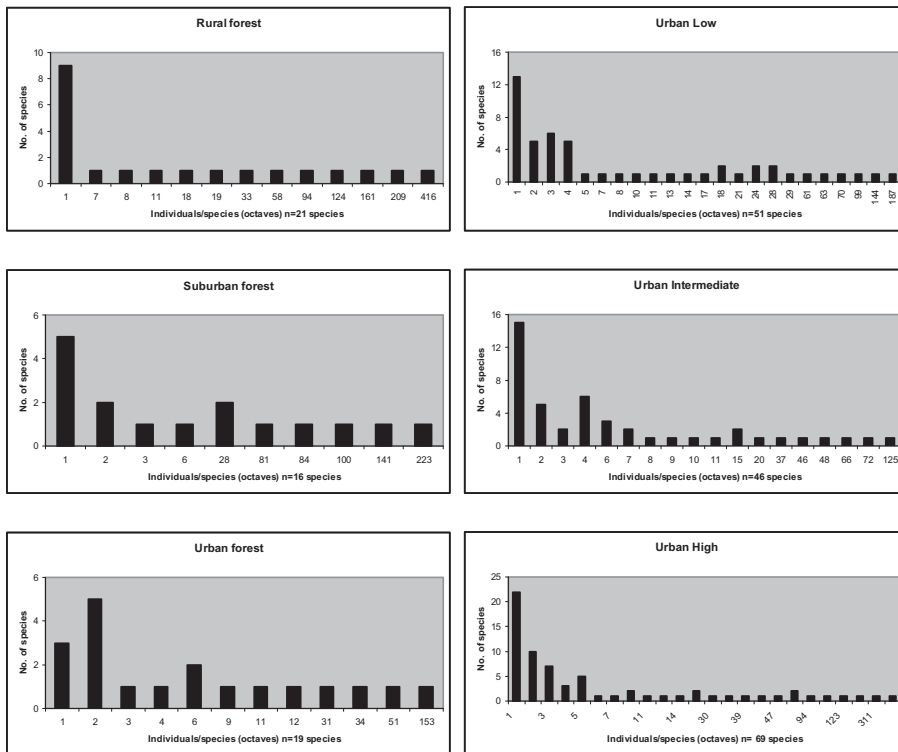
Interestingly macroptery was found to be significantly correlated with body size for the spruce forest data from Finland, Bulgaria and Canada (Paper III). This is perhaps not surprising, as flight requires the presence of both wings and flight muscles, which directly result in an increase in body size (Matalin 2003). However, this does also emphasize the need for caution when analyzing these hypotheses, as some of them could result from correlated factors. For instance, many open habitat carabid species are flight capable and xerophilic, so if open habitat species increase in a particular habitat class, then it is likely that macropterous species and xerophilic species will also increase.

Hypothesis 6 stated that there will be some rare and scarce species in urban habitats. No IUCN classified threatened species were recorded in any of these studies (see Rassi et al. 2010). The spruce forest studies (Papers II and III) did not reveal any particularly uncommon species in the urban sites, though a number of regionally uncommon species were recorded from rural sites in Helsinki, Sofia and Edmonton (Paper III). In the dry meadows carabid study (Paper V), the rarest species were *Amara equestris*, *A. consularis*, *Harpalus rubripes* and *Ophonus schaubergerianus* (Plate 1c). Of these, *A. equestris* was recorded from a site with low-intensity urbanization, *A. consularis* from a high urbanization site, *H. rubripes* from both high and low urbanization sites and *O. schaubergerianus* (Plate 1c) occurred abundantly in all three urbanization categories. It is important to note here that the grassland sites were all located within the urban and suburban parts of the

Helsinki region and urbanization in this study was based on population density adjacent and not on location within the urban infrastructure. This result therefore supports the hypothesis that meadow habitats support the presence of rare carabid species in urban areas though does not support any similar role for spruce forests. However, when considering the biodiversity value of forests, it would be wise to consider data on saproxylic taxa (see Siitonen 2001, Sörensson 2008) rather than just carabid beetles. For open habitat carabid beetles in Helsinki, it has also been shown that *Amara equestris*, which was one of the rarest species recorded in this study, has also been recorded from median strips of busy roads (Koivula *et al.* 2005), though it is not certain whether these constitute a population inhabiting the median strips or whether they are residents from a nearby dry meadow.

In Hypothesis 7 I postulated that the carabid assemblages of forest (Plate 2) and grassland (Plate 3) habitats will follow a log-normal distribution in urban environments. Whilst the ecological explanation of the log-normal distribution for assemblages of undisturbed habitats (Fig. 2) provided by Gray (1987) seems intuitive and has been shown by May (1975) to fit equilibrium communities of many taxa, my studies (Fig. 5) suggest that the model does not apply to the activity-density data of carabid assemblages collected by pitfall trapping from either spruce forests (Plate 2) or dry meadows (Plate 3). The pattern of these assemblages is rather that of Fisher's log series (Fisher *et al.* 1943), which has been shown by Magurran (2004) to apply to entomological data, and which is characterized by the mode being in the smallest class (octave 1). This distribution is also that predicted by Hubbell's (2001) Unified Neutral Theory of Biodiversity and Biogeography for samples of very large sizes.

Both spruce forests and semi-natural grasslands demonstrate the presence of an urbanization gradient, with changes in vegetation composition, for example, with increasing urbanization. Urban spruce forests are characterized by direct fragmentation effects and disruption of the canopy, resulting in a mosaic of patches with near natural conditions interspersed with those that have been converted to open, warm and dry structures, often with erosion of the field layer (Hamberg *et al.* 2009). Urbanization impacts on forests therefore comprise of both quantitative (habitat loss and fragmentation) and qualitative (structural change) components. The results of these changes are a discernible linear gradient response of the vegetation and the reduction or loss of flightless and stenotopic carabid species, including *Carabus glabratus*, *C. hortensis*, *Platynus mannerheimii* and *Pterostichus niger*.



**Fig. 5** Fisher plots of the number of species in subsequent octaves of the number of individuals per octave, beginning with species represented by one individual. Figures on the left are for carabid assemblages of spruce forests for rural, suburban and urban sites, and those on the right are for open grassland sites at low, intermediate and high intensity of urbanization.

In the case of semi-natural grasslands, levels of both nutrients and metals, as well as supplementary open habitat adjacent, vary along the urbanization gradient, resulting in vegetation responses of reduced levels of species diversity and increased dominance by nitrophilic plants. For carabid beetles there is not the same conflict between urbanization effects and physical requirements, as open habitat carabid beetle species tend to favour hot, dry and bright conditions, which are also characteristic of urban regions. The most stenotopic species of these habitats are generally well adapted to highly exposed conditions (Klausnitzer 1993). However, because there is an increase in nitrophilic vegetation with increasing urbanization, this would be expected to result in lush field layer vegetation in urban areas, with microhabitat conditions more suitable for hygrophilic carabid species, such as *Poecilus cupreus*, *Pterostichus melanarius* and *Trechus secalis*, in addition to the mesic *P. niger*. These species were all abundantly caught from the unmanaged matrix grassland habitats. Several of the xerophilic species, such as *Calathus erratus*, *C. melanocephalus* (Plate 1b) and *Syntomus truncatellus*, peaked in urban dry rocky habitats, which have the sparsest vegetation and are less susceptible to the influence of increased nutrient levels. Of those xerophilic species which favoured



the managed dry meadows (Plate 3a), most, such as *Amara communis*, *A. nitida* (Plate 1d), *Ophonus schaubergerianus* (Plate 1c), *Synuchus vivalis* and *Carabus nemoralis*, peaked in rural sites, implying that there is an undetermined component of the urbanization gradient which is unfavourable for such species. The exception was *Amara lunicollis*, which peaked in the urban sites.

It is interesting to note that *Pterostichus niger* and *P. melanarius* were highly abundant in both the forest and grassland studies, implying that they are eurytopic species. *Calathus micropterus*, which was the most abundant species in the forest study and the only species in that study not to respond negatively to urbanization, was the fourth most abundant species in the grassland study, suggesting that it is also eurytopic. In addition to these abundant species, there were also a number of less abundant species, such as *Amara brunnea*, *Cychrus caraboides*, *Leistus ferrugineus* and *Synuchus vivalis*, which occurred in both forest and grassland habitats, indicating that eurytopic species need not necessarily be highly abundant.

#### **4.2 Conclusions and recommendations for enhancing biodiversity in urban habitats**

Fragmentation has a major effect on species assemblages of urban habitats (Paper I, Connor *et al.* 2002, Sharma & Amritphale 2007). This issue should be addressed by trying to conserve intact areas of habitats that have the potential for maintaining biodiversity. In carabids at least, species of small body size and good dispersal power (i.e. flight capacity), benefit from urban environments. Contrastingly large-sized and flightless species generally decline in disturbed urban habitats (Gray 1989), so strategies for maintaining urban biodiversity should consider ways of supporting such taxa. Possible means of fulfilling this requirement would be to enhance the continuity between habitats wherever possible and employing management strategies with low intensities of incurred disturbance. Clearly carabid species associated with forests are foremost amongst those that decline with urbanization. This process could be addressed by managing more urban spruce forests for the retention of typical spruce forest microhabitat conditions. In addition, acknowledged factors such as the provision of a continuum of deadwood (Rassi *et al.* 2010) should not be overlooked.

Homogenization of urban assemblages results from the loss of stenotopic species and the flourishing of eurytopic species (Hartley *et al.* 2007, Niemelä & Kotze 2009). Measures to support stenotopic species would include management strategies aimed at retaining appropriate microhabitat conditions, such as that of spruce forests. Also the recognition and maintenance of other habitat types with potential for maintaining

assemblages of stenotopic species, such as ruderal habitats, gardens and remnant habitats, such as cultural dry meadows, can make an important contribution to the maintenance of urban biodiversity (Papers I, IV & V). Ruderal habitats in particular have the advantage that they have high habitat heterogeneity and generally low nutrient levels without the need for management regimes (Gilbert 1989).

Urbanization does have negative effects on carabid and vascular plant assemblages, as has been clearly demonstrated by most of the urbanization gradient studies reported here and as it probably does on the majority of indigenous taxa. This is not surprising, as urbanization invariably results in habitat loss and fragmentation. However, it is equally clear that it is possible to maintain populations of many species, even including stenotopic species, as long as suitable habitat conditions can be assured (Papers IV & V, Eversham *et al.* 1996). Efforts to maintain urban biodiversity need to be supported by urban ecological studies, to generate information on the habitats with potential for supporting biodiversity. Such research can also help to generate recommendations on how to manage those habitats in order to best fulfil that potential. On the basis of the information presented in this thesis, I propose the following recommendations.

1. Habitats should be retained in as large and contiguous a form as possible. In the case of meadow habitats, this includes the removal of encroaching scrub or woodland vegetation, as well as the occasional mowing of adjacent grasslands to provide larger areas of habitat for meadow species. In the case of forests, this means the recognition of extant areas of valuable microhabitats, and activities to promote the expansion of such habitats, as well as to allow the development of more natural forest conditions, rather than managing urban forests predominantly as recreational resources. In addition to recreational forests, other areas should be left unthinned and undrained, for example, to support biodiversity and provide nature experiences for urban inhabitants.
2. Habitat supplementation, by the restoration of habitats and the creation of artificial habitats, such as artificial meadows, which can be constructed on landfill hills and noise abatement banks, and also green roofs and green walls, which can be designed to supplement and support valuable habitats and their species communities.

I conclude that the spruce forests sampled in these studies contribute relatively little to urban biodiversity, though they probably do have value as venues for recreation and providing nature experiences. Future initiatives to consider the value of urban spruce forests for biodiversity would need to focus on sites where their typical microclimate conditions have been retained, and to determine the proportion of such microhabitats within the forest area.

To enhance urban biodiversity, spruce forests need to be managed by reducing the impact of fragmentation and by maintaining areas of cool, damp and shady microhabitats to enhance their suitability for stenotopic species (Siitonen 2001) and to reduce the incursion of opportunistic species of drier open habitats, which tend to be plentiful in urban areas. If all urban forests are managed primarily for recreation, by thinning to provide light, open, warm and dry conditions, then there is little prospect for maintaining forest biodiversity. An optimal strategy for this purpose would be to distinguish between recreational forests, recreational routes through forests and forests for the purpose of nature experiences and maintaining biodiversity and manage each according to their purpose.

Managing dry meadow habitats (Plate 3a) in urban areas for biodiversity also has its challenges. Firstly they require intensive management, though this management is considerably less intensive than that required to maintain grass lawns. The minimum size of such sites for maintaining vascular plant diversity should be 0.25 ha, though this is perhaps insufficient for species of other taxa. In the case of meadow habitats, the main measures for enhancing biodiversity are the surveying of potential sites and implementation of appropriate management regimes, i.e. the periodic mowing and removal of vegetation, as a general rule sufficiently late in the season to permit seed set by late flowering plant species. Their value for biodiversity can be enhanced by maintaining and appropriately managing adjacent areas of grassland. Protection of urban dry meadow habitats is also necessary, as many such habitats are used for construction or managed inappropriately for the maintenance of dry meadow ecosystems. Also measures should be implemented to reduce the impact of urban disturbance, such as trampling, by maintaining an appropriate network of recreational routes.

Strategies for maintaining urban biodiversity should focus on enhancing the biodiversity value of both forest and grassland habitats. This can not be successfully achieved without the recognition of habitats within forest or grassland cover that have particularly high potential for supporting biodiversity. Such habitats need to be conserved and managed appropriately. Also adjacent areas of habitat should be considered in management strategies to supplement and support such habitats, and avoid encroachment, e.g. of secondary woodland into meadow habitats. Finally, imaginative strategies should be implemented to supplement urban biodiversity, for instance by habitat creation. This can be done in the form of constructing artificial meadow habitats on landfill hills and noise abatement banks, constructing green roofs and walls, and also considering ways of supplementing other habitats with the potential to enhance urban biodiversity.

## Acknowledgements

First and foremost I would like to acknowledge the role of my supervisor, Prof. Jari Niemelä, who initiated the Globenet project, which was the framework for my first ecological research studies. Jari has also played a key role in all of the varied projects that have employed me during virtually the whole time I have been working on this thesis. Secondly I wish to express my deep gratitude to my colleague Doc. Johan Kotze, who has had a major role in most of my papers, and in particular has provided valuable support in the statistical analyses. Thanks are also due to Dr. Bob O'Hara for valuable contributions to the models used in most of these studies. Thanks too to Dr. Tarmo Virtanen, who provided the map figures. Thanks also to my pre-examiners, Prof. Kari Heliövaara and Dr. Gabor Lövei, for their constructive comments on my thesis. Thanks to the departments of Biological Sciences and Environmental Sciences for providing the necessary laboratories, microscopical equipment and other infrastructure and resources. Thanks to Unigrafia's Eeva Hagel and Raimo Nieminen, who radically improved the appearance of my thesis. Thanks to my parents, Michael and Elizabeth, who planted the seeds that led me onto the path towards a career in ecological research, and also to my late Uncle John, who supported my interest in conservation at an early age and also helped steer me towards an academic career. Thanks to my wife Airi and son Konsta for their love, support and toleration throughout the duration of this project. I am also particularly indebted to my mother and father-in-law, Else and Vilho, as well as the rest of my Finnish family, neighbours and friends, who have made me very welcome here in Finland with their warm generosity. Papers IV and V were produced by the Helsinki Meadows project, which benefited greatly from cooperation with Kaarina Heikkonen (City of Helsinki Environment Centre), Tuuli Ylikotila (Helsinki Civil Works Department) and Inkeri Vähä-Piikkiö (Helsinki Urban Facts) and was supported by an urban research grant from Helsinki City. I also acknowledge the support of Academy of Finland (project 126915). Finally I would also like to thank all the colleagues from within the urban ecology research group (UERG) and from the various other research groups and departments that have been around me during the time I have been studying biology at the University of Helsinki.

# References

- Alberti, M. 2008 *Advances in urban ecology: integrating humans and ecological processes in urban ecosystems*. Springer, New York p. 366
- Angelstam, P. & Kuuluvainen, T. 2004 Boreal forest disturbance regimes, successional dynamics and landscape structures – a European perspective. *Ecological Bulletins* **51**: 117-136
- Angold, P.G., Sadler, J.P., Hill, M.O., Pullin, A., Rushton, S., Austin, K., Small, E., Wood, B., Wadsworth, R., Sanderson, R. & Thompson, K. 2006 Biodiversity in urban habitat patches. *Science of the Total Environment* **360**: 196-204
- Balmer, O. & Erhardt, A. 2000 Consequences of succession on extensively grazed grasslands for Central European butterfly communities: rethinking conservation practices. *Conservation Biology* **14**: 746-757
- Blake, S., Foster, G.N., Eyre, M.D. & Luff, M. 1994 Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. *Pedobiologia* **38**: 502-512
- Berkes, K. & Folke, C. (eds.) 1998 *Linking social and ecological systems: Management practices and social mechanisms for building resilience*. Cambridge University Press, Cambridge, UK
- Blair 2004, The effects of urban sprawl on birds at multiple levels of biological organization. *Ecology and Society* **9**: 2 available from [www.ecologyandsociety.org/vol9/iss5/art2](http://www.ecologyandsociety.org/vol9/iss5/art2)
- Bohan, D.A., Boursault, A., Brooks, D.R. & Petit, S. 2011 National scale regulation of the weed seedbank by carabid predators. *Journal of Applied Ecology* **48**: 888-898
- Cajander, A.K. 1949 Forest types and their significance. *Acta Forestalia Fennica* **56**: 1-71
- Chinery, M. 1988 *Pohjois-Euroopan hyönteiset* (In English: Insects of Northern Europe). Helsinki: Painokaari Oy, Tammi. ISBN 951-30-6952-4
- Chinery M 1993 *Collins Field Guide - Insects of Britain and Northern Europe* 3rd edition, Collins, London
- Connell, J.H. 1978 Diversity in tropical rain forests and coral reefs – high diversity of trees and corals is maintained only in a non-equilibrium state. *Science* **199**: 1302-1310
- Connor, E.F., Hafernik, J., Levy, J., Moore, V.L. & Rickman, J.K. 2002 Insect conservation in an urban biodiversity hotspot: The San Fransisco Bay area. *Journal of Insect Conservation* **6**: 247-259
- Czechowski, W. 1982 Occurrence of carabids (Coleoptera, Carabidae) in the urban greenery of Warsaw according to the land utilization and cultivation. *Memorabilia Zoologica* **39**: 3-108
- Czechowski, W. & Pisarski, B. (eds.) 1981 Species composition and origin of the fauna of Warsaw – Part 1. *Memorabilia Zoologica* **34** p. 260
- Den Boer, P.J. 1970 On the significance of dispersal power for populations of carabid beetles (Coleoptera, Carabidae). *Oecologia* **4**: 1-28
- Den Boer, P.J. (ed.) 1971 Dispersal and dispersal power of carabid beetles. *Miscellaneous papers 8* Landbouwhogeschool, Wageningen, The Netherlands p. 151
- Desender, K. 1989 *Dispersievermogen en ecologie van loopkevers (Coleoptera, Carabidae) in België: een evolutionaire benadering* (English: Dispersal power and ecology of carabid beetles (Coleoptera, Carabidae) in Belgium: an evolutionary approach). Koninklijk Belgisch Instituut voor Natuurwetenschappen p. 136

- Digweed, S.C., Currie, C.R., Carcamo, H.A. & Spence, J.R. 1995 Digging out the "digging-in-effect" of pitfall traps: influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). *Pedobiologia* **39**: 561-576
- Eversham, B.C., Roy, D.B. & Telfer, M.G. 1996 Urban, industrial and other manmade sites as analogues of natural habitats for Carabidae. *Annales Zoologici Fennici* **33**: 149-156
- Eyre, M.D. 1994 Strategic explanations of carabid species distributions in northern England. In K. Desender, J.-P. Maelfait, M. Loreau and M. Luff (eds.) *Carabid beetles: Ecology and evolution* Kluwer Academic Publishers, Netherlands, pp. 267-275
- Fisher, R.A., Corbet, A.S. & Williams, C.B. 1943 The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* **12**: 42-58
- Forsythe, T.G. 1982 Feeding mechanisms of certain ground beetles (Coleoptera: Carabidae). *The Coleopterologists Bulletin* **36**: 26-73
- Frankie, G.W. & Ehler, L.E. 1978 Ecology of insects in urban environments. *Annual Reviews of Entomology* **23**: 367-387
- Gaston, K.J. 2010 *Urban Ecology*. Cambridge University Press, Cambridge, UK p. 318
- Gilbert, O.L. 1987 Urban ecology: Progress and problems in I.D. Rotherham (ed.) *Loving the aliens?!!? Ecology, history, culture and management of exotic plants and animals: Issues for nature conservation*. B & B Press, Rotherham, UK. pp. 7-9
- Gilbert, O.L. 1989 *The ecology of urban habitats*. Chapman & Hall, London
- Gray, J.S. 1987 Species-abundance patterns in: J.H.R. Gee and P.S. Giller (eds.) *Organization of Communities, Past and Present*. Blackwell Scientific Publications, Oxford, UK, pp. 53-67.
- Gray, J.S. 1989 Effects of environmental stress on species rich assemblages. *Biological Journal of the Linnean Society* **37**: 19-32
- Greenslade, P.J.M. 1964 Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology* **33**: 301-310
- Grime, J.P. 1974 Vegetation classification by reference to strategies. *Nature* **250**: 26-31
- Grime, J.P. 1977 Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. *The American Naturalist* **111**: 1169-1194
- Grimm, N.B., Grove, J.M., Pickett, S.T.A. & Redman, C.L. 2000 Integrated approaches to long-term studies of urban ecological systems. *Bioscience* **50**: 571-584
- Hahs, A.K., McDonnell, M.J. & Breuste, J.H. 2009 A comparative ecology of cities and towns: synthesis of opportunities and limitations. In A.K. Hahs, M.J. McDonnell and J.H. Breuste (eds.) *Ecology of Cities and Towns: A Comparative Approach* Cambridge University Press, Cambridge pp. 574-596
- Hamberg, L., Lehvävirta, S., Malmivaara-Lämsä, M., Rita, H. & Kotze, D.J. 2009 The effects of habitat edges and trampling on understorey vegetation in urban forests in Helsinki, Finland. *Applied Vegetation Science* **11**: 83-98
- Hanski, I. 1999 *Metapopulation Ecology*. Oxford University Press, UK, p. 328
- Hanski, I. & Ovaskainen, O. 2002 Extinction debt at extinction threshold. *Conservation Biology* **16**: 666-673

- Hartley, D.J., Koivula, M.J., Spence, J.R., Pelletier, R. & Ball G.E. 2007 Effects of urbanization on ground beetle assemblages (Coleoptera, Carabidae) of grassland habitats in western Canada. *Ecography* **30**: 673-684
- Holland, J.M. 2002 *The agroecology of carabid beetles*. Intercept Ltd., Hampshire, UK p. 356
- Hubbell, S.P. 2001 The unified neutral theory of biodiversity and biogeography, *Monographs in Population Biology* **32** Princeton University Press, New Jersey, USA p. 375
- Hunter, M.L. and Gibbs, J. 2007 *Fundamentals of Conservation Biology* 3<sup>rd</sup> edition. Blackwell Publishing, Oxford, UK p. 14
- Hyvärinen, E., Mannerkoski, I., Clayhills, T., Helve, E., Karjalainen, S., Laurinharju, E., Martikainen, P., Mattila, J., Muona, J., Pentinsaari, M., Rassi, P., Rutanen, I., Salokannel, J., Siitonen J. & Silfverberg, H. 2010 Beetles. In P. Rassi, E. Hyvärinen, A. Juslén and I. Mannerkoski (eds.) *The 2010 Red List of Finnish Species*. Ympäristöministeriö & Suomen ympäristökeskus, Helsinki p. 685
- Kalliovirta, M., Rytteri, T., Hæggström, C.-A. , Hakalisto, S., Kanerva, T., Koistinen, M., Lammi, A., Lehtelä, M., Rautiainen, V-P., Rintanen, T., Salonen, V., & Uusitalo A. 2010 Vascular Plants. In P. Rassi, E. Hyvärinen, A. Juslén and I. Mannerkoski (eds.) *2010 The 2010 Red List of Finnish Species*. Ympäristöministeriö & Suomen ympäristökeskus, Helsinki p. 685
- Kinnunen, H., Tiainen, J. & Tukia, H. 2001 farmland carabid beetle communities at multiple levels of spatial scale. *Ecography* **24**: 189-197
- Klausnitzer, B. 1993 *Ökologie der Großstadtf fauna*. (In English: Ecology of the metropolitan fauna) 2<sup>nd</sup> edition. Gustav Fischer, Stuttgart p. 454
- Klausnitzer, B. & Richter, K. 1993 Presence of an urban gradient demonstrated for carabid associations. *Oecologia* **59**: 79-82
- Koivula, M.J., Kotze, D.J. & Salokannel, J. 2005 Beetles (Coleoptera) in central reservations of three highway roads around the city of Helsinki, Finland. *Annales Zoologici Fennici* **42**: 615-626
- Kotze, D.J. & O'Hara, R.B. 2003 Species decline – but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia* **135**: 138-148
- Kotze, D.J., O'Hara, R.B. & Lehvavirta, S. 2012 Dealing with varying detectability, unequal sample sizes and clumped distributions in count data. *PLoS ONE* **7**: e40923
- Krebs, C. 2001 *Ecology – the experimental analysis of distribution and abundance*. Benjamin Cummings, San Francisco
- Kuussaari M., Heliölä, J., Luoto, M. & Pöyry, J. 2007 Determinants of local species richness of diurnal Lepidoptera in boreal agricultural landscapes. *Agriculture, Ecosystems and Environment* **122**: 366-376
- Lindroth, C.H. 1985 *The Carabidae (Coleoptera) of Fennoscandia and Denmark*. Volume 15, part 1, Scandinavian Press Ltd., Denmark p. 225
- Lindroth, C.H. 1986 *The Carabidae (Coleoptera) of Fennoscandia and Denmark*. Volume 15, part 2, Scandinavian Press Ltd., Denmark p. 497
- Lindroth, C.H. 1992 *Ground Beetles (Carabidae) of Fennoscandia – A Zoogeographic Study Part III General Analysis with a Discussion on Biogeographic Principles*. Smithsonian Institution Libraries and The National Science Foundation, Washington D.C. p. 814
- Linusson, A.-C., Berlin, G.A.I. & Olsson, E.G.A. 1998 Reduced community diversity in semi-natural meadows in southern Sweden. 1965-1990 *Plant Ecology* **136**: 77-94

- Luff, M.L. 2007 *The Carabidae (ground beetles) of Britain and Ireland*. Royal Entomological Society and Field Studies Council, St. Albans p. 247
- Luff, M.L., Eyre, M.D. & Rushton, S.P. 1989 Classification and ordination of habitats of ground beetles (Coleoptera, Carabidae) in North-East England. *Journal of Biogeography* **16**: 121-130
- Luoto, M., Rekolainen, S., Aakkula, J. & Pykälä, J. 2003 Loss of plant species richness and habitat connectivity in grasslands associated with agricultural change in Finland. *AMBIO – A Journal of the Human Environment* **32**: 447-452
- Lövei, G.L. & Sunderland, K.D. 1996 Ecology and Behaviour of Ground Beetles (Coleoptera: Carabidae). *Annual Review of Entomology* **41**: 231-256
- McDonnell, M.J. 2011 The history of urban ecology – an ecologist's perspective. In J. Niemelä, J. Breuste, T. Elmqvist, G. Guntenspergen, P. James and N. McIntyre 2011 *Urban Ecology: Patterns, processes and applications*. Oxford University Press, Oxford, UK pp. 5-13
- McDonnell, M.J. & Hahs, A.K. 2008 The use of gradient analysis studies in advancing our understanding of the ecology of urbanising landscapes: Current status and future directions. *Landscape Ecology* **23**: 1143-1155
- McDonnell, M.J., Pickett, S.T.A. & Pouyat, R.V. 1993 The application of the ecological gradient paradigm to the study of urban effects. In: M.J. McDonnell and S.T.A. Pickett, (eds.) 1993 *Humans as components of ecosystems*. Springer-Verlag, N. York, pp. 175-189
- McDonnell, M.J., Pickett, S.T.A., Pouyat, R.V., Parmelee, R.W., Carreiro, M.M., Groffmann, P., Bohlen, P., Zipperer, W.C. & Medley, K. 1997 Ecosystem processes along urban-to-rural gradients. *Urban Ecosystems* **1**: 21-36
- McKinney, M.L. 2002 Urbanization, biodiversity, and conservation. *Bioscience* **52**: 883-890
- McKinney, M.L. 2008 Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems* **11**: 161-176
- Magura, T., Tóthmérész, B. & Molnar, T. 2004 Changes in carabid beetle assemblages along an urbanisation gradient in the city of Debrecen, Hungary. *Landscape Ecology* **19**: 747-759
- Magura, T., Lövei, G.L. & Tóthmérész, B. 2010 Does urbanisation decrease diversity in ground beetle (Carabidae) assemblages? *Global Ecology and Biogeography* **19**:16-26
- Magurran, A.E. 2004 *Measuring Biological Diversity*. Blackwell publishing, p. 257
- Marsh, G.P. 1864 *Man and nature; or, physical geography as modified by human action*. Reprinted 1965 Belknap Press of Harvard University Press, Cambridge
- Marzluff, J.M., Shulenberger, E., Endlicher, E., Alberti, M., Bradley, G., Ryan, C., Simon, U. & ZumBrunnen, C. 2008 *Urban ecology: an international perspective on the interaction between humans and nature*. Springer, New York p. 807
- Matalin, A.V. 2003 Variations in flight ability with sex and age in ground beetles (Coleoptera, Carabidae) of south-western Moldova. *Pedobiologia* **47**: 311-319
- Matteson, K.C., Ascher, J.S. & Langellotto, G.A. 2008 Bee richness and abundance in New York city urban gardens. *Annals of the Entomological Society of America* **101**: 140-150
- May, R.M. 1975 Patterns of species abundance and diversity. In M.L. Cody and J.M. Diamond (eds.) *Ecology and Evolution of Communities* pp. 81-120 Belknap Press, Harvard, USA
- Niemelä, J. 1999 Ecology and urban planning. *Biodiversity and Conservation* **8**: 119-131



- Niemelä, J., Breuste, J., Elmqvist, T., Guntenspergen, G., James, P. & McIntyre, N. 2011 *Urban Ecology: Patterns, processes and applications*. Oxford University Press, Oxford, UK, p. 374
- Niemelä, J. & Kotze, D.J. 2009 Carabid beetle assemblages along urban to rural gradients: A review. *Landscape and urban planning* **92**: 65-71
- Niemelä, J., Haila, Y., Halme, E., Pajunen, T., Punttila, P. & Tukia, H. 1987 Habitat preferences and conservation status of *Agonum mannerheimii* Dej. in Hame, southern Finland. *Notulae Entomologicae* **67**: 175-179
- Niemela, J., Haila, Y. & Punttila, P. 1996 The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography* **19**: 352-368
- Nuorteva, P. 1963 Synanthropy of blowflies (Dipt., Calliphoridae) in Finland. *Annales Entomologica Fennica* **29**: 1-49
- Nuorteva, P. 1971 The synanthropy of birds as an expression of the ecological cycle disorder caused by urbanization. *Annales Entomologica Fennica* **8**: 547-553
- Oertli, S., Müller, A. & Dorn, S. 2005 Ecological and seasonal patterns in the diversity of a species-rich bee assemblage (Hymenoptera: Apoidea: Apiformes). *European Journal of Entomology* **102**: 53-63
- Oksanen, J. 2007 Multivariate Analysis of Ecological Communities in R: vegan tutorial. [http://www.planta.cn/forum/files\\_planta/multivariate\\_analysis\\_of\\_ecological\\_communities\\_in\\_r\\_140.pdf](http://www.planta.cn/forum/files_planta/multivariate_analysis_of_ecological_communities_in_r_140.pdf)
- Paarman, W., Faust, N., Arndt, E., Luchtrath, I. & Rohe, W. 2006 Constant seed size and mandible growth - a fundamental problem for granivorous ground beetle larvae (Coleoptera: Carabidae). *Entomologica Fennica* **17**: 334-339
- Pearson, T.H. & Rosenberg, R. 1978 Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology Annual Review* **16**: 229-311
- Pickett, S.T.A., Kolasa, J., Armesto, J.J. & Collins, S.L. 1989 The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos* **54**: 129-136
- Pickett, S.T.A. & McDonnell, M.J. 1993 Humans as components of ecosystems: a synthesis. In M.J. McDonnell and S.T.A. Pickett (eds.) *Humans as components of ecosystems: subtle human effects and the ecology of populated areas* Springer-Verlag, New York
- Pickett, S.T.A., Parker, V.T. & Fiedler, P. 1992 The new paradigm in ecology: Implications for conservation biology above the species level. In P.L. Fiedler and S.K. Jain (eds.) *Conservation biology: the theory and practice of nature conservation, preservation, and management* Chapman and Hall, New York. pp. 65-68
- Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., Nilon, C.H., Pouyat, R.V., Zipperer, W.C. & Costanza, R. 2008 Urban Ecological Systems: Linking Terrestrial Ecological, Physical, and socioeconomic Components of Metropolitan Areas. In Marzluff, J.M., Shulenberg, E., Endlicher, E., Alberti, M., Bradley, G., Ryan, C., Simon, U. & ZumBrunnen, C. *Urban ecology: an international perspective on the interaction between humans and nature*. Springer, New York pp. 99-122
- Preston, F.W. 1948 The commonness and rarity of species. *Ecology* **29**: 254-283
- Preston, F.W. 1962 The canonical distribution of commonness and rarity. *Ecology* **43**: 410-432
- Pykälä, J. 2003 Effects of restoration with cattle grazing on plant species composition and richness of seminatural grasslands. *Biodiversity and Conservation* **12**: 2211-2226

- Pykälä, J. 2005 Plant species responses to cattle grazing in mesic semi-natural grassland. *Agriculture, Ecosystems and Environment* **108**: 109-117
- Påhlsson, L. 1998 *Vegetationstyper i Norden* (in English: Nordic vegetation types, in Swedish). TemaNord, Nordic Council of Ministers, Copenhagen, Denmark
- Pöyry, J., Lindgren, S., Salminen, J. & Kuussaari, M. 2004. Restoration of butterfly and moth communities in semi-natural grasslands by cattle grazing. *Ecological Applications* **14**: 1656-1670
- Rassi, P., Hyvärinen, E., Juslén, A. & Mannerkoski, I. (eds.) 2010 *The 2010 Red List of Finnish Species*. Ministry of the Environment and Finnish Environment Institute, Helsinki, (In Finnish with English summary)
- Rees, W.E. 1997 Urban ecosystems: the human dimension. *Urban Ecosystems* **1**: 63-75
- Sadler, J.P., Small, E.C., Fiszpan, H., Telfer, M. & Niemelä, J. 2006 Investigating environmental variation and landscape characteristics of an urban-rural gradient using woodland carabid assemblages. *Journal of Biogeography* **33**: 1126-1138
- Saska, P. 2008 Effect of diet on the fecundity of three carabid beetles. *Physiological Entomology* **33**: 188-192
- Saska, P., Vodde, M., Heijerman, T., Westerman, P. & Van der Werf, W. 2007 The significance of a grassy boundary for the spatial distribution of carabids within two cereal fields. *Agriculture, Ecosystems and Environment* **122**: 427-434
- Schmitz, O.J. 2009 Effects of predator functional diversity on grassland ecosystem function. *Ecology* **90**: 2339-2345
- Scholz, H. 1960 Die veränderungen in der ruderaflora Berlins. Ein beitrag zur jüngsten florensgeschichte (in English: The changes in the ruderal flora of Berlin. A contribution to the recent floral history). *Willdenowia* **2**: 379-397
- Schwerk, A. 2000 Ecological aspects of carabid beetle coenoses (Coleoptera: Carabidae) on industrial fallow grounds in the Ruhr Valley Area. In P. Brandmayr, *et al.* eds. *Natural History and Applied Ecology of Carabid Beetles* Pensoft Publishers, Moscow pp. 277-287
- Seto K.C., Fragkias M., Güneralp B., Reilly, M.K. 2011 A meta-analysis of global urban land expansion. *PLoS ONE* **6**: e23777. doi:10.1371/journal.pone.0023777
- Sharma, S. & Amritphale, D. 2007 Effect of urbanization on the population density of aak weevil. *Current Science* **93**: 1130-1134
- Siitonen, J. 2001 Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins* **49**: 11-41.
- Simberloff, D. 1982 A succession of paradigms in ecology. Essentialism to materialism and probabilism. In E. Saarinen (ed.) *Conceptual Issues in Ecology* Reidel (Kluwer) Boston, USA.
- Small, E., Sadler, J.P. & Telfer, M. 2006 Do landscape factors affect brownfield carabid assemblages? *Science of the Total Environment* **360**: 205-222
- Smith, R.M., Thompson, K., Hodgson, J.G., Warren, P.H. & Gaston, K.J. 2006 Urban domestic gardens (IX): Composition and richness of the vascular plant flora, and implications for native biodiversity. *Biological Conservation* **129**: 312-322
- Soulé, M.E. 1985 What is conservation biology? *Bioscience* **35**: 727-734
- Soulé, M.E. & Wilcox, B.A. 1980 *Conservation biology. An evolutionary-ecological perspective*. Sunderland, MA: Sinauer Associates pp. 95-117

- Sousa, W.P. 1984 The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* **15**: 353-391
- Suding, K.N., Collins, S.L., Gough, L., Clark, C., Cleland, E.E., Gross, K.L., Milchunas, D.G. & Pennings, S. 2005 Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *PNAS* **102**: 4387-4392
- Sukopp, H. 1998 Urban ecology: scientific and practical aspects. In J. Breuste, H. Feldmann and O. Uhlmann (eds.) *Urban Ecology*. Springer-Verlag, Berlin. p. 79-98
- Sukopp, H. 2008 On the early history of urban ecology in Europe. In: J.M. Marzluff, E. Shulenberger, W. Endlicher, M. Alberti, G. Bradley, C. Ryan, C. ZumBrunnen and U. Simon, (eds.) 2008 *Urban Ecology – An international perspective on the interaction between humans and nature*. Springer Science and Business Media, New York, pp. 79-97
- Šustek, Z. 1987 Changes in body size structure of carabid communities (Coleoptera, Carabidae) along an urbanisation gradient. *Biologia (Bratislava)* **42**: 145-156
- Šustek, Z. 1992 Changes in the representation of carabid life forms along an urbanization gradient (Coleoptera, Carabidae). *Biologia (Bratislava)* **42**: 417-430
- Symondson, W.O.C., Sunderland, K.D. & Greenstone, M.H. 2003 Can generalist predators be effective biocontrol agents? *Annual Review of Entomology* **47**: 561-594
- Sörensson, M. 2008 AHA – en enkel metod för prioritering av vedentomologiska naturvärden hos träd i sydsvenska park- och kulturmiljöer (in English: AHA – a simple method for evaluating conservation priorities of trees in South Swedish parks and urban areas from an entomo-saproxylic viewpoint). *Entomologisk Tidskrift* **129**: 81-90 ISSN 0013-886x
- Tallamy, D.W. 2009 *Bringing Nature Home*. Timber Press, Portland, USA p. 360
- ter Braak, C.J.F 1994 Canonical community ordination. Part I: Basic theory and linear methods. *Ecoscience* **1**: 127-140
- ter Braak, C.J.F. 1995 Ordination Pages 91-173 in Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. *Data analysis in community and landscape ecology*. Cambridge University Press
- ter Braak, C.J.F. & Prentice, I.C. 1988 A Theory of Gradient Analysis. *Advances in Ecological Research* **34**: 271-317
- Thiele, H.-U. 1977. *Carabid Beetles in Their Environments*. Springer, New York, USA
- Thomas, C.F.G., Parkinson, L. & Marshall, E.J.P. 1998 Isolating the components of activity-density for the carabid beetle *Pterostichus melanarius* in farmland. *Oecologia*, **116**: 103-112
- Tonteri T. & Haila Y. 1990 Plants in a boreal city: ecological characteristics of vegetation in Helsinki and its surroundings, southern Finland. *Annales Botanici Fennici* **27**: 337-352
- Truscott, A.M., Palmer, S.C.F., McGowan, G.M., Cape, J.N. & Smart, S. 2005 Vegetation composition of roadside verges in Scotland: the effects of nitrogen deposition, disturbance and management. *Environmental Pollution* **136**: 109-118
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. 2005 Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters* **8**: 857-874
- UNFPA 2007 *State of the world population 2007: Unleashing the potential urban growth*. United Nations Population Fund, New York

Vallet, J., Daniel, H., Beujouan, V. & Rozé, F. 2008 Plant species responses to urbanization: comparison of isolated woodland patches in two cities of North-Western France. *Landscape Ecology* **23**: 1205-1217

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. 1997 Human domination of earth's ecosystems. *Science* **227**: 494-499

Weller, B. & Ganzhorn, J.U. 2004 Carabid beetles community composition, body size, and fluctuating asymmetry along an urban-rural gradient. *Basic and Applied Ecology* **5**: 193-201

Whittaker, R.H. 1965 Dominance and diversity in land plant communities. *Science* **147**: 250-260

Whittaker, R.H. 1967 Gradient analysis of vegetation. *Biological Reviews* **49**: 207-264

Whittaker, R.H. 1969 Evolution of diversity in plant communities. In: *Diversity and Stability in Ecological Systems* Brookhaven Symposia in Biology, Upton, New York pp. 178-95

Wootton, J.T. Effects of disturbance on species diversity: A multitrophic perspective. *The American Naturalist* **152**: 803-825