# Plants in urban environments in relation to global change drivers at different scales

Dissertation
Zur Erlangung der Würde des Doktors der Naturwissenschaften des Fachbereichs Biologie
der Fakultät für Mathematik, Informatik und Naturwissenschaften
der Universität Hamburg

vorgelegt von

Katharina Johanna Schmidt

aus Heidelberg

Hamburg 2014

Genehmigt vom Fachbereich Biologie
der Fakultät für Mathematik, Informatik und Naturwissenschaften
an der Universität Hamburg
auf Antrag von Professor Dr. K. JENSEN
Weitere Gutachterin der Dissertation:
Frau Professor Dr. E.-M. PFEIFFER
Tag der Disputation: 07. Februar 2014

Hamburg, den 28.Januar 2014

Professor Dr. C. Lohr
Vorsitzender des
Fach-Promotionsausschusses Biologie

# TABLE OF CONTENTS

# LIST OF FIGURES

# LIST OF TABLES

# SUMMARY

Urbanisation and climate change are major global change drivers affecting biodiversity and plant species. In future, more and more people will live in cities and urban land cover will continue to increase. Thus, plant species will be faced with habitat changes and even loss. Concomitantly, climate is changing and this is predicted to result in elevated temperature and atmospheric $CO_2$ levels as well as different precipitation patterns (e.g. less precipitation in summer). Some of today's environmental conditions in urban areas reflect changes expected in the course of climate change. Urban environmental conditions differ strongly from those in rural areas. Urban areas usually feature high degrees of soil sealing, high population density, heavy traffic, enhanced air and soil pollution, high $CO_2$ levels, high nitrogen deposition, and low water availability. Along gradients of decreasing urbanisation from urban to rural areas, these environmental factors decrease in intensity. Another important factor in urban areas is the strong direct human impact.

Conserving and promoting biodiversity in cities is important for the conservation of local biodiversity, environmental education, improvement of human well-being, and maintaining ecosystem functions of vegetation. Urban areas are especially rich in plant species due to small-scale habitat heterogeneity, geological diversity and the occurrence of non-native species. Within a city, species richness is generally lower in highly urbanised areas and highest in moderately urbanised areas. Non-native species are closely associated with urban areas and have increased in proportion during the past century. One reason for their success is preadaptation to the dry and warm environmental conditions in urban areas.

Climate change will influence phenology, range, and distribution of species as well as the composition and dynamics of communities. Some species might go extinct locally, while new species are expected to migrate. Hence, novel communities will develop. Changes in phenology and latitudinal or altitudinal range shifts can disrupt biotic interactions or alter former synchrony between species. Competition and plant-herbivory interactions may also change in future. However, species may also adapt to the changing conditions (i.e. niche shifts).

The studies of this thesis aim to detect patterns in the urban flora of Hamburg (i.e. spontaneously occurring vascular plant species) at different scales and to identify underlying drivers. The analyses range from a general investigation of species distribution in the entire city of Hamburg to analysing species richness in select habitats and to study the responses of a single species to climate change. In all studies, a major focus is on changes along urbanisation gradients.

In Chapter 2, a study was conducted on a large scale considering the entire city of Hamburg. Here, areas of high species richness were identified and richness distribution patterns in the city of Hamburg were assessed by analysing a floristic mapping dataset on the scale of 1 $km^2$. Besides total species richness, proportions of non-native, endangered, and thermophilic species were investigated. Differences in plant species richness were analysed between three

urbanisation zones. With multiple regression analyses, effects of urban structure, habitat, and environmental conditions on the distribution of species richness measures were tested.

Total species richness per 1 km$^2$ was 274 ± 60 on average and differed only slightly between the urbanisation zones in contrast to other cities. Species richness increased with habitat diversity and decreased with Ellenberg indicator values (EIV) for nutrients. The proportion of non-native species increased with mean annual temperature and decreased with EIVs for moisture, while the proportion of endangered species increased with EIVs for moisture and decreased with EIVs for nutrients. The proportion of thermophilic species could be explained by mean annual temperature. Some of the emerging patterns probably differ from those in other cities due to Hamburg's central port harbouring a particular flora. Besides the expected high proportions of non-native species, high proportions of endangered species were also found in this area. The results of the study contribute to identifying drivers of biodiversity in cities and can thus be used to develop measures for the conservation of urban biodiversity.

In Chapter 3 the study aim was to disentangle the effects of environmental conditions and spatial structure on the distribution of plant species on a large scale using the city of Hamburg as a case study. Furthermore, tests dermined whether species proxy data are better suited than original species distribution data for understanding general biodiversity pattern in urban environments.

Using the same floristic mapping data as in Chapter 2, general patterns in plant species distribution were first tested by cluster analysis. Second, redundancy analyses (RDAs) were used to determine the most important environmental variables for species' and species proxies' (genera, communities and traits) distribution patterns. Third, we applied variation partitioning to differentiate between environmental and spatial effects. Considering the complex spatial structure in urban environments, Moran's eigenvector maps (MEM) were used. Species composition reflected Hamburg's geography, indicating effects of both historical environmental conditions and urbanisation on species distribution. The port area and semi-natural habitats were richest in plant species. The variation explained by the considered variables increased in the RDAs from species (24 %) and genera (36 %) to trait (60 %) and community (61 %) data. Including spatial structure in variation partitioning detected the impact of spatially structured environmental variables (induced spatial dependence). Hence, the combination of species proxy data with advanced multivariate analyses accounting for complex spatial pattern is well suited to analyse the distribution of biodiversity in urban systems. Results obtained using species proxy data could be used for comparisons of biodiversity patterns between cities in the future.

Chapter 4 deals with an interdisciplinary study assessing the long-term urban heat island (UHI) in Hamburg. Since long-term data on the UHI are scarce, a new proxy dataset derived from floristic mapping was used: Under the assumptions that plants integrate environmental conditions over time, Ellenberg indicator values for temperature (EIT) were derived to summarise the overall temperature preferences of the occurring plant species. The EIT showed a clear heat island pattern, were highly correlated with existing measurements, and showed increased values in densely built urban classes. Consequently, EIT were considered suitable as UHI proxies. EIT were related to a large number of typical UHI predictors, of which the normalised difference vegetation index (NDVI) explained most variance followed by

temperature variables derived from remote sensing data. Hence, floristic mapping data can be successfully applied in other research fields.

In Chapter 5, species richness and species composition of select habitats along an urbanisation gradient in Hamburg were investigated on a smaller scale than in the previous studies. Vegetation composition and edaphic conditions in two habitat types, riparian (natural) and wasteland habitats (anthropogenic), were analysed to test whether these differ along natural and anthropogenic gradients and whether emerging patterns can be related to urbanisation. Vegetation relevés of vascular plant species were conducted at nine sites of each habitat type and soil samples were taken. With regression models, species numbers, soil pH, and conductivity of river and wasteland sites were related to distance to the city centre as a proxy for urbanisation. Total plant species number, soil pH and soil conductivity were not correlated with distance to the city centre at either site. Species number did not differ between habitat types, while soil pH was higher at wasteland sites and conductivity was higher at riparian sites. Corresponding to the results of Chapter 2, species richness did not differ along the urbanisation gradient on this smaller scale.

The aim in Chapter 6 was to investigate how the non-native species *Senecio inaequidens*, originating from South Africa, responds to biotic interactions with native species under future climate change. In three experiments simulating climate warming, germination of *S. inaequidens* and its performance in response to competition and herbivory were analysed. This study considers potential differences in six populations along an urbanisation gradient in Hamburg on the small scale of individual plants. Germination was favoured by higher temperatures. Interspecific competition and elevated temperature influenced growth and biomass production of *S. inaequidens*. Differences in growth and biomass production between populations could not clearly be related to urbanisation intensity. However, the results of the herbivory experiment indicate that *S. inaequidens* is able to rapidly adapt to local conditions. Plants from highly urbanised areas were more strongly attacked by herbivores than plants from less urbanised areas and they exhibited a different defence strategy against herbivores. Changes in these patterns due to climate warming could not be detected. However, *S. inaequidens* might rapidly adapt to future enemies and changing environmental conditions, and has the advantage that, due to its South-African origin, the species is already adapted to warm and dry conditions.

Overall, the results from the studies of this thesis showed that Hamburg's spatial conditions differ from those of other cities and thus plant species and species richness distribution patterns are rather specific. Urbanisation intensity could be well defined by the definitions of urbanisation derived from environmental and spatial variables as well as by plant species composition. The results of this thesis can be used to compare future species richness and composition with the patterns derived here to estimate future impacts on vegetation in the course of climate change. The application of results from analyses of floristic mapping data is a promising avenue for integrating botanical and floristic studies into other research areas, e.g. climatology.

The analysis of floristic mapping data in this thesis can help identify valuable areas for conservation practice and hence provide important impacts for urban planning. In Hamburg, nature conservation will need to pay special attention to both the port vegetation and the vegetation of semi-natural habitats in Hamburg, since these areas are richest in species and harbour rare and endangered plant species. Hence, conservation measures should focus on dry grasslands, wasteland and semi natural habitats, i.e. by designating nature reserves and developing habitat networks.

More studies on the impact of climate change on urban plant species richness and composition are needed to fully estimate future changes in vegetation patterns. One possible approach is the investigation of single species in experiments: Here, the results of this thesis indicate that the non-native *S. inaequidens* will be able to adapt locally to changing conditions.

# ZUSAMMENFASSUNG

Urbanisierung und Klimawandel sind wichtige Faktoren des globalen Wandels, die Biodiversität und Pflanzenarten beeinflussen. In Zukunft werden immer mehr Menschen in Städten leben und die Verstädterung wird weiter zunehmen. Daher werden Pflanzenarten mit Habitatveränderungen und auch -verlusten konfrontiert sein. Gleichzeitig verändert sich das Klima, so werden ein Anstieg von Temperatur und atmosphärischer $CO_2$-Konzentration sowie sich verändernde Niederschlagsmuster (z.B. ein Rückgang von Sommerniederschlägen) prognostiziert. Einige heutige Umweltbedingungen in Städten spiegeln die im Zuge des Klimawandels zu erwartenden Veränderungen bereits wider. Umweltbedingungen in Städten unterscheiden sich stark von denen in ländlichen Gebieten. Sie zeichnen sich typischerweise durch einen hohen Versiegelungsgrad, hohe Bevölkerungsdichte, starkes Verkehrsaufkommen, erhöhte Luft- und Bodenverschmutzung, hohe $CO_2$-Konzentrationen, hohe Stickstoffdepositionen und geringe Wasserverfügbarkeit in Böden aus. Die Intensität dieser Umweltfaktoren nimmt entlang eines Urbanisierungsgradienten mit zunehmender Distanz zum Stadtzentrum ab. Ein weiterer wichtiger Faktor in Städten ist der starke anthropogene Einfluss.

Schutz und Förderung der Biodiversität in Städten ist wichtig, um sowohl die lokale Biodiversität zu bewahren, Ökosystemfunktionen der Vegetation zu erhalten, als auch das menschliche Wohlbefinden zu verbessern und Umweltbildung zu ermöglichen. Auf Grund kleinskaliger Habitatheterogenität, geologischer Vielfalt und dem Vorkommen von nicht-heimischen Arten ist die Flora von Städten besonders reich an Pflanzenarten. Innerhalb einer Stadt ist der Artenreichtum in stark urbanisierten Bereichen in der Regel am geringsten und in moderat urbanisierten Bereichen am größten. In Städten sind häufig viele nicht-heimische Arten zu finden, ihr Anteil hat im letzten Jahrhundert stark zugenommen. Einwandernde Pflanzenarten sind häufig wärmeliebend und daher gut an die wärmeren und trockenen Bedingungen in Städten angepasst.

Es ist zu erwarten, dass der Klimawandel die Phänologie und die Verbreitung von Arten sowie die Zusammensetzung und die Dynamik von Pflanzengemeinschaften beeinflussen wird. Einige Arten könnten lokal aussterben, andere neu einwandern, dabei würden sich neue Artengemeinschaften bilden. Veränderungen in der Phänologie sowie in der Ausbreitung von Arten können biotische Interaktionen stören und die Synchronisation von Arten verändern. Darüber hinaus können sich künftig Konkurrenzverhältnisse zwischen Pflanzenarten und Pflanzen-Tier-Interaktionen verändern. Es ist aber auch möglich, dass sich Arten an sich verändernde Bedingungen anpassen, z.B. durch eine Verlagerung ihrer ökologischen Nische.

Diese Arbeit hat das Ziel, auf unterschiedlichen Skalen Muster in der urbanen Flora von Hamburg aufzudecken und die zu Grunde liegenden Einflussfaktoren zu identifizieren. Die Untersuchungen reichen von einer Analyse der Artenverbreitung im gesamten Hamburger Stadtgebiet über die Untersuchung von Artenvielfalt in ausgewählten Habitaten bis hin zu Studien zu den Auswirkungen des Klimawandels auf eine einzelne Art. Im Fokus standen dabei jeweils Veränderungen entlang von Urbanisierungsgradienten.

In Kapitel 2 wurde eine Studie durchgeführt, die das gesamte Hamburger Stadtgebiet betrachtet. Durch die Analyse eines Datensatzes einer floristischen Kartierung auf der Skala von 1 km² wurden Gebiete mit hohem Artenreichtum identifiziert und die Verbreitung des Artenreichtums untersucht. Neben dem Gesamtreichtum wurden auch Anteile nicht-heimischer, gefährdeter und thermophiler Arten analysiert. Unterschiede im Artenreichtum wurden zwischen drei Urbanisierungszonen getestet. Mit multiplen Regressionen wurden Effekte von Stadtstruktur, Habitat und Umweltbedingungen auf die Verbreitung der Artenvielfalt getestet.

Der Gesamtartenreichtum pro km² betrug im Mittel 274 ± 60 und unterschied sich – im Unterschied zu anderen Städten – kaum zwischen den Urbanisierungszonen. Die Gesamtartenzahl pro km² nahm mit zunehmender Habitatdiversität zu und mit zunehmendem Ellenberg Zeigerwert (EIV) für Nährstoff ab. Der Anteil nicht-heimischer Arten nahm mit zunehmender mittleren Jahrestemperatur zu und mit zunehmendem EIV für Feuchte ab, der Anteil gefährdeter Arten nahm hingegen mit zunehmendem EIV für Feuchte zu und mit zunehmendem EIV für Nährstoffe ab. Der Anteil thermophiler Arten konnte durch die mittlere Jahrestemperatur erklärt werden. Einige dieser ermittelten Muster unterscheiden sich von denen anderer Städte durch den zentralen Hamburger Hafen, der eine besondere Flora aufweist. Neben dem zu erwartenden hohen Anteil nicht-heimischer Arten kommen im Hafengebiet auch viele gefährdete Arten vor. Die Ergebnisse der Studie tragen zu der Identifizierung von Einflussfaktoren auf Biodiversität in Städten bei und können daher genutzt werden, um Maßnahmen zum Schutz der städtischen Biodiversität zu entwickeln.

Das Ziel der Studie in Kapitel 3 war, die Einflüsse von Umweltbedingungen und räumlicher Struktur auf die Verbreitung von Pflanzenarten im urbanen Raum getrennt zu betrachten. Wieder wurde auf der Skalenebene von ganz Hamburg gearbeitet Außerdem wurde untersucht, ob aus den Artdaten abgeleitete Proxies besser für das Verständnis von Biodiversitätsmustern in urbanen Gebieten geeignet sind als die Artdaten selbst. Hier wurde dieselbe Datengrundlage aus der floristischen Kartierung genutzt wie in Kapitel 2. Zunächst wurde der Datensatz mit einer Clusteranalyse auf generelle Muster in der Verbreitung der Hamburger Pflanzenarten getestet. Danach wurden mit Redundanzanalysen (RDA) die einflussreichsten Umweltvariablen für die Verbreitung der Arten und Artenproxies (Gattung, Pflanzengemeinschaft und ‚traits‘) ermittelt. Dann wurden mithilfe von Variationspartitionierung Umwelt- und Raumeffekte separiert, als Raumvariablen wurden hierbei aufgrund der komplexen Struktur in Städten ‚Moran's eigenvector maps' (MEM) verwendet.

Die Artenzusammensetzung spiegelte die Hamburger Landschaft deutlich wieder, dies deutete auf die Beeinflussung der Artenverbreitung durch sowohl historische Umweltbedingungen als auch Urbanisierung hin. Das zentrale Hafengebiet und naturnahe Habitate waren am artenreichsten. Die Variation, die durch die Umweltvariablen in den RDAs erklärt wurde, nahm von Art-(24 %) und Gattungs- (36 %) zu 'trait'- (60 %) und Pflanzengemeinschaftsdaten (61 %) zu. Die Einbeziehung der räumlichen Struktur in der Variationspartitionierung zeigte den starken Einfluss von räumlich strukturierten Umweltvariablen auf, Raum und Umwelt waren demnach schlecht trennbar. Es wurde gezeigt, dass die Analyse von Artenproxies mit umfangreicher multivariater Statistik unter Einbeziehung der räumlichen Struktur gut geeignet ist, um die Verbreitung von Biodiversität in urbanen Systemen zu analysieren. Die Ergebnisse der Analysen der Artenproxies könnten zukünftig für den Vergleich von Biodiversitätsmustern mit anderen Städten genutzt werden.

Kapitel 4 befasst sich mit einer interdisziplinären Studie, in der die langzeitige städtische Wärmeinsel (UHI) in Hamburg untersucht wird. Da es kaum langfristige Daten zur UHI in Hamburg gibt, wurde ein neuer UHI-Proxy-Datensatz aus Daten aus der o.g. floristischen Kartierung generiert. Unter der Annahme, dass Pflanzen Umweltbedingungen über die Zeit integrieren, wurden Ellenberg Zeigerwerte für Temperatur (EIT) aus den Artdaten ermittelt. Diese repräsentieren die Temperaturpreferenzen von Pflanzenarten in Bezug auf ihr Verbreitungsgebiet. Die EIT wiesen ein deutliches UHI-Muster auf, waren stark mit vorhandenen Messungen korreliert und waren in dicht bebauten Stadtklassen erhöht und daher gut als UHI-Proxy geeignet. Die EIT waren mit zahlreichen typischen UHI-Prädiktoren korreliert, von denen der normalisierte differenzierte Vegetationsindex (NDVI) sowie temperaturbezogene Prädiktoren, die aus Fernerkundungsdaten gewonnen wurden, die meiste Varianz erklärten. Es wurde gezeigt, dass Daten aus floristischen Kartierungen auch in anderen Forschungsgebieten erfolgreich angewendet werden können.

In Kapitel 5 wurden Artenreichtum und Artenzusammensetzung von Pflanzen einzelner Habitate entlang von Urbanisierungsgradienten in Hamburg untersucht, die Untersuchungsskala war hier kleiner als in den vorherigen Kapiteln. Vegetationszusammensetzung und Bodenbedingungen in zwei Habitattypen, entlang eines Flusses (naturnah) und auf Brachflächen (anthropogen), wurden in Hinblick auf Unterschiede entlang von naturnahen und anthropogenen Gradienten und deren Bezug zur Urbanisierung analysiert. Die Gefäßpflanzenvegetation wurde auf jeweils neun Flächen beider Habitattypen aufgenommen, außerdem wurden Bodenproben genommen. Mit Regressionsmodellen wurden Artenzahl, pH-Wert und Leitfähigkeit des Bodens der Fluss- und Brachflächen in Beziehung zur Distanz zur Stadtmitte (als Proxy für Urbanisierung) gesetzt. Artenzahl, pH-Wert und Leitfähigkeit des Bodens waren in beiden Habitattypen nicht mit der Distanz zur Stadtmitte korreliert. Die Artenzahl unterschied sich nicht zwischen den Habitattypen. Der pH-Wert war höher auf den Brachflächen, während die Leitfähigkeit auf den Flussflächen höher war. In Übereinstimmung mit den Ergebnissen aus Kapitel 2 gab es auch auf einer kleineren Untersuchungsskala keine Unterschiede im Artenreichtum entlang des Urbanisierungsgradienten.

In Kapitel 6 wurde untersucht, wie die in Deutschland nicht-heimische Pflanzenart *Senecio inaequidens* (heimisch in Südafrika) auf biotische Interaktionen mit heimischen Arten unter Bedingungen des zukünftigen Klimawandels reagiert. In drei Experimenten, in denen Klimaerwärmung simuliert wurde, wurde Keimung sowie Wachstum und Biomasseproduktion von *S. inaequidens* unter Konkurrenz und Herbivorie analysiert. Diese Studie untersucht auch potentielle Unterschiede zwischen sechs Populationen entlang eines Urbanisierungsgradienten in Hamburg auf der Skala von einzelnen Pflanzen.

Die Keimung von *S. inaequidens* wurde durch erhöhte Temperatur gefördert. Interspezifische Konkurrenz und erhöhte Temperatur beeinflussten Wachstum und Biomasseproduktion. Unterschiede in Wachstum und Biomasseproduktion zwischen Populationen konnten nicht direkt auf Urbanisierungsintensität zurückgeführt werden. Allerdings deuten die Ergebnisse aus dem Herbivorie-Experiment darauf hin, dass sich *S. inaequidens* schnell an lokale Umweltbedingungen anpassen kann. Pflanzen aus stark urbanisierten Gebieten wurden stärker von Fraßfeinden angegriffen als Pflanzen aus weniger stark urbanisierten Gebieten und nutzten eine andere Verteidigungsstrategie gegen Herbivore. Klimawandelbedingte Veränderungen dieser Muster konnten jedoch nicht festgestellt werden. Trotzdem ist zu erwarten, dass sich *S. inaequidens* schnell an zukünftige Fraßfeinde und eine sich verändernde Umwelt anpassen wird. Zudem hat die Art den Vorteil, dass sie aufgrund ihrer Herkunft bereits an warme und trockene Umweltbedingungen angepasst ist.

Zusammengefasst zeigten die Ergebnisse dieser Arbeit, dass sich Hamburgs räumliche Struktur von der anderer Städte stark unterscheidet und daher Artenreichtum und –zusammensetzung recht spezifisch sind. Die Urbanisierungsintensität konnte durch die erarbeiteten Muster aus Pflanzenarten, Umwelt und Raum sehr gut abgebildet werden. Die Ergebnisse dieser Arbeit können mit zukünftigen Mustern des Artenreichtums und der Artenzusammensetzung verglichen werden, um zukünftige Veränderungen der Vegetation durch den Klimawandel genau abschätzen zu können. Die Integration von botanischen und floristischen Studien in andere Forschungsgebiete, z.B. durch die Anwendung in der Klimatologie, ist sehr vielversprechend.

Die Analyse floristischer Kartierungsdaten in dieser Arbeit kann zur Identifizierung wichtiger Gebiete für den Naturschutz beitragen und daher auch wichtige Impulse für die Stadtplanung geben. In Hamburg sollte der Naturschutz ein besonderes Augenmerk auf die Hafenflora und die naturnahen Habitate legen, da diese Gebiete besonders reich an Pflanzenarten, auch an gefährdeten Arten, sind.

Hier sollte der Naturschutz besonders Trockenrasen, Brachflächen und naturnahe Lebensräume fokussieren, indem z.B. neue Schutzgebiete ausgewiesen und Verbundkorridore entwickelt werden. Zudem ist es wichtig, mehr Studien zu den direkten Einflüssen des Klimawandels auf Artenreichtum und –zusammensetzung in Städten durchzuführen, ein möglicher Ansatz ist hier die Untersuchung einzelner Arten in Experimenten. Hierbei haben die Ergebnisse dieser Arbeit gezeigt, dass sich die nicht-heimische Art *S. inaequidens* lokal an sich verändernde Bedingungen anpassen kann.

# 1 INTRODUCTION

## 1.1 URBANISATION

Major drivers of global environmental change, i.e. land use and cover, biogeochemical cycles, climate, hydrosystems, and biodiversity, affect (and are in turn affected by) urban ecosystems (Grimm et al. 2008). In future, more and more people will live in cities. By 2050, 67 % of the world's population is expected to live in urban areas, while for Europe approx. 83 % and for Germany approx. 81 % of the populations are projected to live in cities (United Nations Population Division 2011). Concomitantly, urban land cover is predicted to increase by 1.2 million km² globally by 2030. This is almost three times the area from 2000 (Seto et al. 2012). Urban land expansion differs significantly between regions; most urbanisation will likely take place in developing countries (Seto et al. 2012, Güneralp and Seto 2013). Future expansion of urban land will result in habitat loss for species, especially in global biodiversity hotspots (Seto et al. 2012).

Geographically, a city is defined as a compact settlement area with high population and building density (predominantly multi-storeyed buildings), functional division (e.g. inner city, residential areas, and recreation areas), differentiated social structures and a division of labour, economic efficiency, high traffic density and concentration as well as economic, political and cultural significance for the surrounding rural areas (Heineberg 2006, Schubert and Klein 2011). There is no consistent definition of "urban" worldwide. The U.S. Census Bureau defines urban areas by a minimum population density of 186 people per km² (Pickett et al. 2011), whereas in Europe, a settlement area is considered urban if its population density exceeds 500 people per km² and it has at least 50,000 inhabitants (Federal Statistical Office of Germany 2012). Moreover, the term "urban" is often defined differently in natural and social sciences: social scientists refer to areas with high human population density, while natural scientists refer to areas under human influence (McIntyre et al. 2000). For integrating both views when defining an urban study site, McIntyre et al. (2000) suggest a description of the attributes of demography, physical geography, socioeconomics, and cultural factors in ecological as well as social urban studies. To overcome the problematic urbanisation measures that are solely based on population density and do not distinguish urbanisation intensities within a city's area, attempts have been made to quantify integrative urbanisation measures and to transfer them to other cities (e.g. Luck and Wu 2002, Hahs and McDonnell 2006, du Toit and Cilliers 2011). However, Andersson et al. (2009) point out that it is difficult to generalise patterns and correlations between urbanisation variables. For the city of Stockholm (Sweden), they found the variables of soil sealing, population density and household density to be interchangeable, but this does not necessarily hold true for other cities.

## 1.2 ENVIRONMENTAL CONDITIONS IN URBAN AREAS AND URBANISATION GRADIENTS

Environmental conditions in urban areas are heavily altered by anthropogenic impact. Urban areas are characterised by a high degree of soil sealing, high population density, heavy traffic, enhanced air and soil pollution, high nitrogen deposition, and low water availability (Pouyat and McDonnell 1991, Lovett et al. 2000, McKinney 2002). Along gradients of decreasing urbanisation from urban to rural areas, these environmental factors decrease in intensity. Moreover, urban climatic conditions are extremely variable and differ from those in rural areas.

The morphology of a city (e.g. height, width and density of buildings) differs from rural land surfaces and affects the diurnal pattern of heating (cooling at night and solar heating during the day) (Grimmond 2007). Within urban areas, temperatures are higher compared to their rural surroundings, a phenomenon called the 'urban heat island' (UHI) effect (Oke 1982, Arnfield 2003, Figure 1.1). Due to construction materials, soil sealing, anthropogenic heat flux, and air pollution, the urban surfaces store heat and the cooling process is much slower than in rural areas (Oke 1982, Grimmond 2007). Hence, the UHI is strongest at night during clear and calm conditions (Oke 1982). The maximum heat island intensity increases with greater population size of a city (Oke 1973). Precipitation patterns in urban areas are less certain to explain (Lowry 1998), because they strongly depend on local conditions. Urban areas can provoke higher precipitation on the leeward side of a city (5 % to 51 %; overview in Hoffmann 2009). Wind velocities also differ between urban and rural areas. Wind conditions in cities are highly variable in built-up areas, since strong turbulences and channelling effects can develop on small scales depending on building structure and density (Bornstein and Johnson 1977, Dutt 1991). Furthermore, air pollution is higher than in rural areas as a result of emissions from traffic, industry, power stations, and households, namely the concentrations of NO, $NO_2$, CO, $O_3$, $SO_2$, and particulate matter (Kuttler 2008). $CO_2$-concentrations are also higher in urban areas than in rural surroundings, but vary during the course of days and weeks (Idso et al. 2001, George et al. 2007).

Urban soils are fairly dry, because rain water runs off immediately on sealed soils or drains due to coarse soil compounds. Therefore, water is only available for vegetation for a short time, if at all (Wittig 1991, Arnold and Gibbons 1996). Urban soils are also very heterogenic due to the altered natural soil conditions from agricultural and horticultural use, construction works, introduction of building material from various sources and soil sealing. Cities are more often located in areas with high geological diversity that promoted the ability to grow a settlement into a city (Kuehn et al. 2004). In general, urban soils are more alkaline than rural soils, with higher NaCl concentrations due to the use of de-icing salt (at least in temperate zones) and enhanced heavy metal and nutrient concentrations as a result of atmospheric deposition (Gilbert 1989, Pouyat and McDonnell 1991, Wittig 1991, Pickett et al. 2001, Scheffer 2008, George et al. 2009).

In urban areas, the impact by humans is more pronounced than in less densely populated areas. Human activities like building measures, gardening, and landscaping as well as recreational activities subject urban areas to frequent disturbance (Rebele 1994). Consequently, urban habitats are highly dynamic. The urban landscape is also highly diverse, featuring a patchwork of different habitat types that developed under the influence of geology, land-use history and urbanisation.

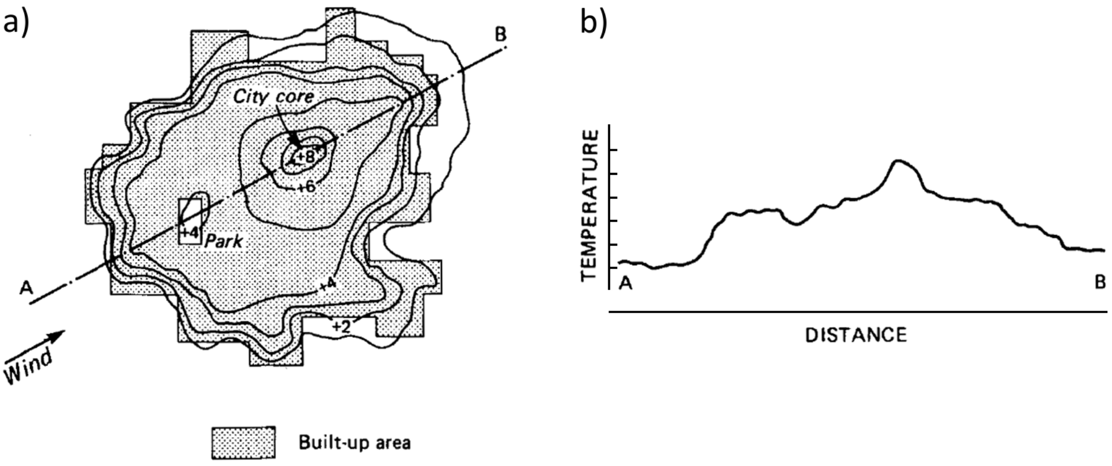

**Figure 1.1** Diagram of a schematic urban heat island (UHI) in a mid-latitude city with clear and calm weather showing the relation of **a)** city structure and **b)** temperature distribution. Modified according to Oke (1982).

## 1.3 HISTORY OF URBAN ECOLOGY

Urban ecology is the study of living organisms in relation to their abiotic and biotic environment in towns and cities (Sukopp 2002). It is “the study of urban systems from an ecological perspective; an emerging field within ecology that strives to understand human interactions in ecological systems in and around urban areas and to develop theories and analyses that include human communities as fundamental components of ecological systems” (Cook et al. 2013).

For a long time, cities have been ignored by ecologists and seen in a rather negative light due to the resulting air, water, and soil pollution (Botkin and Beveridge 1997). However, the study of urban biodiversity has received more and more attention in the last few decades. Early studies analysed the flora of single castles, ruins, walls, gardens, cemeteries, and parks (Sukopp 2002). During and after World War II, several studies on vegetation development on bombed sites and ruins were conducted in Europe (e.g. Salisbury 1943). Consequently, vegetation mappings of entire cities were carried out, spatial and temporal changes in urban plant communities and their causes were assessed, and maps and atlases of city floras were compiled (Pickett et al. 2001, Sukopp 2002).

To fully understand urban effects, urban ecology must not only include the densely populated city areas, but also the less populated surrounding areas (Pickett et al. 2011). Grimm et al. (2000) distinguish between ecology *in* cities and ecology *of* cities. Accordingly, studies on ecology *in* cities investigate how ecological patterns and processes differ in cities compared to other environments. Effects of the city on the ecology of organisms inside and outside of the city are also studied, e.g. distribution and abundance of animal and plant populations, air pollution and meteorology, patch-specific ecological pattern and processes, edge effects, and interactions between native and non-native species. Grimm et al. (2000) define ecology *of* cities as the way cities process energy or matter relative to their surroundings, e.g. whole-system mass balances of nutrients, patch dynamics, effects of land-use change, whole-system metabolism, spatial distribution of resources and populations, and estimation of a city's ecological footprint. Current urban ecological theory "view[s] cities as heterogeneous, dynamic landscapes and as complex, adaptive, socioecological systems, in which the delivery of ecosystem services links society at multiple scales" (Grimm et al. 2008). The role of cities for biodiversity conservation is also gaining in importance, as the conservation of novel urban ecosystems has been proposed due to their ecosystem services and social functions (Kowarik 2011).

## 1.4 URBAN AREAS AND VEGETATION

### 1.4.1 EFFECTS OF URBANISATION ON VEGETATION

Concomitantly with changing environmental conditions along urbanisation gradients, the proportion of semi-natural and natural habitats decreases with increasing urbanisation. Ecosystems in cities can be classified by the "four natures approach" (Kowarik 1992) in regard to their transformation from pristine environmental conditions due to urbanisation. "Nature of the first kind" comprises remnants of the pristine natural landscape, e.g. forests, peatlands and water bodies; "nature of the second kind" is ecosystems that are characterised by agricultural use, e.g. grassland, cropland and horticultural sites. "Nature of the third kind" comprises the ornamental "nature" of e.g. parks, gardens and green roofs, while "nature of the fourth kind" incorporates spontaneous urban vegetation, e.g. on wasteland sites, roadsides, and urban-industrial sites.

The flora of an urban area originates from three sources: species originally present in the area, regionally native species that colonise novel urban habitats, and non-native species introduced by humans (Williams et al. 2009). The authors identify four filters that act as selection pressures on urban vegetation: habitat transformation, habitat fragmentation, urban environmental effects and human preference, of which the latter two are unique to cities. Furthermore, they hypothesise how urbanisation changes floras and predict that novel urban environments will promote simple plant communities. These are comprised of species not usually found in the above-mentioned remnant habitats, which possess particular traits that tolerate urban conditions. Hence, urbanisation also selects for specific species traits (Kuehn et al. 2004, Williams et al. 2005, Thompson and McCarthy 2008, Knapp et al. 2010). For instance, short plants, small- and light-seeded plants as well as plants of forest, riparian and wetland sites are threatened by urbanisation (Dolan et al. 2011, Duncan et al. 2011), while species able to cope with urbanisation are often wind-pollinated, animal-dispersed, have mesomorphic, scleromorphic or succulent leaves and have an annual or biennial life cycle (Knapp et al. 2008). The combination of particular traits can lead to a higher probability of extinction of a species in urban habitats (Williams et al. 2005).

The urban climate leads to a prolonged growing period due to the warmer climate and fewer days of frost and also influences the phenology of plant species. Plants in highly urbanised areas often flower earlier than plants of the same species in less urbanised areas due to the UHI effect (Franzen 1955, Roetzer et al. 2000, Mimet et al. 2009). Furthermore, temperature influences species distribution. Species are therefore expected to mirror temperature conditions (e.g. UHI) in urban areas. Those which prefer or are adapted to rather warm habitats (thermophilic species) are predominantly found in the urban centre, for instance *Ailanthus altissima* (Mill.) Swingle (Kowarik and Saeumel 2007).

Direct human impact is another important effect of urbanisation on vegetation in cities. Socioeconomic factors like family income and housing age can affect plant diversity (Hope et al. 2003); education level and immigration status can be related to vegetation cover (Luck et al. 2009). Moreover, richness of non-native invasive species is strongly correlated with housing variables (housing densities and growth; Gavier-Pizarro et al. 2010). Landscaping or pest control can severely affect urban vegetation. Other activities like pet keeping or bird feeding act primarily on urban fauna (Cook et al. 2013), but can affect vegetation indirectly. Moreover, rather local impacts like trampling or cutting can alter urban vegetation.

Biotic homogenisation can be defined as the replacement of local biota with non-native species, usually introduced by humans, leading to a higher similarity between regions (McKinney and Lockwood 1999), but can also be attributed to urbanisation (Kuehn and Klotz 2006). Since all cities were built for human purposes, disturbance of vegetation took place in a similar way. During urbanisation, habitats of native species are often destroyed while new habitats are created. These appeal for rather few species that are able to adapt to urban conditions. Consequently, the same species become widespread in cities worldwide (McKinney 2006). Wittig and Becker (2010) detected floristic homogenisation between cities within Europe and in comparison to a North-American city when analysing spontaneous vegetation around tree bases. Regarding Germany, homogenisation has been found for native species in urbanised areas, whereas non-native species[1] were more heterogeneous than in less urbanised areas (Kuehn and Klotz 2006). This is confirmed in a study by Lososová et al. (2012b), who further compared the differentiation of non-native species between different urban habitats and found lower differentiation in highly urbanised habitats. They conclude that species not native to the area but already with a long residence time (i.e. archaeophytes: introduced before 1492) contribute to homogenisation, while non-native species with a shorter residence time tend to differentiate floras between European cities. Homogenisation due to increasing urbanisation was also found on the community scale in urban woodlands, where total and native species were most diverse in areas of low urbanisation (Trentanovi et al. 2013). On the contrary, Celesti-Grapow and Blasi (1998) did not detect a homogenisation effect when comparing the flora of five Italian cities.

To detect the impact of urbanisation on vegetation, studies along urbanisation gradients have been useful, since “the magnitude and nature of the change in the physical, chemical, and biotic environments that are associated with urbanisation provide an unprecedented suite of ‘experimental manipulations’ that ecologists can utilise” (McDonnell & Pickett 1990). Studies along urbanisation gradients have been used to analyse changes in plant species composition and functional traits (Williams et al. 2005, Vallet et al. 2008, Brunzel et al. 2009), seed bank and soil characteristics (Pellissier et al. 2008) and ecosystem processes in forest ecosystems (McDonnell et al. 1997); see McDonnell and Hahs (2008) for a review on gradient analyses in the past decades and future research questions. Furthermore, urbanisation gradients can be used as a ’space-for-time substitution’ for projected climatic changes in landscapes, because

---

[1] Throughout this thesis non-native species are defined as species introduced to the area after 1492, so-called neophytes.

factors like temperature and $CO_2$-concentration often change gradually with urbanisation (Ziska et al. 2004, Carreiro and Tripler 2005, George et al. 2009).

In addition, it is important to mention that most of the studies on the effects of urbanisation on biodiversity have been conducted in developed countries – but these effects differ little in developing countries, although here, fewer resources are consumed, pollution is lower and less land is urbanised (Pauchard et al. 2006). However, more research on the effect of urbanisation on ecosystems is needed to improve conservation measures, e.g. in South America (Pauchard et al. 2006).

### 1.4.2 SPECIES RICHNESS IN URBAN AREAS

Cities are generally rich in plant species and the richness is mostly higher than in surrounding rural areas (Pyšek 1993, Kuehn et al. 2004, Wania et al. 2006, see also Jim and Chen 2009 for contradictory results). The numbers of plant species and plant communities increase with growing city sizes and numbers of inhabitants (Pyšek 1993). One reason for high plant species richness is small-scale habitat heterogeneity in urban areas, e.g. the mixture of novel anthropogenic and (semi-)natural remnant habitats arising from differing intensities of human impact and alteration (Pyšek 1993, Zerbe et al. 2003). Another reason is geological diversity: cities have often been established in areas with diverse geological substrates, where natural resources for construction have been provided. This geological diversity promotes plant species richness (Kuehn et al. 2004). In addition, non-native species contribute to urban plant species richness: since cities are centres of trade and traffic, they are often introduced here first and subsequently become naturalised in surrounding rural areas (e.g. Wittig 2004; Kowarik 2011; see 1.4.3.).

Within cities, species richness patterns vary: species richness is generally lower in highly urbanised areas, but can be highest in moderately urbanised areas (Gilbert 1989, Kent et al. 1999, McKinney 2008). Here, habitat diversity is often high, because the typical urban landscape mixes with rural components, e.g. semi-natural remnant habitats like forests. Building density is usually lower and leaves room for gardens etc. Moreover, species richness and composition differ strongly between land-use types (e.g. Celesti-Grapow et al. 2006; Wania et al. 2006, Wang et al. 2012) and can even differ between typical urban land-use types only (Godefroid and Koedam 2007, Lososová et al. 2012a).

### 1.4.3 NON-NATIVE SPECIES IN URBAN AREAS

The successful establishment of non-native plant species in a new range depends on overcoming different barriers and can therefore be divided into different stages (Richardson et al. 2000). First, plants need to overcome geographical barriers aided by human transport (introduction). When environmental barriers, e.g. abiotic and biotic conditions, as well as barriers to reproduction are overcome, naturalisation follows. Subsequent invasion is defined as the “spread into areas away from sites of introduction” (Richardson et al. 2000). For this stage, dispersal barriers must be overcome and the species must cope with abiotic and biotic situations in the area. Often, disturbed communities are invaded, whereas the invasion of undisturbed communities requires the overcoming of a further barrier (Richardson et al. 2000). Possible pathways of introduction are summarised by Hulme et al. (2008), distinguishing between intentional and unintentional introductions.

Species often perform differently in their native range compared to their introduced range. Whether a plant species is able to successfully invade an area can depend on different factors – several hypotheses are discussed in invasion biology (Bossdorf 2013; Figure 1.2.). The enemy release hypothesis states that, during their introduction into a new range, plant species are released from their native herbivores and other enemies. Hence, they are able to rapidly increase in distribution and abundance (Keane and Crawley 2002). Following the observation that invasive plants are often taller and produce more biomass in their new range than in their native range, the hypothesis of evolution of increased competitive ability (EICA) has been formulated (Blossey and Noetzold 1995). The EICA hypothesis predicts that, under the same growing conditions, individuals of a species from the introduced range will produce more biomass than individuals from the native range and that specialised herbivores will perform better on individuals from the introduced range. Plants in the introduced range reallocate resources from herbivore defence to growth and production. Studies testing the EICA hypothesis revealed different results, which have recently been discussed e.g. by Felker-Quinn et al. (2013) who overall found little support for the hypothesis in a meta-analysis. Callaway and Ridenour (2004) attribute invasion success of non-native plant species to the possession of new biochemical weapons that are not present in native species and can therefore affect them negatively (novel weapon hypothesis).

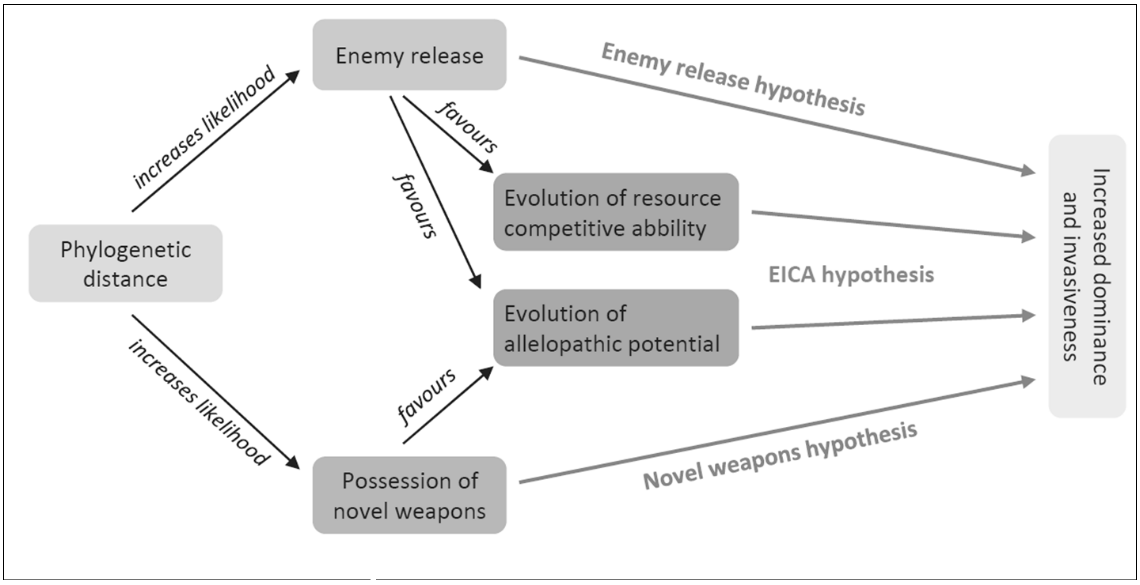

**Figure 1.2** Overview of different hypotheses that attempt to explain the increased dominance and invasiveness of plants in their induced range and the relationships between them. From Bossdorf (2013).

Non-native plant species are often closely associated with urban areas (Roy et al. 1999, Deutschewitz et al. 2003, Pyšek et al. 2004; see 1.4.2.) and comparisons between urban floristic compositions in the past and at present mostly revealed an increase in non-native species (Godefroid 2001, Chocholoušková and Pyšek 2003, Dolan et al. 2011, see also Pyšek et al. (2004), who found no change in the proportion of non-natives). Often originating from warmer regions, many non-native species are pre-adapted to the dry and warm environmental conditions of urban areas. Non-natives are also associated with disturbance (Lake and Leishman 2004), which occurs frequently in most urban ecosystems.

Most non-native species in Europe have been introduced intentionally (Lambdon et al. 2008), e.g. for ornamental purposes like *Fallopia japonica* (Houtt.) Ronse Decraene (Beerling et al. 1994). Ornamental and horticultural plant species can escape from private and public gardens and explore new habitats (Rusterholz et al. 2012), accounting for 52 % of all naturalised non-natives in Europe (Lambdon et al. 2008). The occurrence of non-native species in urban areas is furthermore due to traffic and trade operations. Roadsides and railway tracks can act as migration corridors for invasive species and vehicles can promote long distance dispersal (Ernst 1998, von der Lippe and Kowarik 2007). Trade actions have served as introduction pathways for several non-native species; for example, *Senecio inaequidens* DC. was accidently introduced by wool import from South Africa (Ernst 1998). In Europe, 64 % of all naturalised non-native species occur in industrial habitats and 59 % on arable land, parks, and gardens (Lambdon et al. 2008). Amongst the habitat types invaded most in Denmark were ruderal and man-made habitats, while riparian and swamp habitats were least invaded, also indicating a strong relation between anthropogenic impact and invasions (Thiele et al. 2009). However, projected future species richness of non-natives in Switzerland was driven more by temperature than by urbanisation. Nevertheless, urban regions will gain most in new non-native species (Nobis et al. 2009).

Although Botham et al. (2009) found in a study in Great Britain that non-natives do not necessarily spread from urban habitats into the rural surroundings, the number and percentage of non-native species often decreases with distance to the city centre (e.g. Celesti-Grapow and Blasi 1998; Zerbe et al. 2003, Brunzel et al. 2009).

### 1.4.4 IMPORTANCE OF VEGETATION IN URBAN AREAS

Vegetation in cities is important in various aspects. First of all, since cities are particularly rich in plant species, urban vegetation contributes substantially to regional and worldwide biodiversity. Furthermore, vegetation has a positive influence on urban climate in summer, which can be advantageous for human inhabitants in times of heat waves. Vegetation can reduce mean radiant temperature in cities (Lindberg and Grimmond 2011). Above green areas (e.g. parks, green spaces), temperature increases resulting from the UHI effect can be reduced by vegetation (Oke 1982) due to lower heat storage capacity. Vegetation in urban areas can reduce energy consumption by air-conditioning in buildings through shading and can improve air quality, cool the air by evapotranspiration, and block wind (Akbari 2002, Nowak 2010, Leung et al. 2011).

Vascular plant species richness in urban areas has been shown to be closely related to the richness of other taxa and can therefore be used to predict an area's overall species richness (Bräuniger et al. 2010). Obviously, urban vegetation provides habitats for other organisms and therefore influences animal species richness and distribution (Faeth et al. 2011). Robinson and Lundholm (2012) showed that habitat provision was higher in spontaneous urban vegetation than in managed lawns and semi-natural urban forests. Wasteland sites can also be important habitats for animals (Angold et al. 2006).

Urban areas furthermore play a role in carbon sequestration. Although cities emit large amounts of $CO_2$, urban green space acts as a carbon sink, but carbon storage differs strongly between habitat types (Strohbach and Haase 2012). Urban forests can help reduce atmospheric $CO_2$; Nowak and Crane (2002) estimated that urban trees store 700 million tonnes of carbon in the US.

The importance of spontaneous vegetation in cities is still underestimated and to fully tap into its ecological, social and aesthetic potential, management strategies need to be developed (Del Tredici 2010).

## 1.5 CLIMATE CHANGE AND BIODIVERSITY

Global average surface temperature increased by 0.74°C ± 0.18°C in the 20th century, while the warming rate over the past 50 years (0.13°C/decade) was nearly twice that of the last 100 years (0.07°C/decade) (Trenberth et al. 2007). This increase is very likely a result of the observed rise in anthropogenic greenhouse gas concentrations. During the second half of the 20th century, the increase in greenhouse gas concentration was at least five times higher than in any other period of similar length prior to the industrial era. Concomitantly, average temperatures in the northern hemisphere were higher than in any other 50 year period in the last 500 years (Jansen et al. 2007).
In future, global temperature is projected to increase by 1.7 to 4.4°C (A1B scenario) at the end of the 21st century. Expected future changes in climate vary from region to region (IPCC 2007). In Europe, annual mean temperatures are projected to rise more than the global mean. Future climate projections estimate a temperature increase between 2.3 and 5.3°C (A1B scenario, depending on the model) until the end of the 21st century. Precipitation patterns are not projected to change as consistently as temperature changes: While annual precipitation is expected to increase in northern Europe, a decrease in southern Europe is projected. Overall, precipitation is estimated to change between 0 to 16 % and -27 to -4 % depending on the model (A1B scenario). In central Europe, winter precipitation is projected to increase, while summer precipitation is generally expected to decrease (Christensen et al. 2007).

The warmer climate over the past 30 years has already influenced the phenology, range, and distribution of species as well as the composition and dynamics of communities. Furthermore, recent latitudinal and altitudinal range shifts have often been caused by general warming (Walther et al. 2002). Hence, it can be expected that future climate change will have an even more severe impact on species and communities. Modelling results show that many European species will probably be threatened by climate change; thus the magnitude of climatic impacts differs between biogeographic regions (Huntley et al. 1995, Thuiller et al. 2005). Between 6 and 29 % of plant species in Europe are expected to be extinct by 2050, depending on the intensity of climate change and the dispersal scenario (Thomas et al. 2004). Similarly, species distribution ranges in Germany will shift and some species might go extinct locally. Species with small distribution ranges are most vulnerable (Pompe et al. 2008). Pompe et al. (2009) modelled future distribution ranges of 1,200 plant species in Germany under climate change and found that increasing temperatures would reduce the area of suitable climate conditions for 60 % of the species.
A changing climate offers migration possibilities for new species that are not yet in the area and the Iberian Peninsula was identified as a possible species pool for the future German flora (Bergmann et al. 2009). In future, climate is predicted to change faster than e.g. after the last glacial period due to strong anthropogenic influences (Huntley 1991, IPCC 2007). Consequently, species will need to migrate rapidly; individual migration rates depend on

dispersal mode (Cunze et al. 2013). Parmesan and Yohe (2003) estimated range shifts of 6.1 km on average per decade towards the poles for animal and plant species.

However, effects of future climate change on biodiversity are complex and several interactions between global change drivers and other biodiversity drivers like physiology, natural disturbance and species interactions will lead to various changes in future biodiversity (Figure 1.3). Hence, model results should be interpreted carefully. Willis and Bhagwat (2009) review studies that yielded different results depending on the factors included and the scale studied. Hof et al. (2011) argue that species' ability to cope with rapid climate change might be underestimated, because species have already survived rapid changes in the past.

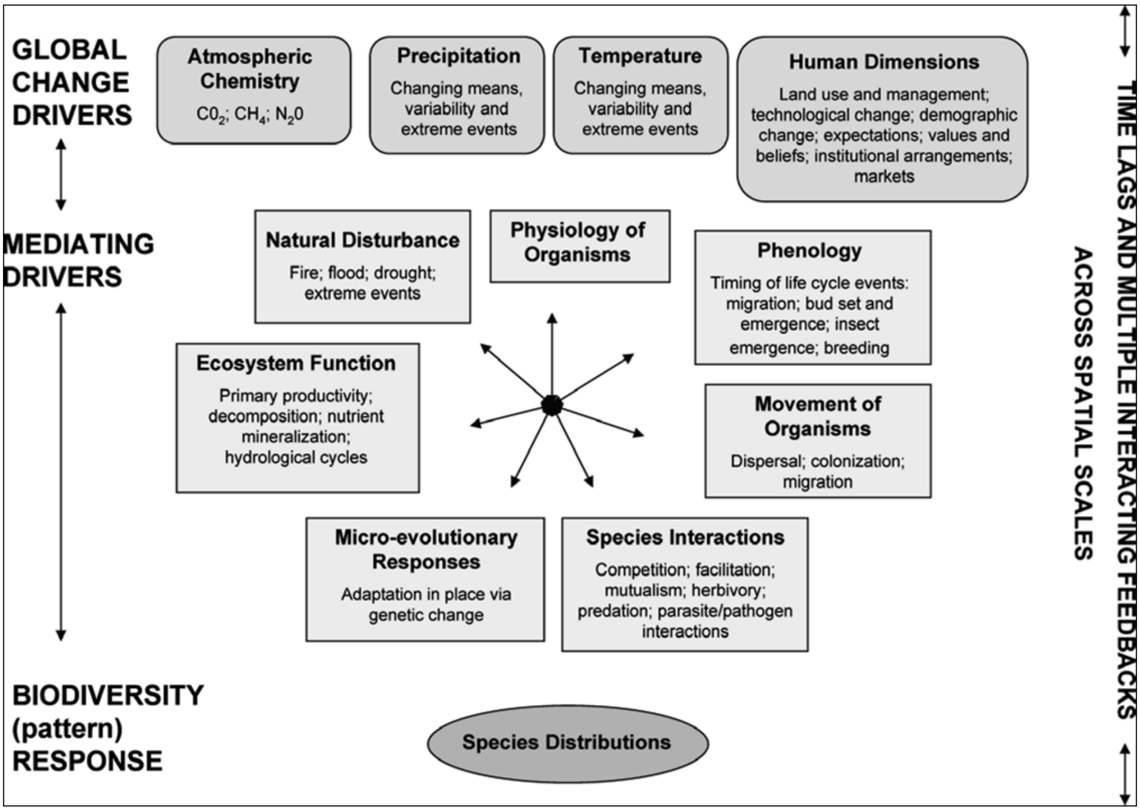

**Figure 1.3** Diagram of the interaction between global change drivers, mediating drivers and biodiversity response in terrestrial ecosystems. From Hagerman and Chan (2009).

According to Bellard et al. (2012) there are three directions of species' response to climate change on the community scale. Species can change along three axes: 1) the spatial axis, e.g. the above-mentioned range shifts, 2) the temporal axis, e.g. the response with a changed phenology to abiotic factors that change cyclically over time, and 3) the 'self' axis, e.g. adapting themselves to changing conditions in physiology or behaviour. If populations fail to adapt along one or more of these axes, they will go extinct locally or even globally.

Changes in phenology as well as latitudinal and altitudinal range shifts can disrupt interactions between species by temporal and spatial mismatches. When the involved species have responded differently to climate change, former synchrony is altered. While some interactions may be disrupted, new interactions may emerge, e.g. former potential interactions between species that have not yet been realised due to different distribution ranges (Schweiger et al. 2010). Effects of climate change on interactions between plants and insects are difficult to determine, because they affect all behavioural, physiological, and molecular interactions on lower organisational scales (DeLucia et al. 2012). Generalist species are likely to profit more than specialists from the combined future effects of climate change and non-native species, for example they may be pre-adapted to switch hosts when conditions change (Schweiger et al. 2010, DeLucia et al. 2012). In the case of a disruption of predator-prey and plant-insect interactions, food sources can become lost or pollinator and host ranges can be diminished – this could consequently lead to species extinctions (Parmesan 2006, Schweiger et al. 2010, DeLucia et al. 2012, Schweiger et al. 2012). Hegland et al. (2009) state that overall, the structure of pollinator networks seems robust against changes due to climate warming. However, insect phenologies can be more advanced than plant phenologies, resulting in lost synchrony (reviewed in Visser and Both 2005). If insects are able to reproduce faster due to warming and generate multiple generations per year, damage to plants may increase. Elevated $CO_2$ can alter plant tissue composition and therefore food quality for herbivores as well as defence mechanisms against herbivores (DeLucia et al. 2012). Studies of interacting effects of elevated temperature and $CO_2$ on plant-insect interactions on any scale are still scarce (DeLucia et al. 2012, see Niziolek et al. 2013 for a study example).

Moreover, competition is an important process regulating plant communities' response to changing climate. The effect of elevated temperature can differ between species grown in monoculture and in mixture (Brooker 2006, Verlinden et al. 2013). The response to elevated $CO_2$ is also strongly species-dependent and can hence alter future competitive dynamics in communities. Furthermore, elevated $CO_2$ can have different impacts on native and non-native species and promote non-native species' dominances (Brooker 2006). Possible changes in competition dynamics cannot (yet) be generalised; more research is needed (Brooker 2006, Verlinden et al. 2013). In future, native competitors that are not able to adapt as fast as the non-native species might suffer even more from changing climate and environmental conditions (Schweiger et al. 2010). Facilitation under climate change has rarely been studied. Facilitative interactions might help plant species survive otherwise less suitable environmental conditions by expanding the realised ecological niche, especially in extreme environments (Brooker 2006).

Generally, future effects of interactions on species are manifold and difficult to predict. Hence, it has proved useful to incorporate interactions into models for predictions of future biodiversity (Urban et al. 2012, Blois et al. 2013).

Instead of range shifts, species may also adapt to the changing conditions in response to climate change (i.e. niche shifts). Adaptation of plant populations to current conditions has been demonstrated in several studies, but little is known about the interaction of local adaptation and climate change (Jump and Penuelas 2005). The role of adaptation seems to be underestimated, but since the rate of climate change is projected to be faster than most species' migration potential, the pressure to adapt to the new conditions will be high (Jump and Penuelas 2005, Cunze et al. 2013). The ability of rapid evolution could lead to a successful adaptation to climate change (Maron et al. 2007, Lachmuth et al. 2011). Over a latitudinal gradient in Europe, Wasof et al. (2013) found evidence of shifts in realised niches in common understorey plant species. Furthermore, phenotypic plasticity can buffer individual plants against environmental changes in the short term. Therefore, plants could be expected to react plastically, also regarding long-term changes due to climate change (Jump and Penuelas 2005).

Concomitantly with local adaptation and phenotypic plasticity, environmental maternal effects and genetic drift can play an important role in phenotypic variation of invasive populations in response to climate (Monty et al. 2013).

Hagerman and Chan (2009) review recent approaches of biodiversity conservation in future climate to reduce extinction risks of species. In regard to adaptation measures, new protected areas should be established and existing reserves should be connected via migration corridors that species are able to shift ranges and to enhance evolution potential by increasing population size and diversity. In addition, they propose the establishment of spatial buffer zones around habitat types that species can migrate outside core reserves in response to climate change and of dynamic reserves, e.g. protected areas whose locations and levels of protection can change over time and space. Lastly, they propose assisted colonisation as an active measure to help species overcome barriers as well as accelerating movements.

## CLIMATE CHANGE AND BIODIVERSITY IN URBAN AREAS

Solecki and Marcotullio (2013) state that “the role of cities in climate change is not well understood” and give three key aspects related to urban biodiversity that are especially vulnerable to climate change: the quality and extent of urban habitats, the provision of green infrastructure and ecosystem functions, and urban wetlands. If climate change causes a decline in urban biodiversity, a large proportion of the world’s population may no longer be in contact with nature and attention to biodiversity conservation may fade. Furthermore, deploying options for adaptation to climate change and maintaining ecosystem functions of vegetation in cities will fail (Solecki and Marcotullio 2013).

In general, urban areas harbour many ruderal species that are able to react quickly to changes in climate. Species introduced from warmer areas which are better adapted to elevated temperature and drought have often established in cities (e.g. *Ailanthus altissima*, *Robinia pseudoacacia* L., *Hordeum murinum* L.; Sukopp and Wurzel 2003). A general increase in thermophilic species in urban areas in the final decades of the 20th century in the Dutch flora was found by Tamis et al. (2005). Urbanisation did not fully explain this change, so it was partly attributed to climate change since concomitantly, temperature was increasing. Not all studies comparing floras and vegetation between two or more time steps in cities related changes in floristic diversity and composition to climate changes (e.g. Tait et al. 2005, Pyšek et al. 2004), but urbanisation and climate change are often difficult to distinguish. The increasing number of non-native plant species in Brussels can be related to suitable habitat conditions in cities that could have been created by both urbanisation and climate warming (Godefroid 2001). Gregor et al. (2012) see the increasing number of non-native species in Frankfurt between 1880 and 2000 linked to climate change. Chocholoušková and Pyšek (2003) found no effects of climate change (indicated by Ellenberg indicator values for temperature) when comparing historical floristic data from 1880 with data from the 1960s and 1990s in Pilsen, although species composition changed. Luo et al. (2007) relate differences in plant phenology in Beijing to both climate and urbanisation (e.g. UHI) and expect phenological responses to be stronger in urban areas than in rural areas.

## 1.6 HAMBURG AS A CASE STUDY

The Free and Hanseatic City of Hamburg is located in the north of Germany and is the country's second largest city with 1.8 million inhabitants and an area of 755 km² (Figure 1.4a). Settlement and traffic areas cover 60 %, 8 % are water bodies, 25 % agriculture and 8 % woodland (Federal Statistical Office of Germany 2011). Furthermore, 8 % of Hamburg's area is nature reserves. Hamburg has Europe's second largest seaport, which is located close to the city centre and covers 72 km²; it covers nearly 10 % of the city area (HPA 2013). The river Elbe crosses through the city and flows into the North Sea. Hence, the river is still under tidal influence in Hamburg and small relic tidal freshwater wetlands can be found. The city of Hamburg is also a federal state of Germany and borders the federal states of Schleswig-Holstein to the north and Lower-Saxony to the south, both separated by the river Elbe.

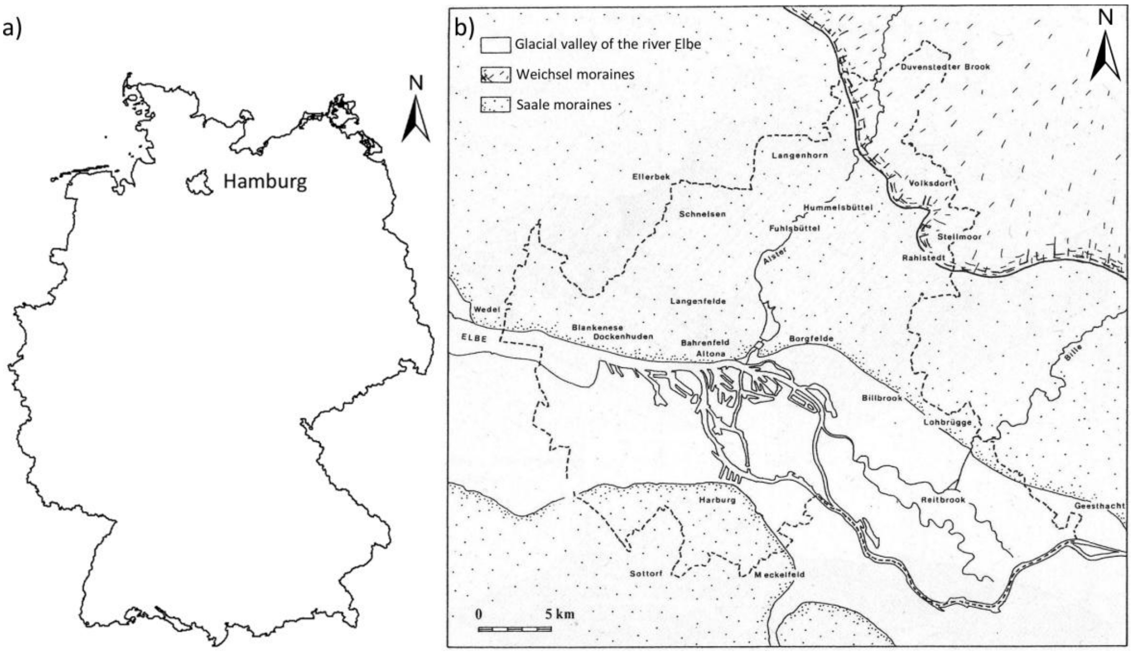

**Figure 1.4 a)** Location of Hamburg in Germany, **b)** Geology of Hamburg influenced by glacial periods (Saale-glaciation and Weichsel-glaciation). Saale moraines were dissected by the glacial valley of the river Elbe, while Weichsel moraines reached Hamburg only in the very north-eastern area. Modified according to Ehlers (1995).

Hamburg's present landscape is heavily influenced by glacial periods. Saale moraines covered large areas of the city and were dissected by the glacial valley of the river Elbe. The later Weichsel moraines only reached Hamburg in the very north-eastern area (Ehlers 1995, Figure 1.4b). During the Holocene, alluvial sediments were deposited in the glacial valley and with sea level rise the region was waterlogged (Ehlers 1995). Fertile marsh habitats developed in the river valley and on the moraine based areas the so-called geest landscapes formed, which are characterised by dry, mostly sandy and unfertile soils. The marsh areas have been under intensive agricultural use for centuries, mainly for vegetable-, flower-, and fruit-growing, and have been heavily anthropogenically altered. The port area is also strongly altered and built up. The geest areas have been used for forestry (since the 18th century) and also for agriculture. Today, the northern geest areas are mostly built-up areas in decreasing density of soil sealing towards the city border (Poppendieck et al. 2010; Figure 1.5).

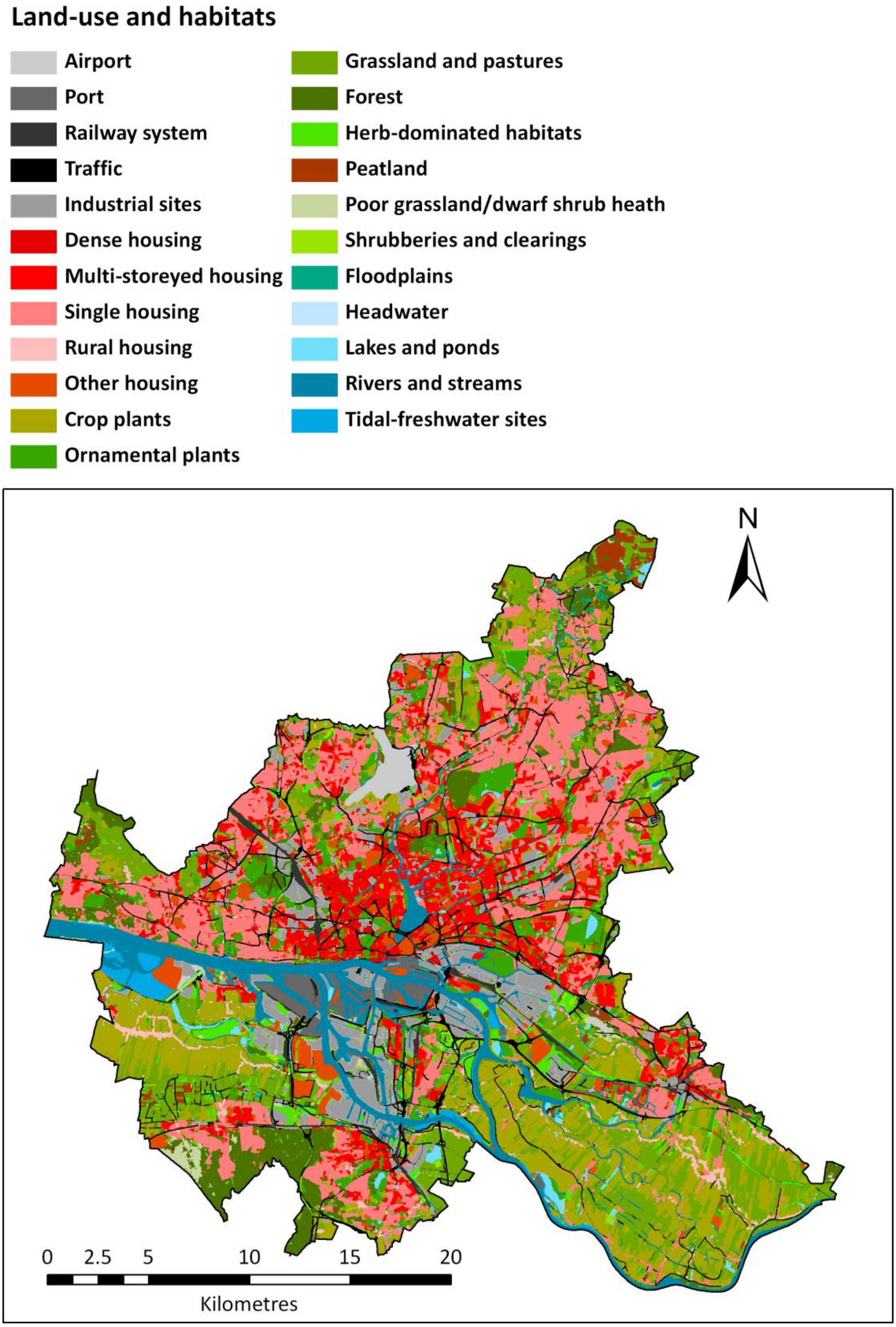

**Figure 1.5** Distribution of land-use and habitat types in Hamburg based on the biotope type mapping of the Ministry for Urban Development and Environment of Hamburg (2006).

Due to its proximity to the North Sea and the Baltic Sea (80 km and 70 km, respectively) the city has a temperate and oceanic climate, characterised by mild winters, moderately warm summers and precipitation throughout the entire year (Hoffmann and Schluenzen 2010). The mean annual temperature is 9°C and annual precipitation is 752 mm (data: German Meteorological Service (DWD) 2010; reference period 1971-2000). The main wind direction is southwest. The precipitation pattern depends on the impact of the “Harburger Berge” in the south and the geest areas at the river Elbe banks. The precipitation maximum is in the north of the city and the minimum in the southeast, which indicates an increasing continental impact (Hoffmann and Schluenzen 2010; Figure 1.6). Despite being a very “green” city, Hamburg exhibited a mean UHI effect of 1.1 K for the decade 1988-1997. The UHI has been found to be more pronounced when minimum temperatures are observed. Here, urban temperatures are up to 3 K higher than those from the rural reference station. Due to the higher building densities, urban surfaces like buildings and sealed areas store heat during the day and release heat during the night, which contributes to higher temperatures at night than in rural areas not built up (Schluenzen et al. 2010; Figure 1.7).

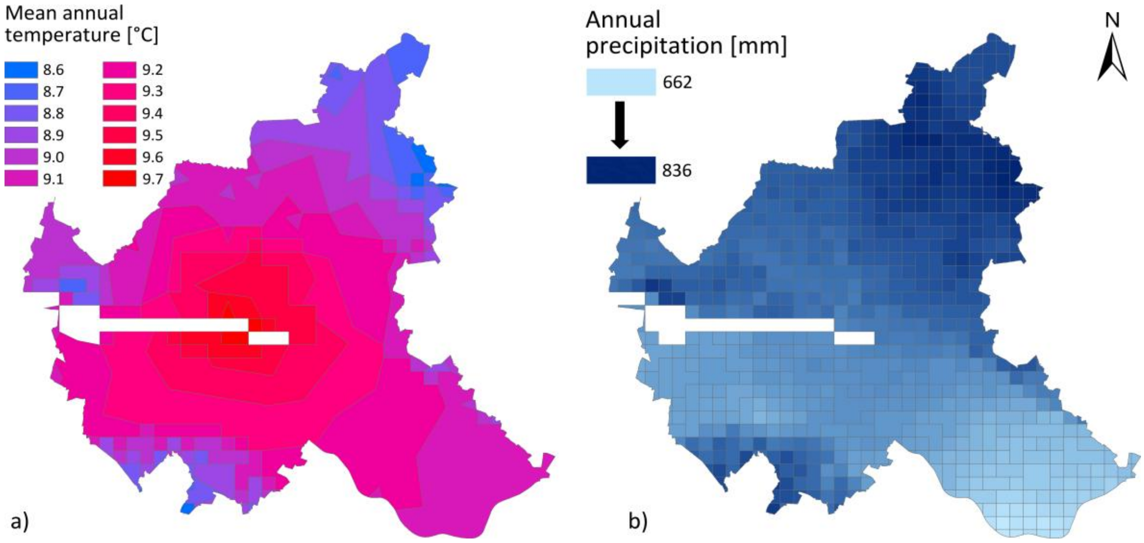

**Figure 1.6** Distribution of **a)** mean annual temperature [°C] and **b)** annual precipitation [mm] in Hamburg for the reference period 1971-2000 (data: German Meteorological Service (DWD) 2010).

Projected future changes in temperature and precipitation for Hamburg have been calculated by Jacob et al. (2008). Here, minimum and maximum changes in both variables are projected from the emission scenarios A1B, B1, A2 for 2021-2050 and 2071- 2100 relative to a control period from 1961-1990 for all seasons. For Hamburg, projected precipitation will change moderately in 2021-2050 (in winter between 4 and 12 % and in summer between -7 and 8 %), but changes will more pronounced for 2071-2100 (in winter between 19 and 23 % and in summer between -13 and -11 %). Temperature is projected to increase by 0.9 to 1.8°C in winter and 0.7 to 1.4°C in summer in 2021-2050 and by 2.5 to 3.6°C in winter and 1.8 to 2.9 in summer in 2071-2100. Overall, precipitation is thus projected to increase in winter and to decrease in summer, while temperature is projected to increase over all seasons, but this will be most pronounced in winter.

Regarding future changes in the UHI, different regional climate models yield different results (Hoffmann et al. 2012): results from the REMO (REgional MOdel; Jacob and Podzun 1997) suggest no change in the average UHI in future, while results from the CLM (Climate Local Model; Rockel et al. 2008) indicate significant changes in UHI. Here, an increase for the months of July and August and a decrease in other months results in a slight decrease if averaged over the year (Hoffmann et al. 2012).

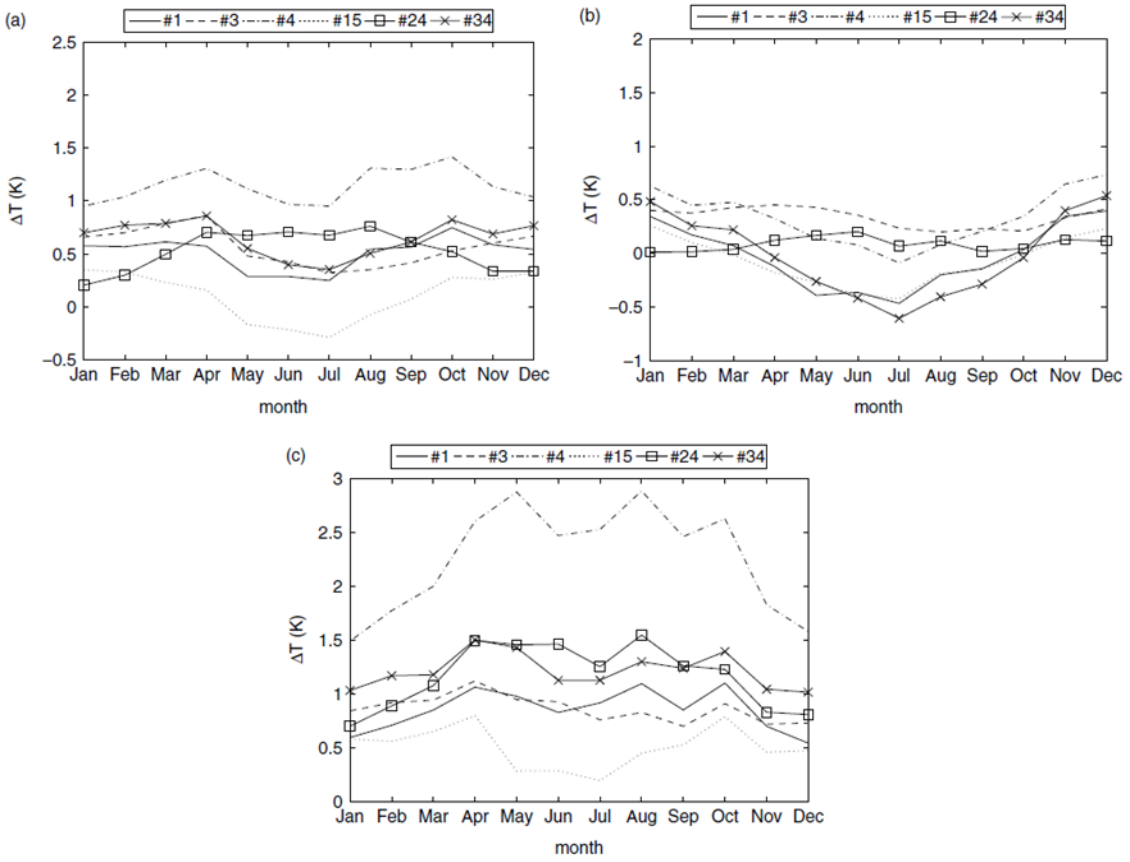

**Figure 1.7** Mean annual cycle of temperature differences [K] for **a)** daily mean temperatures, **b)** daily maximum temperatures and **c)** daily minimum temperatures for the decade 1988-1997. Differences are based on the differences of six climate stations (#1=Fuhlsbüttel, #3=Wandsbek, #4=St.Pauli, #15=Ahrensburg, #24=Kirchwerder and #34=Neuwiedenthal, all in the city of Hamburg with the exception of Ahrensburg) to the climate station Grambek in the eastern rural surroundings of Hamburg. From Schluenzen et al. (2010).

## URBAN ECOLOGY IN HAMBURG

The earliest published study of urban ecology in Hamburg (to the author's knowledge) investigated differences in the beginning of flowering of *Forsythia* x *intermedia* in spring across the city of Hamburg (Franzen 1955). In cooperation with a local newspaper, inhabitants were asked to report the date and the location where at least ten flowers of a plant were open. Plants in densely built-up areas and south-facing slopes of the Elbe river valley flowered earlier than plants in less densely built-up areas in the outskirts. This result is in accordance with studies from other areas (e.g. Roetzer et al. 2000, Mimet et al. 2009) and can be related to the UHI.

Studies on animal species richness revealed decreasing insect species richness with increasing urbanisation (Denys and Schmidt 1998, Weller and Ganzhorn 2004). The members of the Botanical Association of Hamburg e.V. conducted a comprehensive floristic mapping of spontaneous vascular plant species (presence/absence). The mapping took place from 1995 to 2009 and was mainly done by volunteers. The city was divided into grid cells of 1 km² that were mapped repeatedly during different seasons and over the entire mapping period. The resulting distribution maps of the plant species occurring in Hamburg were published in an atlas in 2010 along with articles on Hamburg's nature as well as its different habitats, climate, and soil. Altogether, 1,643 species were mapped (Poppendieck et al. 2010).

## 1.7 AIMS AND OUTLINE OF THE THESIS

The overall aim of this thesis was to detect patterns in the urban flora of Hamburg (i.e. spontaneously occurring vascular plant species) and to identify underlying drivers related to urbanisation and climate change. The analyses were conducted using different scales. These range from a broad macroecological scale to a small-scale investigation of a single species, i.e. from a general investigation of species distribution in the entire city of Hamburg to species richness in select habitats and to responses of a single species to climate change. In all studies, a major focus was placed on changes along urbanisation gradients. The results shall contribute to the discussion of the effects of future climate changes on species richness, species composition, and biotic interactions of non-native and native species.

Why study effects of climate change in urban areas? Since urbanisation is increasing worldwide and cities are particularly rich in plant species, it is important to be able to estimate future changes in urban biodiversity. Urbanisation and climate change have similar effects on ecosystems and plant species, because in urban areas ambient temperature is usually higher than in rural areas (UHI effect) and species' response to elevated temperature therefore can already be studied today. The study of ecological changes along urbanisation gradients can provide insights into expected changes due to global change.

The main research aims were (1) to detect important drivers for plant species richness and plant species distribution in a city, (2) to assess whether plant species richness and plant species distribution differ between urbanisation zones or along urbanisation gradients, (3) to investigate the impact of spatial structure on plant species distribution in an urban area and whether it can be distinguished from environmental drivers, and (4) to estimate to what extend the derived patterns can be related to climate (e.g. temperature and precipitation). Another aim was to investigate (5) whether plant species composition contains information about the long-term air temperature distribution (e.g. UHI) within an urban area. Finally, on the smallest scale, (6) a case study was conducted to assess how an invasive non-native plant species responds to interactions with native species under elevated temperature.

The thesis is structured as follows:

**Chapter 2** deals with the identification of drivers of biodiversity in cities. The distribution of vascular plant species richness in the city of Hamburg is assessed in relation to urban structure, habitat, and environmental conditions with a special focus on non-native, endangered, and thermophilic species. Furthermore, an urbanisation index is developed for the city. The article was published in *Urban Ecosystems* in 2013. The author of this thesis planned the study, prepared the data, conducted the statistical analysis and wrote the manuscript.

> **Schmidt KJ, Poppendieck HH, Jensen K (2014) Effects of urban structure on plant species richness in a large European city. Urban Ecosystems 17(2):427–444. doi: 10.1007/s11252-013-0319-y**

**Chapter 3** aims to disentangle effects of environmental conditions and spatial structure on the distribution of plant species in the city of Hamburg and deals with the study of general plant species distribution patterns and the underlying spatial and environmental effects. The article was submitted to *Landscape Ecology*. The author of this thesis planned the study, prepared the data, conducted the statistical analysis and wrote the manuscript.

**Chapter 4** deals with the introduction of a new proxy dataset for the UHI derived from plant species composition data (plant species' temperature preferences) covering the city of Hamburg. In an interdisciplinary study, UHI proxies were consequently related to a large number of typical UHI predictors. The article was published in *Climate Research* and was written in cooperation with Benjamin Bechtel (Institute of Geography), who is the first author. The author of this thesis prepared the floristic data, wrote the parts of the manuscript that are related to ecological and floristic issues, created Figure 4.3, and contributed to discussing and rewriting parts of the manuscript during the review process.

> **Bechtel B & Schmidt KJ (2011) Floristic mapping data as a proxy for the mean urban heat island. Climate Research 49: 45-58. doi: 10.3354/cr01009**

**Chapter 5** deals with vegetation composition in two select habitat types and changes in species richness along an urbanisation gradient in Hamburg. Scale-wise, by investigating only select habitats, the study connects chapters 2 to 4 comprising the entire city and chapter 6 dealing with a single species. The author of this thesis planned the study, conducted the fieldwork, conducted the statistical analysis and wrote the chapter.

**Chapter 6** deals with the non-native and invasive plant species *Senecio inaequidens* DC. and its biotic interactions with native species in its invaded range under climate change. Experimentally, *S. inaequidens* populations from different origins along an urbanisation gradient in Hamburg were subjected to elevated temperature under herbivory and competition. The author of this thesis planned the study, conducted the competition and germination experiments, supervised the herbivory experiment, conducted the statistical analysis and wrote the manuscript. The herbivory experiment was conducted by Jonathan Steinke und Dennis Schulze in the framework of their BSc. thesises, they both contributed to the discussion.

For consistency throughout this thesis, all published or submitted chapters were changed from American English to British English when necessary and abstracts were left out. Furthermore, the figures and tables were renumbered and all references were summarised at the end of the thesis.

# 2 EFFECTS OF URBAN STRUCTURE ON PLANT SPECIES RICHNESS IN A LARGE EUROPEAN CITY

Katharina J. Schmidt, Hans-Helmut Poppendieck & Kai Jensen

Published in *Urban Ecosystems* (2014) 17(2):427-444. doi: 10.1007/s11252-013-0319-y

**KEYWORDS**
Biodiversity * Ellenberg indicator values * Floristic mapping * Species richness * Spontaneous vegetation * Urban ecology

## 2.1 INTRODUCTION

Environmental conditions in cities are strongly altered compared to the environment of surrounding rural areas. Urban ecosystems have developed under strong anthropogenic impacts, resulting in novel ecosystems. Cities are characterised by a high degree of soil sealing, high population density, heavy traffic, enhanced air and soil pollution, high nitrogen deposition, and low water availability (Pouyat and McDonnell 1991, Lovett et al. 2000, McKinney 2002). These environmental factors decrease in intensity from urban to rural areas. Due to the urban heat island (UHI) effect, cities also feature higher temperatures than the surrounding rural areas (Oke 1982). With more and more people living in cities, urban ecosystems and their biodiversity will be affected even stronger by human activity in the future. The study of urban biodiversity and ecosystems is of great importance, since vegetation in cities contributes to several ecosystem functions like carbon sequestration (Nowak and Crane 2002), temperature reduction (Susca et al. 2011, Lindberg and Grimmond 2011), habitat provision (Faeth et al. 2011, Robinson and Lundholm 2012), and human psychological well-being (Fuller et al. 2007). Therefore, the issue of conservation of typical urban habitats has been raised in several publications (e.g. Niemelä 1999, Lawson et al. 2008, Kowarik 2011). Here, assessments of predictors of species richness in cities might be of great assistance in identifying important areas and developing well-suited measures for conservation. Despite the anthropogenically altered environmental conditions, cities are generally rich in plant species. Often the richness is higher than in rural areas (but see Jim and Chen 2009).

Small-scale habitat heterogeneity, e.g. the mixture of novel anthropogenic and (semi-)natural remnant habitats, is one reason for high plant species diversity (Pyšek 1993, Zerbe et al. 2003). Moreover, geological diversity favours plant species richness: cities have often been established in areas with diverse geological substrates, where natural resources for construction have been provided (Kuehn et al. 2004). High anthropogenic disturbance can also promote particular plant species. Further, plant species richness in urban areas has been related to habitat type (Lososová et al. 2011), city area, number of inhabitants (Pyšek 1993), and socioeconomic factors (Hope et al. 2003). Urbanisation can have different effects on the richness of different groups of plant species. Non-native species are often closely associated with urban areas (Pyšek 1998, Roy et al. 1999, Dunn and Heneghan 2011). Since cities are centres of trade and traffic, non-natives are often found here first and subsequently become naturalised also in more rural areas (e.g. Wittig 2004, Kowarik 2011). Furthermore, they mostly originate from warmer regions and are therefore adapted to the dry and warm conditions of city centres. The number and percentage of non-native species often decreases with distance to the city centre (e.g. Celesti-Grapow and Blasi 1998, Brunzel et al. 2009). On the contrary, the majority of rare and endangered species are absent from urban areas. They are rather restricted to natural and semi-natural habitats and are often specialist species adapted to specific environmental conditions. These habitats, e.g. wetlands or dry grasslands, have been negatively affected the most by urbanisation through fragmentation or even loss. Thus, urbanisation can be a great threat for specialist species (van der Veken et al. 2004, Knapp et al. 2009, Dolan et al. 2011). Since cities show distinct temperature differences, strong temperature preferences of species should have a great impact on plant species distribution within a city (e.g. *Ailanthus altissima* (Mill.) Swingle; Kowarik and Saeumel 2007). Species which prefer or are adapted to rather warm habitats (thermophilic species) are therefore expected to be found predominantly in the urban centre.

Within a city, plant species richness has been found to be generally higher in suburban areas than in urban and rural areas (Gilbert 1989, Kent et al. 1999, Zerbe et al. 2003). Suburban areas are extremely heterogeneous given that urban and rural landscape components intermix here. However, species richness and its predictors are often scale-dependent (Pautasso 2007, Walker et al. 2009). Studies on species richness patterns on smaller scales within an urban agglomeration found that species richness and composition differ strongly between land-use types (e.g. Celesti-Grapow et al. 2006, Wania et al. 2006, Wang et al. 2012). Godefroid and Koedam (2007) even detected differences between typical urban land use types only. However, few studies have analysed urban species distribution data mapped on smaller grid scales of approx. 1 km$^2$ including all existing habitats in a spatially comprehensive way (e.g. Kent et al. 1999, Godefroid 2001, van der Veken et al. 2004).

Our study is conducted in the city of Hamburg, which is considered a hotspot of plant species richness in Germany (approx. 1,100 km$^2$ grid size, Haeupler 2000), harbouring about 1,600 plant species (Poppendieck et al. 2010). The high total species richness can be explained by the encounter of four different landscape regions formed during glacial periods with their respective floras, namely the glacial valley of the river Elbe, Weichsel glaciation moraines and two types of Saale glaciation moraines. Furthermore, the diverse habitats along the river Elbe contribute to species richness (Poppendieck et al. 2002). On smaller scales, however, no comprehensive analysis of the distribution of species richness within the city has been conducted so far.

The aim of our study is to describe the small-scale distribution of plant species richness in Hamburg and to identify its possible predictors by analysing floristic mapping data on a 1 km$^2$ grid. As measures for species richness we use total, non-native, endangered, and thermophilic species richness. First, we test differences in species richness variables between three different urbanisation zones (high, medium and low degree of urbanisation). Second, we relate species richness to several predictors representing urban structure, habitat, and environmental conditions by using multiple regressions.

We address the following questions:

- Does species richness differ between different urbanisation zones?
- How are the four species richness measures distributed in Hamburg, and what patterns emerge?
- Can plant species richness patterns in Hamburg be explained by urban structure, habitat, and environmental conditions?

## 2.2 METHODS

### 2.2.1 STUDY AREA

Hamburg, Germany's second largest city, is situated in the north of the country (53.55 °N, 10.0 °E, 6 m a.s.l), about 80 km from the North Sea and 70 km from the Baltic Sea (Figure 2.1). It has 1.8 million inhabitants and extends over an area of 755 km$^2$. Settlement and traffic areas cover 60 % of the area, 8 % are water bodies - the river Elbe and the port (Europe's second largest seaport) are characteristic for Hamburg. Being a federal state, Hamburg covers not only urban but also rural areas. It comprises 25 % agricultural and 6 % woodland areas (Federal Statistical Office of Germany 2011). Moreover, 8 % of Hamburg's area is covered by nature reserves. The climate is temperate and oceanic with a mean annual temperature of 9°C and annual precipitation of 752 mm (data: German Meteorological Service (DWD) 2010, reference period 1971–2000). Schluenzen et al. (2010) determined a mean urban heat island of 1.1 K for the decade between 1988 and 1997.

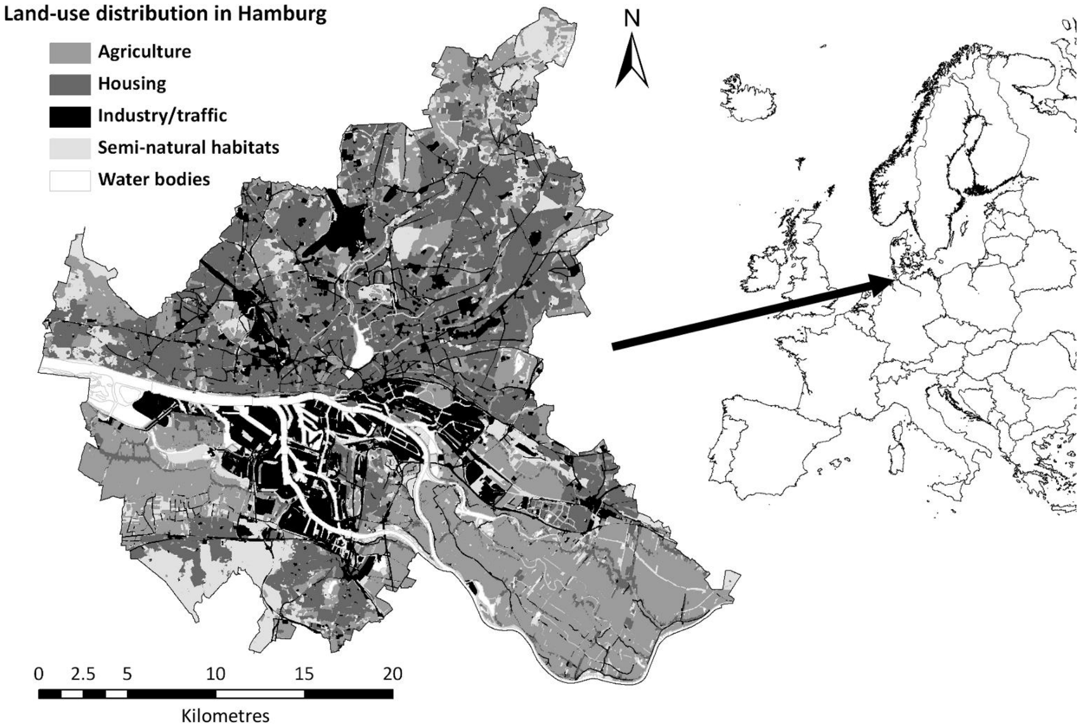

**Figure 2.1** Hamburg's location within Europe and its main land-use distribution

### 2.2.2 SPECIES RICHNESS PATTERNS

Floristic data was recorded over a period of 15 years between 1995 and 2009 by the Botanical Association of Hamburg (Botanischer Verein zu Hamburg e.V.). The presence and absence of all vascular plant species was mapped on a 1 km$^2$ grid. All grid cells were mapped repeatedly and at different times over the year (data set: Regionalstelle für Pflanzenartenschutz, Botanischer Verein zu Hamburg e.V. 2009). Altogether 1,643 plant species were registered in 861 grid cells (Poppendieck et al. 2010). In this study, we only included the 629 grid cells whose area is entirely within the borders of Hamburg. To analyse only spontaneous vegetation, cultivated and ornamental species were excluded from this study. Furthermore, a species list representative for the whole time period surveyed was obtained by excluding all species that are not naturalised, e.g. not (yet) able to reproduce in the area and establish stable populations. Our final species list consisted of 1,217 species. For each grid cell, four species richness measures were calculated (Table 2.1): total species number and proportions of non-native (all non-natives that naturalised in Germany after 1492 (neophytes) according to the status classification of the database BIOLFLOR; Klotz et al. 2002), endangered (according to the Red List for the flora of Hamburg, Poppendieck et al. 2010), and “thermophilic” species. These have an Ellenberg indicator value (EIV; see below) for temperature >5 (Goedde and Wittig 1983, Ellenberg et al. 1992), indicating strong preferences for warm habitat conditions.

**Table 2.1** Descriptive statistics of the four species richness measures (total species richness, proportions of non-native, endangered, and thermophilic species). Species numbers and proportions were generated from a floristic mapping on grid cells of the size of 1 km$^2$.

| Species richness measure | Mean | SD | Min | Max |
|---|---|---|---|---|
| Total species richness | 274.0 | ± 60 | 9.0 | 470.0 |
| Non-native species [%] | 10.4 | ± 3.4 | 0 | 22.2 |
| Endangered species [%] | 8.4 | ± 4.2 | 0 | 27.8 |
| Thermophilic species [%] | 38.3 | ± 5.0 | 18.7 | 53.3 |

### 2.2.3 SPECIES RICHNESS PREDICTORS: URBAN STRUCTURE, HABITAT, AND ENVIRONMENTAL CONDITIONS

As predictors representing urban structure, we used distances of all grid cells to the city centre and to the river Elbe, population density, and soil sealing. Habitat-related predictors for species richness include habitat diversity, soil diversity, and protected area.

Predictors representing environmental conditions comprise information on climate and EIVs for light, temperature, continentality, moisture, reaction, and nutrients. All data was calculated as information referring to the grid of the floristic mapping using ArcGIS 9.3 software (ESRI Inc., Redlands, CA, USA). For detailed information on specific classes of the predictor variables see Table 2.2.

Distance measures were calculated in ArcGIS, taking the distance of the central point of each grid cell to the city centre, defined by the grid cell holding the historic town hall, and the minimum distance to the river Elbe. Data on soil sealing was obtained from a mapping of biotope types. Classes of soil sealing ranged from 0 (hardly paved) to 10 (mostly paved) (data: Ministry for Urban Development and Environment of Hamburg (BSU) 2006). For both soil sealing and population density [inhabitants/ha] (data: Statistics Agency for Hamburg and Schleswig-Holstein 2009) weighted means per grid cell were calculated (weighted by area).

Habitat type data was derived from the biotope type mapping (data: BSU 2005). The original set of 370 biotope types was aggregated on the basis of a classification by Haeupler (2002), but developing a more detailed classification of the urban and industrial habitats, finally resulting in 23 habitat types. Soil data consisted of eight classes (data: Miehlich and Brandt 2010). For habitat type and soil, the proportional areas of the respective classes per grid cell were calculated in ArcGIS. Based on these, habitat and soil diversity per grid cell were calculated using the Shannon-Wiener index (see Krauss et al. 2004). We detected landscape and nature protection areas with the GIS data of the biotope type mapping and calculated the proportion of total protected area per grid cell.

Climate data comprised mean annual temperature and annual precipitation for the reference period 1971–2000 (data: German Meteorological Service (DWD), as a digital map with spatially interpolated values; 2010). EIVs have been assigned to plant species in Central Europe according to habitat preferences and distribution and usually range from 1 to 9 (Ellenberg et al. 1992). EIVs are often used as indicators for environmental conditions of plant species assemblages. EIVs for light indicate the shade tolerance of a species ranging from 1 (shade tolerant) to 9 (not shade tolerant). EIVs for temperature are derived from species' distributional and altitudinal range and transferred to temperature preferences ranging from 1 (high-altitude and cold conditions) to 9 (Mediterranean and warm conditions).

EIVs for continentality are also derived from species distribution. These range from 1 (eu-oceanic) to 9 (eu-continental) and can be seen as a gradient of species' tolerance towards winter frost. EIVs for moisture are an indicator of species' tolerance towards drought and range from 1 (restricted to dry soil conditions) to 12 (submerged plants). EIVs for reaction indicate species' preference for acidic (1) or alkaline (9) soil conditions. EIVs for nutrients were initially assigned to plant species on the basis of nitrogen preferences only, but several studies attributed the value to nutrient availability and productivity in general (e.g. Schaffers and Sykora 2000, Cornwell and Grubb 2003, Klaus et al. 2012). The values range from 1 (nutrient-poor) to 9 (nutrient-rich).

For each grid cell, we calculated the mean EIVs based on species composition. EIVs were available for 1,040 species for light, 773 for temperature, 839 for continentality, 1,008 for moisture, 819 for reaction, and 991 for nutrients. EIVs are ordinal numbers and therefore do not fulfil the requirements for calculating arithmetic means. Nevertheless, the use of average indicator values is widely applied in vegetation ecology, as e.g. mean and median usually do not differ much except in some species-poor communities and potential error resulting from averaging remains small in comparison to other restrictions (Ter Braak and Barendregt 1986, Schaffers and Sykora 2000, Diekmann 2003, Chytrý et al. 2009).

**Table 2.2** Descriptive statistics of the plant species richness predictor variables of urban structure, habitat and environmental conditions used in the analyses. The predictor variables were calculated per 1 $km^2$ grid cell.

| Variable | Classes | Mean | SD | Min | Max |
|---|---|---:|---|---:|---:|
| **Distances to** | City centre [m] | 10525.52 | ± 4850.51 | 0 | 23323.81 |
| | River Elbe [m] | 5279.94 | ± 4843.91 | 0 | 23158.85 |
| **Soil sealing** | [mean degree per grid cell] | 4.99 | ± 1.98 | 1.24 | 9.15 |
| **Population density [inhabitants/ha]** | | 32.00 | ± 36 | 0 | 180.00 |
| **Habitat type** [% of area per grid cell] | Airport | 0.87 | ± 7.09 | 0 | 99.44 |
| | Port | 1.41 | ± 7.04 | 0 | 64.45 |
| | Railway system | 1.43 | ± 3.29 | 0 | 23.86 |
| | Traffic | 3.34 | ± 3.48 | 0 | 19.83 |
| | Industrial sites | 8.22 | ± 14.59 | 0 | 81.80 |
| | Dense housing | 2.56 | ± 6.90 | 0 | 58.53 |
| | Multi-storeyed housing | 8.23 | ± 12.89 | 0 | 74.07 |
| | Single housing | 17.34 | ± 21.48 | 0 | 94.43 |
| | Rural housing | 1.22 | ± 3.36 | 0 | 35.38 |
| | Other housing | 5.52 | ± 8.36 | 0 | 80.60 |
| | Crop plants | 12.98 | ± 20.33 | 0 | 96.43 |
| | Ornamental plants | 6.38 | ± 9.63 | 0 | 73.84 |
| | Grassland/pastures | 10.91 | ± 17.91 | 0 | 86.27 |
| | Forest | 5.08 | ± 11.57 | 0 | 88.63 |
| | Herb-dominated habitats | 2.60 | ± 5.30 | 0 | 52.59 |
| | Peatland | 0.64 | ± 3.06 | 0 | 38.37 |
| | Poor grassland/dwarf shrub heath | 0.34 | ± 1.85 | 0 | 24.72 |
| | Shrubberies/clearings | 1.30 | ± 2.44 | 0 | 30.30 |
| | Floodplains | 0.43 | ± 1.48 | 0 | 14.73 |
| | Headwater | 0.00 | ± 0.02 | 0 | 0.40 |
| | Lakes/ponds | 1.39 | ± 3.17 | 0 | 34.21 |
| | Rivers/streams | 5.70 | ± 12.76 | 0 | 71.85 |
| | Tidal-freshwater sites | 0.65 | ± 4.36 | 0 | 66.18 |
| **Soil** [% of area per grid cell] | Artificial substrate | 14.63 | ± 30.89 | 0 | 100.00 |
| | Clay | 22.65 | ± 35.80 | 0 | 100.00 |
| | Fine sand | 0.34 | ± 2.87 | 0 | 38.17 |
| | Peat | 5.14 | ± 16.56 | 0 | 100.00 |
| | Sand | 35.25 | ± 36.09 | 0 | 100.00 |
| | Sand/silt/clay | 6.78 | ± 13.18 | 0 | 91.17 |
| | Silt | 13.90 | ± 23.32 | 0 | 100.00 |
| | Silt/fine sand | 1.16 | ± 8.45 | 0 | 94.00 |
| **Protected area** [% of area per grid cell] | | 22.10 | ± 30.41 | 0 | 100 |
| **Climate** | Annual precipitation [mm] | 748.37 | ± 34.73 | 667.50 | 821.00 |
| | Mean annual temperature [°C] | 9.19 | ± 0.20 | 8.65 | 9.70 |
| **EIV** | Light | 6.84 | ± 0.20 | 6.16 | 7.31 |
| | Temperature | 5.67 | ± 0.10 | 5.27 | 5.92 |
| | Continentality | 3.84 | ± 0.15 | 3.42 | 4.50 |
| | Moisture | 5.88 | ± 0.56 | 4.82 | 7.68 |
| | Reaction | 6.21 | ± 0.27 | 4.80 | 7.50 |
| | Nutrients | 5.76 | ± 0.22 | 4.66 | 6.50 |

### 2.2.4 STATISTICAL ANALYSES

To test for differences of the four species richness measures (total plant species number, proportion of non-natives, endangered, and thermophilic species) between different degrees of urbanisation in Hamburg, we calculated an 'urbanisation index'. Because of the central and largely paved but uninhabited port area, none of the variables representing urban structure, habitat, and environmental conditions solely accounted for urbanisation.

Therefore, degree of soil sealing, population density, mean annual temperature, and proportion of green space per grid cell were included in the index. The proportion of green space was obtained by adding up the proportions of the eight land-use classes crop plants, ornamental plants, grasslands & pastures, forest, herb-dominated habitats, peat land, poor grassland/dwarf shrub heath, and shrubberies/clearings. The four variables for the index were standardised by zero mean-unit variance prior to analysis to obtain dimensionless numbers. The urbanisation index was calculated as the sum of degree of soil sealing, population density, and mean annual temperature minus the proportion of green space. To divide the index into three groups of high, medium and low urbanisation, we used two different methods for verification: 'equal intervals' and 'natural breaks' as implemented in ArcGIS (see Figure 2.2a for 'natural breaks' division). Differences in species richness measures between urbanisation zones were tested with one-way ANOVAs followed by GT2/Hochberg posthoc tests. If ANOVA assumptions could not be met, Welch-ANOVAs followed by Games-Howell posthoc tests were applied. Prior to analysis, the proportional species richness measures were arcsine-transformed.

Overall species richness pattern in Hamburg was assessed by testing effects of urban structure, habitat, and environmental conditions on species richness for the four species richness measures using stepwise multiple regression analyses. The variables representing species richness in proportions were arcsine-transformed. Predictor variables for species richness were: distance to the city centre and to the river Elbe, degree of soil sealing, annual precipitation, mean annual temperature, proportion of protected area, habitat diversity, soil diversity, and mean EIVs for light, temperature, continentality, moisture, reaction, and nutrients. All predictor variables were standardised by zero mean unit variance. Analysis of collinearity of these variables was conducted beforehand by calculating a matrix of Spearman's correlations and applying Bonferroni correction (Table 2.3). Of all correlations with a Spearman correlation coefficient higher than 0.5, the most redundant predictor variables were omitted. Subsequently, we used mean annual temperature, precipitation, proportion of protected area, habitat diversity, soil diversity, EIV for moisture, and EIV for nutrients as species richness predictors for the multiple regression analyses. The variables of distance to the city centre, distance to the river Elbe, degree of soil sealing, and the EIVs for light, temperature, continentality, and reaction were omitted from further analyses. All final predictor variables were assessed visually in ArcGIS.

Stepwise multiple regressions were followed by analyses of relative importance of the regressors using the metric "lmg" that decomposes $R^2$ into contributions adding up to the total $R^2$ (R-package 'relaimpo', Groemping 2006). Statistical analyses were calculated with R (R Development Core Team 2010) and SPSS (PASW Statistics 18, Version 18.0.0). Figures were created with ArcGIS 9.3 and Sigmaplot 12.0 (Systat Software, Inc. 2011).

**Table 2.3** Correlation matrix of the initially considered predictor variables distance to the city centre [km], distance to the river Elbe [km], degree of soil sealing, population density [inhabitants/ha], habitat diversity, soil diversity, proportion of protected area [%], mean annual temperature [°C], annual precipitation [mm], EIVs for light, temperature, continentality, moisture, reaction, and nutrients. Significant correlations after Bonferroni correction with a Spearman correlation coefficient >0.5 are indicated by bold numbers. Predictor variables in bold have been included in further analyses.

| | D_city | D_Elbe | Seal. | Popd. | **H_div.** | **S_div.** | **Prot.** | **Temp.** | **Prec.** | EIL | EIT | EIC | **EIM** | EIR |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Dist. city | 1 | | | | | | | | | | | | | |
| Dist.Elbe | 0.40 | 1 | | | | | | | | | | | | |
| Soil sealing | **-0.53** | 0.13 | 1 | | | | | | | | | | | |
| Pop. density | -0.29 | 0.33 | **0.67** | 1 | | | | | | | | | | |
| **Habitat div.** | -0.23 | 0.13 | 0.28 | 0.35 | 1 | | | | | | | | | |
| **Soil div.** | -0.01 | 0.24 | 0.11 | 0.25 | 0.18 | 1 | | | | | | | | |
| **Prot. area** | 0.49 | 0.18 | **-0.53** | -0.28 | 0.03 | 0.04 | 1 | | | | | | | |
| **Temperature** | **-0.83** | **-0.61** | 0.26 | 0.01 | 0.12 | -0.1 | -0.46 | 1 | | | | | | |
| **Precipitation** | -0.08 | **0.64** | 0.43 | **0.52** | 0.18 | 0.23 | 0.05 | -0.4 | 1 | | | | | |
| EIL | -0.36 | **-0.64** | -0.02 | -0.35 | -0.03 | -0.23 | -0.38 | **0.68** | **-0.65** | 1 | | | | |
| EIT | **-0.62** | **-0.55** | 0.39 | 0.09 | 0.08 | -0.12 | **-0.55** | **0.71** | -0.28 | **0.67** | 1 | | | |
| EIC | -0.21 | **-0.54** | -0.17 | -0.44 | -0.04 | -0.21 | -0.28 | **0.57** | **-0.68** | **0.83** | **0.51** | 1 | | |
| **EIM** | **0.54** | 0.04 | **-0.74** | **-0.52** | -0.14 | 0.01 | 0.42 | -0.24 | -0.4 | 0.04 | -0.44 | 0.25 | 1 | |
| EIR | -0.31 | -0.45 | 0.02 | -0.15 | -0.05 | -0.12 | -0.37 | **0.54** | -0.44 | **0.58** | **0.58** | **0.69** | 0.08 | 1 |
| **EIN** | -0.09 | -0.13 | -0.02 | 0.05 | -0.12 | 0.03 | -0.18 | 0.19 | -0.17 | 0.04 | 0.17 | 0.21 | 0.17 | **0.65** |

## 2.3 RESULTS

The flora of Hamburg analysed here comprised 140 non-native species (12 %), 429 endangered species (38 %), and 518 thermophilic species (46 %). The most frequently occurring species were *Urtica dioica* L., *Rumex obtusifolius* L., *Cirsium arvense* (L.) Scop., *Plantago lanceolata* L., *Lolium perenne* L., *Poa annua* L., *Ranunculus repens* L., and *Sambucus nigra* L. The total number of species per 1 km$^2$ was 274 ± 60 (Table 2.1) on average and differed significantly between low and medium urbanisation when using 'natural breaks' index division (Figure 2.2b, F=3.1*), but did not differ significantly using 'equal interval' index division (Table 2.4; F=0.4 ns.). For the other species richness measures, the emerging patterns were independent of the method of index division, therefore only the 'natural breaks' division is shown (Figure 2.2). The proportion of non-native species was 10.4 % ± 3.4 per 1 km$^2$ on average and significantly increased with increasing urbanisation intensity (Figure 2.2c; ANOVA, F=343.6***), while the proportion of endangered species (average 8.4 % ± 4.3 per 1 km$^2$) decreased (Figure 2.2d; ANOVA, F=110.7***). The proportion of thermophilic species (average 38.3 % ± 5 per 1 km$^2$) also increased with urbanisation intensity (Figure 2.2e; Welch-ANOVA, F=87.8***).

**Table 2.4** Differences in total species number between different degrees of urbanisation in Hamburg (high, medium, low) according to two methods of index division (equal intervals and natural breaks).

| **Index division** | **Equal intervals** | **Natural breaks** |
|---|---|---|
| *Degree of urbanisation* | *Total species number* | |
| High | 271 ± 49 | 264 ± 56$^a$ |
| Medium | 276 ± 64 | 280 ± 64$^b$ |
| Low | 272 ± 57 | 273 ± 56$^{ab}$ |
| ANOVA results (F- and p-values) | 0.4 ns. | 3.1* |

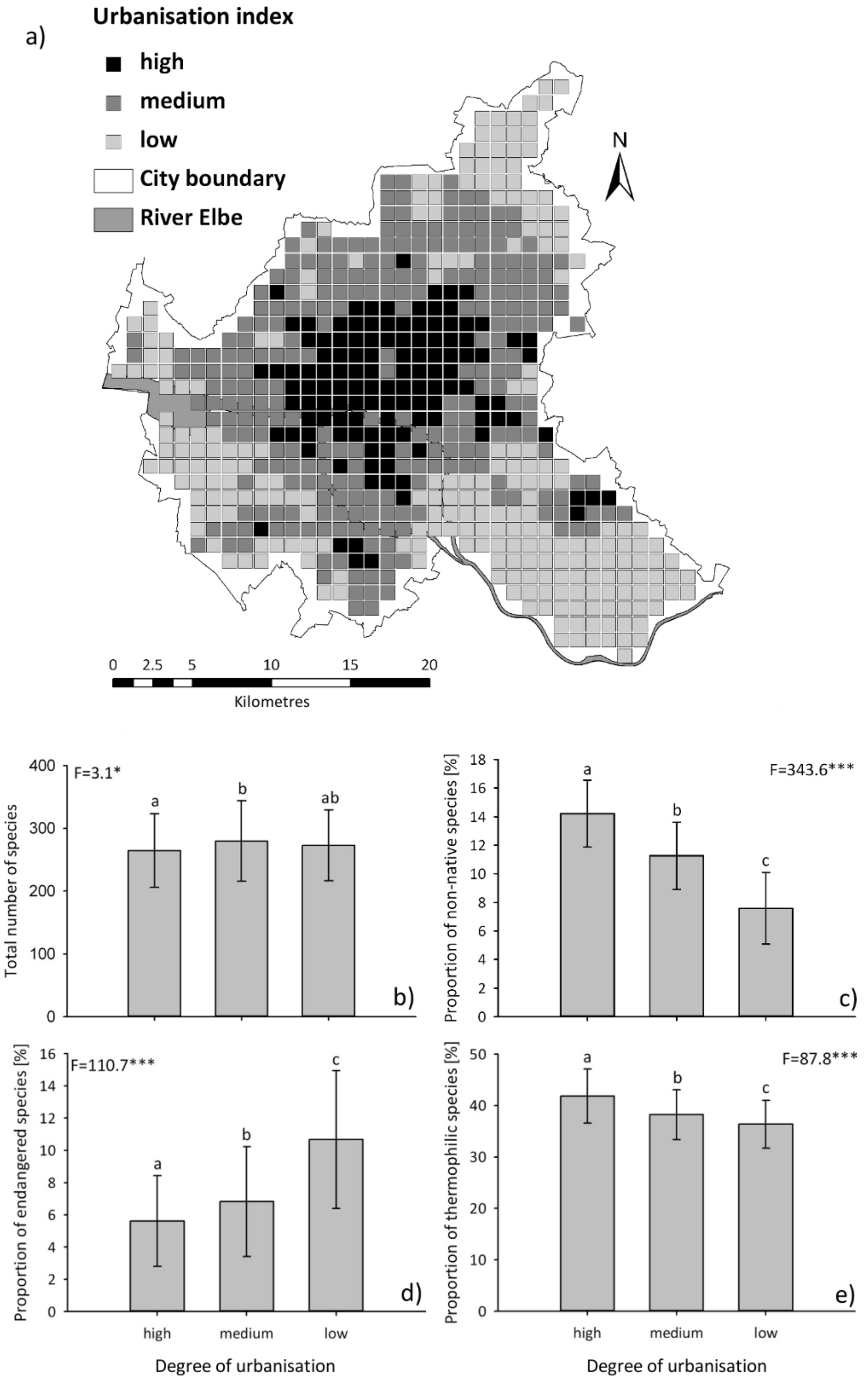

**Figure 2.2** **a)** Location of grid cells with high, medium and low degrees of urbanisation in Hamburg based on the urbanisation index divided by 'natural breaks', and differences in species richness measures between the three urbanisation zones: **b)** total species richness, **c)** proportion of non-native species (square-transformed), **d)** proportion of endangered species (Welch-ANOVA), and **e)** proportion of thermophilic species. Mean and standard deviation are shown in bar plots and ANOVA-results are given.

The spatial pattern of species richness predictor variables differed considerably (Figure 2.3). Protected areas were found exclusively outside of the urban core (Figure 2.3b). Mean annual temperature clearly decreased from urban to rural areas (Figure 2.3c), while precipitation increased towards the north and decreased towards the southeast of the study area (Figure 2.3d). Habitat diversity showed no distinct pattern (Figure 2.3e), nor did soil diversity (Figure 2.3f), which was generally low. None of the two variables was strongly correlated with any of the other predictors. Mean EIV for moisture was rather low in the urban centre and higher in the south-eastern and western parts of Hamburg (Figure 2.3g), while the distribution of mean EIV for nutrients was indistinct and could not be related to urban structure (Figure 2.3h).

The total number of species per grid cell ranged between 9 and 470 (Figure 2.4a). Only four grid cells contained fewer than 100 species, while 21 had more than 400 species. Species richness was distributed rather indistinctly and could not be related to urban structure at first sight. However, multiple regression analysis showed that total species richness decreased with increasing EIV for nutrients and increased with habitat diversity, while climatic variables and the proportions of protected area were less important (Table 2.5). Altogether 30.5 % of the variation in the total number of species was explained by the regression model (multiple $R^2$=0.31). The distribution of the proportion of non-native species per grid cell was already visually related to urban structure. The proportion of non-natives decreased from the urban centre to the rural outskirts (Figure 2.4b). It was negatively associated with increasing EIV for moisture and positively with increasing temperature. This relationship also reflects the spatial urban structure, since both variables were correlated with distance to the city centre (multiple $R^2$=0.72, Table 2.5).The proportion of endangered species was generally higher in rural areas, but also in some grid cells of the city centre (Figure 2.4c). It increased with increasing EIV for moisture and decreased with increasing EIV for nutrients. Furthermore, an increase with increasing proportion of protected area was found (multiple $R^2$=0.66, Table 2.5). The proportion of thermophilic species showed distinct distribution patterns (Figure 2.4d) and increased with increasing temperature. Furthermore, it decreased with increasing precipitation and increasing proportions of protected area (multiple $R^2$=0.58, Table 2.5).

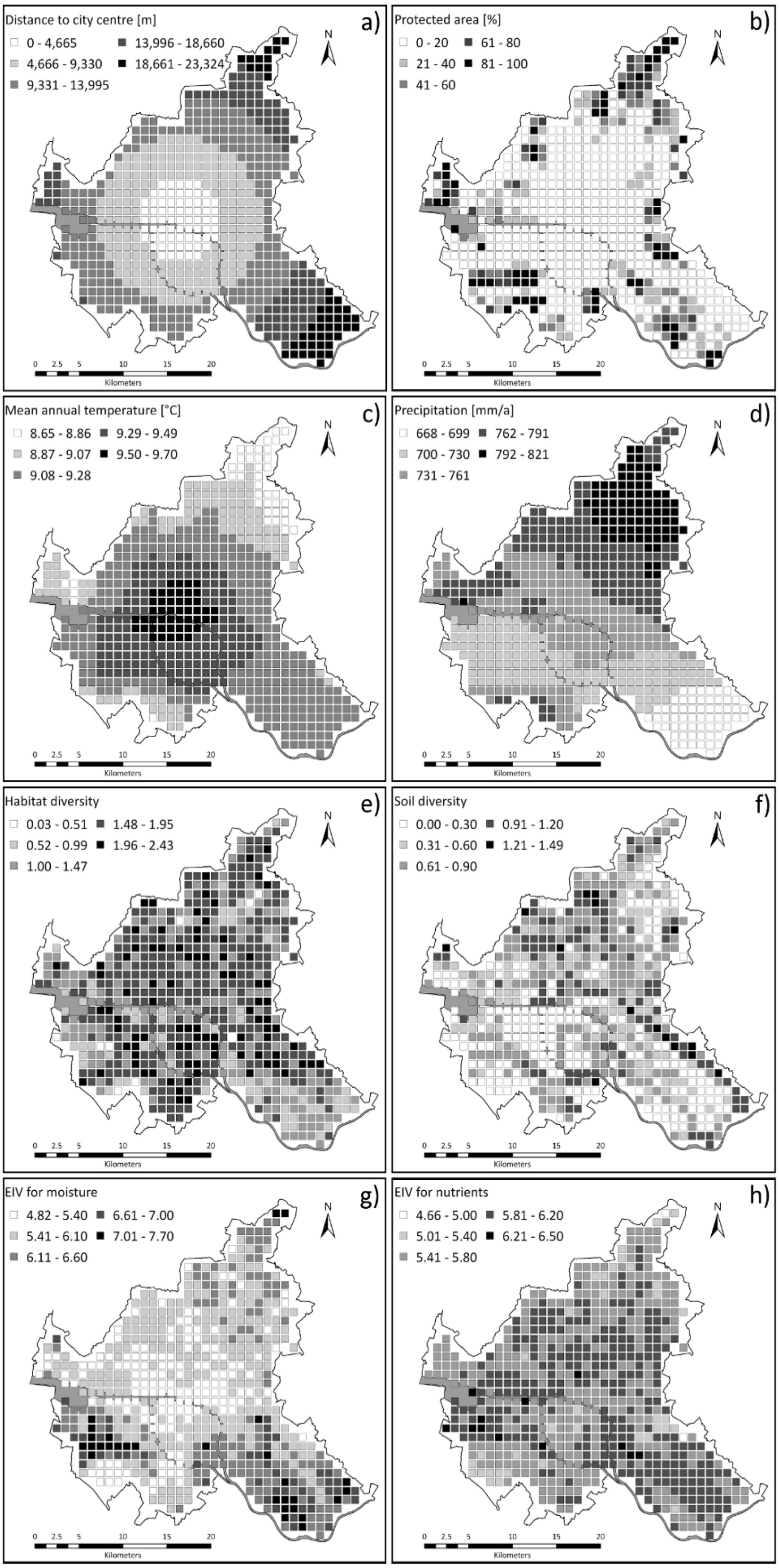

**Figure 2.3** Distribution of species richness predictor variables for plant species richness: **a)** Distance to city centre, **b)** Proportion of protected area, **c)** Mean annual temperature, **d)** Annual precipitation, **e)** Habitat diversity, **f)** Soil diversity, **g)** Mean Ellenberg indicator value for moisture, **h)** Mean Ellenberg indicator value for nutrients. All predictors have been calculated per grid cell. Habitat and soil diversity have been computed using the Shannon-Wiener-Index.

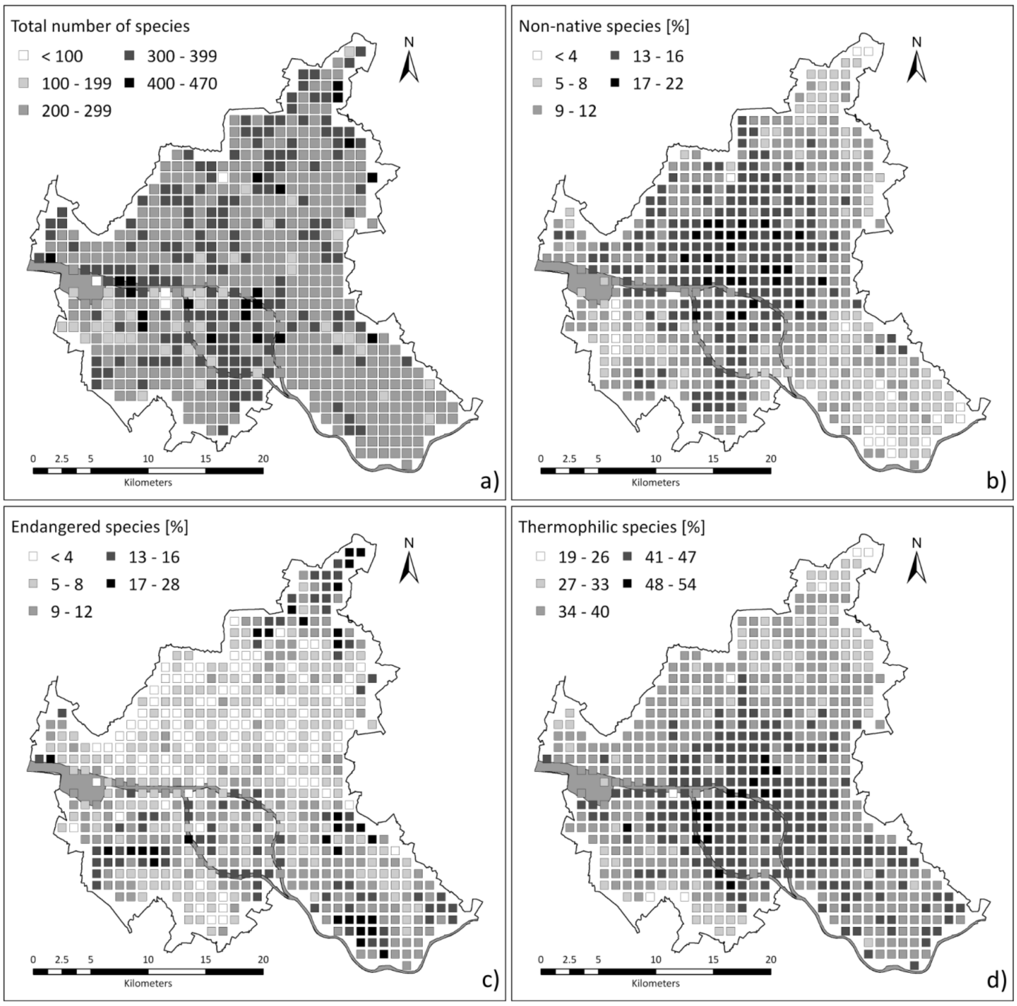

**Figure 2.4** Plant species richness distribution in Hamburg: **a)** total number of plant species, **b)** proportions of non-native species, **c)** proportions of endangered species, and **d)** proportions of thermophilic species. Darker colours indicate higher species numbers or proportions in the respective grid cells.

**Table 2.5** Multiple regressions of the effects of the species richness predictors mean annual temperature, annual precipitation, proportion of protected area, habitat diversity, soil diversity, mean Ellenberg indicator values for moisture (EIM) and for nutrients (EIN) on species richness patterns. Total species numbers and proportions of non-natives, endangered, and thermophilic were used as measures for species richness. Bold numbers indicate most important predictors.

| | **Total species number** | | | **Non-natives [%]** | | | **Endangered [%]** | | | **Thermophilic [%]** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Predictors** | F | p | RI | F | p | RI | F | p | RI | F | p | RI |
| Temperature | 3.2 | ns. | 0.01 | 143.1 | *** | **0.12** | 82.9 | *** | 0.02 | 695.7 | *** | **0.27** |
| Precipitation | 10.8 | ** | 0.01 | 54.2 | *** | 0.08 | 16.4 | *** | 0.08 | 93.5 | *** | **0.12** |
| Protected area | 7.1 | ** | 0.02 | 9.1 | ** | 0.09 | 4.1 | * | 0.10 | 37.1 | *** | 0.10 |
| Habitat diversity | 100.9 | *** | **0.12** | 35.3 | *** | 0.05 | 3.5 | ns. | 0.01 | 2.6 | ns. | 0.01 |
| Soil diversity | | | | | | | | | | | | |
| EIM | 3.2 | ns. | 0.01 | 1302.7 | *** | **0.37** | 583.5 | *** | **0.23** | 42.6 | *** | 0.08 |
| EIN | 148.0 | *** | **0.14** | 42.3 | *** | 0.02 | 498.4 | *** | **0.22** | | | |
| Variance explained [%] | | | 30.5 | | | 71.8 | | | 65.7 | | | 58.3 |

## 2.4 DISCUSSION

Total plant species richness decreased with increasing EIV for nutrients. The highest EIV for nutrients was found in agricultural areas, which are characterised by very fertile soils. Here, species richness is generally lower due to intensive agricultural use. Usually nitrogen deposition is higher in city centres (Lovett et al. 2000), and therefore EIV for nutrients would also be expected to be higher in the urban core (Pellissier et al. 2008). Hope et al. (2003) found increasing species richness with increasing nutrient availability. On the contrary, Hamburg's port area, which is located in the city centre, harbours vegetation like dry grasslands that are colonised by species adapted to low nutrient availability. Urban soils differ from rural soils: they are mostly drier and contain more sand. Therefore, deposited nitrogen is washed out rather quickly and available nitrogen for plants is reduced, which might compensate for the higher input. The total species number increased further with increasing habitat diversity. This result is in accordance with Deutschewitz et al. (2003), who showed an increase in species richness with spatial heterogeneity and the amount of habitats on a regional scale. In the city of Berlin, species richness was also positively influenced by habitat diversity, which in turn was related to an underlying urban-to-rural gradient (Zerbe et al. 2003). In Hamburg, we could not detect any relation between habitat diversity and urban structure. This might be due to the short gradient considered. Since we were restricted by the data set covering only the city state of Hamburg, we could not define the gradient by landscape features and extend it to more rural areas outside of Hamburg.

Using different methods of dividing the urbanisation index into categories led to different results in total species richness. Along urban-to-rural gradients, the highest species richness usually occurs in suburban areas (Gilbert 1989, Kent et al. 1999, Zerbe et al. 2003). These areas are very heterogeneous due to a mixture of residential areas in different stages of development, as well as agricultural and natural remnant habitats. In contradiction, we found only slightly differing plant species numbers between the different urbanisation zones in Hamburg. The higher species richness in grid cells with medium degrees of urbanisation is not as pronounced as in the above-mentioned studies. Hamburg's spatial conditions probably account for this result: the urban centre comprises both typical urbanised landscapes with high building and population density, but also the uninhabited port area with industrial and wasteland sites and surprisingly high plant species richness. The rural areas in the periphery of Hamburg are also species-rich, as they contain several semi-natural habitats and nature reserves. Therefore, we could only identify a tendency of decreasing species richness towards the urban core, which was reported by other studies (Kent et al. 1999, McKinney 2008, see also Celesti-Grapow et al. 2006, who found lower species richness in more disturbed areas).

The distribution of the richness of non-native species in Hamburg is consistent with general patterns of non-native species distribution: number and percentage of non-native species decrease with distance to the urban core (e.g. Celesti-Grapow and Blasi 1998, Brunzel et al. 2009). Non-native species often first occur in the centre of cities and then spread towards the surrounding areas (von der Lippe and Kowarik 2008). Since they mostly originate from warmer regions, they can better naturalise in warm and dry city centres, which is reflected in our results.

In Hamburg, non-native occurrences can also be related to trade actions in the port area, where several species arrived first (Meyer 1955, Jehlîk 1989). A striking example is *Senecio* *inaequidens* DC., whose subsequent spread from the port to the surroundings can be retraced in the mapping data over the years (Poppendieck et al. 2010). The proportion of non-native species (neophytes) of the total flora of Hamburg of 12 % was rather low compared to other European cities (e.g. average over 54 Central European cities: 25 % (Pyšek 1998); Frankfurt (Germany): 23 % (Gregor et al. 2012)). This discrepancy is probably due to our rather strict criteria for generating the species list: not naturalised species and ornamentals were excluded, most of which might have also been included as neophytes in other studies.

The proportion of endangered species increased with increasing EIV for moisture and decreasing EIV for nutrients. As expected, it further increased with increasing proportion of protected area. The EIV for moisture was negatively correlated with the degree of soil sealing and obviously represents less urbanised and more natural habitats. In general, these habitats are often nutrient-poor, which is reflected in low EIV for nutrients. Rather natural or semi-natural habitats are usually found in areas less disturbed by human influence, e.g. in the rural areas. In Hamburg, these habitats are bogs, heathlands, forests, and inland dunes harbouring specialist species. These are adapted to environmental conditions that are no longer found in more urbanised areas. For example, the endangered species *Drosera rotundifolia* L. and *Eriophorum angustifolium* Honck. occur in bog habitats, which are characterised by low nutrient availability, low soil pH and high moisture. *Corynephorus canescens* (L.) P. Beauv. and *Carex arenaria* L. are restricted to sandy habitats that feature low nutrient availability, low soil pH, and drought. Overall, our results are in accordance with Knapp et al. (2009), who found that species adapted to low soil pH and cool habitats are especially threatened by urbanisation.

Surprisingly, high proportions of endangered species were also found in the port area. This area is under great anthropogenic impact and features some remarkable habitat types, some with specific habitat conditions like low nutrient availability, high temperature, and drought. Numerous wasteland sites are found here, which are usually species-rich (Zerbe et al. 2003, Muratet et al. 2007). Poppendieck et al. (2010) attribute the port’s species richness further to the traditional use of spoil areas that created rather unique habitats. Silt was dredged from the river Elbe and then spread out to dry on large fields. The contained seeds germinated and species spread into the surrounding habitats. Furthermore, sand fillings created new unoccupied habitats where succession took place. Dry grasslands often developed here, forming a special feature of the flora of Hamburg. The wasteland sites are also habitats for garden and agricultural weeds, especially for thermophilic species that prefer alkaline soils. Additionally, seeds unintentionally escaped during loading activities, e.g. at flour and oil mills (Jehlîk 1981, Poppendieck et al. 2010). These species in particular increase species richness over time in the port area. Within the 15 years of mapping, several species appeared and disappeared again, of which several are considered endangered. However, even though a species-rich and unique port flora has developed in the past few decades, today this is threatened by port expansion and container use. Moreover, improved processes of seed cleaning prevent invasions of new species today (Poppendieck et al. 2010).

Natural habitats like the rare tidal marshes and forests in the port area also contribute to high species richness. Here, *Oenanthe coinoides* and *Deschampsia wibeliana* occur, and both are endemic plants of the river Elbe. Their habitats are threatened by channel dredging for shipping and altered courses of dikes (Poppendieck et al. 2010). As expected, thermophilic species were mainly influenced by mean annual temperature. Moreover, their proportions decreased with increasing precipitation. They seem to be favoured by warm and dry conditions typical for urban habitats. Obviously the EIV for temperature, by which the measure was classified, corresponds well with actual temperatures in the study area. Non-native species are often also thermophilic and one could expect them to contribute considerably to the proportion of thermophilic species. However, EIVs for temperature patterns of only native species show basically the same distribution in Hamburg (Bechtel and Schmidt 2011).

### 2.4.1 CONCLUSIONS

Patterns of Hamburg’s plant species richness can be related to the specific city structure: the port, as part of the city centre, is particularly species-rich over time due to high disturbance (frequent urban redevelopment) and its dry and nutrient-poor conditions that also favour endangered species. Hence, we cannot clearly confirm that suburban areas are generally species rich. The distribution pattern of the proportions of non-natives, however, follows general patterns with a strong decrease towards rural areas. Endangered species richness depends on moist habitats and low nutrient availability, which can be found in rural and also port areas. These species are especially threatened by urbanisation. Thermophilic species richness is strongly influenced by temperature patterns and is thus generally higher in urban areas. Our results can help identify areas of high urban biodiversity for conservation. Moreover, semi-natural remnants in cities need to be further protected from urbanisation to maintain their high species richness.

## 2.5 ACKNOWLEDGEMENTS

We are grateful to the Botanischer Verein zu Hamburg e.V. and the Regionalstelle für Pflanzenartenschutz for providing the extensive data set on plant species distribution and all volunteers who contributed to mapping the flora of Hamburg. We wish to thank the German Meteorological Service (DWD), the Ministry for Urban Development and Environment of Hamburg (BSU) and G.Miehlich & I.Brandt for the provision of data on predictors and Melissa Kostelecky for linguistic proofreading of the manuscript. We also thank two anonymous reviewers for helpful comments that improved our manuscript. The work was funded by the Federal Ministry for Education and Research within the research project KLIMZUG-NORD (grant number 01LR0805D).

# 3 PLANT SPECIES DISTRIBUTION CLEARLY REFLECTS THE STRUCTURE OF HAMBURG (GERMANY) ON A MESO-SCALE

Katharina J. Schmidt, Hans-Helmut Poppendieck & Kai Jensen

Submitted to *Landscape Ecology*, under review

j

**KEYWORDS**
Cluster analysis * Floristic mapping * Moran's eigenvector maps (MEM) * Spontaneous vegetation * Urban ecology * Urban flora * Variation partitioning

**ABBREVIATIONS:**
EIV = Ellenberg indicator values, MEMs = Moran's eigenvector maps, MEM+ = positively spatially correlated MEMs, MEM- = negatively spatially correlated MEMs

## 3.1 INTRODUCTION

Urban development is one of the most important global drivers for land-use change and consequently also affects biodiversity. Although cities often harbour high plant species richness, urbanisation has strong impacts on species composition and selects for species with specific traits that can tolerate urban conditions (Kuehn et al. 2004, Thompson and McCarthy 2008, Williams et al. 2009, Knapp et al. 2010). Due to both similar species compositions of typical urban habitats and the occurrence of non-native species, an increasing homogenisation of floras of different cities worldwide has been reported (Kuehn and Klotz 2006, McKinney 2006, Wittig and Becker 2010). Regarding conservation, a better understanding of the effects of urbanisation on species distribution patterns is important. Conserving and promoting biodiversity directly in cities is crucial for several reasons, e.g. conservation of local biodiversity, environmental education, and general improvement of human well-being (Miller 2005, Dearborn and Kark 2010). Urban vegetation contributes to ecosystem functions like carbon sequestration (Nowak and Crane 2002), temperature reduction in summer (Lindberg and Grimmond 2011), habitat provision (Robinson and Lundholm 2012) and human psychological well-being (Fuller et al. 2007). Concomitantly, studies of urban biodiversity patterns and processes can facilitate the integration of ecology into urban planning (Niemelä 1999, Sushinsky et al. 2013, McDonnell and Hahs 2013).

Species distribution patterns and extinction rates in cities have been shown to be affected by the history of urbanisation (Chocholoušková and Pyšek 2003, Hahs et al. 2009, Dolan et al. 2011), which in turn is dependent on historical environmental conditions and landscape topography. Thus, both natural landscape conditions and urban development shaped present environmental conditions in a city. Environmental conditions often vary spatially along urbanisation gradients: Soil sealing, population density, traffic, air and soil pollution, nitrogen deposition, temperature and drought generally have the highest intensity in city centres and generally decrease towards the surroundings (Oke 1982, Pouyat and McDonnell 1991, Lovett et al. 2000, McKinney 2002). Since these conditions directly affect plant species distribution, species distribution pattern can reflect urban structure (Kent et al. 1999). However, biotic processes like dispersal, competition or herbivory and direct human impact (e.g. trampling or gardening) additionally influence urban species distribution patterns (von der Lippe and Kowarik 2007, Maurel et al. 2010, Bertoncini et al. 2012). Thus, disentangling the origin of variation for plant species distribution in cities is a challenging task in urban ecology.

Recent literature emphasises the importance of accounting for spatial variation in ecological analyses (McIntire and Fajardo 2009, Dray et al. 2012). The higher similarity of samples that are taken from close-by locations compared to samples farther apart can either be directly related to biotic processes (spatial autocorrelation) or indirectly to environmental processes that are spatially structured (induced spatial dependence; Dray et al. 2006, Peres-Neto and Legendre 2010). Over the past two decades, several methods have been developed to incorporate spatial structure into multivariate analyses (e.g. Borcard et al. 1992, Borcard and Legendre 2002, Legendre et al. 2005, Dray et al. 2012). Moran's eigenvector maps (MEM), an eigenvector decomposition of a connectivity map, have been recently introduced as an option for multivariate spatial analysis in ecology (Dray et al. 2006). Here, positive MEMs are positively spatially correlated (MEM+), they represent broad scale spatial correlation and describe global structures, e.g. large-scale drivers of environmental, historical or biotic origin (Dray et al. 2006, Dray et al. 2012). Negative MEMs are negatively spatially correlated (MEM-), representing processes on a fine spatial scale and local structures related to biotic interactions, micro-site effects of unmeasured environmental variables or dispersal processes (Dray et al. 2006, Dray et al. 2012) or fine-scale geological patterns (Mikulyuk et al. 2011). Variation partitioning can be used to differentiate between effects of environmental and spatial factors (Borcard et al. 1992, Peres-Neto and Legendre 2010). So far, few studies dealt with spatially structured species distribution pattern in urban contexts: For instance, Chytrý et al. (2012) detected spatial structure caused by dispersal limitation in several organism groups across cities, while Sattler et al. (2010) found only weak spatial structure in urban animal communities in selected habitats. In a study by Lososová et al. (2012a), spatial structure explained more variation than climate in plant species composition across cities.

We use the city of Hamburg (Germany) as a case study to disentangle effects of environmental conditions and spatial structure on urban plant species distribution. Hamburg comprises different urbanisation zones, including urban settlement areas, the central port area, peripheral agricultural land, and semi-natural habitats. We analyse the effect of environmental conditions and spatial structure on plant species distribution in Hamburg on a meso-scale (1 km²) using species data and three species proxy data sets (genera, communities and traits) obtained from a floristic mapping. The analysis of proxies derived from species data can be seen as a method of reducing variation by agglomerating species into broader categories. By using species proxy data additional insights into vegetation pattern might be achieved (Thompson and McCarthy 2008). We assume that the spatial structure can indicate neighbourhood effects of close-by sites due to historical effects, e.g. urbanisation. To our knowledge, so far only few studies have accounted for spatial structure in the analysis of species distribution data mapped on a regular grid (Petřík and Wild 2006, plant species in

Czech Republic; Titeux et al. 2004, bird species in Belgium). However, when using grid based data it is especially important to account for spatial structure, because grids closer together probably share environmental conditions (induced spatial dependence) and species (spatial autocorrelation) (Titeux et al. 2004).

We ask the following questions:

- Does plant species distribution reflect the structure of Hamburg?
- What are the most influential environmental variables for plant species distribution?
- What impact do environmental conditions and spatial structure have on species composition and can they be distinguished?
- Are species proxy data suitable to represent species distribution in an urban context?

## 3.2 METHODS

### 3.2.1 STUDY AREA

Hamburg, Germany's second largest city, is located in Northern Germany (53.55 °N, 10.0 °E, 6 m a.s.l), about 80 km from the North Sea and 70 km from the Baltic Sea (Figure 3.1). The climate is temperate and oceanic with a mean annual temperature of 9°C and an annual precipitation of 752 mm (data: German Meteorological Service (DWD) 2010; reference period 1971-2000). Schluenzen et al. (2010) determined a mean urban heat island of 1.1 K for the decade between 1988 and 1997. Hamburg has 1.8 million inhabitants and extends over an area of 755 km². Settlement and traffic areas cover 60 %. 8 % are water bodies – the river Elbe and the port (Europe's second largest seaport) are characteristic for Hamburg. The city covers also rural areas: It comprises 25 % agricultural and 6 % woodland areas (Federal Statistical Office of Germany 2011). Moreover, 8 % of the area is declared as nature reserves. Large areas of Hamburg comprise moraines of the second last glaciation (Saale glacial). The Elbe river valley dissects these moraines (Ehlers 1995). Here, holocene marshes developed after the last glaciation. During the past 1000 years, these marshes have been diked to obtain land for settlement and agriculture.

### 3.2.2 SPECIES AND SPECIES PROXY DATA

Floristic data were recorded over a period of 15 years between 1995 and 2009 by the Botanical Association of Hamburg (Botanischer Verein zu Hamburg e.V.). Presence-absence of all vascular plant species was mapped on a 1 km² grid. All grid cells were mapped repeatedly and at different times over the year (data set: Regionalstelle für Pflanzenartenschutz, Botanischer Verein zu Hamburg e.V. 2009). Altogether 1,643 plant species were registered in 861 grid cells (Poppendieck et al. 2010). In this study, we only included the 629 grid cells whose area is entirely within the borders of Hamburg.

To analyse only spontaneous vegetation, cultivated and ornamental species were excluded for this study. Furthermore, all species that are not naturalised, e.g. are not able to reproduce in the area (yet) and establish populations, were excluded. Species that only occurred in one or two grid cells were omitted, resulting in a final data set of 1,088 species. The average number of species per grid cell was 274 ± 60 (mean ± SD).

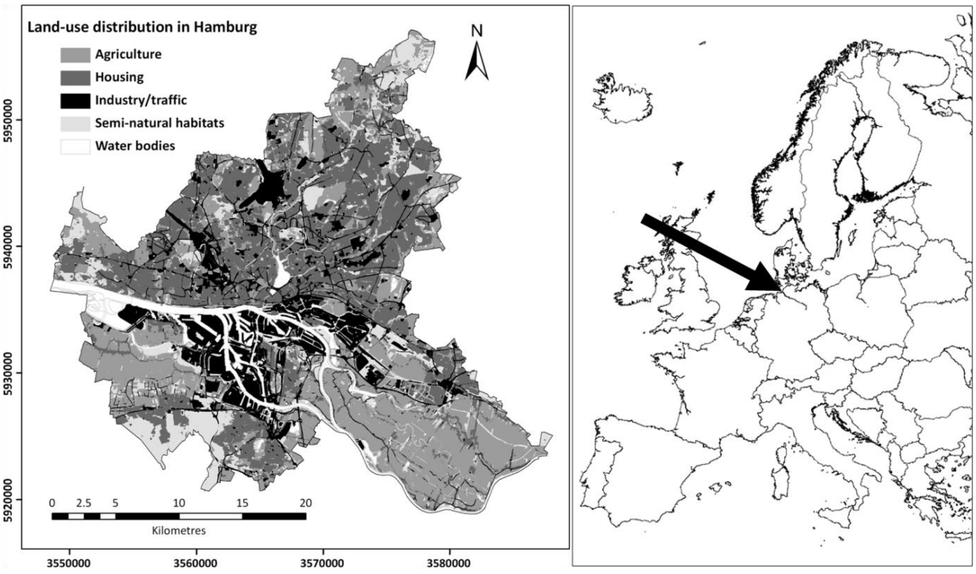

**Figure 3.1** Hamburg's location within Europe, main land-use distribution (data: Ministry for Urban Development and Environment of Hamburg (BSU) 2005; Gauss-Krueger 3 grid) and the river Elbe. Industry & traffic in the centre are mainly port related, former marshland (now agriculture) is located in the south-east and far south-west, semi-natural habitats are restricted to peripheral areas.

Beside presence-absence data of species composition (hereafter called species), we used three data sets of species proxies:

1) Genera: We calculated the number of species per genus and grid cell. Altogether 440 different genera were obtained.

2) Communities: We derived the affiliations of each species to a phytosociological class from the database BIOLFLOR (Klotz et al. 2002) and consequently calculated the percentage of species affiliated to a particular class per grid cell. Due to interdependency, the percentages were transferred into abundance classes from 0 (no occurrence) to 10 (over 10 %). The data contained many zero entries (16 %), hence, replacing them for compositional analysis is not advised (Martín-Fernández et al. 2003). Information on class affiliation was available for 898 species. Several species had more than one affiliation, adding up to 2887 entries for the 54 differentiated phytosociological classes (Appendix, Table A 3.1).

3) Traits: Using the BIOLFLOR database we assigned the traits strategy type (Competition-Stress-Ruderal; CSR; available for 877 species), life form (available for 918 species), life cycle (available for 916 species) and urbanity (available for 870 species) to the species set. Altogether, we analysed 25 trait variables (Appendix, Table A 3.2). We excluded five grid cells with species numbers lower than 100, because the available information on traits was too scarce. For each trait the proportions of species of the trait categories was calculated per grid cell. Again, we created compositional data and centred log-ratio transformations were applied using the R package "compositions" (van den Boogaart et al. 2013) to break the constraint that proportions add up to 100 % (Aitchison 1982, Martín-Fernández et al. 2003, Pawlowsky-Glahn and Egozcue 2006). Since we only had about 3 % of zero entries in the data, zero entries were replaced with the proportion one trait variable would have if only one species of all species of the respective a grid cell would have expressed that trait (following Knapp et al. 2008). The non-zero entries of that grid cell were reduced by the corresponding amount (Martín-Fernández et al. 2003, Knapp et al. 2008).

### 3.2.3 ENVIRONMENTAL DATA

Environmental data contained information on soil sealing, population density, climate, habitat type, soil, and Ellenberg indicator values (EIV) for light (EIL), temperature (EIT), continentality (EIC), moisture (EIM), reaction (EIR), and nutrients (EIN) (Ellenberg et al. 1992) (see Table 3.1 for detailed information). All data were calculated as information referring to the 1 km² grid (Gauss-Krueger 3 grid) of the floristic mapping using ArcGIS 9.3 software (ESRI Inc., Redlands, CA, USA).

Data on soil sealing was derived from a mapping of biotope types as classes of soil sealing ranging from 0 (hardly sealed) to 10 (mostly sealed) (data: Ministry for Urban Development and Environment of Hamburg (BSU) 2006). Climate data comprised mean annual temperature and annual precipitation for the reference period 1971-2000 (data: German Meteorological Service (DWD) 2010, as a digital map with spatially interpolated values). For soil sealing, climate and population density [inhabitants/ha] (data: Statistics Agency for Hamburg and Schleswig-Holstein 2009) weighted means per grid cell were calculated (weighted by area).

Habitat type data were derived from the biotope type mapping of Hamburg (data: Ministry for Urban Development and Environment of Hamburg (BSU) 2005). The original 370 biotope types were aggregated on the basis of a classification by Haeupler (2002), but by developing a more detailed classification of the urban and industrial habitats. We finally generated six classes: industry & traffic, high density housing, low density housing, semi-natural habitats, agriculture and water bodies. Here, the proportional areas of the respective classes of habitat type per grid cell were calculated in ArcGIS.

Soil data originally consisted of eight classes (data: Miehlich and Brandt 2010), but due to results from a Principal Component Analysis (PCA) we reduced these to the five most important classes.

Mean EIV were calculated for each grid cell based on species composition. EIV are ordinal numbers and therefore do not fulfil the requirements for calculating arithmetic means. Nevertheless, the use of average indicator values is widely applied in vegetation ecology (Diekmann 2003). Recently, difficulties of using mean EIV have been discussed by Zeleny and Schaffers (2012), but the authors also stated that “in most cases [of studies tested in a literature analysis], however, the potential bias was of only minor importance and did not influence interpretation of the results“.

### 3.2.4 STATISTICAL ANALYSES

#### SPECIES DISTRIBUTION AND SPECIES RICHNESS

To compare species distribution with the structure of Hamburg, we identified groups with similar species composition by conducting a hierarchical cluster analysis on presence-absence species data using Bray-Curtis dissimilarity index as distance measure and Ward’s minimum variance method for agglomerative clustering. The number of clusters to be calculated was assessed by applying the “cascadeKM” function in R (‘vegan’ package, Oksanen et al. 2012) using the simple structure index (ssi-criterion) to detect the best number of clusters. The results were displayed in ArcGis and visually related to city structure. Differences in species number per km² between the obtained clusters were tested with Welch-ANOVA (due to heterogeneity of variance in the data) followed by Games-Howell post-hoc test.

## SPECIES DISTRIBUTION & ENVIRONMENT

To identify the most influential environmental variables for plant species distribution, the impact of environmental variables on species composition was analysed by ordination techniques. We used species and species proxy data for genera, communities and traits as response matrices. Since the lengths of gradient obtained by Detrended Correspondence Analyses (DCA) in all four response data sets were rather short (<2 SD; Lepš and Šmilauer 2003) we conducted direct Redundancy Analyses (RDA) using the R-package 'vegan' (Oksanen et al. 2012). Initially, we included all environmental variables and ran a stepwise selection to identify the significant variables to be used in the final models (see Appendix, Table A 3.3 for significant variables and biplot scores). All variables were standardised (zero mean - unit variance) prior to analyses and correlations of variables with RDA-axes were calculated.

**Table 3.1** Descriptive statistics of environmental variables. Mean, standard deviation (SD) and minimum (Min) and maximum (Max) values are given (n=629).

| Variable | | Mean | SD | Min | Max |
|---|---|---|---|---|---|
| **Soil sealing** | [mean degree per grid cell] | 4.99 | ± 1.98 | 1.24 | 9.15 |
| **Population density [inhabitants/ha]** | | 32.00 | ± 36 | 0 | 180.00 |
| **Climate** | Annual precipitation [mm] | 748 | ± 35 | 667.50 | 821.00 |
| | Mean annual temperature [°C] | 9.2 | ± 0.2 | 8.65 | 9.70 |
| **Habitat type** [% of area per grid cell] | Industry & traffic | 15.28 | ± 19.56 | 0 | 99.44 |
| | High density housing | 16.32 | ± 20.40 | 0 | 82.00 |
| | Low density housing | 18.55 | ± 21.27 | 0 | 94.43 |
| | Semi-natural habitats | 9.96 | ± 14.07 | 0 | 92.81 |
| | Agriculture | 30.27 | ± 30.08 | 0 | 100 |
| | Water bodies | 8.17 | ± 14.37 | 0 | 74.93 |
| **Soil** [% of area per grid cell] | Artificial substrate | 14.63 | ± 30.89 | 0 | 100.00 |
| | Clay | 22.65 | ± 35.80 | 0 | 100.00 |
| | Fine sand | 0.34 | ± 2.87 | 0 | 38.17 |
| | Sand | 35.25 | ± 36.09 | 0 | 100.00 |
| | Silt | 13.90 | ± 23.32 | 0 | 100.00 |
| **EIV** | Light | 6.84 | ± 0.20 | 6.16 | 7.31 |
| | Temperature | 5.67 | ± 0.10 | 5.27 | 5.92 |
| | Continentality | 3.84 | ± 0.15 | 3.42 | 4.50 |
| | Moisture | 5.88 | ± 0.56 | 4.82 | 7.68 |
| | Reaction | 6.21 | ± 0.27 | 4.80 | 7.50 |
| | Nutrients | 5.76 | ± 0.22 | 4.66 | 6.50 |

## SPECIES DISTRIBUTION, ENVIRONMENT AND MEASURES OF SPATIAL STRUCTURE

Preliminary analyses using simple distance measures (distance to city centre and river Elbe) showed that these variables failed to represent the complex spatial structure in our data. Hence, more elaborate methods were needed. To account for complex spatial structure, we applied multivariate spatial analyses (following Dray et al. 2012) using Moran's eigenvector maps (MEM, an eigenvector decomposition of a connectivity map; Dray et al. 2006) as variables representing the spatial structure of our data sets. This method is an extension of the approach of principal coordinate analysis of neighbour matrices (PCNM; Borcard and Legendre 2002). The spatial relationships among the sampling site's coordinates are translated into explanatory variables that can be directly used in regression or canonical analyses and represent spatial effects at different scales (Dray et al. 2006, Peres-Neto and Legendre 2010).

Following Dray et al. (2012), we chose a simple distance based matrix as a spatial weighting matrix, where cells with shared borders and corners counted as neighbours (queen's connection; see Legendre (1998) for other matrix types). We used this rather simple approach, because the floristic sampling was conducted on a regular rectangular grid (Legendre 1998). We calculated the matrix with the R-package 'spdep' (Bivand et al. 2012). From this matrix we calculated MEMs with the "scores.listw" function of the R-package 'spacemakeR' (Dray 2010), and tested their significance of Moran's I (measure of spatial autocorrelation). Then, we conducted RDAs with species and species proxy data as response matrices and all significant MEMs (MEM+ representing broad scale and MEM- representing fine scale spatial correlations) as explanatory matrices, where the significant MEMs were subjected to a forward selection procedure (Blanchet et al. 2008) using the package 'packfor' (Dray et al. 2011). Thus, we obtained MEM+ and MEM- for the species (105 MEM+, 4 MEM-), genera (70, 7), community (60, 2) and traits (51, 2) data sets.

To differentiate between the explanatory power of environmental variables and complex spatial structure, we conducted variation partitioning with three explanatory matrices: environmental data (ENV, significant variables only), MEM+ and MEM-. We obtained seven single and shared fractions of variation explained, which were presented in stacked bar diagrams. The effects of the single fractions were tested for significance with permutation tests ("anova.cca" function; package 'vegan').

All statistical analyses were conducted with R (R development core team 2012) except Welch-ANOVA, which was performed using SPSS (PASW Statistics 18, Version 18.0.0). Figures were created with ArcGis 9.3., Sigmaplot 12.0 (Systat Software, Inc. 2011), CANOCO (Ter Braak & Šmilauer 1997) and GIMP 2.6.8 (The GIMP Development Team 2008).

## 3.3 RESULTS

### SPECIES COMPOSITION AND SPECIES RICHNESS

Cluster analysis of species data revealed seven clusters. The dendrogram showed a division between the clusters 1, 2, 3 and the clusters 4, 5, 7 (Figure 3.2). Cluster 6 was separated from all other clusters. The distribution of the clusters displayed a distinct spatial pattern for Hamburg (Figure 3.3). The species distribution pattern reflected the structure of Hamburg: Based on their spatial location we referred to the clusters as 1) City (comprising 113 grid cells), 2) Settlement & forest (195), 3) Semi-natural (51), 4) Former marshland (122), 5) Settlement & agriculture (85), 6) Port & river (27) and 7) Urban & industry (36). Of the 1088 species investigated, all seven clusters had 533 plant species in common. 23 species were restricted to grid cells of only one cluster, of which 13 species occurred solely in the cluster 'Semi-natural' (Table 3.2). Mean species numbers per grid cell differed significantly between clusters (F=47.8***; Table 3.2). The cluster 'Urban & industry' was richest in species (352 ± 43 species), followed by 'Semi-natural' (320 ± 50). The cluster 'River & industry" had the lowest (180 ± 73) and 'Former marshland' the second lowest species numbers (242 ± 40 species).

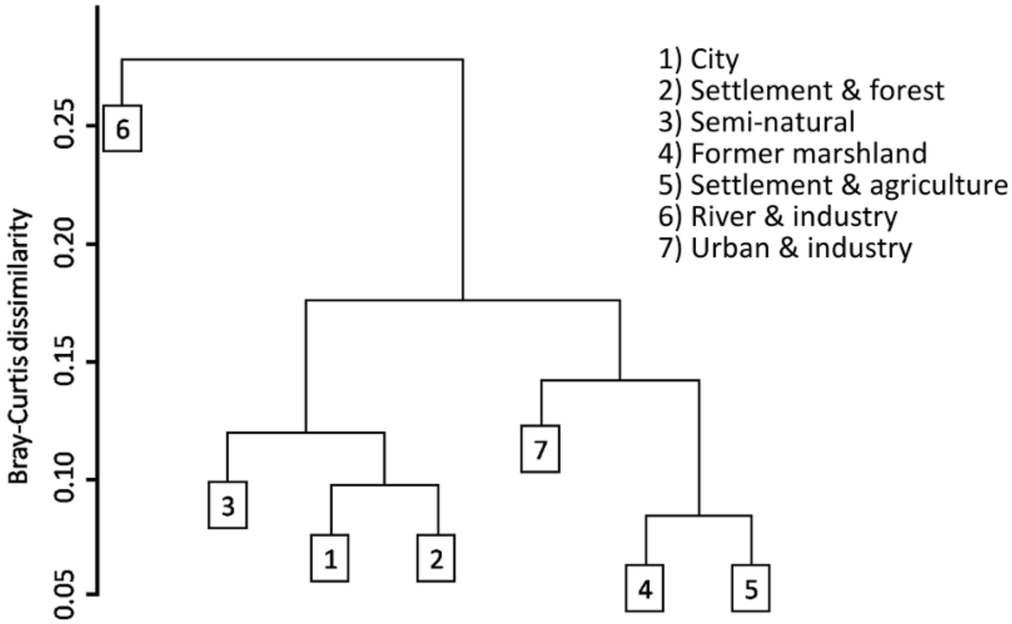

**Figure 3.2** Dendrogram of the seven clusters revealed by cluster analysis of plant species composition (presence/absence data) in Hamburg, using Bray-Curtis dissimilarity index as distance measure and Ward's minimum variance method for agglomerative clustering (n=629).

**Table 3.2** Species numbers of the seven clusters. Descriptive statistics including mean and standard deviation (SD), minimum (Min) and maximum (Max) values are given. Different letters show significant differences in species numbers between clusters. Numbers of species exclusively occurring in the respective cluster and number of grid cells per cluster are shown.

| Cluster | Mean ± SD | | Number of Species<br>Min | Max | Exclusive | Number of grid cells |
|---|---|---|---|---|---|---|
| 1) City | 276 ± 57 | ab | 176 | 458 | 0 | 113 |
| 2) Settlement & forest | 271 ± 44 | b | 180 | 405 | 2 | 195 |
| 3) Semi-natural | 320 ± 50 | c | 190 | 458 | 13 | 51 |
| 4) Former Marshland | 242 ± 40 | d | 132 | 346 | 5 | 122 |
| 5) Settlement & agriculture | 293 ± 55 | ac | 189 | 447 | 1 | 85 |
| 6) River & industry | 180 ± 73 | e | 9 | 317 | 0 | 27 |
| 7) Urban & industry | 352 ± 43 | f | 254 | 418 | 2 | 36 |

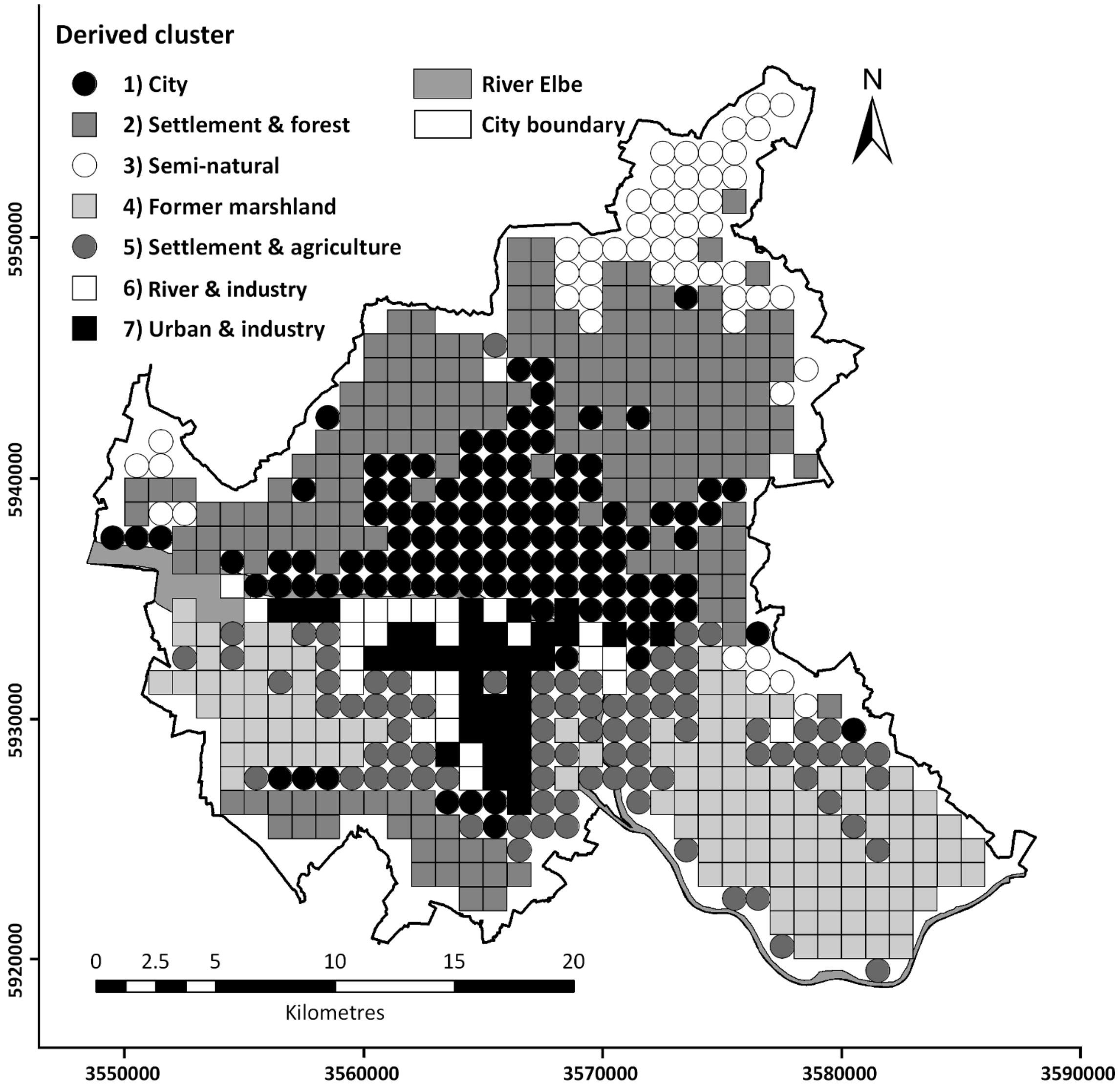

**Figure 3.3** Spatial distribution of the assignment of grid cells to seven clusters revealed by cluster analysis of plant species composition (presence/absence data, n=629). The size of the grid cells is 1 km² (Gauss-Krueger 3). According to their spatial location in the city of Hamburg the clusters were referred to as 1) City, 2) Settlement & forest, 3) Semi-natural, 4) Former marshland, 5) Settlement & agriculture, 6) River & industry and 7) Urban & industry.

## SPECIES DISTRIBUTION & ENVIRONMENT

In the calculated RDAs, the amount of variation explained by the considered environmental variables increased in the RDAs from species (23 %) and genera (35 %) to traits (60 %) and community (61 %) data (Table 3.3). 'Low density housing' was the only variable that was not significant in any analysis. The number of significant variables ranged from 16 (traits), 17 (communities) to 19 (genera) and 20 (species) (Appendix, Table A 3.3).

The first RDA-axes were strongly correlated with EIM, soil sealing, and agriculture (except for traits), separating species and species proxies characteristic for the urban core (urbanophilic species, short-lived species, dry habitats) from those of semi-natural sites (urbanophobic species, long-lived species, moist sites) (Table A 3.3, Figure 3.4, RDA-graphs from other species data not shown). The second axes were strongly correlated with temperature (mean annual temperature, EIT, and EIC) and light (EIL), further to precipitation and reaction (EIR). Here, species and species proxies of open and rather warm habitats were separated from forest and shrub dominated habitats. The third axis was correlated with EIN in all RDAs analyses.

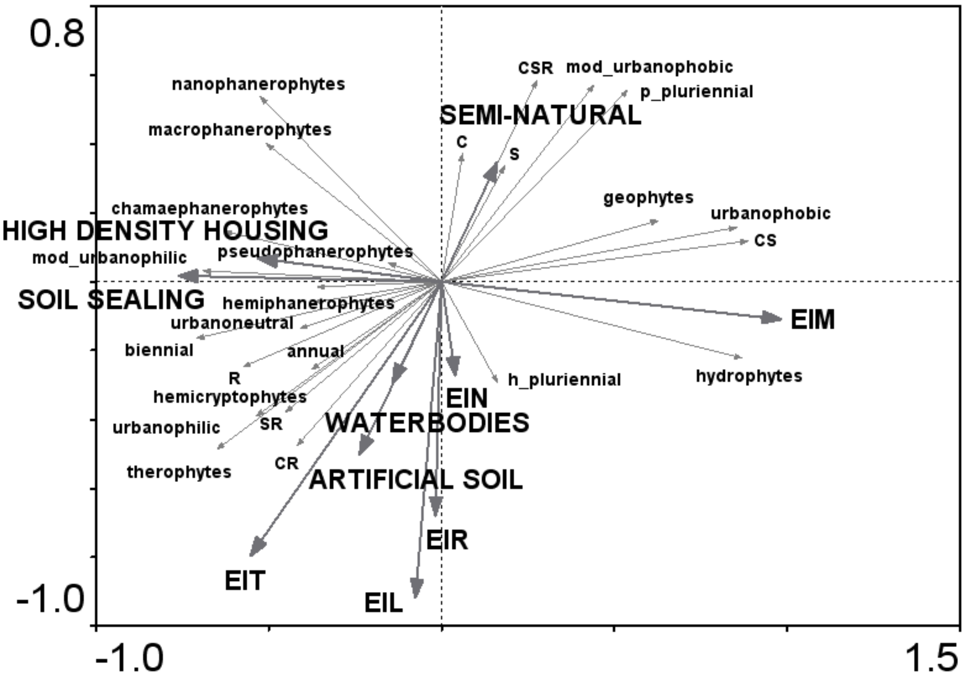

**Figure 3.4** RDA with traits as species proxies and environmental variables. For clarity, only ten environmental variables are shown (n=624). Abbreviations environmental variables: Artificial soil = proportion of artificial substrate, semi-natural = proportion of semi-natural habitats, waterbodies = proportion of waterbodies, high density housing = proportion of high density housing, EIL = Ellenberg indicator value (EIV) for light, EIT = EIV for temperature, EIM = EIV for moisture, EIR = EIV for reaction, EIN = EIV for nutrients. Abbreviations traits: h_pluriennial = hapaxanthic, p_pluriennial = pollakanthic, mod. = moderately, CSR correspond to Grime's strategy types. For descriptive statistics of the actual proportions of the trait groups see Table A 3.2.

### SPECIES DISTRIBUTION, ENVIRONMENT AND SPATIAL STRUCTURE

In variation partitioning including all significant environmental variables and MEMs, the highest total variation was explained in the RDAs of communities and traits (63 %) and the least in the RDAs of species (28 %) (Table 3.3, Figure 3.5). The percentage of explained variation was increased in all four analyses compared to the RDAs not considering MEMs. Generally, MEM- did not explain a considerable amount of variation; neither did all three matrices together. The effects of all single fractions on the response data were significant (Table 3.4). In all four analyses, most variation was explained by ENV and MEM+ in combination. In species and genera, single MEM+ contributed more to the explained variation in total than in communities and traits. Single ENV explained more variation in communities and traits than in species and genera.

**Table 3.3** Explained variance [%] by two methods of Redundancy analysis (RDA) of species, genera, communities and traits data (n=629, except for traits data: n=625). 1) **ENV**: RDAs using significant environmental variables as explanatory matrix. 2) **ENV + MEM**: Serial RDAs applying variation partitioning using environmental variables (ENV) and Moran's eigenvector maps (MEM) as explanatory matrices.

| RDA method | Species | Genera | Communities | Traits |
|---|---|---|---|---|
| 1) ENV | 22.82 | 35.18 | 60.51 | 60.18 |
| 2) ENV + MEM | 27.71 | 40.5 | 62.94 | 63.17 |

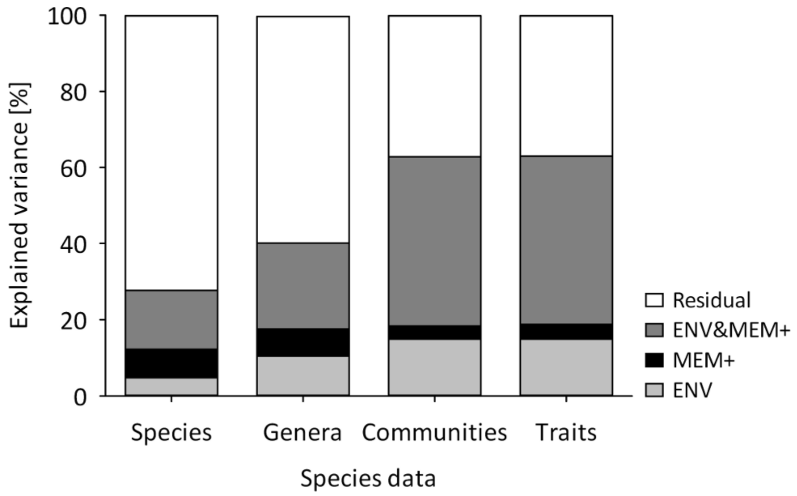

**Figure 3.5** Variation partitioning of species, genera, communities and traits data as response variables with environmental and spatial structure matrices as explanatory variables. Stacked bar diagrams show the proportions of variance [%] explained by environment (ENV; all significant environmental variables), by positively spatially correlated Moran's eigenvector maps (MEM+), by both (ENV & MEM+) and residual (unexplained) variance. Due to little explained variance MEM- (negatively spatially correlated Moran's eigenvector maps) and MEM- combinations as well as the combination of ENV, MEM+ and MEM- are not shown.

**Table 3.4** Permutation tests of the explanatory variables' single fractions from variation partitioning with species and the species proxies genera, communities and traits as response data (n=629, except for traits data: n=625) and environmental and spatial variables (Moran's eigenvector maps, MEM): ENV (significant environmental variables), MEM+ (positively spatially correlated) and MEM- (negatively spatially correlated) as explanatory matrices. F-values and p-values (**=p<0.01) are given.

| **Response data** | **Fractions** | | |
|---|---|---|---|
| | **ENV** | **MEM+** | **MEM-** |
| Species | 2.74** | 1.59** | 1.23** |
| Genera | 6.10** | 2.03** | 1.45** |
| Communities | 14.41** | 1.94** | 1.77** |
| Traits | 15.45** | 2.25** | 2.54** |

## 3.4 DISCUSSION

### SPECIES COMPOSITION AND SPECIES RICHNESS

We showed that plant species distribution clearly reflected the city's structure. Hamburg's geography was almost exactly matched by the results of the cluster analysis: This finding is in good agreement with Kent et al. (1999), who detected urban structure patterns reflected in the flora of Plymouth (U.K.) on the same scale of 1 km². The match is remarkable regarding the meso-scale of the floristic mapping and the fact that nearly half of the analysed species occurred in grid cells of all clusters. Hence, the remaining species obviously accounted for incisive differences between the grid cells.

The cluster analysis separated the grid cells first into two main groups representing the major landscape types formed during glacial periods (marshlands of the Elbe river and moraines; see Ehlers 1995) and then into further groups representing different degrees of urbanisation and historical landscape development based on hydrological and edaphic conditions. Furthermore, the river Elbe has been shown to influence the ambient temperature of its surrounding (Schluenzen et al. 2010), resulting in milder conditions that might also influence species composition. The further division of the grid cells can be attributed to differences in population density, soil sealing and land-use. The clusters 'Urban & industry' and 'Semi-natural' exhibited by far the highest species richness: This corresponds both to the generally high plant species richness in urban habitats due to habitat heterogeneity, geological diversity and anthropogenic disturbance (Kuehn et al. 2004, Muratet et al. 2007, Schmidt et al. 2013) and the high species richness of European semi-natural habitats (Wilson et al. 2012).

### SPECIES DISTRIBUTION & ENVIRONMENT

The most influential environmental variables for plant species distribution represented both historical environmental conditions and urbanisation. In all RDAs, the first axis represented an urbanisation gradient ranging from central sealed, dry and warm conditions to peripheral less sealed, moist and colder conditions. Urban habitat characteristics like higher temperature and drier soil favouring R-strategists with a short lifespan were also demonstrated by Prach et al. (2001) and Knapp et al. (2008). The second axis could be related to a turn-over from habitats under influence of the river valley to moraine habitats distant to the river, further representing a gradient from open to shaded habitats. At the one end, the gradient was characterised by high EIL, EIC and low precipitation, indicating open habitats of milder climate. The higher EIC might result from the occurrence of river corridor plants along the river Elbe originating from more continental climate zones (Burkart 2001) or relate to conditions in settlement areas (Lososová et al. 2006). EIV have repeatedly been shown to be associated with urbanisation: Cities had higher values than their surroundings in all EIV except EIM (Wittig and Durwen 1982, Chocholoušková and Pyšek 2003) and the urban heat island (UHI) was strongly correlated with EIT in Hamburg (Bechtel and Schmidt 2011). At the other end of the gradient, long-living species and species proxies affiliated with colder and shaded (forest) habitats distant to the river occurred, which is in accordance with Prach et al. (2001).

### SPECIES DISTRIBUTION, ENVIRONMENT AND SPATIAL STRUCTURE

Both spatial structure and environmental conditions affected species composition, but spatially structured environmental conditions had the largest impact, and could hence not be distinguished completely. Variance explained by the shared fraction of ENV and MEM+ was largest in all analyses, indicating induced spatial dependence (Dray et al. 2006, Gravel et al. 2008, Dray et al. 2012). This shared fraction could represent the history of urban development in Hamburg in consequence of historical environmental conditions. In Hamburg, soil developed under glacial influence and although it has been strongly altered by urbanisation, glacial patterns are still reflected in species distribution. The river Elbe had a certain impact on its surroundings leading to moist soils that have been more suitable for agriculture than for settlement. In turn, urbanisation alters environmental conditions over time. Hence, species occurrence is shaped by both environmental conditions and urban development.

Variance explained by the fraction of spatially structured environment is large in comparison with a meso-scale study of Petřík and Wild (2006) in a mountain range, but small in comparison with results of Dainese and Poldini (2012). However, both studies were not conducted predominantly in urban areas. In community and traits analyses, the single environmental fraction explained a much greater proportion of variance than the single spatial fraction. Direct environmental factors might thus be more important than historical processes for the distribution of species' proxies in cities (see discussion below). Nevertheless, the spatial fraction alone explained a large amount of variation in species and genera, indicating that historical urbanisation processes may have led to the structure of present species communities. On the contrary, Sattler et al. (2010) found a near absence of spatial structure for animal species in urban areas. They suggest that anthropogenic disturbances play a major role in urban habitats and overlay spatially structured environmental variables and biotic processes. We argue that the impact of spatial structure is scale dependent: Sattler et al. (2010) investigated only select green area habitats, whereas our study scale included all habitat types and represented the entire city of Hamburg.

Fine scale processes represented by MEM- did not influence species and species proxy composition in Hamburg. This finding might be simply caused by the broad scale of the floristic mapping and the use of presence-absence data. Fine scale structures are often related to small scale community processes such as dispersal, predator-prey interactions or competition (Borcard et al. 2004, Hájek et al. 2011, Dray et al. 2012). Hence, insights into small scale spatial structures on a 1 km² meso-scale are not likely to detect.

## SUITABILITY OF SPECIES PROXIES

We found species proxy data to be very suitable to represent species distribution in an urban context. Explained variance increased from 23 % in species data to 61 % in species proxy data. Our study reinforces the statement of Thompson and McCarthy (2008) that the analysis of traits can reveal important patterns in vegetation that cannot be derived from purely floristic analyses. Moreover, we showed that the affiliation to phytosociological classes is a reasonable proxy variable for species composition, being not directly related to species traits. Long-term changes in frequencies of phytosociological class affiliation have been successfully used to detect urbanisation and management effects (Pyšek et al. 2004, Catorci et al. 2011).

Contrary to the results of the cluster analysis, in RDA analyses species distribution itself is not very useful to explain patterns in an entire city. In studies dealing with select urban habitats, however, species composition could be much better explained by environmental variables (Godefroid et al. 2007, Vallet et al. 2008, Lososová et al. 2011). When accounting for complex spatial structure using MEMs, only in the community and trait data the single environmental fraction explained a substantial amount of variation. Species proxies might be under less direct spatial impact and thus be better explained by environmental variables, because variability in group composition is lower than at species level. Furthermore, community and trait data are almost independent from rare species that cause a lot of zero entries in large species data matrices. Another reason is that traits also represent species' adaptation to their environment. However, the environmental variables might have also been too broadly scaled to reveal effects on species composition.

### 3.4.1 CONCLUSIONS

Generally, plant species distribution on the analysed meso-scale was primarily affected by historical landscape and urbanisation. Hamburg's central port area and semi-natural habitats had the highest species richness. Especially in the port area, where several dry grassland and wasteland sites contribute to high plant species richness, conservation measures should include the designation of new reserves as well as temporary conservation approaches to maintain disturbance regimes (e.g. Kattwinkel et al. 2011). The semi-natural areas should be protected from further urbanisation.

Spatially structured environmental conditions explained most variation in species composition, species and genera were more affected by spatial structure alone than communities and traits. Overall, we conclude that the combination of species proxy data with advanced multivariate analyses accounting for complex spatial pattern is a promising avenue for further research on the distribution of biodiversity in urban systems. Moreover, results obtained using species proxy data can be easily compared between cities. Even if the actual species composition is different between cities from different geographic regions, traits are still comparable and e.g. the endangerment or vulnerability of species and communities can be assessed by analysing traits (e.g. Duncan et al. 2011).

## 3.5 ACKNOWLEDGEMENTS

We are grateful to the Botanischer Verein zu Hamburg e.V. and the Regionalstelle für Pflanzenartenschutz for providing the extensive data set on plant species distribution and all volunteers who contributed to mapping the flora of Hamburg. We also wish to thank G. Miehlich & I. Brandt, the German Meteorological Service (DWD), the Ministry for Urban Development and Environment of Hamburg (BSU), and the Statistics Agency for Hamburg and Schleswig-Holstein for the provision of data on predictors. K. J. Schmidt thanks the School of Integrated Climate System Science (SICSS) for organisational support. The work was funded by the Federal Ministry for Education and Research within the research project KLIMZUG-NORD (grant number 01LR0805D).

## 3.6 APPENDIX

**Table A 3.1** Descriptive statistics of phytosociological class affiliation of the species per grid cell (629 grid cells considered). Mean, standard deviation (SD), minimum (Min) and maximum (Max) values [%] of the proportion of species affiliated to a particular phytosociological class are given.

| Communities of | Community | Mean | SD | Min | Max |
|---|---|---|---|---|---|
| **Freshwaters, river banks, springs and silted areas** | *Lemnetea minoris* | 0.26 | ±0.28 | 0.00 | 1.31 |
| | *Potamogetonetea pectinati* | 0.55 | ±0.56 | 0.00 | 3.61 |
| | *Utricularieta intermedio-minoris* | 0.01 | ±0.02 | 0.00 | 0.27 |
| | *Isoeto-Littorelletea uniflorae* | 0.19 | ±0.18 | 0.00 | 0.95 |
| | *Montio-Cardaminetea* | 0.23 | ±0.17 | 0.00 | 0.93 |
| | *Phragmito-Magnocaricetea* | 2.97 | ±1.63 | 0.11 | 8.56 |
| **Swamps, fens and bogs** | *Isoeto-Nanojuncetea bufonii* | 0.61 | ±0.21 | 0.00 | 1.43 |
| | *Scheuchzerio-Caricetea nigrae* | 0.56 | ±0.51 | 0.00 | 3.12 |
| | *Oxycocco-Sphagnetea* | 0.07 | ±0.13 | 0.00 | 1.22 |
| **Brackish and salt marshes** | *Spartinetea maritimae* | 0.01 | ±0.03 | 0.00 | 0.22 |
| | *Ruppietea maritimae* | 0.01 | ±0.04 | 0.00 | 0.34 |
| | *Thero-Salicornietea* | 0.01 | ±0.03 | 0.00 | 0.15 |
| | *Saginetea maritimae* | 0.01 | ±0.03 | 0.00 | 0.15 |
| | *Asteretea tripolii* | 0.61 | ±0.15 | 0.00 | 1.18 |
| **Pioneer rock vegetation** | *Asplenietea trichomanis* | 0.48 | ±0.22 | 0.00 | 1.27 |
| | *Parietarietea judaicae* | 0.33 | ±0.14 | 0.00 | 0.89 |
| | *Thlaspietea rotundifolii* | 0.41 | ±0.18 | 0.00 | 1.08 |
| | *Violetea calaminariae* | 0.52 | ±0.13 | 0.00 | 1.39 |
| **Dune, meadow, dry and poor grassland** | *Ammophiletea arenariae* | 0.35 | ±0.13 | 0.00 | 0.92 |
| | *Koelerio-Corynephoretea* | 2.65 | ±0.80 | 0.85 | 5.41 |
| | *Festuco-Brometea* | 2.95 | ±0.60 | 1.29 | 6.12 |
| | *Molinio-Arrhenatheretea* | 8.26 | ±1.01 | 6.26 | 13.99 |
| | *Agrostietea stoloniferae* | 4.69 | ±0.70 | 3.02 | 9.19 |
| | *Nardetea strictae* | 1.39 | ±0.43 | 0.60 | 3.53 |
| | *Seslerietea albicantis* | 0.05 | ±0.06 | 0.00 | 0.33 |
| **Ruderal and arable weeds** | *Cakiletea maritimae* | 0.14 | ±0.10 | 0.00 | 0.70 |
| | *Bidentetea tripartitae* | 2.03 | ±0.57 | 0.00 | 4.53 |
| | *Polygono arenastri-Poetea annuae* | 2.29 | ±0.44 | 0.80 | 5.26 |
| | *Sisymbrietea officinalis* | 7.01 | ±1.75 | 1.95 | 12.48 |
| | *Artemisietea vulgaris* | 6.64 | ±1.23 | 2.44 | 10.62 |
| | *Stellarietea mediae* | 7.13 | ±1.46 | 2.21 | 11.92 |
| **Shrubs and herbs adjacent to forests** | *Trifolio-Geranietea sanguinei* | 1.31 | ±0.32 | 0.44 | 2.63 |
| | *Stellario nemorum-Geranietea sylvatici* | 1.30 | ±0.33 | 0.00 | 2.63 |
| | *Melampyro-Holcetea mollis* | 0.66 | ±0.23 | 0.00 | 1.76 |
| | *Epilobietea angustifolii* | 4.79 | ±0.53 | 3.26 | 6.76 |
| | *Galio-Urticetea dioicae* | 5.79 | ±0.62 | 3.50 | 9.08 |
| **Dwarf shrubs** | *Rhododendro hirsurti-Ericetea carneae* | 0.08 | ±0.09 | 0.00 | 0.34 |
| | *Loiseleurio-Vaccinietea* | 0.02 | ±0.05 | 0.00 | 0.27 |
| | *Salicetea herbaceae* | 0.08 | ±0.06 | 0.00 | 0.27 |
| | *Calluno-Ulicetea* | 0.83 | ±0.38 | 0.00 | 3.12 |
| **Shrubberies and hedges** | *Betulo carpaticae-Alnetea viridis* | 0.64 | ±0.25 | 0.00 | 1.59 |
| | *Franguletea* | 1.69 | ±0.45 | 0.44 | 3.38 |
| | *Carici-Salicetea cinereae* | 2.66 | ±0.75 | 1.11 | 5.19 |
| | *Salicetea purpureae* | 2.11 | ±0.51 | 0.74 | 4.84 |
| | *Rhamno-Prunetea spinosae* | 7.24 | ±1.38 | 3.30 | 10.75 |
| **Forests and woods** | *Alnetea glutinosae* | 3.13 | ±0.94 | 1.10 | 5.95 |
| | *Carpino-Fagetea* | 7.56 | ±1.60 | 2.79 | 12.95 |
| | *Quercetea robori-petraeae* | 2.07 | ±0.69 | 0.51 | 4.79 |
| | *Quercetea pubescentis-petraeae* | 2.03 | ±0.57 | 0.41 | 3.44 |
| | *Pulsatillo-Pinetea sylvestris* | 0.35 | ±0.17 | 0.00 | 1.06 |
| | *Erico-Pinetea* | 0.75 | ±0.30 | 0.00 | 2.63 |
| | *Vaccinio-Piceetea* | 0.92 | ±0.46 | 0.00 | 2.97 |
| | *Vaccinio uliginosi-Pinetea* | 0.60 | ±0.32 | 0.00 | 2.17 |

**Table A 3.2** Descriptive statistics of trait frequency per grid cell (625 grid cells considered). Mean, standard deviation, minimum and maximum values are given. Abbreviations are: Pluriennial_H = pluriennial-hapaxanthic, Pluriennial_P = pluriennial-pollakanthic, mod. = moderately.

| Trait | Subgroup | Mean | SD | Min | Max |
|---|---|---|---|---|---|
| **CSR –strategy** | C | 38.58 | ± 3.86 | 27.17 | 52.23 |
| (**C**ompetition- | CR | 16.19 | ± 3.48 | 6.92 | 28.36 |
| **S**tress- | CS | 13.52 | ± 4.90 | 3.83 | 32.08 |
| **R**uderal) | CSR | 17.94 | ± 2.55 | 10.99 | 26.71 |
| | R | 10.70 | ± 2.67 | 1.54 | 17.24 |
| | S | 0.71 | ± 0.56 | 0.00 | 4.40 |
| | SR | 2.36 | ± 1.43 | 0.00 | 8.57 |
| **Life cycle** | Annual | 25.43 | ± 5.13 | 9.47 | 42.57 |
| | Biennial | 7.88 | ± 2.11 | 2.52 | 13.93 |
| | Pluriennial_H | 1.81 | ± 0.75 | 0.00 | 4.20 |
| | Pluriennial_P | 64.89 | ± 7.04 | 45.95 | 84.46 |
| **Life form** | Hydrophyte | 3.92 | ± 3.37 | 0.00 | 17.10 |
| | Chamaephyte | 2.82 | ± 0.70 | 0.97 | 4.80 |
| | Geophyte | 9.35 | ± 2.11 | 4.88 | 16.67 |
| | Hemicryptophyte | 46.69 | ± 2.18 | 40.00 | 54.24 |
| | Macrophanerophyte | 8.68 | ± 2.12 | 0.56 | 14.34 |
| | Nanophanerophyte | 6.52 | ± 2.11 | 0.00 | 13.15 |
| | Pseudophanerophyte | 0.75 | ± 0.34 | 0.00 | 1.95 |
| | Hemiphanerophyte | 0.61 | ± 0.37 | 0.00 | 3.19 |
| | Therophyte | 20.66 | ± 4.32 | 7.29 | 34.46 |
| **Urbanity** | Urbanophobic | 12.42 | ± 6.06 | 2.53 | 40.63 |
| | Mod. urbanophobic | 38.92 | ± 3.61 | 26.98 | 48.78 |
| | Urbanoneutral | 40.92 | ± 5.92 | 18.70 | 59.40 |
| | Mod. urbanophilic | 6.97 | ± 2.15 | 1.25 | 13.95 |
| | Urbanophilic | 0.74 | ± 0.73 | 0.00 | 3.41 |

**Table A 3.3** Redundancy analyses (RDA) biplot scores resulting from RDAs of species/species proxies and environmental variables. Only biplot scores of significant environmental variables are shown and were included in the models.

| | **Species** | | | **Genera** | | | **Communities** | | | **Traits** | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Environmental variable** | **RDA1** | **RDA2** | **RDA3** | **RDA1** | **RDA2** | **RDA3** | **RDA1** | **RDA2** | **RDA3** | **RDA1** | **RDA2** | **RDA3** |
| Soil sealing | -0.78 | -0.11 | 0.11 | -0.74 | 0.16 | 0.11 | -0.74 | -0.15 | -0.01 | -0.76 | -0.02 | -0.19 |
| Population density | -0.58 | 0.06 | 0.14 | -0.49 | 0.26 | 0.01 | | | | | | |
| Annual precipitation | -0.55 | 0.63 | -0.14 | -0.26 | 0.77 | 0.07 | -0.52 | 0.52 | -0.25 | -0.36 | -0.61 | 0.02 |
| Mean annual temperature | -0.20 | -0.78 | -0.04 | -0.38 | -0.63 | 0.30 | -0.16 | -0.72 | 0.14 | -0.35 | 0.66 | -0.02 |
| Industry & traffic | -0.38 | -0.51 | -0.20 | -0.45 | -0.32 | 0.35 | -0.39 | -0.39 | 0.37 | -0.48 | 0.43 | 0.28 |
| High density housing | -0.53 | -0.01 | 0.24 | -0.51 | 0.16 | -0.08 | | | | -0.53 | -0.07 | -0.32 |
| Low density housing | | | | | | | | | | | | |
| Semi natural habitats | 0.07 | 0.38 | -0.36 | 0.25 | 0.37 | 0.14 | 0.01 | 0.51 | 0.19 | 0.16 | -0.33 | 0.54 |
| Agriculture | 0.76 | -0.04 | 0.16 | 0.63 | -0.32 | -0.28 | 0.76 | -0.05 | -0.02 | | | |
| Waterbodies | -0.03 | -0.44 | -0.20 | -0.12 | -0.35 | 0.32 | -0.05 | -0.39 | 0.01 | -0.14 | 0.30 | 0.32 |
| Artificial substrate | -0.09 | -0.58 | -0.25 | -0.20 | -0.47 | 0.36 | -0.12 | -0.45 | 0.30 | -0.24 | 0.51 | 0.42 |
| Clay | 0.62 | -0.38 | 0.19 | 0.38 | -0.59 | -0.18 | 0.63 | -0.35 | 0.05 | 0.52 | 0.44 | -0.18 |
| Finesand | -0.02 | 0.12 | -0.01 | | | | | | | 0.01 | -0.12 | -0.02 |
| Sand | -0.42 | 0.61 | 0.05 | -0.18 | 0.68 | -0.12 | -0.42 | 0.52 | -0.11 | | | |
| Silt | -0.35 | 0.29 | 0.06 | -0.22 | 0.39 | -0.01 | -0.31 | 0.17 | -0.30 | | | |
| EIL | 0.14 | -0.94 | -0.11 | -0.12 | -0.89 | 0.33 | 0.16 | -0.82 | 0.49 | -0.07 | 0.91 | 0.16 |
| EIT | -0.40 | -0.83 | -0.16 | -0.52 | -0.57 | 0.52 | -0.31 | -0.84 | 0.22 | -0.55 | 0.79 | -0.04 |
| EIC | 0.34 | -0.80 | -0.06 | 0.05 | -0.87 | 0.16 | 0.34 | -0.73 | 0.14 | 0.16 | 0.83 | 0.06 |
| EIM | 0.97 | 0.11 | -0.03 | 0.91 | -0.26 | -0.25 | 0.98 | 0.13 | -0.08 | 0.98 | 0.11 | -0.05 |
| EIR | 0.08 | -0.68 | 0.28 | -0.23 | -0.71 | -0.05 | 0.14 | -0.85 | -0.43 | -0.02 | 0.66 | -0.54 |
| EIN | 0.07 | -0.25 | 0.71 | -0.26 | -0.38 | -0.56 | 0.11 | -0.51 | -0.80 | 0.04 | 0.25 | -0.86 |

# 4 FLORISTIC MAPPING DATA AS A PROXY FOR THE MEAN URBAN HEAT ISLAND

Benjamin Bechtel & Katharina J. Schmidt

Published 2011 in *Climate Research* 49: 45-58. doi: 10.3354/cr01009

**KEYWORDS**
Floristic mapping * Urban heat island * Ellenberg indicator values * UHI predictors * Local climate zones * Infrared thermography

## 4.1 INTRODUCTION

The urban heat island (UHI) is the 'most obvious manifestation of urbanisation' (Landsberg 1981) and remains the most intensively studied climatic feature of cities (Oke 1973, Oke 1988, Souch and Grimmond 2006). The intensity of the UHI is usually defined as urban–rural air temperature difference, although the meanings of the terms urban and rural are somewhat blurred (Stewart and Oke 2009). Published case studies cover a variety of towns, cities and metropolitan agglomerations on almost all continents, very different spatiotemporal scales and a broad methodological spectrum. Therefore, the UHI has been measured and analysed for virtually any period between a single night and a full century, which makes general conclusions difficult. Frequently used methodological approaches to characterise the UHI are comprised of measurements from meteorological stations and mobile sensors, numerical and physical modelling, and aerial and satellite remote sensing. Each of them has advantages and limitations in terms of coverage, spatial and temporal resolution as well as representativeness and accuracy. However, these studies suggest that observed air temperature differences between urban and rural areas as well as within cities depend on numerous factors and processes (e.g. Lowry 1977, Oke 1988, Matzarakis 2001, Souch and Grimmond 2006, Hart and Sailor 2009), which are partially indicated in the conceptual overview in Figure 4.1.

Considering climate change and the likely increase of summer heat waves, the UHI, which can have human health and thermal comfort consequences (Hart and Sailor 2009), will gain further importance, even in a maritime climate. More detailed knowledge about the impact of different urban morphologies on mean air temperature would help to adapt urban infrastructures to climate change-related risks in time. However, the frequent lack of long-term UHI data severely limits such analysis.

We therefore examined a new proxy dataset, which has potential to indicate the mean annual to mean decadal heat island intensity for a whole city at a spatial resolution of 1 km in a consistent manner. This dataset was derived from the mapping of spontaneous occurring plant species in Hamburg, Germany, which was conducted over a period of 15 yr. The underlying idea is that the species composition in a certain area yields information about the respective climatic and ecological conditions (Ellenberg et al. 1992). Although this approach might be uncommon in urban climatology, it is appropriate considering the long tradition of phenology in urban climatology, especially in Hamburg (cf. Franken 1955). Goedde and Wittig (1983) presented a thermal division of Münster, Germany, on a vegetational basis which visually represented typical zoning of urban microclimatic conditions. In this study we not only interpreted patterns from the floristic dataset visually, but also conducted an empirical analysis, and further refined the data as a proxy for UHI intensity. To gain more detailed knowledge of the UHI intensity, its spatiotemporal structure and influencing factors, the UHI intensity is often related to different descriptors of the urban surface. These are more or less associated with some of the processes shown in Figure 4.1 (e.g. Oke 1973, Roth et al. 1989, Voogt and Oke 2003, Bottyán et al. 2005, Nichol et al. 2009, Wong et al. 2009, Yokobori and Ohta 2009). Another major motivation to relate descriptors of urban structures to air temperature is to assess and correct for urbanisation effects in long-term climate records for estimations of global near surface temperature and corresponding trends (Karl et al. 1988, Gallo et al. 1993, Gallo and Owen 1999, Hansen et al. 2010, Parker 2010). Some of the most common predictors and selected case studies are listed in Table 4.1.

Our main hypothesis was that the plant species composition, and especially the percentage of thermophilic plants, yield relevant information about the long-term air temperature distribution within an urban agglomeration. Furthermore, we assumed that floristic data are suitable as a proxy for long-term climatic conditions in a city. We expected UHI predictors to be significantly correlated with the ‘floristic heat island’.

The following research questions were posed:

- What information does the plant species composition contain about the long-term air temperature distribution within an urban agglomeration?
- Are the proxy data that are derived from plant species composition related to long-term air temperature measurements, and do the proxy data differ between areas with different urban morphological structures?
- Are the temperature proxy data derived from plant species composition related to common UHI predictors, and which predictors show the strongest correlation?

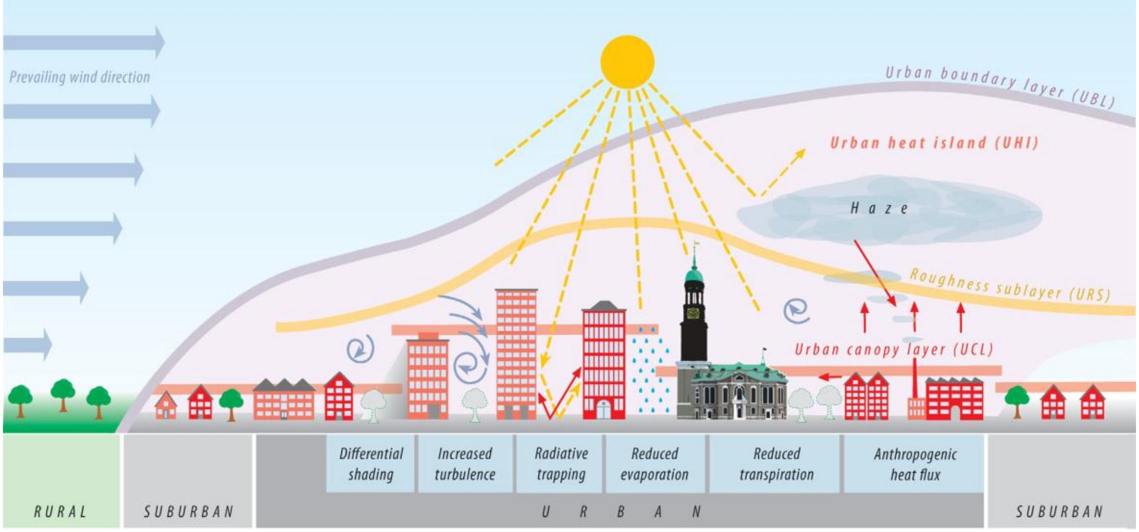

**Figure 4.1** Urban climate is a superposition of various effects and processes; adapted from Ossenbruegge & Bechtel (2010).

**Table 4.1** Predictors related to the urban heat island (UHI) in the literature and selected case studies.

| Predictor class | Notes & examples | Case studies |
|---|---|---|
| Thermal imagery | Air- and spaceborne | Eliasson 1992, Gallo et al. 1993, Gallo and Owen 1998, Gallo and Owen 1999, Roth et al. 1989, Voogt and Oke 2003, Nichol et al. 2009, Wong et al. 2009, Balázs et al. 2009 |
| Vegetation | Normalised difference vegetation index (NDVI) | Gallo et al. 1993, Gallo and Owen 1998, Gallo and Owen 1999, Wong et al. 2009 |
| Urban morphology parameters | Building density, building height, soil sealing | Kuttler et al. 1996, Bottyán et al. 2005, Alcoforado and Andrade 2006, Hart and Sailor 2009, Wong et al. 2009, Buttstaedt et al. 2010 |
| Nightlight radiance | | Gallo and Owen 1998, Hansen et al. 2010 |
| Population | Absolute and density | Oke 1973, Karl et al. 1988, Hansen et al. 2010 |
| Vegetated area and waterbodies | | Alcoforado and Andrade 2006, Yokobori and Ohta 2009, Hart and Sailor 2009 |
| Land use data | | Yokobori and Ohta 2009, Hart and Sailor 2009 |
| Topoclimatic factors | e.g. altitude | Kuttler et al. 1996, Alcoforado and Andrade 2006 |

## 4.2 DATA AND METHODS

### 4.2.1 CITY OF HAMBURG AND REGIONAL CLIMATE

The Free and Hanseatic City of Hamburg (53.55° N, 10.0° E) is the second largest city in Germany with about 1.77 million inhabitants within the administrative borders and about 4.3 million in the metropolitan region.

In Hamburg, 4 distinctive natural regions converge: Saale glaciation moraines of Lüneburg Heath and Schleswig-Holstein, eastern Weichsel glaciation moraines and the glacial valley of the Elbe River – all leading to a high habitat diversity and therefore high plant species richness (Poppendieck et al. 2002). Water and especially the Elbe River are dominant landscape elements (water bodies cover 8% of Hamburg’s area) with the characteristic harbour area (nearly 10% of the city’s area). Furthermore, nature reserves comprise 8% of the area, preserving habitats like bogs, forests and grassland as well as the unique tidal floodplain forests. Nevertheless, 60% of the area is covered by settlement and traffic elements (Statistisches Bundesamt, www. statistik-portal.de/ statistik-portal/de_jb09_jahrtabf1. asp).

Hamburg covers an area of 755 km$^2$ and is situated in the northern German lowlands about 80 km from the North Sea and 70 km from the Baltic Sea. Consequently, air temperature extremes are quite moderate (with a yearly mean of 9.0°C) and mean wind speeds are comparably high (monthly means between 3.2 and 4.7 m s$^{-1}$, Rosenhagen et al. 2011). The urban climate in Hamburg has thus far been less thoroughly investigated than other cities.

Reidat (1971) was the first to measure the UHI and discover a mean air temperature difference of 0.6 K in January and 1.0 K in July between meteorological stations in St. Pauli (a densely built district close to the inner city) and at the airport in Fuhlsbüttel in the periphery. Schluenzen et al. (2010) analysed the mean daily heat island of 5 stations in Hamburg and 1 station in Ahrensburg, a town close to Hamburg, for the decade between 1988 and 1997. They reported a mean heat island of 1.1 K for St. Pauli and 0.6 K for Fuhlsbüttel compared to a reference station in Grambek east of Hamburg. The mean heat island and further information about all stations is given in Table 4.2.

### 4.2.2 FLORISTIC MAPPING DATA AND ELLENBERG INDICATORS

The flora of Hamburg was mapped for the past 15 yr (1995–2009) by the Botanischer Verein zu Hamburg e.V. (subsequently called Botanical Association). Presence and absence of all vascular plant species were recorded on a 1 km² Gauß-Krüger zone 3 grid, a traditional German transverse Mercator projection. All grid cells were mapped repeatedly and at different times over the year (data set: Regionalstelle für Pflanzenartenschutz, Botanischer Verein zu Hamburg e.V. 2009). Altogether 1643 plant species (taxa) were registered (Poppendieck et al. 2010).

Based on the total list of the vascular plant species mapped, we generated a modified species list. We excluded non-established species (to obtain a long-term and relatively persistent floristic composition) as well as ornamental plants (to analyse only spontaneous vegetation). Furthermore, all tree and shrub species were excluded to avoid intentionally planted individuals. Aquatic plants were also eliminated, since they are expected to be more dependent on water temperature. The corresponding plant species were identified by linking the species data set with the BIOLFLOR database (Klotz et al. 2002), where the status of plant species as well as life form characteristics are available. The final species list consists of 902 vascular plant species (authors' unpubl. data).

Ellenberg indicator values describe the ecological behaviour of plants towards climatic and soil-related habitat conditions (Ellenberg et al. 1992). Each plant species is assigned an indicator value between 1 (low value) and 9 (high value). The Ellenberg indicator value for temperature (EIT) reflects the species' main geographical distribution and preferred position along the altitudinal gradient. The indicator values for temperature range from (1) indication of extremely cold conditions (e.g. plants from alpine altitudes), to (9) indication of extremely warm conditions (e.g. plants from the Mediterranean area). For the final set of species, mean EITs ($EIT_m$) were calculated per cell of the original grid of the Botanical Association. Ellenberg indicator values are ordinal numbers and therefore do not fulfil the requirements for calculating arithmetic means. Nevertheless, the use of average indicator values is widely applied in vegetation ecology (Ellenberg et al. 1992, Ewald 2003, Petřík and Wild 2006, Godefroid and Koedam 2007). To control for potential errors, the percentages of 'thermophilic plants', which were defined to have an EIT of at least 6 (EIT>5) by Goedde and Wittig (1983), were generated. Overall, 625 species have distinct EITs and were included in the analysis.

EITs do not directly correspond to determined air temperature values, since they were not calibrated from measured temperature conditions in ecological experiments. Nevertheless, EITs are better related to physical environmental conditions than other Ellenberg indicator values like moisture, light or nitrogen (Ewald 2003). (Ellenberg et al. 1992) also stated that there are strong correlations between mean indicator values for temperature and measured air temperatures as well as phenological observations.

Cities commonly have many established non-native plant species (e.g. Pyšek 1998). These species need to be considered when analysing indicator values for temperature in urban areas, because they often originate from warmer regions. Therefore, they might have higher EITs and thus contribute to increased mean indicator values per grid cell. We calculated the percentage of non-native species from the modified species list. The status of plant species (indigenous, pre-1500 non-native [first occurence in Germany before 1500] and post-1500 non-native [first occurrence in Germany after 1500] was also available in the database BIOLFLOR (Klotz et al. 2002). Altogether we considered 103 non-native plant species (11.4% of the species set).

The time period of the floristic mapping of 15 yr seems appropriate to reflect the climatic conditions in Hamburg, because major changes in species composition are not expected. For instance, Goedde and Wittig (1983) stated that plants integrate climatic conditions over an extended period. Further, our species list contains only established species. Non-native species in particular require stable conditions for a considerable period of time for reproduction and spreading. The species set also includes annual species which might be considered as not very persistent. Nevertheless, they are usually rapid colonisers, and as cities are characterised by a high habitat turnover rate, new habitats are always available, so the main annual species composition per grid cell is not expected to change severely over time.

### 4.2.3 URBAN MORPHOLOGY DATA - LOCAL CLIMATE ZONES

Local climate zones (LCZs, also thermal climate zones) were introduced by Stewart and Oke (2009) to overcome the urban–rural dichotomy in urban climatology. They are defined as local-scale regions of relatively homogeneous air temperature in the canopy layer. A big advantage compared to rather qualitative older schemes is that Stewart and Oke (2009) provided a hierarchical typology and a detailed fact sheet containing important quantitative features for every class. A disadvantage thus far is that although the authors intended to create a generic scheme without cultural biases, the classes are clearly related to North American urban morphologies. Therefore, Daneke et al. (2010) derived a more differentiated typology of European typical morphologies that can be aggregated to the original LCZs. The authors digitised LCZ data from topographical maps and aerial imagery. In our study, we only used the original LCZ classes for the urban series.

### 4.2.4 UHI PREDICTORS

Regarding the selection of UHI predictors, special attention was given to remotely sensed and urban morphology parameters. The latter describe the urban form and can easily be linked to land use scenarios (Wong et al. 2009). The selected UHI predictors are the normalised difference vegetation index (NDVI), surface temperature ($T_s$), 2 parameters describing the annual cycle in $T_s$ (yearly amplitude of surface temperature, YAST; and mean annual surface temperature, MAST), nighttime city light (NIGHTLIGHT), land use (WATERSHARE, the percentage of the surface area comprising water bodies; SOILSEAL, the percentage of sealed surface area) and morphological characteristics (BUILDDENS, building density; GFZ, floor space index), positional and topographical parameters (ALTITUDE, SLOPE, ASPECT) as well as population density. These predictors are defined and described below, and a selection is shown in Figure 4.2. All data were reprojected and resampled to the target grid of the Botanical Association using an area weighted average. Furthermore, water bodies were excluded from the remote sensing data (except NIGHTLIGHT), since they are not predominantly determined by the surface energy balance, and the vegetation inventory was conducted on land only. Landsat data are freely available (datasets beginning in 1982). Landsat 4 and 5 carry the Thematic Mapper (TM), which has a 10.4 to 12.5 µm thermal band in 120 m spatial resolution. Landsat 7 carries the Enhanced Thematic Mapper (ETM+) with a spatial resolution of 60 m. We selected 36 scenes, excluding scenes with cloud contamination or scan line correction error. Hamburg is situated between 2 Landsat orbits (path 195 and 196). Landsat 5 and Landsat 7 cover the full area of Hamburg in 1 scene (row 23) for both paths. For Landsat 4, a small corner is missing in the north at path 196. We processed the scenes with the SAGA (Boehner et al. 2008, www.saga-gis.org) command line interpreter in a Perl script as follows. The digital numbers were calibrated to radiance, using the calibration constants delivered in the metadata and the procedure given by Chander et al. (2009). Atmospheric correction based on the radiative transfer code ‘moderate resolution atmospheric transmission 4’ (MODTRAN 4) was conducted with the National Aeronautics and Space Administration (NASA) atmospheric correction parameter calculator (Barsi et al. 2003, Barsi et al. 2005) for 26 of the scenes. To calculate the surface temperature, the emissivity ε of the surface is needed. The moderate-resolution imaging spectroradiometer (MODIS) offers daily emissivity data at about 1 km resolution from a generalised split window approach for 2 bands (band 31: 10.78 to 11.28 µm, band 32: 11.77 to 12.27 µm), which together cover roughly half of the TM/ETM+ band.

To evaluate the importance of spatial variability in ε, we analysed 1 scene (MOD11A2, version 5 from 15 May 2007). Within the Hamburg area, the emissivities for the 2 bands were 0.979 ± 0.004 (SD) and 0.983 ± 0.003, respectively. Hence, the spatial variability at the regarded scale is substantially smaller than the 2% given by Roth et al. (1989). Therefore, a constant emissivity was considered sufficient and according to the MODIS data, ε=0.98 was chosen, which is slightly above typical values in the literature for urban areas (e.g. Landsberg 1981).

The long-term air temperature regime is influenced by dominant patterns of surface temperatures, rather than individual surface temperatures (seen at random acquisition times). The annual cycle of the 26 scenes is described by 2 parameters, MAST and YAST (Bechtel 2011). The NDVI was calculated from the Landsat bands 3 (red) and 4 (near infrared, NIR) of the same scenes. Atmospheric correction was not considered necessary here, since the band ratio roughly compensates for atmospheric conditions as long as the adjacent bands are comparably affected. The nighttime city light data (NIGHTLIGHT) represents the mean nighttime radiance from cloudfree images between March 1996 and February 1997. The dataset was taken from DMSP/OLS (Defense Meteorological Satellite Program/Operational Linescan System) data described by Imhoff (1997) and has a spatial resolution of 30 arc seconds (~900 m). The data are freely provided by the National Oceanic and Atmospheric Administration (NOAA, www. ngdc. noaa. gov/ dmsp/ download_rad_ cal_ 96-97.html).

For urban morphology parameters, the storeys were given a typical height, according to their period of construction and function. The subsequent parameters, BUILDDENS and floor space index, were derived from the buildings’ area and number of storeys. The degree of soil sealing (SOILSEAL) was taken from the European Environment Agency Fast Track Service Precursor Sealing (Product 2, ‘European Mosaic’). The percentage of water bodies WATERSHARE) was taken from the above classification. Furthermore, topographical and spatial parameters were included. The topographical parameters (especially altitude, slope and aspect) were calculated from the NASA Shuttle Radar Topography Mission (SRTM) dataset, which is freely available worldwide at a resolution of 3 arc seconds (~90 m). Furthermore, 2 parameters describing the relative position within the city were derived by distance transformation (Borgefors 1986). DIST2CEN describes the distance to the city centre, and DIST2MWB is the distance to the closest major water body. The population density was calculated from census data at the district level.

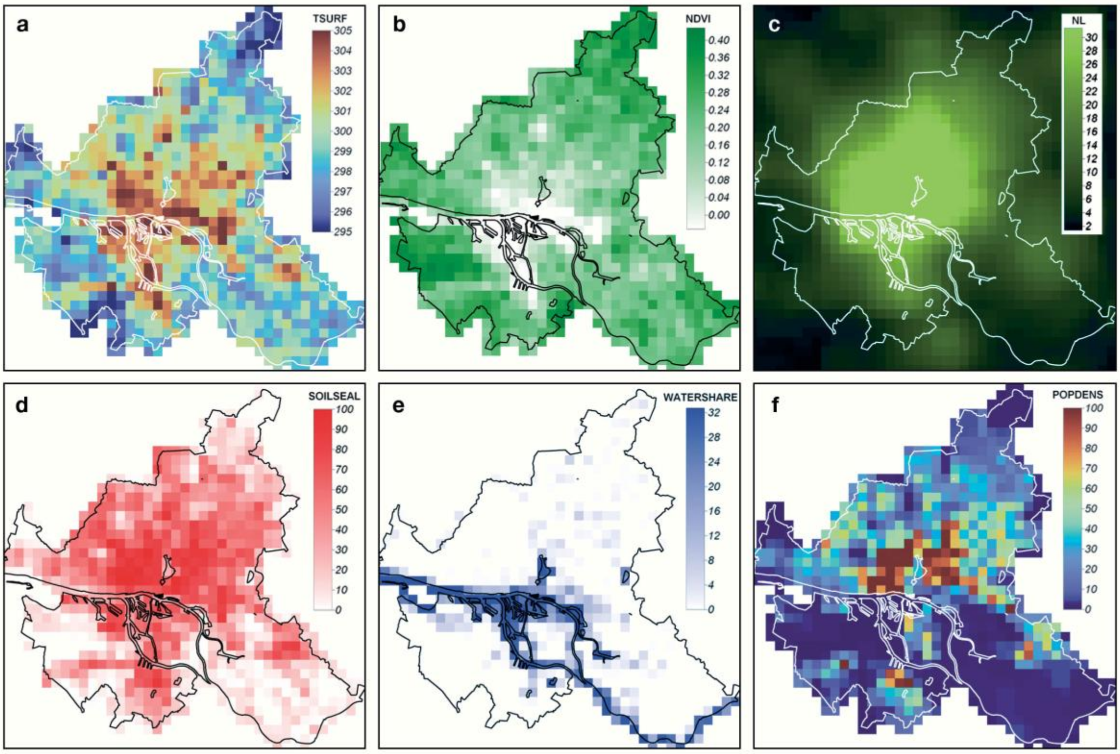

**Figure 4.2** Example predictors for Hamburg, Germany. **a)** Surface temperature (K), **b)** normalised difference vegetation index (NDVI); **c)** NIGHTLIGHT radiance ($10^{-9}$ W $cm^{-2}sr^{-1}$ ); **d)** soil sealing; **e)** water coverage (%); **f)** population density (inhabitants $ha^{-1}$).

### 4.2.5 STATISTICAL ANALYSIS

We had to assume a certain temporal persistence of the long-term UHI pattern, since station data, floristic mapping and predictors comprised different time spans. However, the UHI pattern can be expected to mostly depend on the shape of the urban fabric and therefore the change in urban morphology within the regarded timeframe can be considered. The urban land use was compared for the years 1990 and 2000 using digitised map data from Daneke et al. (2010) regarding the settings around the climate stations, the assumption of persistence of urban morphology (and consequently negligible alterations of urban climate) was essentially confirmed by the data. For the whole city, the overall urban structure was mostly persistent in the relevant decade, although a few areas experienced distinct change. However, this remaining uncertainty is intrinsic to any study of urban climate, since urban structures tend to be dynamic and therefore never remain completely constant for a climatologically relevant time scale. To assess whether the EITs contain substantial information about urban climate and UHI, we evaluated species distribution patterns and possible influence from other ecological factors. All analyses were conducted on the grid of the Botanical Association. Further, all grid cells with at least 100 species with EITs were taken into account, if not marked otherwise.

To test the hypothesis that EITs reflect the inner urban long-term air temperature distribution, we calculated Pearson correlation coefficients as well as non-parametric Spearman rank correlation coefficients of EITs with the mean decadal UHI intensity data of Schluenzen et al. (2010) for the Hamburg stations. Therefore, each station was assigned to the respective cell in the km grid, even if it was not necessary in the centre or representative for the entire cell. For the control, a weighted average of surrounding cells was computed with comparable results. Since these data were only available for 5 stations, the sample size was very small. For a comparison of the urban morphology on the EITs, they were evaluated for different LCZs. Differences in $EIT_m$ between the LCZ classes were analysed by a 1-way analysis of variance (ANOVA) followed by a Tukey-HSD post hoc test. On a km scale, subscale variation of land use is likely; therefore, each cell was assigned to an LCZ, if the dominant land use covered ≥75% of the area. This introduced additional variance to the classes but possibly also systematic errors due to typical class combinations. For instance, many agricultural cells contain built-up areas. Furthermore, the remaining area might include completely different habitats and therefore more than 25% of the species in the grid cell. The initial exclusion of tree and shrub species from the species list resulted in lower species numbers in forest areas than in other habitat types. To include forest areas as LCZs in the analysis, we only excluded grid cells with less than 80 species with EITs. The LCZ ‘compact housing’ was excluded from the analysis due to limited sample size.

To derive the floristic UHI pattern from the proxy data, a linear regression of the measured mean decadal UHI intensity with $EIT_m$ was calculated. The obtained model was used to predict the heat island for the whole study area from the $EIT_m$. The predicted values were used in the subsequent analyses as UHI data. Here, an EIT subscript was added to the UHI pattern from the floristic proxy data ($UHI_{EIT}$) for discrimination from the measured UHI intensity data. As this pattern is derived from mean decadal UHI intensity data by a linear regression model, a decade is roughly the time span it can be associated with, but its representativeness has to be considered with care. Since the $UHI_{EIT}$ values are calibrated with the measured UHI data and inherit any bias, the pattern is more reliable than the absolute numbers. Further, the determination of regression parameters is restricted by the sample size, and gradients in the derived pattern might differ somewhat. However, due to the linearity of the transformation, all further correlation results apply to $UHI_{EIT}$ and $EIT_m$ equally (explained variance is invariant against linear transformation). To test the predictors, the pattern correlations (Santer et al. 1993) between $UHI_{EIT}$ and common UHI predictors were calculated, which are essentially product moment correlations of the selected grid cells. For consistency, the same selection of grid cells (with at least 100 species) was used in this analysis, even where different predictors were related. Additionally, we conducted a multiple regression with the principal component of 13 *z*-transformed predictors to assess the overall explaining capacity and redundancy of the predictors. Here, a few cells had to be excluded due to missing values of single predictors.

## 4.3 RESULTS AND DISCUSSION

### 4.3.1 INFLUENCE OF FURTHER ECOLOGICAL FACTORS IN THE EIT

The spatial distribution of the EITs in Hamburg (see Figure 4.4 for general pattern) suggests that the EITs contain substantial information about the urban climate and especially the UHI. The distribution follows the settlement structures and shows a concentric pattern, with high EITs in the city centre and decreasing values outwards. Besides climate, species distribution is certainly influenced by numerous factors, e.g. land use, soil conditions, disturbance, soil sealing or microclimatic conditions. Furthermore, the distribution pattern of the proportion of non-native species is similar to that of the EITs. An increase of non-native species towards the city centre has also been detected in other studies (e.g. McKinney 2002). However, the solitary EITs of indigenous species also show a distinct UHI pattern, so the increased EITs in the city centre are not only due to more frequent occurrence of thermophilic non-native species. Summarising, the EITs predominantly reflect the inner urban mean air temperature distribution, but to a certain degree also other ecological and climatic factors.

### 4.3.2 COMPARISON OF THE EIT WITH AVAILABLE MEASUREMENTS

Both the mean EIT of all species ($EIT_m$) and the percentage of thermophilic plants ($EIT>5$) were positively correlated with the mean decadal UHI intensity. The Pearson correlation coefficients were 0.88 for $EIT> 5$ and 0.89 for $EIT_m$. The respective Spearman rank correlation coefficients were 1.00 and 0.90. Besides the small sample size, all correlations are significant. These strong relations are clear evidence that the species composition is sensitive to air temperature and that the EITs contain substantial information about the inner urban air temperature distribution. However, air temperature cannot exactly be specified as shelter height in this case, since many of the included plants are found in the ground vegetation layer, and therefore different air temperatures are integrated by the proxy data.

### 4.3.3 FLORISTIC THERMAL CHARACTERISTICS OF LCZS

The $EIT_m$ differed significantly between 3 classes of LCZs ($p < 0.001$; Figure 4.3). The results support the UHI interpretation of the EIT pattern, because urban classes showed greater mean $EIT_m$ than agricultural classes. $EIT_m$ of the LCZs old core and industry were significantly higher than $EIT_m$ of the LCZs grassland, agriculture, and regular housing, while forest cells had significantly lower $EIT_m$. Although compact housing was excluded from the analysis due to the small sample size, its mean was between regular housing and old core, which is consistent with increasing morphological density.

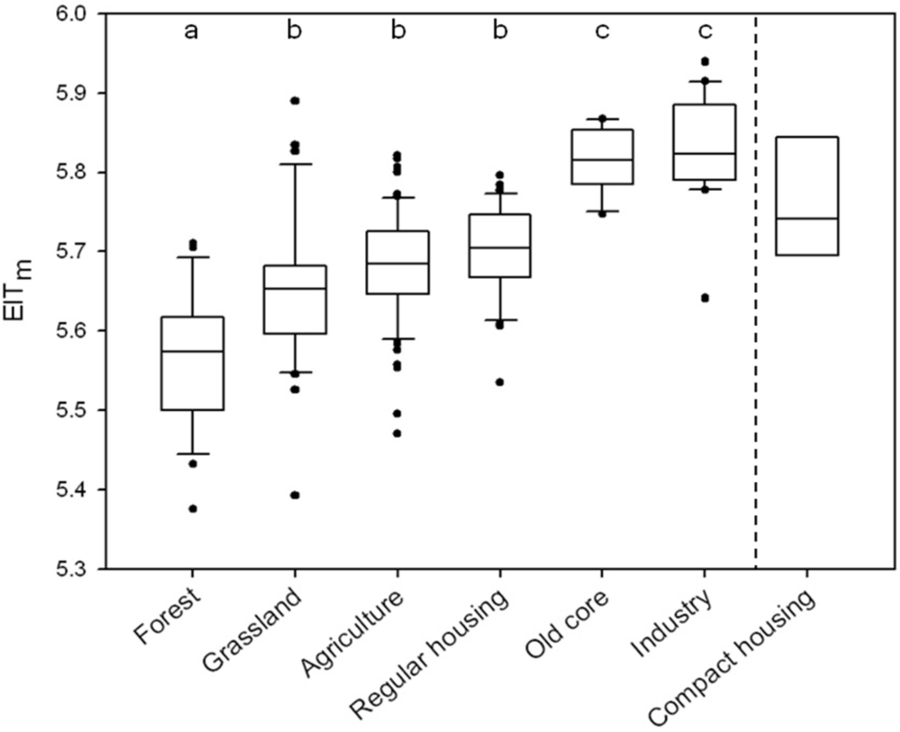

**Figure 4.3** Mean Ellenberg indicator values for temperature ($EIT_m$) for different local climate zones (LCZs). Plots show the median (central line), interquartile range (box), whiskers (90th and 10th percentiles) and outliers (dots). Letters indicate significant differences (ANOVA $p < 0.05$) between $EIT_m$ of the local climate zones (Tukey HSD). The LCZ 'compact housing' is shown but not included in the analysis due to limited sample size.

## 4.3.4 FLORISTIC HEAT ISLAND PATTERN FROM ELLENBERG INDICATOR VALUES

To determine the floristic heat island pattern, a linear regression model was fitted from $EIT_m$ and long-term mean UHI measurements from station data (Schluenzen et al. 2010), resulting in the following empirical model: $UHI_{EIT} = 2.15 \times EIT_m - 11.56$. A comparison of the regression results from $EIT_m$ and the measured values of the mean decadal UHI for the 5 stations showed good agreement (Table 4.2). However, the sample size was small and no independent validation data are available. Hence, the determination of the regression parameters is limited. Further, the model cannot be directly transferred to other cities since it incorporates a specific regional climate. The resulting 'floristic heat island' pattern from Ellenberg indicator values ($UHI_{EIT}$) is shown in Figure 4.4. The pattern shows greater $UHI_{EIT}$ in the densely built city core and harbour area with a radial decrease towards the periphery and therefore agrees with conceptual UHI models. The areas close to the water bodies (e.g. the river island in the west) and in the wetlands southeast of Hamburg showed greater $UHI_{EIT}$. This might indicate that the species composition expressed in the EIT is not only sensitive towards mean but also towards minimum air temperatures. However, the station in Kirchwerder also showed a mean UHI of 0.69 K. This might be a bias of the reference station chosen by Schluenzen et al. (2010) but could also partly be attributed to the river, which is heat contaminated by a nuclear power plant nearby. Overall, it can be stated that EITs contain substantial information about the mean heat island and that their application as a proxy is reasonable. However, the species distribution is determined by various ecological factors which also influence the EITs. Consequently, it cannot be determined to which degree a specific value is influenced by further factors and the results must be evaluated carefully. If, as in Hamburg, no measurements with high spatial coverage are available, the EITs at least represent some picture of the spatial variation of the long-term UHI. This particularly applies to the spatial pattern but only with some restrictions to the absolute numbers.

**Table 4.2** Mean decadal heat island (K) for the available stations ($UHI_{station}$) versus urban heat island derived from Ellenberg indicator values by linear regression ($UHI_{EIT}$).

| Station | $UHI_{station}$ | $UHI_{EIT}$ | Surroundings/Local climate zone |
|---|---|---|---|
| Fuhlsbüttel | 0.58 | 0.48 | Airport |
| Kirchwerder | 0.69 | 0.76 | Agriculture and regular housing |
| Neuwiedenthal | 0.82 | 0.82 | Regular housing, partly commercial area |
| Sankt Pauli | 1.15 | 1.04 | Old core, compact housing and water |
| Wandsbek | 0.63 | 0.77 | Regular and compact housing |

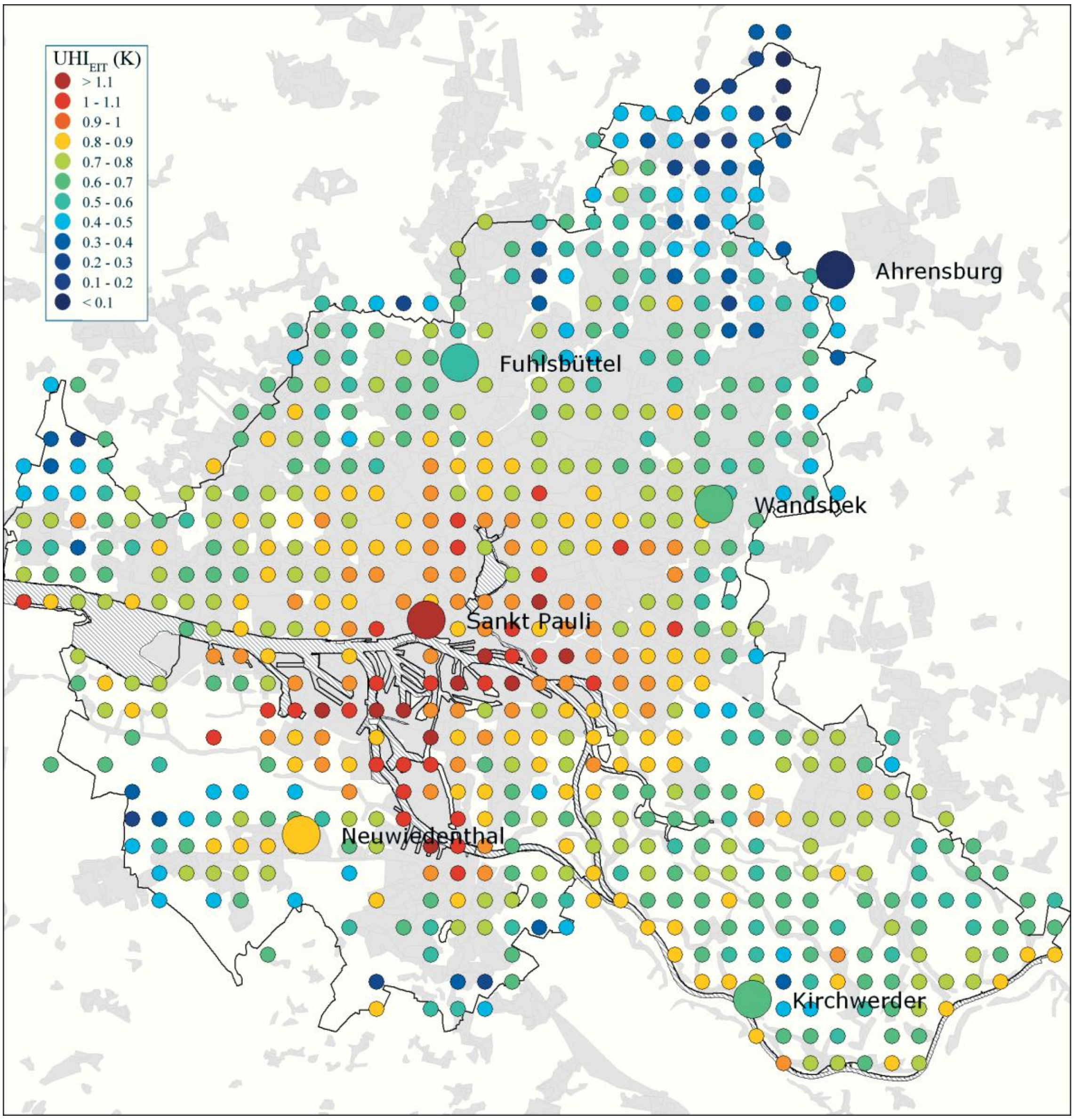

**Figure 4.4** Mean heat island intensity for Hamburg, Germany, derived from mean Ellenberg indicator values for temperature ($UHI_{EIT}$). Large circles: values measured by Schluenzen et al. (2010); small circles: predicted values on a km$^2$ raster.

### 4.3.5 TEST OF UHI PREDICTOR SUITABILITY

Table 4.3 shows the pattern correlation results for chosen predictors. Correlations for SLOPE are not significant. All other correlations are highly significant ($p < 0.001$). The remotely sensed predictors 'radiance at the top of the atmosphere' ($L_{TOA}$), $T_s$ and NDVI show a strong correlation with the derived $UHI_{EIT}$ (i.e. $EIT_m$). The pattern correlation for selected scenes is 0.67 for $L_{TOA}$ and $T_s$ (scene no. 2: Landsat Scene Identifier LE71950232001131EDC00) and –0.76 for NDVI (scene no. 1: Landsat Scene Identifier LE71950231999254 EDC00). Since the results of EIT>5 are comparable, errors due to the averaging of ordinal numbers can be excluded. The better performance of NDVI is in accordance with Gallo et al. (1993) and Gallo and Owen (1999), although their results become more differentiated when looking at a monthly time scale. The results of the selected scenes are not representative and are expected to change with season and atmospheric conditions. Therefore, the pattern correlations of different scenes are compared in the following section. The regression results for the selected scenes are shown in Figure 4.5 (a, b).

**Table 4.3** Pattern correlation of different predictors (by category) with the urban heat island derived from Ellenberg indicator values by linear regression ($UHI_{EIT}$) and percentage of thermophilic plants with Ellenberg indicators >5 ($EIT_{>5}$). NDVI: normalised difference vegetation index; $L_{TOA}$: radiance at the top of the atmosphere; TIR: thermal infrared; DMSP/OLS: Defense Meteorological Satellite Program/Operational Linescan System; SRTM: NASA Shuttle Radar Topography Mission data. All correlations are highly significant, except SLOPE (not significant). Square brackets: landscape scene identifier of respective scene.

| **Predictor** | **$UHI_{EIT}$** | **$EIT_{>5}$** | **Description** |
|---|---|---|---|
| **Remote Sensing** | | | |
| NDVI | –0.761 | –0.743 | NDVI [scene LE71950231999254EDC00] |
| $L_{TOA}$ | 0.673 | 0.675 | TIR radiance [LE71950232001131EDC00] |
| $T_s$ | 0.675 | 0.677 | Surface temp. [LE71950232001131EDC00] |
| YAST | 0.647 | 0.648 | Yearly amplitude of surface temperature |
| MAST | 0.556 | 0.565 | Mean annual surface temperature |
| $L_{TOA}$ | 0.644 | 0.645 | TIR radiance [LT51950232007124MOR00] |
| $T_s$, $\varepsilon = 0.98$ | 0.645 | 0.646 | Surface temperature with constant emissivity/epsilon [same scene] |
| $T_s$, MOD $\varepsilon$ | 0.652 | 0.653 | Same as above description, with MODIS emissivity [MOD11A2 v.5] |
| NIGHTLIGHT | 0.504 | 0.490 | Nightime city light (DMSP/OLS) |
| **Urban morphology, position & population** | | | |
| WATERSHARE | 0.393 | 0.358 | % of waterbodies |
| SOILSEAL | 0.540 | 0.546 | Soil sealing |
| BUILDDENS | 0.509 | 0.520 | Building density |
| GFZ | 0.410 | 0.412 | Floor space index |
| DIST2CEN | –0.597 | –0.579 | Distance to center |
| DIST2MWB[a] | –0.653 | –0.648 | Distance to major water bodies |
| ALTITUDE | –0.361 | –0.358 | Above sea level from SRTM |
| SLOPE | –0.057 | –0.065 | |
| ASPECT | –0.101 | –0.089 | |
| POPDENS[a] | 0.257 | 0.263 | Population density |

[a] one or two cells excluded

To analyse the influence of differential emissivity, the surface temperature for a single scene (no. 3: Landsat Scene Identifier LT51950232007124MOR00) was calculated with constant emissivity and with spatially differentiated emissivity from a MOD11A2 dataset from the same date. The surface temperatures with differential emissivity show only a negligible improvement in explanation of $UHI_{EIT}$, which does not justify the additional effort. The parameters for the yearly cycle are also well correlated with $UHI_{EIT}$, but less than the best single scene. Thereby, the amplitude of the yearly cycle performs better than the mean surface temperature. Hence, the multitemporal approach seems suitable to derive material properties of surfaces (the correlation R between YAST and SOILSEAL is 0.81). The smaller correlation of MAST compared to $T_s^{(no.2)}$ can be related to single scenes with different patterns, which are assumed to be contaminated by cirrus uncinus clouds. Figure 4.6 shows the pattern correlation of $L_{TOA}$ of all scenes with the $UHI_{EIT}$ pattern, and clearly indicates that some scenes perform much worse than the average. This is not the case for NDVI where all scenes (except a single scene, which has obvious cloud contamination and should have been excluded) have an absolute R of more than 0.64. Two main reasons may account for this. Firstly, thin cirrus clouds have a smaller impact on visible transmission than on thermal emission, and secondly, the band ratio in the NDVI partly compensates for differential atmospheric conditions as stated above. Surprisingly, NDVI pattern correlations do not show strong seasonal variation, but this changes if a higher resolution and all Landsat 7 scenes are selected. Furthermore, all NDVI patterns show strong correlations with $T_s^{(no.2)}$ (+) of about -0.8. In contrast, many of them agree less with the $L_{TOA}$ patterns of the same scene at the time of acquisition. This again is especially the case for the presumably cloud-contaminated scenes. To summarise, NDVI was observed to be more robust and therefore more suitable as a long-term UHI predictor, while for surface temperature, scenes with very clear and homogenous atmospheric conditions are especially suitable. The urban morphology parameters show a varying picture, but SOILSEAL and BUILDDENS show pattern correlations of more than 0.5. The floor-space index shows a correlation of 0.41, and WATERSHARE has a correlation R of 0.39.

Regarding the location in the city, $UHI_{EIT}$ is negatively correlated with both patterns, DIST2CEN and DIST2MWB. In principle, this is not surprising considering the partially radial shape of the city. However, the higher correlation with DIST2MWB also includes the higher EITs at the river that were discussed above. The altitude shows a negative correlation of only -0.36. This is as expected regarding the rather flat topography. SLOPE and ASPECT show very weak correlations, which partly excludes errors from differential solar radiation. NIGHTLIGHT turned out to be too smooth to show inner urban differences on a kilometre scale while it is very well correlated with DIST2CEN (R=-0.79). However, it still performed almost as well as building density and is certainly sufficient to define a threshold for rural areas. Oppositely, population density was too specific on a kilometre scale, since many built-up areas (like the harbour or commercial centres) have no or only few inhabitants. Since the predictors are highly redundant, the linear partial correlation coefficients between pairs of predictor variables controlling for $EIT_m$ were checked. As expected, partial correlations between $T_s$, $L_{TOA}$ as well as YAST and MAST are very high (e.g. $T_s^{(no.2)}$ and YAST/MAST each 0.86). The morphology parameters SOILSEAL and BUILDDENS also show a high partial correlation (0.85). Also not surprisingly, NIGHTLIGHT and DIST2CEN show a strong negative partial correlation of -0.71. On the other hand, DIST2MWB, WATERSHARE and ALTITUDE are quite independent.

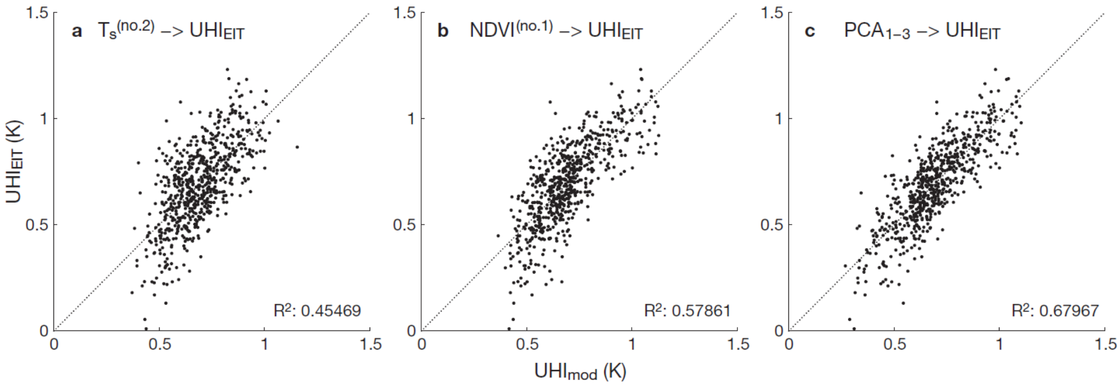

**Figure 4.5** Modelled urban heat island ($UHI_{mod}$, *x*-axis) of different linear regression models against values from floristic proxy data ($UHI_{EIT}$, *y*- axis) in Kelvin. Predictors used: **a)** Surface temperature $T_s^{(no.2)}$, **b)** normalised difference vegetation index NDVI(no.1), **c)** first 3 principal components of 13 predictors PCA1-3.

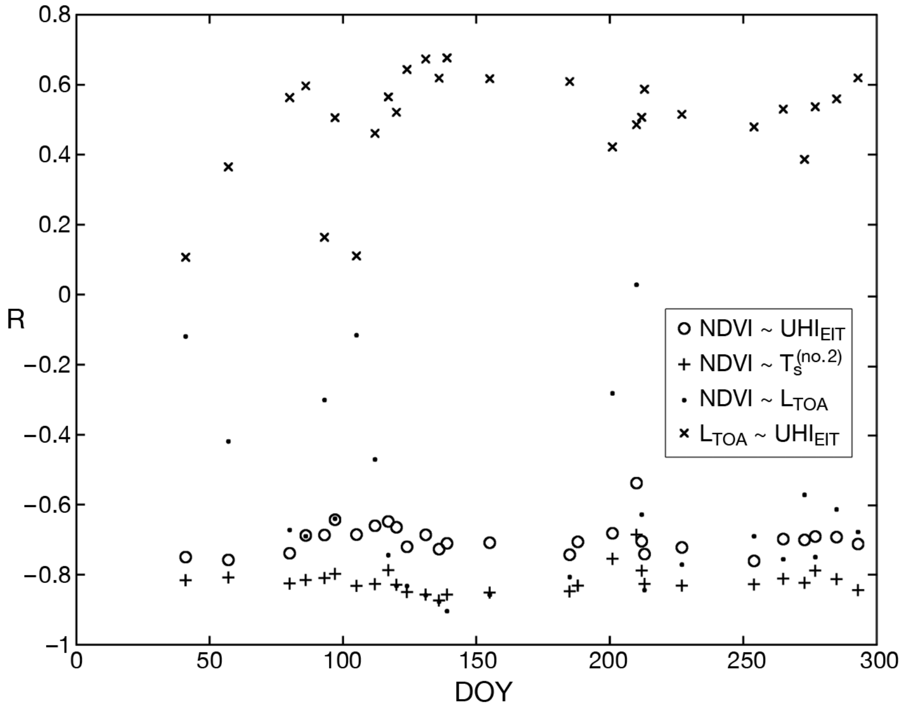

**Figure 4.6** Pattern correlations of remote sensing parameters for different scenes in the order of their acquisition time (day of year, DOY). (×), (s): Correlation of the floristic heat island pattern $UHI_{EIT}$ (urban heat island derived from Ellenberg indicator values) with thermal radiance ($L_{TOA}$) and normalised difference vegetation index (NDVI), respectively, of a scene acquired on that day. (+) Correlation of the NDVI of this scene with the surface temperature of scene no. 2 ($T_s^{(no.2)}$). (•) Correlation between $L_{TOA}$ and the NDVI of the same scene.

In the multiple regression of the principal components of 13 predictors, the first 3 principal components explained 68.0% of the variance in the $UHI_{EIT}$ (cf. Figure 4.5c); the first 5 components explained 68.7%, and all chosen predictors together 70.1%. This agreement underpins that there is a relevant relation between the predictors und the 'floristic' heat island as well as the redundancy in the dataset.

### 4.3.6 DISCUSSION OF THE PREDICTOR SUITABILITY

The overall high coherence with the 'floristic' heat island can be seen as a further proof of relevant information in the proxy data, although it cannot exactly be attributed to air temperature at a certain height. Goedde and Wittig (1983) stated that 'congenial organisms such as plants may be better indicators [for human well-being] than non-animated mercury or alcohol columns […] – although they do not give exact figures'. This indicates the important fact that air temperature alone is insufficient to assess biometeorological impacts. Therefore, all meteorological parameters influencing the human energy balance need to be considered, most importantly the mean radiant temperature (Mayer et al. 2008).

On the other hand, the comparison of UHI predictors can also be seen as a contribution to an empirical analysis of the underlying factors of the UHI, or as Hart and Sailor (2009) put it, whilst 'the general causes of the urban heat island are well known, it is not well understood how much influence different urbanisation characteristics (e.g. land-use, road density, vegetation coverage) have on the intensity of the UHI'. Deeper understanding of this influence would also contribute to improve urban surface parameters in order to develop 'more fundamental surface descriptors' (Voogt and Oke 2003), which should be more comprehensive and physically linked to the relevant surface-atmosphere exchange processes. Likewise, such an understanding of the underlying factors would address the question that was posed by Martilli (2007): 'how much complexity is necessary […] to have a satisfactory representation of urban areas (or, in other words, which are the most important urban parameters that define a city)'. However, for the empirical development of such fundamental surface descriptors, the given database is not sufficient. Even if the floristic data were shown to contain relevant information about the innerurban air temperature distribution, it is 'important to keep in mind that gradients of indicator values are still floristic gradients, even if the original floristic information is transformed' (Schmidtlein 2005). Therefore, the analysis should be complemented with 'real' measured data, which certainly are more credible in a quantitative sense.

## 4.4 CONCLUSIONS AND OUTLOOK

In this paper we introduced Ellenberg indicator values derived from inner urban distributions of spontaneously occurring vascular plant species as a UHI proxy. We tested their suitability as a proxy for long-term spatial inner urban air temperature distributions with very good results. This is in agreement with conceptual heat island models as well as the available climatic measurements and shows a pattern correlation of 0.89 with measured decadal mean UHI, although only 5 stations are available. Furthermore, the LCZs within the city show significantly different EITs. Therefore, EITs of a comprehensive floristic mapping can be used to generate a long-term mean heat island pattern, $UHI_{EIT}$, from floristic data. Although such a pattern is certainly influenced by additional factors, it can give a valuable estimation about the spatial distribution of heat-related risks within an urban area. However, the method will probably not become operational in urban climatology because of the large effort of the floristic mapping as well as the limited representativeness, which should be examined further. Nevertheless, from our point of view the pattern given in this study represents the best available inner-urban differentiation of the long-term UHI for Hamburg.

Furthermore, we compared the floristic heat island pattern with a large number of common predictors (mostly remote sensing and urban morphology data) in UHI studies. The remotely sensed parameters explained more of the spatial variation in $UHI_{EIT}$ than the urban morphological parameters, with an explained variance of up to 58% for a single parameter. NDVI was very robust, while for surface temperature, scenes with very clear and homogenous atmospheric conditions were particularly strongly correlated with the $UHI_{EIT}$ pattern. Regarding the urban morphology, BUILDDENS and SOILSEAL had relevant correlations. Moreover, the position within the city (i.e. the distance to major water bodies) played a notable role, which might reflect the sensitivity of the plant species composition not only to mean but also to minimum air temperatures. These high correlations further prove that the proxy dataset comprises spatial information about the long-term heat island.

On the other hand, several predictors showed a relevant pattern correlation with the ‘floristic’ mean UHI. Therefore, the predictors can also be considered applicable for (at least qualitative) assessment of inner-urban UHI and exposure to heat-related risks. To further evaluate their capacity to deliver quantitative UHI information, the consistent comparison of predictors should be continued with measured data at different scales. Therefore, a mobile measurement campaign with high spatial coverage and an integrated database of available measurements are being planned. The yearly cycle in surface temperature could potentially be used to determine specific material properties of the surface, such as heat conductivity and heat storage, and to classify LCZs, which we will examine further.

## 4.5 ACKNOWLEDGEMENTS

We thank the Regionalstelle für Pflanzenartenschutz, the Botanischer Verein zu Hamburg e.V. and especially H.H. Poppendieck for providing the data on plant species distribution, which was mapped voluntarily. We also thank C. Daneke for the LCZ data, P. Hoffmann and K. H. Schlünzen for the station UHI data as well as all further data providers for the UHI predictors. For their valuable comments on the manuscript we especially thank S. Bakan, M. Bock, J. Böhner and K. Jensen. The work was funded by the cluster of excellence CliSAP and partly funded by the BMBF within the research project KLIMZUG-NORD (grant number 01LR0805D). Further, we thank the reviewers for their comprehensive and constructive remarks on the first manuscript, which helped to substantially improve the paper.

# 5 PLANT SPECIES DIVERSITY IN SELECT HABITATS ALONG AN URBANISATION GRADIENT

## 5.1 INTRODUCTION

Urban areas are subject to frequent anthropogenic disturbance and consequently characterised by highly dynamic habitats. This human impact varies along urbanisation gradients. Concomitantly, temperature, soil sealing, air and soil pollution, soil compaction and alkalinity, $CO_2$-concentration, and population density increase, whereas water availability decreases with urbanisation intensity (McKinney 2002, Pataki et al. 2007, George et al. 2007). Accordingly, the proportion of semi-natural and natural habitats decreases. Vegetation patterns correspond to these changes in environmental conditions: plant species and functional traits compositions change with increasing urbanisation (Williams et al. 2005, Pellissier et al. 2008, Vallet et al. 2008, Brunzel et al. 2009).
Along urbanisation gradients, species richness is often highest in moderately urbanised (suburban) areas (Gilbert 1989; Kent et al. 1999; Zerbe et al. 2003). These areas are very heterogeneous due to a mixture of residential areas in different stages of development, as well as agricultural and natural remnant habitats. The number and percentage of non-native species often decreases with distance to the city centre (e.g. Celesti-Grapow and Blasi 1998; Brunzel et al. 2009).

To investigate species richness and species composition on a smaller scale than the meso-scale used in the previous analyses of this thesis (Chapter 2 and 3), vegetation composition in two habitat types, riparian (natural) and wasteland habitats (anthropogenic), along an urbanisation gradient was analysed. The aim of the study was to test whether natural and anthropogenic gradients differ in species richness and composition (also focussing on non-native species) and if emerging patterns were related to the urbanisation gradient.

Hypotheses were:

- Species richness of wasteland sites increases with urbanisation, whereas species richness of riparian habitats decreases with urbanisation.

- Number and proportion of non-native species decrease along the gradient towards the less urbanised areas.
- More non-natives occur at wasteland sites than at riparian sites.
- Soil parameters differ between the habitat types and change gradually along the urbanisation gradient.

## 5.2 METHODS

Plant species composition was assessed along two urbanisation gradients of riparian (natural) and wasteland habitats (anthropogenic) from the city centre of Hamburg towards the north eastern rural areas (Ahrensburg) in 2010 (Figure 5.1). The first gradient ran along the river Wandse, a small urban river that is rather natural and only canalised close to the city centre. Therefore, it was chosen to represent the natural gradient. Parallel to the first gradient, wasteland sites were selected to represent a gradient under strong anthropogenic influence. During the selection of the study sites, some problems were encountered: Management regime and recreational use along the river Wandse differed in manner and intensity between sites. Hence, exact similar conditions for sites could not be considered. The selection of suitable wasteland sites was conducted visually through aerial images and then confirmed by visiting the site. Here, the main problem was the scarcity of suitable sites along the gradient (especially in less urbanised areas), hence, e.g. duration of abandonment could not be considered as primary criterion of choice.

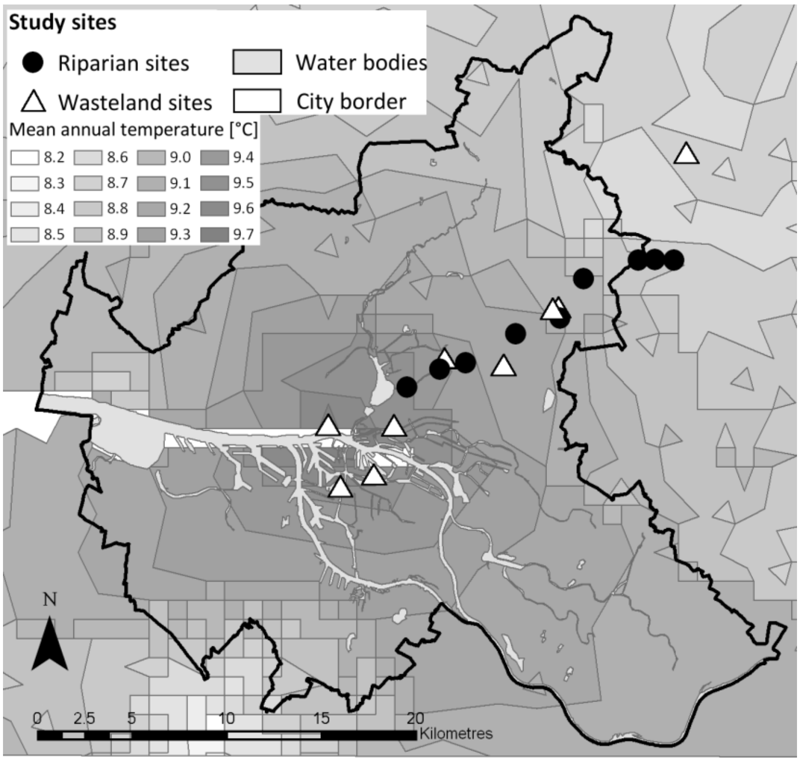

**Figure 5.1** Location of study sites in Hamburg: Nine riparian (circles) and nine wasteland sites (triangles) were studied. The background shows differences in mean annual temperature [°C] across the study area (data: DWD 2010).

Ten vegetation relevés of vascular plant species were conducted recording plant species cover (scale: Londo G. 1976) at each of nine sites along both gradients. At the riparian sites, the relevés were taken close to the river and along a 110 m river stretch (each 10 m apart from the next relevé). At the wasteland sites ten locations were randomly chosen using the GIS application 'Hawths tool' (Beyer 2004) and then relocated in the field.

Furthermore, soil samples were taken around each relevé by combining three samples into one mixed sample per relevé. Due to the rocky and compacted soil at the wasteland sites, samples were restricted to 0-15 cm. Soil samples were analysed for pH and conductivity, the analysis of N, P, K and $C_{org}$ was planned initially to further characterise the respective habitats, but could not be conducted within this thesis.

### STATISTICAL ANALYSES

Differences in plant species richness and soil characteristics were related to urbanisation intensity. Furthermore, differences in these variables between the two habitat types were tested: With linear and nonlinear regression analyses linear, exponential and hump-shaped models were tested to find out whether species numbers of river and wasteland sites were related to distance to the city centre. Further regression analyses investigated the relation of soil pH and soil conductivity to distance to the city centre. With analyses of variance differences in species number, soil pH and soil conductivity were tested between the two habitat types. Statistical analyses were calculated with SPSS (IBM SPSS Statistics, Version 21, 2012) and PAST (Hammer et al. 2001).

## 5.3 RESULTS

Total plant species number, soil pH and soil conductivity were not significantly correlated with distance to the city centre at either riparian or wasteland sites in all models (Figure 5.2). Species number did not differ significantly between habitat types (F=1.4 ns.; Figure 5.3a). Soil pH was significantly higher at wasteland sites (F=365.8***; Figure 5.3b), while conductivity was significantly higher at riparian sites (F=24.48***; Figure 5.3c).

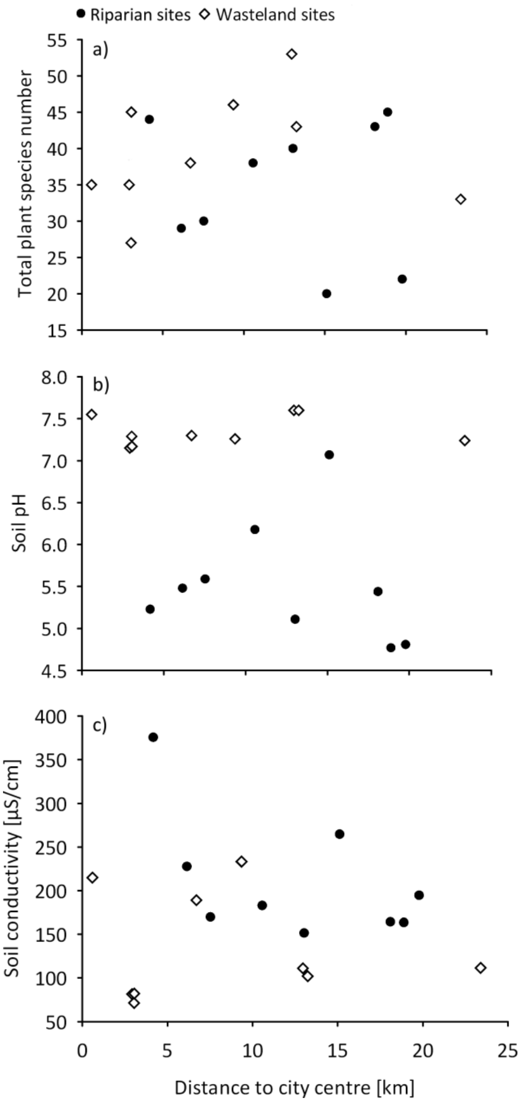

**Figure 5.2** Scatter plots of **a)** total plant species number, **b)** soil pH and **c)** soil conductivity [µS/cm] in relation to distance to the city centre [km] for riparian (circles) and wasteland sites (diamonds); n=9.

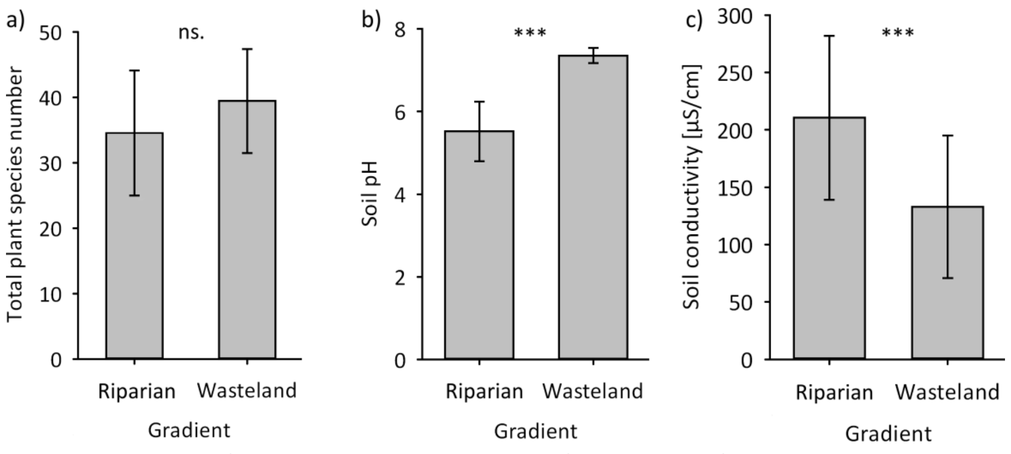

**Figure 5.3** Differences in **a)** total plant species number, **b)** soil ph and **c)** soil conductivity between sites along riparian and wasteland gradients. Mean and standard deviation are given, n=9.

## 5.4 DISCUSSION AND OUTLOOK

Plant species number did not differ between habitat types and was not correlated with distance to the city centre, which is contradictory to other studies (Zerbe et al. 2003, Ranta and Viljanen 2011). Hence, the hypothesis that species richness of wasteland sites increases with urbanisation and that of riparian sites decreases with urbanisation could not be confirmed. Species richness was generally very variable, which could be attributed to the chosen sites that might have not been very comparable regarding age of wasteland sites which influences species composition. The riparian sites were under a stronger human impact than expected beforehand. Since nature conservation organisations and authorities apply restoration measures (e.g. remove non-native species) and sites in more rural areas are influenced by agriculture, the river and its riparian vegetation was altered. The initial aim to investigate the distribution of non-native species along the gradient could therefore not be corresponded to.

Soil pH was higher and soil conductivity lower at wasteland sites. Contradictory to Trammell et al. (2011), who found decreasing soil pH and conductivity with increasing distance from highways, both variables were not correlated with distance to the city centre. The higher pH can be attributed to anthropogenic impact at wasteland sites, since these have been previously build-up and alkaline building materials mixed with the soil. Soil pH was rather constant along the gradient for wasteland sites, indicating that anthropogenic influence acts similar in urbanised and less urbanised areas. At the river sites, soil pH was more variable with an outlier at a moderately urbanised site. The higher soil conductivity at riparian sites can be explained by drainage processes. The river Wandse has a catchment area of 88 $km^2$. Large areas of the city drain into the river. Here, transported nutrients and minerals can accumulate in the riparian sites and lead to high soil conductivity.

The hypotheses concerning non-native species richness could neither be confirmed nor rejected, because altogether too little non-native species were found to conduct a comprehensive analysis. This may be also due to management practise along the river Wandse including the removal of non-native species.

For further analysis it would be desirable to include more sites in the analysis and extend the gradient further to the rural areas. Also, more similar sites would be better for a coherent comparison. Besides species number, diversity indices could be calculated and compared along and between gradients to analyse differences between the sites further. Ordination methods could be applied to look deeper into plant species composition changes along the gradient (see Pellissier et al. 2008). Often the analysis of functional traits can reveal additional information that cannot be drawn from species composition only (Williams et al. 2005, Lososová et al. 2006, Thompson and McCarthy 2008).

# 6 BIOTIC INTERACTIONS OF *SENECIO INAEQUIDENS* DC. WITH NATIVE SPECIES IN ITS INTRODUCED RANGE UNDER CLIMATE WARMING

Katharina J. Schmidt, Dennis Schulze, Jonathan Steinke & Kai Jensen

Manuscript

**KEYWORDS**
Climate change * Competition * Herbivory * Local adaptation * Non-native species * Invasion * Urbanisation gradient

## 6.1 INTRODUCTION

Climate change and non-native species affect native biodiversity and biotic interactions (Brooker 2006, Walther et al. 2009, Schweiger et al. 2010). Hence, native species have to cope with both changing environmental conditions and invading species. Therefore, the future effects of interactions on species – both native and introduced – are manifold and difficult to predict (Blois et al. 2013). Invasive non-native species might benefit from climate change and their establishment could be facilitated (Dukes and Mooney 1999). But during invasion of a new range non-native species are exposed to new biotic interactions with enemies, competitors and mutualists. These interactions with native species will take place under different environmental conditions than in the invader's native range (Mitchell et al. 2006). Climate change and non-native species in combination will lead to the development of novel communities. Here, generalist species are likely to profit from new interactions, while specialists are more likely to be negatively affected (Schweiger et al. 2010, Urban et al. 2012). Climate change will influence phenology and can cause temporal mismatches between species, e.g. resulting in interrupted plant-insect interactions (Parmesan 2006, Schweiger et al. 2010, DeLucia et al. 2012). However, non-native species could also compensate for those lost native interactions (Schweiger et al. 2010).

In recent decades, several studies have analysed why invasive species become so successful in their introduced range. Several hypotheses have been formulated, e.g. the enemy release hypothesis (Keane and Crawley 2002), the evolution of increased competitive ability hypothesis (EICA) (Blossey and Noetzold 1995, see also Felker-Quinn et al. 2013), and the novel weapon hypothesis (Callaway and Ridenour 2004). For relationships between these hypotheses see Bossdorf (2013). Successful invaders can have higher growth rates and size than non-invasive or native species (Garcia-Serrano et al. 2005, van Kleunen et al. 2010, see also Hamilton et al. 2005 and Hawkes 2007), greater phenotypic plasticity (Daehler 2003), less pathogen damage (Hawkes 2007), higher specific leaf area (Lake and Leishman 2004), and increased potential for rapid microevolutionary changes and corresponding adaptation to changing conditions (Maron et al. 2004, Schweiger et al. 2010, Lachmuth et al. 2011). See Pyšek and Richardson (2007) and Pyšek et al. (2009) for comprehensive reviews on traits of invading species. Especially the ability of rapid evolution could also lead to successful adaptation to climate change (Maron et al. 2007).

When non-native species become introduced into novel ranges and communities they are under different competition regimes and encounter new enemies. Generally, invasive species are seen as superior competitors to native species (Vilà and Weiner 2004, Verlinden et al. 2013, see Daehler 2003 for constraints). However, competition from native plants can also reduce the invader's establishment and performance (Scherber et al. 2003, Levine et al. 2004). Regarding climate change, invasive species from warmer and drier regions might be superior to native species. Potential native competitors that are not able to adapt to higher temperature and lower water availability or are not able to adapt as fast as the non-native species might be more negatively affected by changing climatic conditions (Walther et al. 2009, Schweiger et al. 2010). Regarding interactions with new enemies, herbivory usually affects invader's establishment and performance negatively (Levine et al. 2004), but invaders are usually protected better against generalist than specialist herbivores in their invaded range (van der Meijden 1996, Joshi and Vrieling 2005).

Experimental studies on biotic interactions between native and non-native species under future elevated temperature are generally scarce. It has been shown that in competition with a native species photosynthetic rates can be increased in invasive species (Verlinden et al. 2013) and competitive ability is generally higher (He et al. 2012). In a study by Lu et al. (2013) warming increased insect herbivore and hence decreased invasive plant growth. Warming in combination with elevated $CO_2$ could increase foliage damage in soybean by herbivory (Niziolek et al. 2013). Overall, it has been proved useful to incorporate interactions into models for predictions of future biodiversity (Urban et al. 2012).

We chose *Senecio inaequidens* DC. as a study species, because it has been spreading rapidly and invading ruderal sites in Germany during the past decades (Asmus 1988, Heger and Boehmer 2005). The species is able to adapt rapidly to different environmental conditions (Monty and Mahy 2009, Lachmuth et al. 2011) and exhibits a high invasive ability in disturbed habitats (Lopez-Garcia and Maillet 2005). Its invasion success could be related to its higher growth rate compared to native *Senecio* species as well as to its early flowering (Garcia-Serrano et al. 2004, Garcia-Serrano et al. 2005). Furthermore, the species is of growing interest regarding agriculture and health, since it contains pyrrolizidine alkaloids (PA) for herbivore defence. These are toxic for animals and even humans (McLean 1970). The plants usually contain a certain content of PA as constitutive protection against herbivores. Herbivore attack may hence induce plant defence mechanisms and the expression of more PA. Constitutive defence can be of advantage when the risk of being attacked by generalist herbivores is high,

while a positive induction of PA for defence is advantageous when herbivore pressure is low or unpredictable (van Dam et al. 1993). As herbivores, molluscs and aphids can have a significant effect on plant fitness of *S. inaequidens* (Scherber et al. 2003, Bossdorf et al. 2008). The native *Senecio jacobaea* L., which also contains toxic PAs, already invaded agricultural land in Germany. In *S. inaequidens'* native South African range, poisoning of cattle could be traced back to the species (Dimande 2007). Therefore, the species is likely to become a threat to livestock also in Europe.
Different ecotypes (from different regions in Europe) of *S. inaequidens* have been shown to differ in morphological parameters, herbivore response and genetic variation (Scherber et al. 2003, Monty and Mahy 2009, Lachmuth et al. 2010, Monty and Mahy 2010). Several studies compared native and invading populations of *S. inaequidens* (e.g. Bossdorf et al. 2008, Cano et al. 2009, Lachmuth et al. 2010, Thebault et al. 2012) or the non-native with native species of the same genus (Garcia-Serrano et al. 2005, Vanparys et al. 2011). Monty and Mahy (2009) found decreasing height and biomass along an altitudinal gradient in France, which indicates an influence of temperature on *S. inaequidens'* performance.

To our knowledge, it has not been investigated yet, whether differentiation between ecotypes is also recognisable on smaller regional scales. Urban areas seem suitable to study local adaptation within a smaller region, because environmental conditions differ strongly along urbanisation gradients (McDonnell and Pickett 1990, Carreiro and Tripler 2005). Temperature and $CO_2$-concentration decrease with decreasing urbanisation intensity, while water availability increases (McKinney 2002, George et al. 2007, Pataki et al. 2007). Schluenzen et al. (2010) detected a mean urban heat island effect of 1.1 K difference between urban and rural areas in Hamburg. We hypothesise, that *S. inaequidens* adapts quickly to local environmental conditions also on a rather small scale of urbanisation in Hamburg and assume the species has adapted to a warmer, drier and more polluted environment in urbanised areas. Furthermore, general animal species richness is decreasing with increasing urbanisation intensity, also in Hamburg (Denys and Schmidt 1998, McKinney 2002, Weller and Ganzhorn 2004). Hence we assume an adaptation of *S. inaequidens* to lower herbivore pressure in areas of high urbanisation intensity.

The response of *S. inaequidens* to native species and communities has been analysed in some studies (Scherber et al. 2003, Bossdorf et al. 2008, Cano et al. 2009), but to our knowledge so far only very few studies included a changing climate by experimentally elevating temperature (e.g. Verlinden and Nijs 2010, Verlinden et al. 2013). Consequently, we compared populations from different origins along an urbanisation gradient from the city centre to the surroundings of Hamburg to test if differences between ecotypes can also be detected on a small scale. To investigate how *S. inaequidens* responds to interactions with native species under future climate change, we analysed germination, competition and herbivory of six populations along an urbanisation gradient.

We asked the following questions:

- How does growth and productivity of *S. inaequidens* respond to interactions with native species under elevated temperature?
- Does the response to competition with a native species change with elevated temperature?
- Are there gradual tendencies in growth and production along an urbanisation gradient?
- Does the response to herbivory of a native species change with elevated temperature?
- Does the response to herbivory differ along an urbanisation gradient?

## 6.2 METHODS

### 6.2.1 STUDY SPECIES

The invasive species *Senecio inaequidens* DC. (South African ragwort, narrow-leafed ragwort; native to South Africa) of the Asteraceae family first appeared in Europe at the end of the 19th century and was accidentally introduced by wool import. The perennial dwarf shrub prefers dry and warm sites and is favoured by disturbance (e.g. Asmus 1988). It has a remarkable long flowering period, which lasts from May to December (Boehmer 2001). The species is mainly dispersed by wind and is able to disperse seeds over long distances; dispersal can be enhanced by vehicles (Ernst 1998, Monty et al. 2008). *S. inaequidens* is able to adapt rapidly to local conditions, e.g. competitive regimes (Lachmuth et al. 2011).

In Northern Germany, *S. inaequidens* first occurred in Bremen (1896) and Hanover (1889, Kuhbier 1977). During the past decades it spread rapidly, preferably along railway tracks, motorways, and other main roads (Griese 1996, Ernst 1998). Recently, Lachmuth et al. (2010) found evidence that the Northern German populations were not descendants from the Bremen population but from the more rapidly spreading population from an introduction centre in Verviers (Belgium). This finding also explains the previously called long “lag-phase” between introduction and spread in Northern Germany that was often related to demographic, evolutionary and climatic change (Lachmuth et al. 2010).

*S. inaequidens’* first occurrence in Hamburg in 1988 can be located precisely and the dispersal process over the past decades can be retraced by a floristic mapping of Hamburg. From the central port area (Jehlîk 1989) the species spread more or less concentrically to the rural surroundings (data set: Regionalstelle fur Pflanzenartenschutz, Botanischer Verein zu Hamburg e.V. 2009).

### 6.2.2 STUDY POPULATIONS ALONG AN URBANISATION GRADIENT

We chose six study populations along an urbanisation gradient from Hamburg city centre and port area to Ahrensburg in Schleswig-Holstein (Figure 6.1). The location along the gradient is hereafter referred to as urbanisation intensity. The populations grew either along a main road or at a parallel railroad track. Since *S. inaequidens* first occurred in the port area (Jehlîk 1989) and subsequently spread to the surroundings, this is a likely dispersal path. We assume that populations closer to the city centre had more time to adapt to local conditions. Populations were chosen due to different mean annual temperatures over the reference period 1971-2000 (data: German Meteorological Service (DWD), as a digital map with spatially interpolated values; 2010) representing an urbanisation gradient. Furthermore, we tried to find populations with similar habitat conditions at ruderal sites. The temperature gradient was 1 K and ranged from 9.7°C in the highly urbanised area to 8.7°C in the less urbanised surrounding of Hamburg. For further characterisation of the study populations see Table 6.1. We randomly collected seeds from the chosen populations in November 2010. Seeds were dried and kept in the dark at room temperature until the experiments started. Mean seed mass per population was determined.

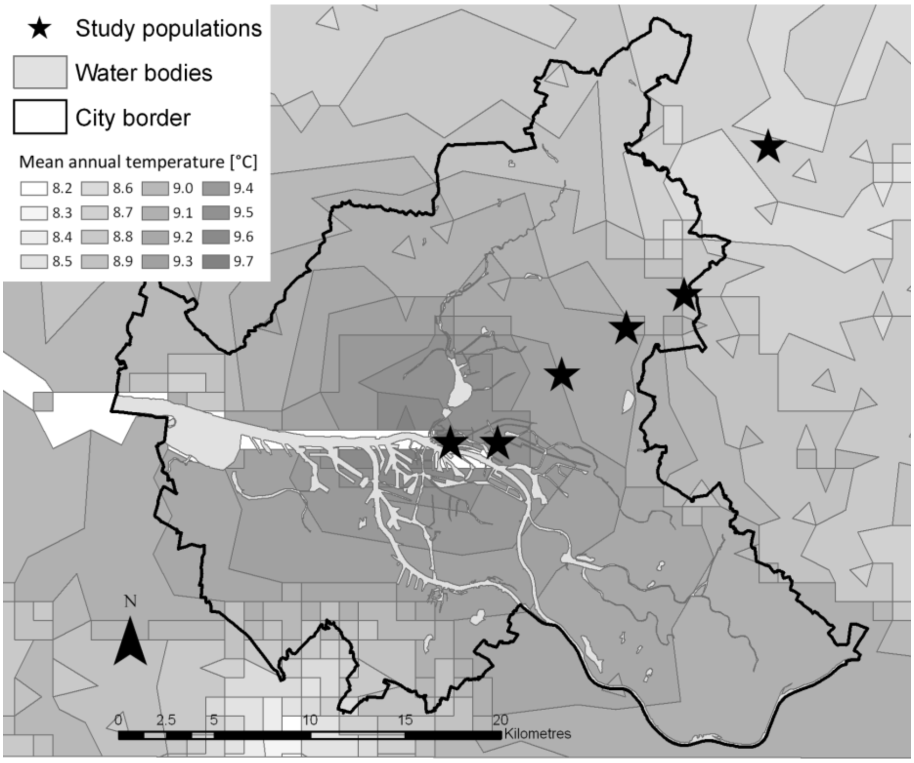

**Figure 6.1** Location of the six study populations within Hamburg and its surroundings. Differences in mean annual temperature [°C] are indicated (data: German Meteorological Service (DWD) 2010; reference period 1971-2000).

**Table 6.1** Characterisation of the six study populations by urbanisation measures and climate. Geographical coordinates, distance to the city centre of Hamburg, degree of soil sealing, population density, proportion of green area and mean annual temperature, number of summer days, annual precipitation, number of frost days and number of snow days per year are given. The data for degree of soil sealing, population density, and proportion of green area were derived from Schmidt et al. (2013) and climate data from DWD 2010. The sixth population is situated in Ahrensburg, Schleswig-Holstein, where data availability is different to Hamburg. Therefore, information on soil sealing and green area for the area around the population could not be obtained.

| **Pop.** | **Coordinates*** | | **Urbanisation** | | | | **Climate** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | **X** | **Y** | **Dist. city centre [km]** | **Soil sealing** | **Pop. density [inh./ha]** | **Green area [%] per km²** | **Mean ann. temp. [°C]** | **Summer [d/a]** | **Annual prec. [mm]** | **Frost [d/a]** | **Snow [d/a]** |
| 1 | 3566289 | 5934843 | 1.0 | 6.4 | 22.6 | 0.9 | 9.7 | 28 | 737 | 55 | 19 |
| 2 | 3568750 | 5934849 | 3.3 | 7.7 | 37.5 | 5.1 | 9.5 | 27 | 747 | 57 | 19 |
| 3 | 3572126 | 5938422 | 7.2 | 6.9 | 41.5 | 19.8 | 9.2 | 27 | 776 | 61 | 19 |
| 4 | 3575503 | 5940879 | 11.4 | 6.3 | 53.0 | 15.2 | 9.1 | 27 | 783 | 66 | 20 |
| 5 | 3578533 | 5942634 | 14.9 | 4.4 | 36.4 | 51.9 | 8.8 | 25 | 801 | 71 | 24 |
| 6 | 3582956 | 5950430 | 23.0 | -- | 9.0† | -- | 8.7 | 25 | 798 | 73 | 25 |

*Gauss-Krüger coordinate system

†Population density is only given for the entire city of Ahrensburg (data: www.ahrensburg.de; retrieved 17th October 2013)

### 6.2.3 EXPERIMENTS

**GERMINATION EXPERIMENT**

To assess how temperature influences the germination percentages of *S. inaequidens*, seeds from each of the six populations from areas of different urbanisation intensity (50 seeds each) were germinated in Petri dishes at two temperature regimes (n=5): 15°C/10°C and 20°C/15°C (day and night, respectively) in climate cabinets (*Rumed*). The ambient temperature was chosen on the basis of temperature data of the DWD (German Meteorological Service (DWD) 2010, as a digital map with spatially interpolated values; reference period 1971-2000) by averaging monthly mean temperatures over the vegetation period and we added 5°C for the elevated temperature treatment. Altogether, 60 Petri dishes were used. For two weeks, the number of germinated seeds was determined daily and germinated seeds were removed. Non-germinated seeds were tested for viability. The percentages of germinated seeds from the number of viable seeds were calculated.

**COMPETITION EXPERIMENT**

To assess how temperature influences the performance of *S. inaequidens* in biotic interaction with a native plant species, a competition experiment of *S. inaequidens* seedlings under different treatments was conducted. We set up a three-factorial experiment with the factors urbanisation intensity (origin of the population on the urbanisation gradient), temperature (15°C/10°C and 20°C/15°C), and competition density (interspecific competition with *Achillea millefolium* L. using none, one and three competitor individuals). According to Asmus (1988), *S. inaequidens* is often displaced by *A. millefolium* amongst other species and has similar life-history traits.

On February 28th 2011, seeds of all six populations were sown on trays containing potting soil (*Floragard® Floradur B fein*) and put in a climate chamber (*Weiss Technik*) at 15°C/10°C (day/night-) temperature for a month. On March 31th, 30 random seedlings per population were planted in flower pots of 12 cm diameter and repotted again on May 10th in pots of 14 cm diameter. The substrate contained 50 % sand (*Quarzsand Korngröße 0.1-0.3 mm; Hakibau GmbH*) and 50 % potting soil (*Floragard® Floradur B fein*). We set up two competition treatments using different densities of *A. millefolium* planting one (low density) or three seedlings (high density) next to one seedling of *S. inaequidens* and a control with one *S. inaequidens* seedling without competition; hereafter called competition densities. All groups were replicated 10 times, adding up to 30 pots per population and 180 pots in total. The plants were grown for three more months until June 2011. The pots were distributed randomly and rotated several times per week during the experiment due to differences in light intensity in the chamber. The plants were watered on a regular basis and fertilised twice (in March and in May).

On 24th of June 2011 the same experiment was set up again with an elevated temperature of 20°C/15°C (day/night) representing an elevated temperature due to climate change. The experiment was also conducted for four months altogether and was completed at the end of October 2011. Due to limited availability of climate chambers we had to conduct both temperature treatments separately.

As response variables for growth we measured height of stem [cm], number of branches per individual plant, lengths and widths of longest leaf. Reproduction variables were number of flower heads per plant and number of flowering plants per treatment. Above- and belowground biomass were also determined. Aboveground biomass was dried for 48 hours at 60°C and dry weight [g] was measured. Belowground biomass was rinsed carefully to wash of the substrate and dried for 48 hours at 60 °C. Since preparing the root samples turned out to be extremely time-consuming, we only used 5 replicates per treatment. Belowground biomass of the two species could not be separated by hand, hence, we analysed the combined samples using Near-infrared-spectroscopy (NIRS) to distinguish the roots of both species following Roumet et al. (2006). Dried root samples were ground to 1 mm particle size.

Samples were scanned with a FT-NIR Spectroscope Vector 22/N (Bruker GmbH, Germany) in duplicate over the range of 1046 to 2715 nm. 50 samples with defined ratios of combined root material of *S. inaequidens* and *A. millefolium* ranging from 1.65/98.35 % to 98.45/1.55 % were used for calibration. We used the 'test-set-validation' method to develop several models, where the calibration data set was divided into two sets, a calibration and a validation set, by the computer software Quant 2 (Bruker Optics). Four different runs of validation for each species were conducted with different spectra for calibration and validation to find the best model. For more detailed descriptions of developing NIRS-models see Stolter et al. (2006). For each species the model with lowest mean variances of the differences between predicted and actual values were chosen to calculate the root proportions of *S. inaequidens* and *A. millefolium* ($R^2_{SI}$=98.25 % and $R^2_{AM}$=97.96 %). The final models were based on calibration data sets of 30 spectra for *S. inaequidens* and 37 spectra for *A. millefolium* and validation data sets of 50 (*S. inaequidens*) and 43 spectra (*A. millefolium*). If predicted root proportions of the two species did not add up to 100 %, we recalculated the proportions using the sum of both values as 100 %. These proportions were then used to calculate the belowground biomass [g] for both species from the weight of the combined root samples.

### HERBIVORY

To assess how temperature influences the performance of *S. inaequidens* in biotic interaction with a native animal species, a herbivory experiment of *S. inaequidens* seedlings under different treatments was conducted. We set up a three-factorial experiment with the factors urbanisation intensity (origin of the population on the urbanisation gradient), temperature (ambient and elevated), and herbivory (no herbivory and herbivory by snails).

In February 2011, seeds of the populations 1, 3 and 6 (Table 6.1) were sown in the greenhouse on trays with potting soil (*Floragard® Floradur B fein*) and in March, 50 seedlings per population were planted in flower pots of 12 cm diameter. The substrate contained 50 % sand (*Quarzsand Korngröße 0.1-0.3 mm; Hakibau GmbH*) and 50 % potting soil (*Floragard® Floradur B fein*). The pots were distributed randomly in the greenhouse and due to differences in light intensity rotated regularly during the experiment. The plants were watered on a regular basis and fertilised once in May. Since the plants exhibited strong increase in height rather than in width and density, which would be preferable for a feeding experiment, we needed to cut the main stem off at 20 cm height in May. Subsequently, all plants performed compensatory growth from lateral buds.

Molluscs can have a significant effect on plant fitness of *S. inaequidens* (Scherber et al. 2003). We used *Cepaea hortensis* and *C. nemoralis* as herbivores. Both species occur in mixed populations but do not hybridise (Jones et al. 1977, Bogon 1990), are generalist species and have the same food range (Carter et al. 1979). At the end of May 2011, 100 adult snails were collected in ruderal habitats and kept in plastic boxes until the experiment started. All snails weighed between 1.5 and 2.5 g and were kept without food for at least 24 h prior to the experiment. Five plants per population were treated with three snails each over a period of 14 days (herbivory treatment), five plants served as control without snails. All 60 plants were covered in gauze (mesh width 500 µm) to assure consistent herbivore density. After the herbivory period, all plants were subjected to a reaction period of another 14 days.

The experiment was conducted in a rigid-frame greenhouse in two chambers: an outer chamber next to the door represented ambient temperature conditions and an inner chamber without a door elevated temperature to simulate effects of climate warming. This chamber was additionally heated by a radiator at night time. For a detailed description of the installation of the temperature treatment see Baldwin et al. (2013). Temperature was recorded every 20 minutes with dataloggers (Ebro Serie EBI 20; Ebro GmbH, Ingolstadt, Germany). During our experiment, the average temperature difference between the chambers was 3.78 K over the four weeks of the experiment. But due to a warm weather period the herbivory treatment period was approx. 2 K warmer than the reaction period and the difference between day (8 am to 7.40 pm) and night (8 pm to 7.40 am) temperature was more pronounced in the ambient than in the elevated temperature chamber.

**Measurements of growth and production variables**

As response variables for growth and production we counted the number of leaves with feeding marks per individual plant and measured aboveground biomass, belowground biomass (both dried for 48 hours at 60°C to calculate dry weight [g]), height of stem [cm], number of branches per individual plant, number of flower heads per individual plant, and number of flowering plants per population. For a detailed description of the methods see Schulze (2011).

**Measurement of pyrrolizidine alkaloid (PA) content**

For the determination of pyrrolizidine alkaloid (PA) content five leaves of each plant were collected at the same time of day (van Dam et al. 1993), lyophilised immediately and then kept at -20°C. For analyses, the leaf samples were pulverised and homogenised. The alkaloid monocrotalin served as reference to determine the PA content, because its structure is similar to the Senecionin derivatives of the genus *Senecio*.

The PAs were extracted following Boer (1999) modified after Hartmann and Zimmer (1986). Finally the extracted PAs were determined by photometric analysis (at λ=n 562 nm) of “colour reaction” with Ehrlich reagent Boer (1999) modified after Mattocks (1967). A wavelength of 562 nm has been shown to be the mean extinction maximum of typical PA compositions of *Senecio* species (Mattocks 1967). The measured extinctions were converted into PA concentrations per mg dry weight. For a detailed description of the methods see Steinke (2011).

PA content was calculated with the following equation:

**PA content [µg/mg d.w.] = (E562 / 0.0207) * 1.135,**

where 0.0207 is the slope of the regression line and 1.135 is the recovery factor resulting from the relation of the extinction values of the measured reference E1 (colour reaction) and E2 (colour reaction + extraction).

Since it is impossible to obtain leaves with induced as well as not induced PA-contents from an individual plant, the induction intensity was calculated indirectly: We subtracted the average PA contents of the control group from the five replicate plants of each group and obtained induction intensity values that account for the mean inductive response (deviation from mean constitutive level) for each individual plant.

### 6.2.4 STATISTICAL ANALYSES

We conducted three-factorial ANOVAS with the factors urbanisation intensity (origin of the sample population along the urbanisation gradient), temperature (ambient/elevated), and native species treatment, i.e. herbivory (yes/no) and competition density (control (no competition)/low/high/). When assumptions of ANOVA could not be met, data was log- or square-transformed. Spearman rang correlations were calculated for seed mass and germination percentage with all growth and production variables for both temperature treatments separately. Since we did not obtain enough data for the reproduction measures in the competition experiment (only 21 % of all plants produced flower heads and 7 % flowered in total) statistical analyses could not be conducted.

Statistical analyses were carried out using SPSS (IBM SPSS Statistics, Version 21, 2012) and R (R development core team 2012) as well as Sigmaplot 12.0 (Systat Software, Inc. 2011) and GIMP 2.6.8 (The GIMP Development Team 2008) for plotting.

## 6.3 RESULTS

### GERMINATION

Seed mass differed significantly between all six populations (Figure 6.2a, Table 6.2). It could not be related to urbanisation intensity; on the contrary, the two populations farthest apart had similar seed masses. Germination percentage also differed significantly between populations and could not be related to urbanisation intensity (Figure 6.2b, Table 6.2). Germination was higher at elevated temperature, but the differences between germination at ambient and elevated temperature differed between populations (significant interaction). At ambient temperature, with increasing seed mass stem height ($\rho=0.89^{*}$), length of longest leaf ($\rho=0.83^{*}$) and above-ground biomass ($\rho=0.94^{**}$) significantly increased. At elevated temperature only stem height significantly increased with increasing seed mass ($\rho=1.0^{**}$). Germination percentage was not correlated with any variable, not even with seed mass.

**Table 6.2** Results of one- and two-factorial ANOVAs on the response variables seed mass and germination percentage of *Senecio inaequidens* with the factors urbanisation intensity and temperature. F-values and p-values (***=p<0.001, **=p<0.01, *=p<0.05, (*)=p< 0.1) are given.

| | | Seed mass [mg] | | Germination [%] | |
|---|---|---|---|---|---|
| **Source of variation** | **d.f.** | **F** | **p** | **F** | **p** |
| Urbanisation | 5 | 24.8 | *** | 17.5 | *** |
| Temperature | 1 | - | | 94.5 | *** |
| Temperature*Urbanisation | 5 | - | | 5.5 | *** |

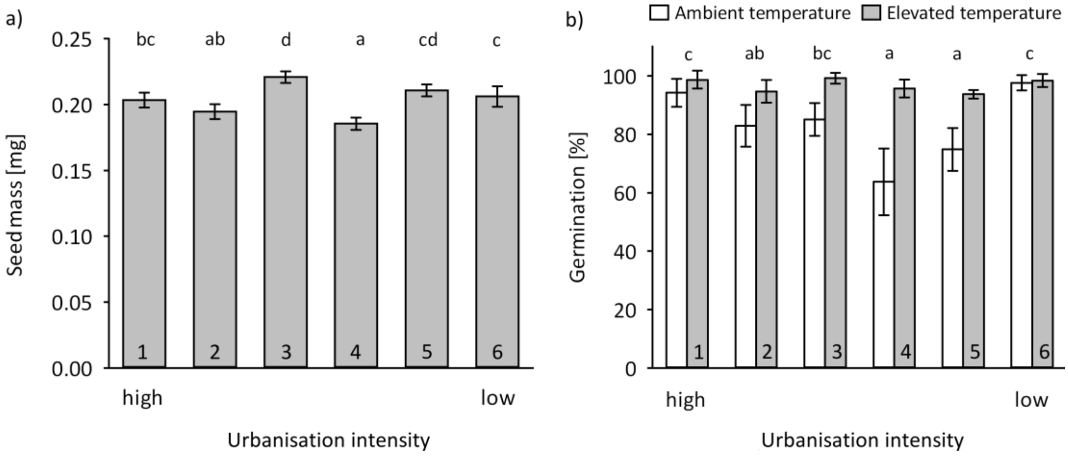

**Figure 6.2** Differences in **a)** seed mass between urbanisation intensity (populations from different origin along an urbanisation gradient) and **b)** germination percentage between urbanisation intensity and two temperature treatments (ambient and elevated). Numbers represent the six populations along the urbanisation gradient from areas of high urbanisation intensity (1) to areas of low urbanisation intensity (6), n=5. Mean and standard error are shown. For ANOVA results see Table 6.2.

## COMPETITION

All response variables (with the exception of number of branches) differed significantly between populations from areas of different urbanisation intensities (Figure 6.3, Table 6.3). Gradual differences due to urbanisation intensity could not be detected in any variable. With increasing temperature plants significantly grew taller (F=277.9***), produced longer (F=8.8**) and narrower leaves (F=36.4***) and less branches (F=54.4***). Contrarily, biomass (above- and belowground) was reduced with increasing competition density ($F_{\text{above}}$=369.5***, $F_{\text{below}}$=131.8***) and increasing temperature ($F_{\text{above}}$=142.1***, $F_{\text{below}}$=379.7***). Here, differences between temperature and competition density were more pronounced than those of leaf size. Competition had a significant negative effect on all variables: they decreased with increasing competition density. Leaf length and width differed significantly between urbanisation intensities at different temperatures ($F_{\text{length}}$=2.7*, $F_{\text{width}}$=3.8**). Stem height and aboveground biomass were significantly different in response to competition density under the two temperature treatments (stem height: low at ambient and decreasing at elevated temperature, F=3.7*; aboveground biomass: stronger decrease at ambient temperature, F=11.2***).

Fewer plants produced flower heads with increasing competition density. The number of plants producing flower heads was higher at elevated temperature, while at ambient temperature, not all populations had plants with flower heads (Figure 6.4).

**Table 6.3** Results of three-factorial ANOVAs of the response variables stem height [cm], number of branches (branches), length of longest leaf (leaf length) [cm], width of longest leaf (leaf width) [cm], aboveground biomass (abovegr. bm.) [g] and belowground biomass (belowgr. bm) [g] of *Senecio inaequidens* with the factors urbanisation intensity, temperature, and competition density and the respective interactions. The response variable stem height was log-transformed prior to analyses to meet ANOVA assumptions. F-values and p-values (***=p<0.001, **=p<0.01, *=p<0.05, (*)=p< 0.1) are given.

| Source of variation | d.f. | Stem height | | Branches | | Leaf length | | Leaf width | | Abovegr. Bm. | | Belowgr. Bm. | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | F | p | F | p | F | p | F | p | F | p | F | p |
| Urbanisation | 5 | 6.2 | *** | 1.2 | ns. | 11.6 | *** | 3.7 | ** | 6.8 | *** | 2.7 | * |
| Temperature | 1 | 277.9 | *** | 54.4 | *** | 8.8 | ** | 36.4 | *** | 142.1 | *** | 379.7 | *** |
| Competition | 2 | 48.8 | *** | 64.5 | *** | 79.4 | *** | 17.2 | *** | 369.5 | *** | 131.8 | *** |
| Urb * Temp | 5 | 0.6 | ns. | 1.2 | ns. | 2.7 | * | 3.8 | ** | 1.3 | ns. | 1.0 | ns. |
| Urb * Comp | 10 | 1.3 | ns. | 0.3 | ns. | 0.9 | ns. | 1.3 | ns. | 1.5 | ns. | 0.5 | ns. |
| Temp * Comp | 2 | 3.7 | * | 1.0 | ns. | 0.4 | ns. | 0.8 | ns. | 11.2 | *** | 0.9 | ns. |
| Urb * Temp * Comp | 10 | 0.8 | ns. | 1.2 | ns. | 1.3 | ns. | 0.4 | ns. | 1.7 | (*) | 0.5 | ns. |

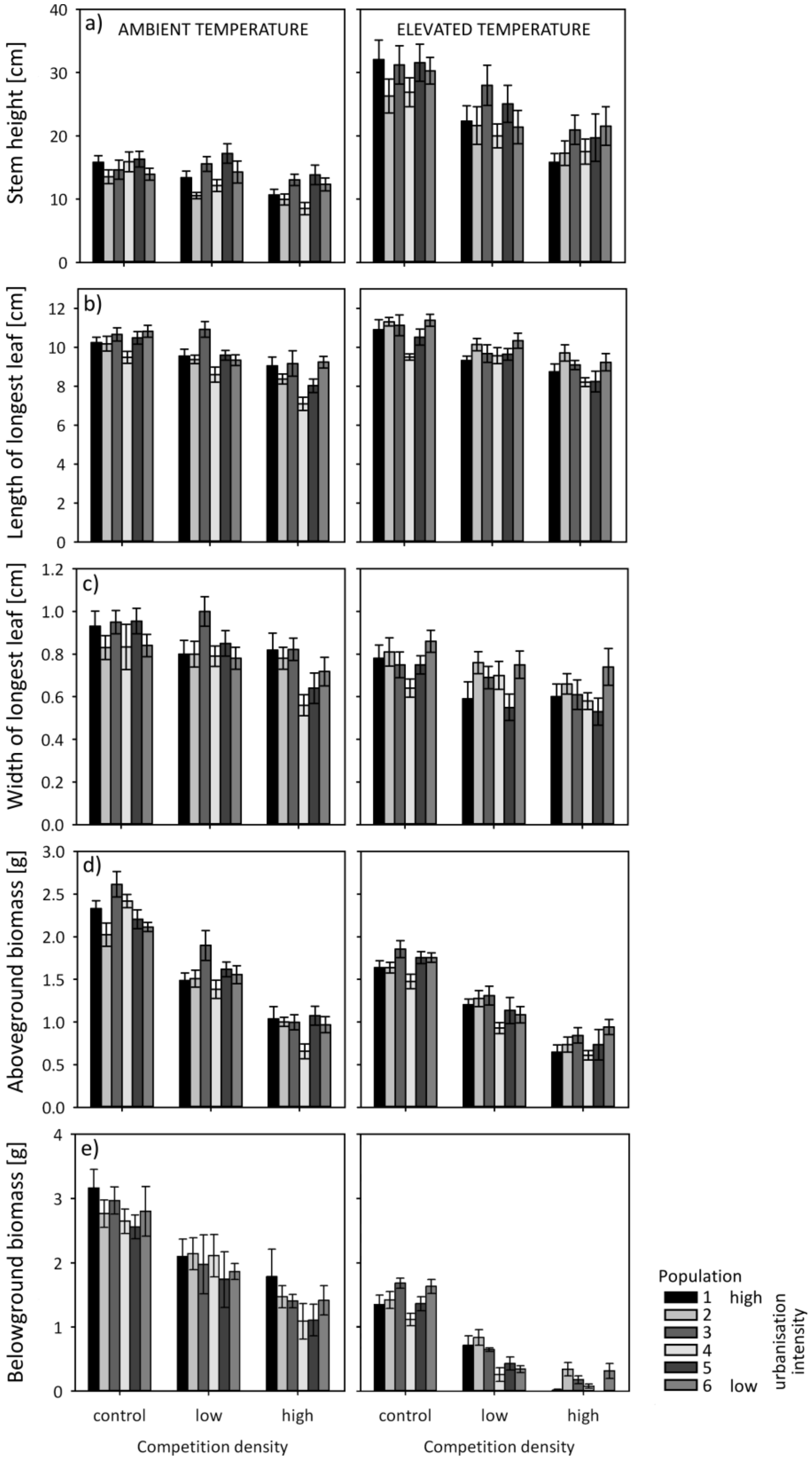

**Figure 6.3** Differences in **a)** stem height, **b)** length and **c)** width of longest leaf, **d)** above- and **e)** belowground biomass of *Senecio inaequidens* in competition with *Achillea millefolium* in different densities (low = one *A. millefolium* plant; high = three *A. millefolium* plants and a control without competition) under two temperature treatments (ambient and elevated). Bars represent the six populations from areas of decreasing urbanisation intensities from left (1, black) to right (6, dark grey), n=10. Mean and standard error are shown. For ANOVA results see **Table 6.3**.

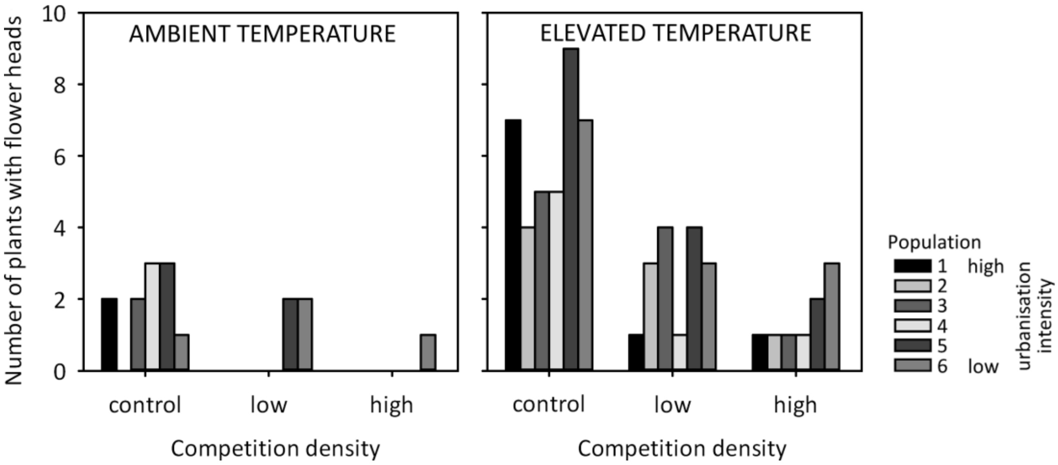

**Figure 6.4** Differences in number of plants with flower heads of *Senecio inaequidens* in competition with *Achillea millefolium* in different densities (low = one *A. millefolium* plant; high = three *A. millefolium* plants and a control without competition) under two temperature treatments (ambient and elevated). Bars represent the six populations from areas of decreasing urbanisation intensities from left (1, black) to right (6, dark grey), n=10.

**HERBIVORY**

Urbanisation intensity, temperature, and herbivory had no significant effect on stem height and number of branches (Table 6.4). Leaves were significantly shorter at elevated temperature (F=5.6*) and under herbivore treatment (F=6.2**, Figure 6.5, Table 6.4) and their response to temperature differed between urbanisation intensities (F=7.9**). Leaf width was smallest in highly urbanised areas (F=8.4***, Table 6.4). Stem diameter was significantly higher at ambient temperature (F=9.4**) and also higher in the group with herbivore treatment (F=10.9**, Figure 6.6, Table 6.4). Aboveground and belowground biomass only differed between urbanisation intensities; both were significantly lower in the highly urbanised area (F=6.7** and F=6.5**, Figure 6.7, Table 6.4). Number of flower heads was lower under elevated temperature, but not significantly.

The PA-content was slightly higher in the group with herbivory treatment (F=3.1$^{(*)}$, Figure 6.8, Table 6.5). This difference was largest in the highly urbanised population (Urbanisation*Herbivory F=2.4$^{(*)}$). The induced PA-content differed significantly between urbanisation intensities (F=7.2**), it generally decreased with decreasing urbanisation intensity (Figure 6.9a, Table 6.5). At elevated temperatures the induced PA-content was significantly lower (F=5.5*), but the pattern varied between temperatures (interaction F=7.6**): At ambient temperature, plants from the highly urbanised area induced most PA. At elevated temperatures, no clear pattern could be detected, variations were large, and standard errors were generally very high. At elevated temperature, slightly (but not significantly) less leaves had been fed on by snails (Figure 6.9b, Table 6.5). More leaves had been attacked by snails at plants from highly urbanised areas, no differences in medium and low urbanised populations were found.

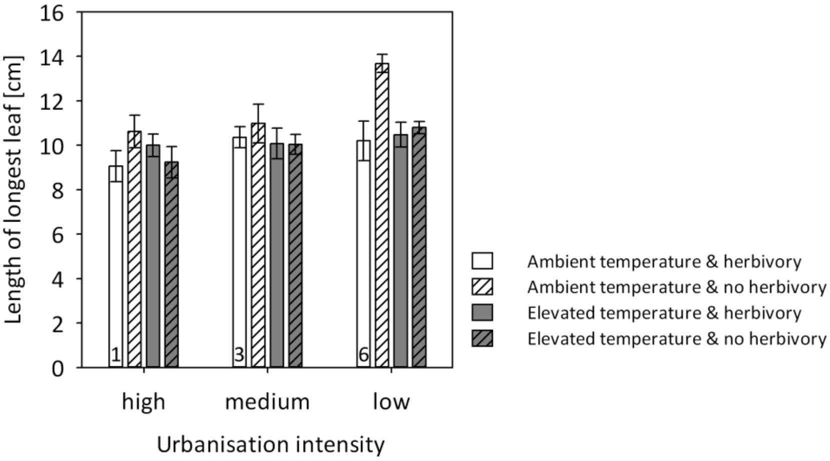

**Figure 6.5** Differences in length of longest leaf [cm] of *Senecio inaequidens* between urbanisation intensity, temperature (ambient and elevated), and herbivory treatment (herbivory and no herbivory). Numbers correspond to the populations from the competition experiment and represent the urbanisation gradient from areas of high urbanisation intensity (1) to low urbanisation intensity (6). Mean and standard error are shown. For ANOVA results see **Table 6.4**.

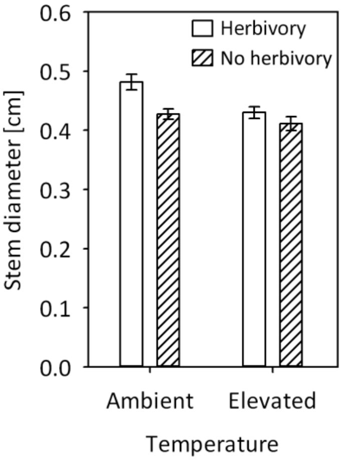

**Figure 6.6** Differences in stem diameter [cm] of *Senecio inaequidens* between temperature (ambient and elevated), and herbivory treatment (herbivory and no herbivory). Mean and standard error are shown. For ANOVA results see **Table 6.4**.

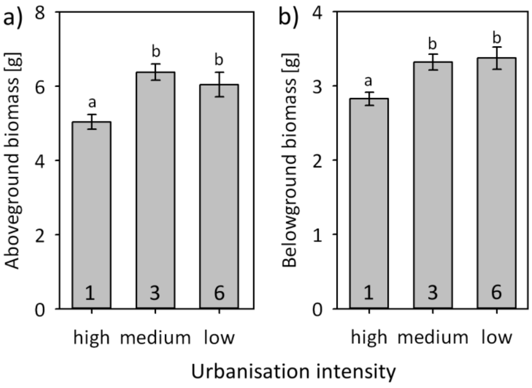

**Figure 6.7** Differences in **a)** aboveground and **b)** belowground biomass of Senecio inaequidens between urbanisation intensities. Different letters show significant differences in biomass between urbanisation intensities. Numbers correspond to the populations from the competition experiment and represent the urbanisation gradient from areas of high urbanisation intensity (1) to low urbanisation intensity (6). Mean and standard error are shown. For ANOVA results see **Table 6.4**.

**Table 6.4** Results of three-factorial ANOVAs of the response variables stem height [cm], number of branches (# branches), length of longest leaf (leaf length) [cm], width of longest leaf (leaf width) [cm], stem diameter (stem diam.) [cm], aboveground biomass (abovegr. bm.) [g] and belowground biomass (belowgr. bm) [g], and number of flower heads with the factors urbanisation intensity, temperature, and herbivory and the respective interactions. The response variable aboveground biomass was square-transformed prior to analyses to meet ANOVA assumptions. F-values and p-values (***=p<0.001, **=p<0.01, *=p<0.05, (*)=p< 0.1) are given.

| **Source of variation** | **d.f.** | **Stem height** | | **Branches** | | **Leaf length** | | **Leaf width** | | **Stem diameter** | | **Abovegr. bm.** | | **Belowgr. bm.** | | **Flower heads** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | **F** | **p** | **F** | **p** | **F** | **p** | **F** | **p** | **F** | **P** | **F** | **p** | **F** | **p** | **F** | **p** |
| Urbanisation | 2 | 0.4 | ns. | 0.7 | ns. | 3.8 | (*) | 8.4 | *** | 0.2 | ns. | 6.7 | ** | 6.5 | ** | 0.7 | ns. |
| Temperature | 1 | 0.5 | ns. | 0.1 | ns. | 5.6 | * | 1.4 | ns. | 9.4 | ** | 0.8 | ns. | 2.6 | ns. | 3.0 | (*) |
| Herbivory | 1 | 2.5 | ns. | 2.2 | ns. | 6.2 | ** | 0.0 | ns. | 10.9 | ** | 0.1 | ns. | 2.5 | ns. | 0.1 | ns. |
| Urb * Temp | 2 | 2.6 | (*) | 1.1 | ns. | 7.9 | ** | 0.5 | ns. | 0.9 | ns. | 1.4 | ns. | 0.2 | ns. | 1.9 | ns. |
| Urb * Herb | 2 | 2.2 | ns. | 0.4 | ns. | 0.8 | ns. | 0.9 | ns. | 0.9 | ns. | 0.2 | ns. | 0.1 | ns. | 2.0 | ns. |
| Temp * Herb | 1 | 3.2 | (*) | 0.1 | ns. | 2.0 | ns. | 0.1 | ns. | 2.6 | ns. | 0.2 | ns. | 2.3 | ns. | 0.5 | ns. |
| Urb * Temp * Herb | 2 | 1.1 | ns. | 0.4 | ns. | 1.0 | ns. | 0.7 | ns. | 1.5 | ns. | 0.1 | ns. | 1.0 | ns. | 1.3 | ns. |

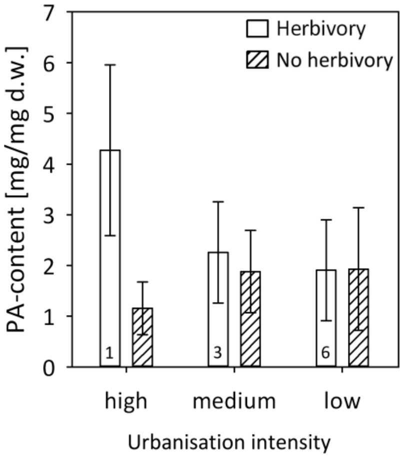

**Figure 6.8** Differences in pyrrolizidine-alkaloid-content (PA-content) between urbanisation intensities and herbivory treatment (herbivory or no herbivory). Numbers correspond to the populations from the competition experiment and represent the urbanisation gradient from areas of high urbanisation intensity (1) to low urbanisation intensity (6). Mean and standard error are shown. For ANOVA results see **Table 6.5**.

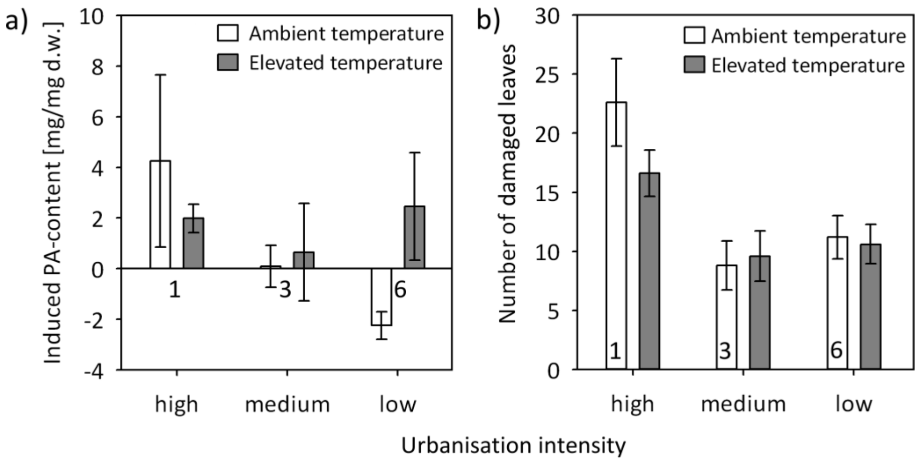

**Figure 6.9** Differences in **a)** induced pyrrolizidine-alkaloid-content (induced PA-content) and **b)** number of damaged leaves by snails between urbanisation intensities and temperature (ambient and elevated). Numbers correspond to the populations from the competition experiment and represent the urbanisation gradient from areas of high urbanisation intensity (1) to low urbanisation intensity (6). Mean and standard error are shown. For ANOVA results see **Table 6.5**.

**Table 6.5** Results of two and three-factorial ANOVAs of the response variables pyrrolizidine-alkaloid-content (PA-content), induced pyrrolizidine-alkaloid-content (induced PA-content) and number of damaged leaves by snails (# damaged leaves) with the factors urbanisation intensity, temperature, and herbivory and the respective interactions. The response variable induced Pa-content was log-transformed prior to analyses to meet ANOVA assumptions. F-values and p-values (***=p<0.001, **=p<0.01, *=p<0.05, (*)=p< 0.1) are given.

| | | **PA-content** | | **Induced PA-content** | | **# Damaged leaves** | |
|---|---|---|---|---|---|---|---|
| **Source of variation** | **d.f.** | **F** | **p** | **F** | **p** | **F** | **p** |
| Urbanisation | 2 | 1.0 | ns. | 7.2 | ** | 11.5 | *** |
| Temperature | 1 | 0.0 | ns. | 5.5 | * | 1.0 | ns. |
| Herbivory | 1 | 3.1 | (*) | - | | - | |
| Urbanisation*Temperature | 2 | 0.2 | ns. | 7.6 | ** | 1.2 | ns. |
| Urbanisation *Herbivory | 2 | 2.4 | (*) | - | | - | |
| Temperature*Herbivory | 1 | 0.7 | ns. | - | | - | |
| Urb*Temp* Herb | 2 | 1.8 | ns. | - | | - | |

## 6.4 DISCUSSION

### GERMINATION

Germination percentage was generally very high, but even higher under elevated temperature. This result is in accordance with Lopez-Garcia & Maillet (2005), who detected an optimum germination temperature range between 14 and 30°C. Germination takes course very rapidly, e.g. within a few days (Lopez-Garcia and Maillet 2005, Lenzewski 2010, K.J. Schmidt, unpublished results). These findings suggest that elevated temperature in course of future climate change may promote germination. The species might be superior to other species that do not germinate so effectively under elevated temperature. But also seedling establishment needs to be considered, which differs between habitats and seasons (Mediterranean area, Cano et al. 2007). The positive responses of *S. inaequidens*' germination to elevated temperature may be explained by the warmer and drier conditions in its native South-African distribution range.

## COMPETITION

Generally, our results show that interspecific plant competition and elevated temperature significantly influenced growth and biomass production of *Senecio inaequidens*. Furthermore, we detected differences in growth and biomass production between populations from areas of different urbanisation intensities.

As expected, competition had a negative effect on growth and biomass production of *S. inaequidens*. The higher the density of the competitors the greater was the effect. Our results confirm previous studies showing that competition reduced growth and reproduction in *S. inaequidens* (Scherber et al. 2003). Generally, competition with native species can have negative effects on the establishment and performance of invading non-native species (Levine et al. 2004). In contrast, several studies showed that non-native species are superior in competition with native species (Vilà and Weiner 2004, Verlinden et al. 2013, see Daehler 2003 for constraints). *S. inaequidens* is able to adapt to local competitive regimes (Lachmuth et al. 2011) and has been shown to be more competitive than native *Senecio* species (Verlinden et al. 2013). However, competitiveness of non-natives can depend on the performance of the competing native species and habitat conditions (Garcia-Serrano et al. 2007). In future, native competitors, who are not able to adapt as fast as the non-native species might suffer even more from changing climate and environmental conditions (Schweiger et al. 2010). But also differences between closely related non-natives were found: *S. inaequidens* was less sensitive than *S. pterophorus* to limited water availability and had a greater competitive ability under moderate stress conditions (Garcia-Serrano et al. 2004). With future climate change, competitive interactions might also be altered, because changes in different environmental conditions, e.g. elevated $CO_2$-concentration or atmospheric N deposition affect plant species differently (see Brooker 2006 for a review).

According to Grime (1974, 1979), *S. inaequidens* is assigned an intermediate ecological strategy type between competitor and stress-tolerator (CS), while *Achillea millefolium* is assigned the competition type (C). The C-type is characterised by efficient capture and utilisation of light, water, nutrients and space. These plants do usually not occur in habitats subjected to stress or disturbance (Grime 1974). The mixed CS-type is characterised by e.g. a perennial life cycle, but lower maximum potential growth rates than species with a C-type strategy and usually occur in habitats with moderate productivity and low disturbance intensity. In our study, biomass of both *S. inaequidens* and *A. millefolium* (results not shown) decreased with increasing temperature and increasing competition density, which indicates a similar response to competition of both species.

The competitive ability of invading species can be increased under climate warming (He et al. 2012). *S. inaequidens*' response to elevated temperature with higher growth and less above- and belowground biomass production indicates that the species may be affected by climate change. The reallocation from biomass to height might result from competition for light. *S. inaequidens* might outcompete smaller species or species that cannot adapt so quickly to changing conditions and eventually hinder them by shading. Contrarily to our results, Verlinden et al. (2013) found increased biomass for *Senecio inaequidens* in competition with *Plantago lanceolata* L. under elevated temperature. They related this finding to a higher photosynthetic rate under elevated temperature originating from acclimation. However, the species showed no response to warming regarding biomass production in another experiment without competition (Verlinden and Nijs 2010). If the native competitor is not able to react to elevated temperature as quickly as *S. inaequidens*, its growth might be limited. Competition for light could have also been biased by the artificial climate chamber conditions. Light quality is different and light quantity was lower than under field conditions.

Concomitantly with elevated temperature, soil water content can decrease, resulting in drought. Since we used the same watering routine under both temperatures, growth conditions might have been drier under elevated temperature due to higher evaporation. As a drought avoidance strategy, plants often allocate to roots, but we could not confirm this with our study: With elevated temperature belowground biomass decreased even more than aboveground biomass. Furthermore, *S. inaequidens* is adapted to drought (Ellenberg et al. 1992) and able to outcompete closely related species under moderate drought conditions (Garcia-Serrano et al. 2005).

Populations growing at different locations along urbanisation gradients are prone to different environmental conditions, which might affect growth and biomass production of plants. As *S. inaequidens'* first occurrence was recorded in the central port area in Hamburg, we assumed that the species gradually spread into less urbanised areas. The significant interactions of urbanisation and temperature in leaf length and leaf width might indicate local adaptation to temperature. However, we found no gradual tendency in the response variables along the urbanisation gradient. Local environmental conditions of microhabitats as well as population structure and genetics (e.g. maternal effects) seem to have a stronger effect than gradually changing environmental variables on a larger scale. Especially maternal effects seem to be a major cause for these population differences, because some growth variables were correlated with seed mass. Seed size, for instance, is considered as a trait with large maternal effects (Roach and Wulff 1987). Monty and Mahy (2009) found decreasing height and aboveground biomass of *S. inaequidens* with increasing altitude along a transect in France, but by comprising 200 km, their gradient was considerably longer than the one in our study. Therefore, differences in temperature and summer drought were probably more pronounced.

Furthermore, *S. inaequidens* exhibits a high plastic response across habitats and treatments. The species is able to cope with different environmental conditions over a wide gradient and competes successfully across this wide range of conditions (Cano et al. 2007, Garcia-Serrano et al. 2007). Different ecotypes of the species from three European regions, analysed by Scherber et al. (2003), differed significantly in morphological parameters and herbivore response. On a broader scale, Monty et al. (2013) could not clearly detect local adaptation of *S. inaequidens* to climate.

With our analysis we cannot disentangle local adaptation and phenotypic plasticity, hence, genetic analyses or transplantation studies should be conducted (see Monty et al. 2013 for a comprehensive approach using *S. inaequidens* as a case study species).

Urbanisation, e.g. the related urban heat island effect (see Schluenzen et al. 2010 for UHI in Hamburg), leads to differences in flowering time between urban and rural areas (Franzen 1955, Roetzer et al. 2000, Mimet et al. 2009). Regarding phenology, no differences were detected between flowering time and number of flowers between the six populations in the experiments. Nevertheless, in the highly urbanised city centre of Hamburg, *S. inaequidens* flowered earlier and set seed earlier than in surrounding less urbanised areas (K.J. Schmidt, pers. observation). In all populations, at elevated temperature more flower heads and flowers were produced and plants flowered earlier during the experiment. Differences between populations are most likely also attributed to maternal effects and general genetic constitution, but not to environmental impacts due to location on the urbanisation gradient.
We conclude that the species is able to react quickly to environmental conditions across a wide range due to phenotypic plasticity (see above: Cano et al. 2007). All populations react in their plastic range to environmental conditions and therefore also differ under the exact same conditions in the climate chamber environment. Local differences in their natural environment seem not to have influenced the populations and their genetic constitution (yet). Haider et al. (2012) could detect adaptation to the environment in non-native species, but on an altitudinal gradient with more pronounced differences in conditions. By using a longer gradient in our study, we might have encountered the problem that species in more rural parts have not been in the area for a sufficient period of time to adapt to local conditions.

### Limitations of the study

Results from the competition of only two species in controlled environment cannot be extrapolated to communities without uncertainties (see also Verlinden et al. 2013). Our results are merely a hint how *S. inaequidens* might respond to climate change in future. Environmental conditions in the climate chamber were artificial, e.g. the light regime might have been too dark compared to natural light. Furthermore, the lengths of day and night of 12 h is not always representative for the invaded range of *S. inaequidens*. Also growing conditions in pots can differ strongly from natural conditions and alter plant water relations and root structure (Gurevitch et al. 2002). In general, it would have been advantageous to have conducted genetic analyses to fully comprehend *S. inaequidens'* dispersal path and the relationships between the populations. It needs to be considered that due to the efficient dispersal of the species by vehicles and possible long distance dispersal, the spread may not only have occurred rather gradually, but also over further distances. Possibly, populations in less urbanised areas have been colonised by populations in highly urbanised areas because they are connected by some transport structure.

## HERBIVORY

Generally, plants from populations in highly urbanised areas had smaller leaves and less biomass then plants from populations in moderately and lowly urbanised areas. Temperature only had an effect on leaf length and stem diameter (both shorter and smaller at elevated temperature). Contrarily to the results of the competition experiment, stem height was not affected by temperature; this can be attributed to the cutting of all plants during the growing time previous to the experiment. Herbivory also only affected leaf length and stem diameter (reduced leaf length and higher diameter).

More leaves had been attacked by snails at plants from highly urbanised areas than at plants from medium and lowly urbanised populations. Accordingly, induced PA-content was higher in populations from highly urbanised areas, although it differed between temperature treatments. The measured PA contents of *S. inaequidens* were very variable between individuals; this is often the case in *Senecio* species (Vrieling et al. 1993, Carvalho et al. 2013). Nevertheless, the values are of similar magnitude as measured PA-contents of *Senecio squalidus* L. and *Senecio jacobaea* (Mattocks 1967, van Dam et al. 1993, Vrieling et al. 1993).
In agreement with predictions based on optimal defence theory, at sites with low herbivore pressure, populations are less constitutively protected against herbivore attacks. At sites with high herbivore pressure, populations are better constitutively protected (Zangerl and Rutledge 1996). Highly urbanised areas often harbour less potential herbivore species (McKinney 2002, Sadler et al. 2006, Lososová et al. 2011; see Magura et al. 2004 for contradictory results), which has also been shown for Hamburg (Denys and Schmidt 1998, Weller and Ganzhorn 2004). This leads to a gradient of decreasing herbivore pressure with increasing urbanisation intensity. Hence, in our study, the population from the highly urbanised area has been attacked most (number of damaged leaves is highest); most likely due to less constitutive defence, hence the induction of PA was high. The populations from the lesser urbanised areas have been attacked less due to better constitutive protection.

Regarding the detected differences between temperature regimes, plants in the colder chamber (ambient temperature) had increasing constitutive PA-content with decreasing urbanisation (increasing herbivore pressure). In the population from the highly urbanised area most PA was induced, in the medium urbanised population PA induction was low and in the less urbanised even negative. Here, PA content was reduced after herbivore attack, because resources were allocated to regrowth (see van Dam et al. 1993 for *Senecio jacobaea*). In the warmer chamber the tendencies were less clear: the population from the medium urbanised area had the highest and the less urbanised the lowest constitutive PA-content. This finding cannot be related to an urbanisation gradient featuring gradual herbivore pressure, but could be explained by abiotic factors that can influence PA synthesis, e.g. drought stress (Briske and Camp 1982, Vrieling et al. 1993, Kirk et al. 2010). Furthermore, the significant interaction of urbanisation and temperature in leaf length might indicate local adaptation to temperature.

According to the EICA hypothesis, plants from the invaded range have a stronger competitive ability than plants of the same species from the native range due to the lack of coevolved enemies and evolve lower defence but higher growth and reproduction, because resources are allocated (Blossey and Noetzold 1995, e.g. discussed in Bossdorf et al. 2005, Bossdorf 2013, Felker-Quinn et al. 2013). Transferred to our analysis of populations from areas of different urbanisation degrees, one could hypothesise that plants that do not invest in constitutive defence (in our case the “urban” plants), would exhibit higher growth and reproductive output. However, plants from the higher urbanised area had smaller leaves and produced less biomass than plants from lesser urbanised areas. One explanation is that the respective population would generally have reduced growth and less biomass due to genetic reasons or maternal effects (parental plants might have had insufficient nutrient supply or were prone to higher pollution). Against maternal effects one can argue that the highly and lowly urbanised populations did not differ significantly in seed mass. Also, in the competition experiment, the most urbanised population was not always smaller and less productive than the other two, which further indicates a connection to the herbivory treatment. In a study of *S. inaequidens* populations from different altitudes maternal effects were not found either (Monty et al. 2009).

The population originating from the area of medium urbanisation degree had most biomass and was less attacked. Concordantly, in the competition experiment plants from this population often had most aboveground biomass and longest leaves (e.g. control treatment at ambient temperature). Maybe this finding can be explained solely by genetic reasons or maternal effects. Maternal effects were related to seed mass (Monty et al. 2013) and to seed size (Roach and Wulff 1987). In comparison with our seed mass results, the higher above-ground biomass of the moderately urbanised population can be related to its larger seed mass. This population grew right next to a railroad track, and maybe evolved differently due to adaptations to local environmental conditions that differ from the other sites. Another explanation would be a higher gene flow caused by the efficient seed dispersal by train (Ernst 1998).

Although our results were not all significant and some were merely tendencies, they revealed *Senecio inaequidens'* ability to local adaptation on a small scale and indicate that climate warming might affect the interaction between *Senecio inaequidens* and its herbivores in the invaded range. A broader approach including all components of herbivore defence might have revealed clearer results than only looking at the PA-content (e.g. using bioassays, see Kempel et al. 2011).

**Limitations of the study**

Snails have obviously not been the best herbivores of choice but due to low abundances of *Longitarsus suturellus* (a specialised beetle species) in spring, we could not use beetles as initially planned. Due to the high ambient temperatures during the herbivory phase, snail activity was probably reduced in the chamber with elevated temperature treatment. To prevent snails from death, the plants under elevated temperature treatments were put in the colder chamber during three days of extreme heat. Hence, the temperature differences were not the same over the whole two weeks of herbivory treatment.

Instead of counting the leaves that have been fed on by snails it would have been more precise to determine the total area of the leaves damaged by herbivores per plant. When using molluscs as herbivores, this could be difficult, because these animals do not produce holes in the leaves like many insects. Therefore, it can be complicated to estimate the former total leaf area.

Regarding the PA measurements, the cutting of all plants during the growth phase could have provoked an early induction (van Dam et al. 1993). It would have been more precise to analyse PA content in all leaves and preferably also flowers, which usually express higher PA contents. But due to a limited timeframe and the fact that plants had to be also used for growth and production measurements, this was not possible.

In conclusion, elevated temperature in course of climate change will affect *Senecio inaequidens'* germination, growth, biomass production, and reproduction. The effects on future interactions with native species are less clear. Competition already influences growth of

*S. inaequidens* negatively today. This pattern did not change under simulated climate warming. But other factors like elevated $CO_2$ levels may have a different impact. Competition regimes will also depend on plant species composition in the invaded habitats, here, studies on more potential competitors are desirable. We found evidence for local adaptation on a small scale, but could not detect clear patterns under elevated temperature that bear hints for changes in future. However, *S. inaequidens* might adapt rapidly to future enemies and changing environmental conditions, and has the advantage that due to its South-African origin, the species is already adapted to warm and dry conditions.

## 6.5 ACKNOWLEDGEMENTS

We thank Sebastian Schmidt for valuable discussions and contributing ideas to the experimental design, Detlef Böhm and Thomas Tumforde for their help with the laboratory analysis of the pyrrolizidine alkaloid content, Klaas Vrieling (Universität Leiden, NL) for his comprehensive manual of the PA-analysis and advice on the interpretation, and Caroline Stolter for her assistance with the NIRS analysis. K. J. Schmidt thanks the School of Integrated Climate System Science (SICSS) for organisational support. The work was funded by the Federal Ministry for Education and Research within the research project KLIMZUG-NORD (grant number 01LR0805D).

# 7 GENERAL DISCUSSION & SYNTHESIS

## 7.1 INTRODUCTION

This study contributes to the understanding of biodiversity patterns in urban areas. McDonnell and Hahs (2013) state: “If cities are to successfully conserve biodiversity at local scales, the impacts of urbanisation on the biodiversity and ecology of urban areas need to be understood. This understanding must then be incorporated into the design, construction and management of our cities and towns to improve urban biodiversity outcomes.” In this thesis, richness, distribution, and performance of spontaneously occurring vascular plant species in Hamburg were analysed at different scales. On the largest scale, examining the entire city of Hamburg, vascular plant species richness and distribution patterns were analysed and related to potential drivers and spatial impact. On the same scale, the application of floristic mapping results to urban climatology was tested to analyse whether plant species’ temperature preferences can serve as proxy data for the long-term urban heat island (UHI). On a smaller scale, looking at select habitats, species richness along an urbanisation gradient was analysed, comparing anthropogenic with semi-natural habitats. Finally, on the smallest scale, responses of a non-native species to biotic interactions at elevated temperatures were studied along an urbanisation gradient.

The main questions addressed in this thesis were: How are plant species and species richness distributed in Hamburg and what drivers affect these distribution patterns? What role does the urbanisation gradient play? Can differences in vegetation patterns be related to urbanisation intensity? Can data derived from species distribution be applied in other research areas? Finally, how does a non-native species respond to biotic interactions with native species at elevated temperatures?

## 7.2 DEFINING URBANISATION

Since urbanisation measures are difficult to define and generalise (McIntyre et al. 2000, McDonnell and Hahs 2008, Raciti et al. 2012), in this thesis two attempts were made to define urbanisation intensity for Hamburg. In Chapter 2 an index was calculated to account for Hamburg’s particular structure. Here, urbanisation cannot be defined by a single variable like population density or distance to the city centre; hence, several variables were integrated into the index. The pattern resulting from the division of the grid cells by the index into high, medium, and low urbanisation intensity is well reflected in the land-use distribution in Hamburg (Figure 1.5, Chapter 1). In Chapter 3, tests determined whether plant species distribution reflects the urban structure of Hamburg. Patterns in species composition based on presence-absence data were analysed by cluster analysis. Floristic composition revealed a strong correlation to Hamburg’s geography and was attributed to different urbanisation zones. These were first separated by the former glacial valley of the river Elbe and moraine landscape and further by urbanisation intensity distinguishing city centre, suburban and rural areas. The results match findings for the city of Plymouth (UK), where urban structure patterns were reflected in the city's flora on the same scale (Kent et al. 1999). Dana et al. (2002) divided the city of Almeria (Spain) into different zones according to plant species composition. These zones were then related directly to urbanisation, i.e. age of building: 1) built up until 1850, 2) up until 1960-70s, and 3) recently urbanised and harbours rural fragments next to typical urban communities.

A general problem in urban areas is the collinearity of environmental variables. Several environmental conditions change gradually along urbanisation gradients (e.g. McKinney 2002) and are hence strongly intercorrelated. In this thesis, temperature, soil sealing, Ellenberg indicator for moisture (EIM), and Ellenberg indicator value for temperature (EIT) were highly correlated with both distance to the city centre and population density; soil sealing was further correlated with proportion of protected area (Chapter 2). These relationships indicate how challenging it can be to disentangle environmental effects in urban areas, even more so since the variables are also spatially influenced. To reveal the effects of environmental conditions on plant species composition, it is important to integrate spatial analyses in studies of species composition (e.g. Dray et al. 2012). In Chapter 3, spatial variables were used to partition the variation in species composition between environmental and spatial impact. The analysis revealed that both environmental conditions and spatial structure affected species composition, but spatially structured environmental conditions had the largest impact. Hence, space and environment could not be distinguished completely. So far, the few studies in urban areas including space in a similar way in species composition analysis report differing results: In a study of several organism groups across cities, Chytrý et al. (2012) detected spatial structure caused by dispersal limitation, while pure environmental variables explained rather little variation. In contrast, Sattler et al. (2010) found only weak spatial structure in urban animal communities in select habitats. In conclusion, the definitions of urbanisation derived from environmental and spatial variables as well as by species composition for Hamburg developed in this thesis seem to be good measures for urbanisation intensity. Nevertheless, the transferability of these measures to other cities still needs to be tested.

## 7.3 PLANT SPECIES RICHNESS, DISTRIBUTION AND APPLICATION OF FLORISTIC MAPPING DATA

Overall species richness of spontaneously occurring vascular plant species in Hamburg was 1,217 species, of which 12 % were non-natives and 38 % were endangered (Chapter 2). In comparison with other European cities, Hamburg has the sixth highest total plant species richness and the ninth highest proportion of non-native species (Figure 7.1, Kelcey and Müller 2011). The proportion of non-native species ranges between 9 % (Bratislava, Sofia, Vienna, Warsaw) and over 30 % (London, Moscow); thus, Hamburg ranges in the bottom third. As discussed in Chapter 2, this could be attributed to the rather strict definition of non-native species applied in this thesis.

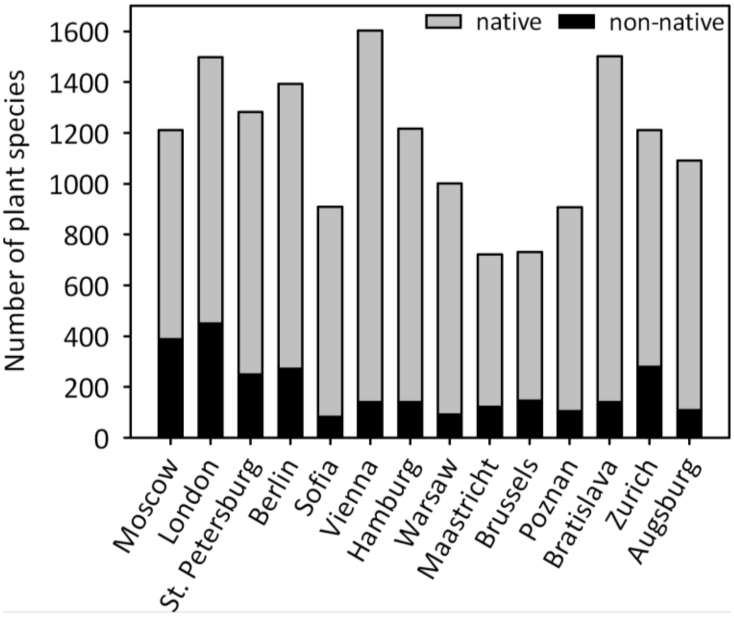

**Figure 7.1** Plant species numbers of native (grey) and non-native species (black) for different European cities in comparison to Hamburg. Cities are arranged by their human population size in decreasing order from left to right. The bar plot is adapted from Kelcey and Müller (2011), who published reports on plant species and habitats of European cities. Data for Hamburg were added from the results of this thesis.

Urbanisation intensity affected plant species richness measures differently. Total plant species richness differed only slightly between the different urbanisation zones. In contrast to other studies, species richness in grid cells with medium degrees of urbanisation was not highest (e.g. Kent et al. 1999, Zerbe et al. 2003, Lososová et al. 2011). Non-native and thermophilic species richness increased with urbanisation, while endangered species richness decreased. One the one hand, the resulting patterns in richness and distribution of spontaneously occurring vascular plant species in the city of Hamburg were in agreement with the results of studies of other areas, but on the other hand they reflected some special features of Hamburg's particular landscape that differ from other cities.

First of all, moderately urbanised areas (e.g. "suburban" or residential areas) in Hamburg were not richest in plant species. This finding is in contrast to what has been demonstrated in and across other cities (see above). At two different scales, neither plant species richness of the entire city nor that of select habitats peaked in moderately urbanised areas in Hamburg (Chapter 2 and Chapter 5). Since species richness has been attributed to habitat diversity (Chapter 2), one could have anticipated that these areas – which are generally seen as very heterogeneous urban landscapes – were also richest in species. Obviously, Hamburg has other areas rich in species that exceed these heterogeneous suburban areas in species richness. Generally, densely built-up areas affect species richness negatively (Godefroid and Koedam 2007, McKinney 2008, Ranta and Viljanen 2011). However, the results presented in Chapter 2 showed that grid cells in the central port area were among the cells richest in species, and in Chapter 3 the "urban & industry" cluster was identified as the cluster with the highest species richness. Here, many of the associated grid cells were located in the port area. The port's special features leading to high species richness were discussed in Chapter 2. The "semi-natural" cluster was the second richest in plant species and comprises bog, heath and forest habitats. Large parts of its area are nature reserves. It is also the northernmost cluster apart from a few outliers and harbours several psychrophilic species, indicating a less urbanised area. Furthermore, it harbours several endangered species and a substantial amount of forest area.

Second, patterns revealed of non-native species matched previously detected patterns in other studies: number and percentage decrease from city centre to the surroundings along with decreasing urbanisation (e.g. Celesti-Grapow and Blasi 1998; Zerbe et al. 2003, Brunzel et al. 2009), while Ranta and Viljanen (2011) detected the highest number of non-native species in suburban areas. Non-native species were correlated with decreasing EIM, increasing mean annual temperature and high degree of soil sealing, and decreasing proportion of protected areas reflecting conditions found in highly urbanised areas. With distance to the city centre these variables change gradually (Chapter 2). On the smaller scale, non-native species richness could not be assessed, as non-native species were removed at some sites in the course of conservation management (Chapter 5).

Third, richness patterns of endangered species mostly matched previously detected patterns. In general, urbanisation threatens rare species. Therefore, these are often restricted to semi-natural remnant habitats or protected areas usually located outside the urban centre (Knapp et al. 2009, Kowarik 2011). However, in calcareous grasslands along an urbanisation gradient, the number of endangered species generally decreased with increasing urbanisation, but some of them occurred only in urban sites (Albrecht and Haider 2013). In addition, rare plant species in urban landscapes are not necessarily prone to extinction and small isolated plant populations in California (U.S.) performed as well in urban as in rural landscapes (Lawson et al. 2008). However, urbanisation has negative impacts especially on species restricted to wetland and nutrient-poor sites (Knapp et al. 2010, Dolan et al. 2011). In this thesis, endangered species richness was positively related to high EIM and low Ellenberg indicator value for nutrients (EIN). It further increased with the proportion of protected area, which correlated with distance to the city centre and also with the availability of unsealed habitats. The pattern of endangered species richness followed general understandings: More extreme habitats are usually found in areas less disturbed by anthropogenic influence, e.g. rural areas. Here, semi-natural remnant habitats occur more frequently than in more disturbed areas. In Hamburg these are bogs, heath lands, forests, and the inland dunes at ‘Boberger Niederung’. These habitats harbour specialist species that are adapted to extreme conditions (e.g. low nutrition availability, low soil pH, high moisture) not found in urbanised areas. These conditions are also reflected by the mean Ellenberg indicator value (EIV) per cluster. Those species (and their habitats, respectively) are especially threatened by urbanisation (Knapp et al. 2009). Yet in the urban-industrial areas as well, high proportions of endangered species were found. This is probably also due to extreme habitat conditions: dry and sandy soils, higher temperatures as well as frequent disturbance, and has been elaborately discussed in Chapter 2.

The environmental gradients identified in Chapter 3 by ordination techniques were strongly related to urbanisation intensity, i.e. the first gradient ranged from central, sealed, dry and warm conditions to peripheral, less sealed, moist and colder conditions, while the second gradient represented a turn-over from open habitats under the influence of the river valley to more shaded moraine habitats distant to the river. Along these gradients, both non-native and endangered species can be located via specific species traits.

Urban characteristics like higher temperature and drier soil favour R-strategists, annuals and therophytes (Prach et al. 2001, Knapp et al. 2008). Since the most important drivers for non-native species richness were higher temperatures and drier soil (Chapter 2), several non-native species can be located here. The arrival of new non-native species via the central port is also a reason for high numbers of non-natives in the city centre, e.g. by escaping during port activities (see *Senecio inaequidens*; Chapter 6). Williams et al. (2009) predict that urbanisation will support simple plant communities from a narrow range of families with traits that can tolerate urban conditions.

On the contrary, many specialist species have habitat requirements that are more complex and in a narrower range of tolerable conditions. Endangered and rare species are often species with specific and narrow habitat requirements (Rabinowitz 1981). At the less urbanised end of the gradients, rather long-living species and species proxies associated with forest habitats distant to the river were found. This corresponds well to Prach et al. (2001), who found perennials associated with less humanly altered and forested sites. These could provide suitable habitats for species threatened by urbanisation. In the studies of this thesis, the port flora harboured several endangered species that seem to tolerate some urban conditions. By trait analysis only, these species might not have been identified as endangered and rare species due to their traits and habitat requirements, which are more similar to traits of common “urban” species.

The previously discussed patterns are mostly somewhat related to the temperature distribution in Hamburg, and temperature is certainly influenced by urbanisation intensity. Most distinctly, the distribution pattern of thermophilic species richness (i.e. species with an EIT higher than 5; Goedde and Wittig 1983) was influenced by mean annual temperature. Hence, proportions of thermophilic species reflected the pattern of the UHI (Chapter 2). The proportion of thermophilic species was highest in the urban core and a few other highly urbanised areas (Neugraben/Neuwiedenthal and Harburg in the south). Consequently, the EIT were used in Chapter 4 serving as temperature values integrating a longer time period. Since the city of Hamburg does not maintain a spatially comprehensive network of measuring stations for climatic data, the floristic values provided a good proxy for long-term temperature measurements and were strongly correlated with UHI data calculated by Schluenzen et al. (2010). This study demonstrates a promising possibility for the application of floristic mapping data in urban climate research.

Values derived from floristic mapping data can also be applied in other areas. The plant species composition in a city is very specific to the respective area and high turnover is found on the scale of 1 km². Species richness is a measure derived from species composition that can help shed light on areas within a city that are important for biodiversity and hence nature conservation. Species-rich habitats should be the focus of conservation measures and be maintained and promoted. However, more abstract measures can also be derived from species composition and indicate possible vulnerable areas and features. For instance, besides temperature preferences in Chapter 4, the species proxies phytosociological classes and traits have been used to explain drivers of urban plant species composition more accurately (Chapter 3). Since both proxies are representatives of the actual species composition, but on a much coarser scale, they can be compared between cities. When analysing species composition of an area, looking at species proxies seems a promising way to generalise findings and make them comparable. According to Thompson and McCarthy (2008), the analysis of traits can reveal important patterns in vegetation that cannot be derived from purely floristic analyses.

In summary, Hamburg's spatial conditions differ from those of other cities. The central city centre comprises typical urban landscapes with high building and population density, but also the port area with large industrial areas, low population density, and surprisingly high species richness. Therefore, we could confirm neither a decrease in species richness towards the urban core as reported by other studies nor a peak in species richness in suburban areas (e.g. McKinney 2008).

## 7.4 POSSIBLE IMPACTS OF CLIMATE CHANGE ON URBAN VEGETATION

The influence of urbanisation along urban-to-rural gradients on species distribution and ecosystem processes has been investigated in many studies (see McDonnell and Hahs 2008 for a review). Some present urban environmental conditions represent conditions expected under future climate change, i.e. elevated temperature (Oke 1982), drier soils (Wittig 1991), elevated atmospheric $CO_2$ levels (George et al. 2007), and hence earlier flowering (Roetzer et al. 2000) and prolonged growth periods (Luo et al. 2007). Besides examining the effects of urbanisation on species and communities, urbanisation gradients have been used to analyse possible future effects of climate change. Conditions in urban areas were used as a 'space-for-time substitution' for climate change (e.g. Ziska et al. 2003, Carreiro and Tripler 2005, George et al. 2009, O'Brien et al. 2012 ).

Nevertheless, Carreiro and Tripler (2005) also state that "many factors co-vary in space and time along urban-rural gradients and their individual effects may be impossible to separate". In the studies of this thesis, urbanisation intensity seemed to have a stronger impact on vegetation than climate. For instance, climate variables could not be clearly separated from distance to the city centre and soil sealing variables (Chapter 3). Hence, climate could not be related to plant species distribution patterns directly. Furthermore, land use history depends on urban development and has a strong effect on vegetation. In Chapters 2 and 3, agricultural areas of Hamburg were shown to be especially species-poor, but this can be attributed more to intensive land use than to environmental conditions. Since this area is former marsh land, the soil is still moist and nutrient-rich, which could have favoured species richness under less intensive agricultural use.

It can be concluded that the approach of 'space-for-time substitution' along urbanisation gradients could not be applied successfully in this thesis. Too many correlated factors blur the climatic effects and these could not be distinguished from other influences. In Chapter 3 for instance, environmental conditions were shown to be strongly spatially structured and the environmental variables were themselves intercorrelated (Chapter 2). Moreover, in Chapter 6, differences in the performance of the non-native species *Senecio inaequidens* could not be related to an urbanisation gradient representing temperature decrease. However, local adaptations to different degrees of herbivore pressure resulting from urbanisation were shown.

The studies of this thesis show that vegetation is sensitive to climatic conditions (Chapter 4), but climatic effects are always intermixed with urbanisation impact. Hence, impacts of climate change can only be estimated. The analysis of floristic mapping data from only one point in time cannot properly reveal changes in floras over time and hence lead to certain predictions of changes in future. One can conclude that temperature does have an effect on species distribution and range shifts can be expected with climate change. Furthermore, species that now occur in the urban centre but are not adapted to warmer and dry conditions might migrate to the surrounding areas where their habitat preferences are met better in future. Several non-native species occurring in cities today originate from Mediterranean habitats; these could extend their range within the city (Wittig et al. 2012). Consequently, suburban areas might experience higher species richness in future – if habitat heterogeneity and the possibility to reach those habitats are maintained by urban planning and development. However, currently protected areas that are located mainly in less urbanised (rural) areas might also experience changes in species composition. In combination with increasing urbanisation, climate change might drive species adapted to rather cool habitats to extinction in the study area and induce range shifts further north. Moreover, effects of urbanisation and climate change need to be distinguished: urbanisation might reduce the habitat availability of semi-natural habitats not under protection directly or restrict it by fragmentation, whereas climate change might alter habitat conditions due to warming and decreasing summer precipitation, especially towards 2100. The species-rich flora of the port area is probably already better adapted to climate change since conditions here are similar to those expected in future. Here, urban development and port development will probably be a stronger threat to species. Conservation needs to take action, so that particular species-rich habitats, e.g. dry grasslands and wasteland sites, will not be lost. However, new species are expected that migrate from other regions and may already be well adapted to future conditions in Hamburg. Thus, overall species richness altogether will probably not be affected much, but most likely the ratio of native and non-native species will change towards more non-native species.

To investigate effects of climate change on species in detail, elaborate studies on single species need to be carried out, as conducted in Chapter 6. When investigating single species, "flagship" species should be chosen that represent groups of species with a similar background, life history, and traits, as such analyses are very complex and time-consuming. For instance, choosing *Senecio inaequidens* as a study species served as an example of a non-native species that spread rapidly in Europe and results might hence be carefully projected to species with a similar invasion history. In the case of *S. inaequidens,* its special herbivore defence strategy has to be considered. Hence, the response of *S. inaequidens* to elevated temperature cannot be transferred directly to other species, but it might be related to other species of the genus *Senecio.* Since Bergmann et al. (2009) identified the Iberian Peninsula as a possible future species pool for Germany, more native and non-native species of that genus might migrate to Central Europe (see Garcia-Serrano et al. 2004, Garcia-Serrano et al. 2005 for studies on *Senecio* species in Spain).

Climate change and non-native species will create novel plant communities in future (Schweiger et al. 2010). When non-native species become introduced into new ranges and communities, they encounter different competition regimes and new enemies. *S. inaequidens* seems to be a strong competitor and has adapted to local enemies (Chapter 6). The increase in germination percentage and the rapid germination course of *S. inaequidens* under elevated temperature in combination with higher flower production and earlier flowering suggests that *S. inaequidens'* reproduction will be favoured by climate change. Consequently, seed output and the reproduction rate may increase. Its flowering period is terminated by frost (Ernst 1998), but in the course of climate warming, winter frost may be delayed, resulting in a prolonged flowering period.

The ability of rapid local adaptation has been confirmed in Chapter 6. Here, different pyrrolizidine alkaloid (PA) contents (a toxic secondary metabolite compound) in leaves of *S. inaequidens* between populations from areas of different urbanisation degrees have been identified. These differences could be attributed to local herbivore pressure, which is lowest in urbanised areas. Local adaptation has also been shown for *S. inaequidens* by Lachmuth et al. (2011), but the scale considered in the study of this thesis is much smaller. Differences in growth and biomass production between populations are most likely further attributed to maternal effects and general genetic constitution. The local adaptation to herbivore pressure could not be clearly related to increased temperatures and hence be transferred to possible future climate. However, the ability of local adaptation indicates that *S. inaequidens* will be able to adapt to future enemies and changing environmental conditions.

The results concerning biotic interactions with native species are not directly transferable to other species since these interactions are species-specific. Climate change will affect all species in a specific way and thus change species communities of urban habitats. Non-native species might compensate for native species that are lost due to climate change and the expected range shifts as well as phenological interruptions (Visser and Both 2005, Parmesan 2006, Schweiger et al. 2010). Some species might need to switch hosts (Schweiger et al. 2010) and hence newly introduced species like *S. inaequidens* may serve as new hosts for native species.

## 7.5 APPLICATIONS FOR BIODIVERSITY CONSERVATION IN URBAN AREAS

Although biodiversity in cities is rather homogenous across the world (Kuehn and Klotz 2006, McKinney 2006, Wittig and Becker 2010) and Germany does not have a legal obligation to protect urban biodiversity (Wittig et al. 2012), motivations behind conservation in urban areas are manifold. They include conservation of local biodiversity, the creation of stepping stones in habitat networks to promote dispersal of natural populations, understanding species' response to global change for better protection in future, environmental education, provision of ecosystem services, and general improvement of human well-being (Dearborn and Kark 2010). Urban areas are still mostly disregarded by nature conservation (e.g. by the European Commission's Habitats Directive; Kelcey and Müller 2011), but several studies emphasise the importance of integrating urban habitats into conservation measures and urban planning (e.g. Niemelä 1999, Kattwinkel et al. 2011, Kowarik 2011, Sushinsky et al. 2013). Special attention should be paid to those species that are endangered or area-specific and therefore indicate valuable habitats that are worth protecting.

Floristic mapping data and the results from the analyses of this thesis can be used to identify valuable areas for conservation practice and hence provide important impacts for urban planning (e.g. Dana et al. 2002). Muratet et al. (2008) developed an index of floristic interest from richness, nativeness, typicality, and rarity of species that can be integrated into conservation practice to decide on preservation of biodiversity in urban areas. The analysis of floristic mapping data as a proxy for the UHI (Chapter 4) can be used to identify areas in cities that are prone to heat stress and might negatively affect human well-being. Areas of high species richness and larger numbers of rare species should be considered for conservation measures.

The results of this thesis show that in Hamburg special attention needs to be paid to both the port vegetation and the vegetation of semi-natural habitats, since these areas are richest in species and harbour rare and endangered plant species. In the port area, measures should include the protection of the valuable dry grasslands that are specific to Hamburg's landscape (Poppendieck et al. 2010) and are amongst the species-richest habitats in Europe (Wilson et al. 2012, Habel et al. 2013). Therefore, these areas should be incorporated into nature conservation practice in Hamburg and be designated as nature reserve.

Another focus should be on the conservation of wasteland sites as habitats. In the course of a dynamic nature conservation approach, Kattwinkel et al. (2011) suggest 'temporary conservation' for wasteland sites. The authors found the highest conservation values (i.e. species richness of plant and animals) on wasteland sites after 15 years of abandonment and conclude to leave urban areas open for such a period of time before redevelopment. They further propose promoting different successional stages in an area and hence focusing on the landscape scale instead of single sites only. This approach could be integrated into urban planning in Hamburg.

The protection of semi-natural remnant habitats in urban areas is important for biodiversity conservation, since typical man-made urban habitats are not suitable for a wide range of species (Kowarik 2011). Conservation of the semi-natural habitats should focus on maintaining or extending their conservation status by law and prevent further fragmentation by urban development. Plant species already inhabiting these ecosystems should be protected and new species should be allowed to migrate. Therefore, a functional habitat network needs to be established and maintained. Recent studies suggest including private gardens in such networks (Rudd et al. 2002, Goddard et al. 2010), which could improve habitat connections and thus enhance biodiversity. This approach could also yield potential for nature conservation in Hamburg, since private green space covers large areas in the city.

Besides the conservation of semi-natural habitats, new species assemblages and novel ecosystems should be part of conservation strategies. Non-native species included in new species assemblages after habitat transformation are likely to be better adapted to the new conditions than previous native species communities (Kowarik 2011). Regarding future urban planning, promoting spontaneously occurring plant species would be advantageous, because these are adapted best to prevalent climatic conditions (Wittig et al. 2012). Hence, urban development should leave more room for spontaneous flora and incorporate extensively managed areas into urban green space and local parks.

A further motivation to protect urban nature is education of the human urban population. Since more and more people will live in cities in future, their main contact with biodiversity and vegetation will be via urban nature. Hence, awareness and appreciation need to be raised amongst the population for integrating nature conservation measures into urban planning. Conservation scientists need to interact with urban planners, land managers, policy-makers, and the public (Miller 2005). Environmental education of the public will be an important task in future as “the critical factor in preserving plant species diversity will be developing public support for natural areas in parks” (DeCandido 2004). People need to reconnect with nature, as experiences with biodiversity and wildlife are essential for global conservation action. People are not likely willing to invest in protection if they do not value nature because it is not properly integrated in their day-to-day life (Miller 2005, Faeth et al. 2011). More appreciation for urban vegetation could be achieved by incorporating environmental education into school curricula so that children learn to value nature from a very young age.

## 7.6 OUTLOOK

The results of this thesis could be used to compare future species richness and composition with the patterns derived here. Good examples for comparable studies are those by Godefroid (2001), Chocholoušková and Pyšek (2003), Tamis et al. (2005), and Knapp et al. (2010), who revealed important results regarding the change of floras over time in relation to urbanisation. Correspondingly, the impact of climate change could also be assessed more thoroughly when comparing data from two points of time. Moreover, the comparisons of the results across cities (e.g. Lososová et al. 2012a) would be desirable. Generalisations in a broader global context could thus be derived, which is a task worth pursuing in future urban ecology (McDonnell and Hahs 2013). In urban areas, environmental variables are highly intercorrelated (see above), so the analyses revealed no clear impact of temperature or precipitation patterns yet. Furthermore, climate (i.e. temperature and water availability) acts differently on plants in different phases of their life cycle. To identify possible effects of climate change on vegetation in cities, it may be promising to focus on single species or communities (see Chapter 6), since climate change can be directly simulated in experiments by elevating temperature or $CO_2$, while fully excluding other impacts. If analyses were conducted on several important “flagship” species, the results could then be possibly transferred to the flora of a city. One could also focus on traits or phytosociological classes and hence project the results via species proxy distributions. Since humans are dominant in urban areas and human impact can vary between urban quarters, more socioeconomic factors should be integrated into analyses. However, these can sometimes be difficult to combine with floristic mapping on a 1 $km^2$ grid scale, since not all population-related data are available in such a resolution. Often, data are only available on the district scale.

The application of floristic mapping data, e.g. for temperature distribution and UHI (Chapter 4), is a promising avenue for integrating botanical and floristic studies into other research areas. Not only climatology, but also urban planning and landscape architecture may benefit from plant sciences and vice versa. For instance, in the course of adaptation to climate change, the design of green space may profit from species adapted to certain conditions. Floristic mapping data may reveal suitable areas, from which urban green space could be colonised.

Floristic mapping data could also be used to analyse a city in regard to other habitat preferences of species, e.g. moisture or nutrients. However, to integrate results from science into urban development and urban biodiversity conservation, the questions planners, designers, and decision-makers need answered have to be translated into ecologically relevant questions that can then be addressed by urban ecology research. Consequently, the results can be used for planning advice (McDonnell and Hahs 2013).

Overall, however, the potential of pursuing such intensive floristic analyses, e.g. between two points of time, depends strongly on the work of voluntary associations such as the Botanical Association of Hamburg. Numerous volunteers conducted the mapping over 15 years and the knowledge and work that is needed to obtain such data is often underestimated. This enormous voluntary work needs to be much more highly valued and appreciated as well as properly funded. Species determination qualifications and abilities must also be promoted in education. Without this work, changes in floras would be nearly impossible to detect.

# 8 REFERENCES

Aitchison J (1982) The statistical analysis of compositional data. Journal of the Royal Statistical Society Series B - Methodological 44(2):139–177

Akbari H (2002) Shade trees reduce building energy use and $CO_2$ emissions from power plants. Environmental Pollution 116:S119

Albrecht H, Haider S (2013) Species diversity and life history traits in calcareous grasslands vary along an urbanization gradient. Biodiversity and Conservation 22(10):2243–2267

Alcoforado M, Andrade H (2006) Nocturnal urban heat island in Lisbon (Portugal): main features and modelling attempts. Theoretical and Applied Climatology 84(1-3):151–159

Andersson E, Ahrné K, Pyykönen M, Elmquist T (2009) Patterns and scale relations among urbanization measures in Stockholm, Sweden. Landscape Ecology 24(10):1331–1339

Angold PG, Sadler JP, Hill MO, 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(1-3):196–204

ArcGIS 9.3 software (2008) ESRI Inc., Redlands, CA, USA

Arnfield AJ (2003) Two decades of urban climate research: A review of turbulence, exchanges of energy and water, and the urban heat island. International Journal of Climatology 23(1):1–26

Arnold CL, Gibbons CJ (1996) Impervious surface coverage - The emergence of a key environmental indicator. Journal of the American Planning Association 62(2):243–258

Asmus U (1988) Das Eindringen von Neophyten in anthropogen geschaffene Standorte und ihre Vergesellschaftung am Beispiel von *Senecio inaequidens* DC. Flora 180:133–138

Balázs B, Unger J, Gál T, Sümeghy Z, Geiger J, Szegedi S (2009) Simulation of the mean urban heat island using 2D surface parameters: empirical modelling, verification and extension. Meteorological Applications 16(3):275–287

Baldwin AH, Jensen K, Schönfeldt M (2013) Warming increases plant biomass and reduces diversity across continents, latitudes, and species migration scenarios in experimental wetland communities. Global Change Biology, doi: 10.1111/gcb.12378

Barsi JA, Schott JR, Palluconi FD, Hook SJ, Butler JJ (2005) Validation of a web-based atmospheric correction tool for single thermal band instruments. In: Butler JJ (ed) Earth Observing Systems X. Proc SPIE 58820, pp 1–7

Barsi J, Barker J, Schott J (2003) An atmospheric correction parameter calculator for a single thermal band earth-sensing instrument. International Geoscience and Remote Sensing Symposium 2003 (IGARSS '03). Proc 2003 IEEE Int 5:3014–3016

Bechtel B (2011) Multitemporal Landsat data for urban heat island assessment and classification of local climate zones. Joint Urban Remote Sensing Event. Proc 2011 IEEE Int:129–132

Bechtel B, Schmidt KJ (2011) Floristic mapping data as a proxy for the mean urban heat island. Climate Research. 49(1):45–58

Beerling DJ, Bailey JP, Conolly AP (1994) *Fallopia japonica* (Houtt.) Ronse Decraene. Journal of Ecology 82(4):959

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. Ecology Letters 15(4):365–377

Bergmann J, Pompe S, Ohlemüller R, Freiberg M, Klotz S, Kuehn I (2009) The Iberian Peninsula as a potential source for the plant species pool in Germany under projected climate change. Plant Ecology 207(2):191-201

Bertoncini AP, Machon N, Pavoine S, Muratet A (2012) Local gardening practices shape urban lawn floristic communities. Landscape and Urban Planning 105(1-2):53–61

Beyer H (2004) Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools

Bivand R, Altman M, Anselin L, Assunção R, Berke O, Bernat A, Blanchet G, Blankmeyer E, Carvalho M, Christensen B, Chun Y, Dormann CF, Dray S, Halbersma R, Krainski E, Legendre P, Lewin-Koh N, Li H, Ma J, Millo G, Mueller W, Ono H, Peres-Neto PR, Piras G, Reder M, Tiefelsdorf M, Yu D (2012) spdep. Spatial dependence: weighting schemes, statistics and models. R package version 0.5-52/r463. http://R-Forge.R-project.org/projects/spdep/

Blanchet FG, Legendre P, Borcard D (2008) Forward selection of explanatory variables. Ecology 89(9):2623–2632

Blois JL, Zarnetske PL, Fitzpatrick MC, Finnegan S (2013) Climate change and the past, present, and future of biotic interactions. Science 341(6145):499–504

Blossey B, Noetzold R (1995) Evolution of increased competitive ability in invasive non-indigenous plants - a hypothesis. Journal of Ecology 83(5):887–889

Boehner J, Blaschke T, Montanarella L (eds) (2008) SAGA –seconds out. Hamburger Beiträge zur Physischen Geographie und Landschaftsökologie. 2. Geographisches Institut der Universität Hamburg

Boer NJ de (1999) Pyrrolizidine alkaloid distribution in *Senecio jacobaea* rosettes minimises losses to generalist feeding. Entomologia Experimentalis et Applicata 91(1):169–173

Bogon K (1990) Landschnecken. Biologie, Ökologie, Biotopschutz. Natur Verlag, Augsburg

Boehmer HJ (2001) Das Schmalblättrige Greiskraut (*Senecio inaequidens* DC. 1837) in Deutschland. Eine aktuelle Bestandsaufnahme. Floristische Rundbriefe 35(1/2):47–54

Borcard D, Legendre P (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling 153(1-2):51–68

Borcard D, Legendre P, Avois-Jacquet C, Tuomisto H (2004) Dissecting the spatial structure of ecological data at multiple scales. Ecology 85(7):1826–1832

Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. Ecology 73(3):1045–1055

Borgefors G (1986) Distance transformations in digital images. Computer Vision, Graphics, and Image Processing 34(3):344–371

Bornstein RD, Johnson DS (1977) Urban-rural wind velocity differences. Atmospheric Environment 11(7):597–604

Bossdorf O (2013) Enemy release and evolution of increased competitive ability: at last, a smoking gun! New Phytologist 198(3):638–640

Bossdorf O, Auge H, Lafuma L, Rogers WE, Siemann E, Prati D (2005) Phenotypic and genetic differentiation between native and introduced plant populations. Oecologia 144(1):1-11

Bossdorf O, Lipowsky A, Prati D (2008) Selection of preadapted populations allowed *Senecio inaequidens* to invade Central Europe. Diversity and Distributions 14(4):676–685

Botham MS, Rothery P, Hulme PE, Hill MO, Preston CD, Roy DB (2009) Do urban areas act as foci for the spread of alien plant species? An assessment of temporal trends in the UK. Diversity and Distributions 15(2):338–345

Botkin DB, Beveridge CE (1997) Cities as environments. Urban Ecosystems 1:3–19

Bottyán Z, Kircsi A, Szegedi S, Unger J (2005) The relationship between built-up areas and the spatial development of the mean maximum urban heat island in Debrecen, Hungary. International Journal of Climatology 25(3):405–418

Bräuniger C, Knapp S, Kuehn I, Klotz S (2010) Testing taxonomic and landscape surrogates for biodiversity in an urban setting. Landscape and Urban Planning 97(4):283–295

Briske DD, Camp BJ (1982) Water-stress increases alkaloid concentrations in Threadleaf Groundsel (*Senecio longilobus*). Weed Science 30(1):106–108

Brooker RW (2006) Plant-plant interactions and environmental change. New Phytologist 171(2):271–284

Brunzel S, Fischer SF, Schneider J, Jetzkowitz J, Brandl R (2009) Neo- and archaeophytes respond more strongly than natives to socio-economic mobility and disturbance patterns along an urban-rural gradient. Journal of Biogeography 36(5):835–844

Burkart M (2001) River corridor plants (Stromtalpflanzen) in Central European lowland: a review of a poorly understood plant distribution pattern. Global Ecology and Biogeography 10(5):449–468

Buttstaedt M, Sachsen T, Ketzler G, Merbitz H, Schneider C (2010) Urban temperature distribution and detection of influencing factors in urban structure. International Seminar on Urban Form 2010, Hamburg Available at www.isuf2010.de/Papers/Buttstaedt_Mareike.pdf

Callaway RM, Ridenour WM (2004) Novel weapons: invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2(8):436–443

Cano L, Escarré J, Sans FX (2007) Factors affecting the invasion success of *Senecio inaequidens* and *S. pterophorus* in Mediterranean plant communities. Journal of Vegetation Science 18(2):281–288

Cano L, Escarré J, Vrieling K, Sans FX (2009) Palatability to a generalist herbivore, defence and growth of invasive and native *Senecio* species: testing the evolution of increased competitive ability hypothesis. Oecologia 159(1):95–106

Carreiro MM, Tripler CE (2005) Forest remnants along urban-rural gradients: Examining their potential for global change research. Ecosystems 8(5):568–582

Carter MA, Jeffery RCV, Williamson P (1979) Food overlap in co-existing populations of the land snails *Cepaea nemoralis* (L.) and *Cepaea hortensis* (Müll). Biological Journal of the Linnean Society 11(2):169–176

Carvalho S, Macel M, Schlerf M, Moghaddam FE, Mulder PPJ, Skidmore AK, van der Putten WH (2013) Changes in plant defense chemistry (pyrrolizidine alkaloids) revealed through high-resolution spectroscopy. ISPRS Journal of Photogrammetry and Remote Sensing 80:51–60

Catorci A, Ottaviani G, Cesaretti S (2011) Functional and coenological changes under different long-term management conditions in Apennine meadows (central Italy). Phytocoenologia 41(1):45–58

Celesti-Grapow L, Blasi C (1998) A comparison of the urban flora of different phytoclimatic regions in Italy. Global Ecology and Biogeography 7(5):367–378

Celesti-Grapow L, Pyšek P, Jarosik V, Blasi C (2006) Determinants of native and alien species richness in the urban flora of Rome. Diversity and Distributions 12(5):490–501

Chander G, Markham BL, Helder DL (2009) Summary of current radiometric calibration coefficients for Landsat MSS, TM, ETM+, and EO-1 ALI sensors. Remote Sensing of Environment 113(5):893–903

Chocholoušková Z, Pyšek P (2003) Changes in composition and structure of urban flora over 120 years: a case study of the city of Plzen. Flora 198(5):366–376

Christensen JHB, Busuioc A, Chen A, Gao X, Held I, Jones RK, Kwon W, Laprise R, Magaña Rueda V, Mearns L, Menéndez C, Räisänen J, Rinke A, Sarr A, Whetton P (2007) Regional Climate Projections. In: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambride University Press, Cambridge, United Kingdom and New York, NY, USA

Chytrý M, Hejcman M, Hennekens SM, Schellberg J (2009) Changes in vegetation types and Ellenberg indicator values after 65 years of fertilizer application in the Rengen Grassland Experiment, Germany. Applied Vegetation Science 12(2):167–176

Chytrý M, Lososová Z, Horsák M, Uher B, Čejka T, Danihelka J, Fajmon K, Hájek O, Juřičková L, Kintrová K, Láníková D, Otýpková Z, Řehořek V, Tichý L (2012) Dispersal limitation is stronger in communities of microorganisms than macroorganisms across Central European cities. Journal of Biogeography 39(6):1101–1111

Cook, E.M., Hale R, Kinzig A, Grove JM (2013) Urban–Suburban Biodiversity. In: Editor-in-Chief: Simon A. Levin (ed) Encyclopedia of Biodiversity (Second Edition), Second Edition. Academic Press, Waltham, pp 304–313

Cornwell WK, Grubb PJ (2003) Regional and local patterns in plant species richness with respect to resource availability. Oikos 100(3):417–428

Cunze S, Heydel F, Tackenberg O, Roberts DL (2013) Are plant species able to keep pace with the rapidly changing climate? PLOS ONE 8(7):e67909

Daehler CC (2003) Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. Annual Review of Ecology and Systematics 34:183–211

Dainese M, Poldini L (2012) Plant and animal diversity in a region of the Southern Alps: the role of environmental and spatial processes. Landscape Ecology 27(3):417–431

Dana ED, Vivas S, Mota JF (2002) Urban vegetation of Almeria City - a contribution to urban ecology in Spain. Landscape and Urban Planning 59(4):203–216

Daneke C, Bechtel B, Langkamp T (2010) Classification scheme of urban structures based on climatic characteristics, designed for land use modeling applications. International Seminar on Urban Form 2010, Hamburg. Available at www.isuf2010.de/Papers/Daneke_Christian.pdf

Dearborn DC, Kark S (2010) Motivations for conserving urban biodiversity. Conservation Biology 24(2):432–440

DeCandido R (2004) Recent changes in plant species diversity in urban Pelham Bay Park, 1947–1998. Biological Conservation 120(1):129–136

Del Tredici P (2010) Spontaneous Urban Vegetation: Reflections of Change in a Globalized World. Nature + Culture 5(3):299–315

DeLucia EH, Nabity PD, Zavala JA, Berenbaum MR (2012) Climate Change: Resetting Plant-Insect Interactions. Plant Physiology 160(4):1677–1685

Denys C, Schmidt H (1998) Insect communities on experimental mugwort (*Artemisia vulgaris* L.) plots along an urban gradient. Oecologia 113(2):269–277

Deutschewitz K, Lausch A, Kuehn I, Klotz S (2003) Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. Global Ecology and Biogeography 12(4):299–311

Diekmann M (2003) Species indicator values as an important tool in applied plant ecology - a review. Basic and Applied Ecology 4(6):493–506

Dimande A (2007) The toxicity of *Senecio inaequidens* DC. Dissertation, Universiteit van Pretoria

Dolan RW, Moore ME, Stephens JD (2011) Documenting effects of urbanization on flora using herbarium records. Journal of Ecology 99(4):1055–1062

Dray S (2010) spacemakeR. Spatial modelling. R package version 0.0-5/r101. http://R-Forge.R project.org/projects/sedar/

Dray S, Legendre P, Blanchet G (2011) packfor. Forward Selection with permutation (Canoco p.46). R package version 0.0-8/r100. http://R-Forge.R-project.org/projects/sedar/

Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling 196(3-4):483–493

Dray S, Pelissier R, Couteron P, Fortin M, Legendre P, Peres-Neto PR, Bellier E, Bivand R, Blanchet FG, Caceres M de, Dufour A, Heegaard E, Jombart T, Munoz F, Oksanen J, Thioulouse J, Wagner HH (2012) Community ecology in the age of multivariate multiscale spatial analysis. Ecological Monographs 82(3):257–275

Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? Trends in Ecology and Evolution 14(4):135–139

Duncan RP, Clemants SE, Corlett RT, Hahs AK, McCarthy MA, McDonnell MJ, Schwartz MW, Thompson K, Vesk PA, Williams NSG (2011) Plant traits and extinction in urban areas: a meta-analysis of 11 cities. Global Ecology and Biogeography 20(4):509–519

Dunn C, Heneghan L (2011) Composition and diversity of urban vegetation. In: Niemelä J, Breuste J, Elmquist T, Guntenspergen G, James P, McIntyre NE (eds) Urban Ecology. Patterns, Processes, and Applications. Oxford University Press, Oxford, pp 103–114

du Toit MJ, Cilliers SS (2011) Aspects influencing the selection of representative urbanization measures to quantify urban–rural gradients. Landscape Ecology 26(2):169–181

Dutt AJ (1991) Wind flow in an urban environment. Environmental Monitoring and Assessment 19(1-3):495–506

Ehlers J (1995) Hamburg. In: Benda L (ed) Das Quartär Deutschlands : mit 30 Tabellen. Borntraeger, Berlin [u.a.], pp 14–22

Eliasson I (1992) Infrared thermography and urban temperature patterns. International Journal of Remote Sensing 13(5):869–879

Ellenberg H, Düll R, Wirth W, Werner W, Paulißen D (1992) Zeigerwerte von Pflanzen in Mitteleuropa, 2nd edn. Erich Goltze KG, Göttingen

Ernst WHO (1998) Invasion, dispersal and ecology of the South African neophyte *Senecio inaequidens* in the Netherlands: from wool alien to railway and road alien. Acta Botanica Neerlandica 47(1):131–151

Ewald J (2003) The sensitivity of Ellenberg indicator values to the completeness of vegetation releves. Basic and Applied Ecology 4(6):507–513

Faeth SH, Bang C, Saari S (2011) Urban biodiversity: patterns and mechanisms. In: Ostfeld RS, Schlesinger WH (eds) The year in ecology and conservation biology, vol 1223. Blackwell Science Publications, Osney Mead, Oxford, England, pp 69–81

Federal Statistical Office of Germany (2011) http://www.statistik-portal.de/statistik-portal/de_jb09_jahrtabf1.asp; retrieved 5th October 2012

Federal Statistical Office of Germany (2012) https://www.destatis.de/DE/ZahlenFakten/LaenderRegionen/Regionales/Gemeindeverzeichnis/Administrativ/Archiv/Definition_STL_bis_30122011.pdf?__blob=publicationFile; retrieved 2nd November 2013

Felker-Quinn E, Schweitzer JA, Bailey JK (2013) Meta-analysis reveals evolution in invasive plant species but little support for Evolution of Increased Competitive Ability (EICA). Ecology and Evolution 3(3):739–751

Franzen E (1955) Der Beginn der Forsythienblüte in Hamburg 1955. Ein Beitrag zur Phänologie der Großstadt. Meteorologische Rundschau 8(7/8):113–115

Fuller RA, Irvine KN, Devine-Wright P, Warren PH, Gaston KJ (2007) Psychological benefits of greenspace increase with biodiversity. Biology Letters 3(4):390–394

Gallo K, Owen T (1998) Assessment of urban heat islands: a multi-sensor perspective for the Dallas-Ft. Worth, USA region. Geocarto International 13:35–41

Gallo KP, McNab AL, Karl TR, Brown JF, Hood JJ, Tarpley JD (1993) The use of NOAA AVHRR data for assessment of the urban heat island effect. Journal of Applied Meteorology 32(5):899–908

Gallo KP, Owen TW (1999) Satellite-based adjustments for the urban heat island temperature bias. Journal of Applied Meteorology 38(6):806–813

Garcia-Serrano H, Escarré J, Garnier E, Sans FX (2005) A comparative growth analysis between alien invader and native *Senecio* species with distinct distribution ranges. Ecoscience 12(1):35–43

Garcia-Serrano H, Escarré J, Sans FX (2004) Factors that limit the emergence and establishment of the related aliens *Senecio inaequidens* and *Senecio pterophorus* and the native *Senecio malacitanus* in Mediterranean climate. Canadian Journal of Botany 82(9):1346–1355

Garcia-Serrano H, Sans FX, Escarré J (2007) Interspecific competition between alien and native congeneric species. Acta Oecologica 31(1):69–78

Gavier-Pizarro GI, Radeloff VC, Stewart SI, Huebner CD, Keuler NS (2010) Housing is positively associated with invasive exotic plant species richness in New England, USA. Ecological Applications 20(7):1913–1925

George K, Ziska LH, Bunce JA, Quebedeaux B (2007) Elevated atmospheric $CO_2$ concentration and temperature across an urban-rural transect. Atmospheric Environment 41(35):7654–7665

George K, Ziska LH, Bunce JA, Quebedeaux B, Hom JL, Wolf J, Teasdale JR (2009) Macroclimate associated with urbanization increases the rate of secondary succession from fallow soil. Oecologia 159:637–647

Gilbert OL (1989) The ecology of urban habitats. Chapman and Hall Ltd., London

Goddard MA, Dougill AJ, Benton TG (2010) Scaling up from gardens: biodiversity conservation in urban environments. Trends in Ecology and Evolution 25(2):90–98

Godefroid S (2001) Temporal analysis of the Brussels flora as indicator for changing environmental quality. Landscape and Urban Planning 52(4):203–224

Godefroid S, Koedam N (2007) Urban plant species patterns are highly driven by density and function of built-up areas. Landscape Ecology 22(8):1227–1239

Godefroid S, Monbaliu D, Koedam N (2007) The role of soil and microclimatic variables in the distribution patterns of urban wasteland flora in Brussels, Belgium. Landscape and Urban Planning 80(1-2):45–55

Goedde M, Wittig R (1983) A preliminary attempt at a thermal division of the town of Munster (North Rhine-Westphalia, West-Germany) on a floral and vegetational basis. Urban Ecology 7(3):255–262

Gravel D, Beaudet M, Messier C (2008) Partitioning the factors of spatial variation in regeneration density of shade-tolerant tree species. Ecology 89(10):2879–2888

Gregor T, Boensel D, Starke-Ottich I, Zizka G (2012) Drivers of floristic change in large cities - A case study of Frankfurt/Main (Germany). Landscape and Urban Planning 104(2):230–237

Griese D (1996) Zur Ausbreitung von *Senecio inaequidens* DC. an Autobahnen in Nordostdeutschland. Braunschweiger Naturkundliche Schriften 5:193–204

Grime JP (1974) Vegetation classification by reference to strategies. Nature 250(5461):26–31

Grime JP (1979) Plant strategies and vegetation processes. Wiley, Chichester, New York

Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM (2008) Global change and the ecology of cities. Science 319(5864):756–760

Grimm NB, Grove JM, Pickett STA, Redman CL (2000) Integrated approaches to long-term studies of urban ecological systems. BioScience 50(7):571–584

Grimmond S (2007) Urbanization and global environmental change: local effects of urban warming. Berichte des Meteorologischen Instituts der Albrecht-Ludwig-Universität Freiburg. 5th Japanese-German Meeting on Urban Climatology, Freiburg, Oktober 2008 173(Part 1):83–88

Groemping U (2006) Relative importance for linear regression in R: The package relaimpo. Journal of Statistical Software 17(1):1-27

Güneralp B, Seto KC (2013) Futures of global urban expansion: uncertainties and implications for biodiversity conservation. Environmental Research Letters 8(1):14025

Gurevitch J, Scheiner SM, Fox GA (2002) The ecology of plants. Sinauer Associates, Sunderland, Mass

Habel JC, Dengler J, Janišová M, Török P, Wellstein C, Wiezik M (2013) European grassland ecosystems: threatened hotspots of biodiversity. Biodiversity and Conservation 22(10):2131–2138

Haeupler H (2000) Die ungleiche Verteilung der Artenvielfalt innerhalb Deutschlands - eine Antwort. Floristische Rundbriefe 34(1):17–24

Haeupler H (2002) Die Biotope Deutschlands. Schriftenreihe für Vegetationskunde (38):247–272

Hagerman SM, Chan KM (2009) Climate change and biodiversity conservation: impacts, adaptation strategies and future research directions. F1000 Biology Reports 1:16

Hahs AK, McDonnell MJ (2006) Selecting independent measures to quantify Melbourne's urban–rural gradient. Landscape and Urban Planning 78(4):435–448

Hahs AK, McDonnell MJ, McCarthy MA, Vesk PA, Corlett RT, Norton BA, Clemants SE, Duncan RP, Thompson K, Schwartz MW, Williams NSG (2009) A global synthesis of plant extinction rates in urban areas. Ecology Letters 12(11):1165–1173

Haider S, Kueffer C, Edwards PJ, Alexander JM (2012) Genetically based differentiation in growth of multiple non-native plant species along a steep environmental gradient. Oecologia 170(1):89–99

Hájek M, Roleček J, Cottenie K, Kintrová K, Horsák M, Poulíčková A, Hájková P, Fránková M, Díte D (2011) Environmental and spatial controls of biotic assemblages in a discrete semi-terrestrial habitat: comparison of organisms with different dispersal abilities sampled in the same plots. Journal of Biogeography 38(9):1683–1693

Hamilton MA, Murray BR, Cadotte MW, Hose GC, Baker AC, Harris CJ, Licari D (2005) Life-history correlates of plant invasiveness at regional and continental scales. Ecology Letters 8(10):1066–1074

Hammer Ø, Harper D, Ryan P (2001) PAST: paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4(art. 4):9pp., 178 KB

Hansen J, Ruedy R, Sato M, Lo K (2010) Global surface temperature change. Reviews of Geophysics 48(4): RG4004

Hartmann T, Zimmer M (1986) Organ-specific distribution and accumulation of pyrrolizidine alkaloids during the life history of two annual *Senecio* species. Journal of Plant Physiology 122(1):67–80

Hart MA, Sailor DJ (2009) Quantifying the influence of land-use and surface characteristics on spatial variability in the urban heat island. Theoretical and Applied Climatology 95(3-4):397–406

Hawkes CV (2007) Are invaders moving targets? The generality and persistence of advantages in size, reproduction, and enemy release in invasive plant species with time since introduction. American Naturalist 170(6):832–843

Heger T, Boehmer H (2005) The invasion of central Europe by *Senecio inaequidens* DC. - a complex biogeographical problem. Erdkunde 59:34–49

Hegland SJ, Nielsen A, Lázaro A, Bjerknes A, Totland Ø (2009) How does climate warming affect plant-pollinator interactions? Ecology Letters 12(2):184–195

Heineberg H (2006) Stadtgeographie. 8 Tabellen, 3rd edn. Uni-Taschenbücher, vol 2166. Schöningh, Paderborn, München [u.a.]

He W, Li J, Peng P (2012) Simulated warming differentially affects the growth and competitive ability of *Centaurea maculosa* populations from home and introduced ranges. PLOS ONE 7(1): e31170

Hof C, Levinsky I, Araújo MB, Rahbek C (2011) Rethinking species' ability to cope with rapid climate change. Global Change Biology 17(9):2987–2990

Hoffmann P (2009) Modifikation von Starkniederschlägen durch urbane Gebiete. Diplomarbeit, Universität Hamburg

Hoffmann P, Krueger O, Schluenzen KH (2012) A statistical model for the urban heat island and its application to a climate change scenario. International Journal of Climatology 32(8):1238–1248

Hoffmann P, Schluenzen KH (2010) Das Hamburger Klima. In: Poppendieck HH, Bertram H, Brandt I, Engelschall E, v.Prondzinski J (eds) Der Hamburger Pflanzenatlas. von a bis z. Dölling und Galitz Verlag, München, Hamburg, pp 28–31

Hope D, Gries C, Zhu WX, Fagan WF, Redman CL, Grimm NB, Nelson AL, Martin C, Kinzig A (2003) Socioeconomics drive urban plant diversity. Proceedings of the National Academy of Science of the United States of America, PNAS 100(15):8788–8792

HPA (2013) http://www.hamburg-port-authority.de/de/der-hafen-hamburg/zahlen-und-fakten/Seiten/default.aspx; retrieved 01st July 2013

Hulme PE, Bacher S, Kenis M, Klotz S, Kuehn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J, Pyšek P, Roques A, Sol D, Solarz W, Vilà M (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. Journal of Applied Ecology 45(2):403–414

Huntley B (1991) How plants respond to climate change - migration rates, individualism and the consequences plant-communities. Annals of Botany 67(1):15–22

Huntley B, Berry PM, Cramer W, McDonald AP (1995) Special Paper: Modelling present and potential future ranges of some European higher plants using climate response surfaces. Journal of Biogeography 22(6):967

IBM Corp. (2012) IBM SPSS Statistics for Windows, Version 21.0. Armonk, NY: IBM Corp.

Idso CD, Idso SB, Balling RC (2001) An intensive two-week study of an urban $CO_2$ dome in Phoenix, Arizona, USA. Atmospheric Environment 35(6):995–1000

Imhoff M (1997) Using nighttime DMSP/OLS images of city lights to estimate the impact of urban land use on soil resources in the United States. Remote Sensing of Environment 59(1):105–117

IPCC (2007) Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambride University Press, Cambridge, United Kingdom and New York, NY, USA

Jacob D, Bülow K, Kotova L, Moseley C, Petersen J, Rechid D (2008) Regionale Klimaprojektionen für Europa und Deutschland: Ensemble Simulationen für die Klimafolgenforschung. CSC Report 6, Climate Service Center, Hamburg

Jacob D, Podzun R (1997) Sensitivity studies with the regional climate model REMO. Meteorology and Atmospheric Physics 63(1-2):119–129

Jansen E, Overpeck J, Briffa K, Duplessy J, Joos F, Masson-Delmotte V, Olago D, Otto-Bliesner B, Peltier W, Rahmstorf S, Ramesh R, Raynaud D, Rind D, Solomina O, Villalba R, Zhang D (2007) Palaeoclimate. In: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambride University Press, Cambridge, United Kingdom and New York, NY, USA

Jehlîk V (1981) Beitrag zur synanthropen (besonders Adventiv-) Flora des Hamburger Hafens. Tuexenia 1:81–97

Jehlîk V (1989) Zweiter Beitrag zur synanthropen (besonders Adventiv-) Flora des Hamburger Hafens. Tuexenia 9:253–266

Jim CY, Chen WY (2009) Urbanization effect on floristic and landscape patterns of green spaces. Landscape Research 34(5):581–598

Jones JS, Leith BH, Rawlings P (1977) Polymorphism in *Cepaea*: A problem with too many solutions? Annual Review of Ecology and Systematics 8(1):109–143

Joshi J, Vrieling K (2005) The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. Ecology Letters 8(7):704–714

Jump AS, Penuelas J (2005) Running to stand still: adaptation and the response of plants to rapid climate change. Ecology Letters 8(9):1010–1020

Karl TR, Diaz HF, Kukla G (1988) Urbanization: Its Detection and Effect in the United States Climate Record. Journal of Climate 1(11):1099–1123

Kattwinkel M, Biedermann R, Kleyer M (2011) Temporary conservation for urban biodiversity. Biological Conservation 144(9):2335–2343

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution 17(4):164–170

Kelcey JG, Müller N (2011) Plants and habitats of European cities. [Almería, Augsburg, Berlin, Bratislava, Brussels, Bucharest, London, Maastricht, Milton Keynes, Moscow, Poznań, St. Petersburg, Sofia, Vienna, Warsaw, Zurich]. Springer, New York [u.a.]

Kempel A, Schaedler M, Chrobock T, Fischer M, van Kleunen M (2011) Tradeoffs associated with constitutive and induced plant resistance against herbivory. Proceedings of the National Academy of Science of the United States of America, PNAS 108(14):5685–5689

Kent M, Stevens RA, Zhang L (1999) Urban plant ecology patterns and processes: a case study of the flora of the City of Plymouth, Devon, UK. Journal of Biogeography 26(6):1281–1298

Kirk H, Vrieling K, van der Meijden E, Klinkhamer PG (2010) Species by environment interactions affect pyrrolizidine alkaloid expression in *Senecio jacobaea*, *Senecio aquaticus*, and their hybrids. Journal of Chemical Ecology 36(4):378–387

Klaus VH, Kleinebecker T, Boch S, Mueller J, Socher SA, Prati D, Fischer M, Hoelzel N (2012) NIRS meets Ellenberg's indicator values: Prediction of moisture and nitrogen values of agricultural grassland vegetation by means of near-infrared spectral characteristics. Ecological Indicators 14(1):82–86

Klotz S, Kuehn I, Durka W (2002) BIOLFLOR - Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Schriftenreihe für Vegetationskunde 38, Bonn: Bundesamt für Naturschutz

Knapp S, Kuehn I, Bakker JP, Kleyer M, Klotz S, Ozinga WA, Poschlod P, Thompson K, Thuiller W, Roemermann C (2009) How species traits and affinity to urban land use control large-scale species frequency. Diversity and Distributions 15(3):533–546

Knapp S, Kuehn I, Stolle J, Klotz S (2010) Changes in the functional composition of a Central European urban flora over three centuries. Perspectives in Plant Ecology, Evolution and Systematics 12(3):235–244

Knapp S, Kuehn I, Wittig R, Ozinga WA, Poschlod P, Klotz S (2008) Urbanization causes shifts in species' trait state frequencies. Preslia 80(4):375–388

Kowarik I (1992) Das Besondere der städtischen Flora und Vegetation. In: Deutscher Rat für Landespflege. Natur in der Stadt - Der Beitrag der Landespflege zur Stadtentwicklung. Gutachtliche Stellungnahme und Ergebnisse eines Kolloquiums des Deutschen Rats für Landespflege. Vol 61, pp 33–47

Kowarik I (2011) Novel urban ecosystems, biodiversity, and conservation. Environmental Pollution 159(8-9, SI):1974–1983

Kowarik I, Saeumel I (2007) Biological flora of Central Europe: *Ailanthus altissima* (Mill.) Swingle. Perspectives in Plant Ecology Evolution and Systematics 8(4):207–237

Krauss J, Am Klein, Steffan-Dewenter I, Tscharntke T (2004) Effects of habitat area, isolation, and landscape diversity on plant species richness of calcareous grasslands. Biodiversity and Conservation 13(8):1427–1439

Kuehn I, Brandl R, Klotz S (2004) The flora of German cities is naturally species rich. Evolutionary Ecology Reseaerch 6(5):749–764

Kuehn I, Klotz S (2006) Urbanization and homogenization - Comparing the floras of urban and rural areas in Germany. Biological Conservation 127(3):292–300

Kuhbier H (1977) *Senecio inaequidens* DC. - ein Neubürger der nordwestdeutschen Flora. Abhandlungen Naturwissenschaftlicher Verein zu Bremen 38(21):383–396

Kuttler W (2008) The urban climate - basis and applied aspects. In: Marzluff JM, Shulenberger E, Endlicher W, Alberti M, Bradley G, Ryan C, Zumbrunnen C, Simon U (eds) Urban Ecology. An international perspective on the interaction between humans and nature. Springer, New York, pp 233–248

Kuttler W, Barlag A, Robmann F (1996) Study of the thermal structure of a town in a narrow valley. Atmospheric Environment 30(3):365–378

Lachmuth S, Durka W, Schurr FM (2010) The making of a rapid plant invader: genetic diversity and differentiation in the native and invaded range of Senecio inaequidens. Molecular Ecology 19(18):3952–3967

Lachmuth S, Durka W, Schurr FM (2011) Differentiation of reproductive and competitive ability in the invaded range of Senecio inaequidens: the role of genetic Allee effects, adaptive and nonadaptive evolution. New Phytologist 192(2):529–541

Lake JC, Leishman (2004) Invasion success of exotic in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. Biological Conservation 117(2):215–226

Lambdon PW, Pyšek P, Basnou C, Hejda M, Arianoutsou M, Essl F, Jarošik V, Pergl J, Winter M, Anastasiu P, Andriopoulos P, Bazos I, Brundu G, Celesti-Grapow L, Chassot P, Delipetrou P, Josefsson M, Kark S, Klotz S, Kokkoris Y, Kuehn I, Marchante H, Perglová I, Pino J, Vilà M, Zikos A, Roy D, Hulme PE (2008) Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. Preslia 80(2):101–149

Landsberg H (1981) The urban climate. Academic Press, New York

Lawson DM, Lamar CK, Schwartz MW (2008) Quantifying plant population persistence in human-dominated landscapes. Conservation Biology 22(4):922–928

Legendre L (1998) Numerical ecology, 2nd edn. Elsevier, Amsterdam [u.a.]

Legendre P, Borcard D, Peres-Neto PR (2005) Analyzing beta diversity: Partitioning the spatial variation of community composition data. Ecological Monographs 75(4):435–450

Lenzewski N (2010) Einfluss von Temperatur und Salinität auf die Keimung von *Senecio inaequidens* DC. BSc. thesis, Universität Hamburg

Lepš J, Šmilauer P (2003) Multivariate analysis of ecological data using CANOCO. Cambridge Univesity Press, Cambridge

Leung DYC, Tsui JKY, Chen F, Yip W, Vrijmoed LLP, Liu C (2011) Effects of urban vegetation on urban air quality. Landscape Research 36(2):173–188

Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters 7(10):975–989

Lindberg F, Grimmond CSB (2011) Nature of vegetation and building morphology characteristics across a city: Influence on shadow patterns and mean radiant temperatures in London. Urban Ecosystems 14(4):617–634

Londo G. (1976) The decimal scale for relevés of permanent quadrats. Vegetatio 33(3):61–64

Lopez-Garcia MC, Maillet J (2005) Biological characteristics of an invasive south African species. Biological Invasions 7(2):181–194

Lososová Z, Chytrý M, Kuehn I, Hájek O, Horáková V, Pyšek P, Tichý L (2006) Patterns of plant traits in annual vegetation of man-made habitats in central Europe. Perspectives in Plant Ecology, Evolution and Systematics 8(2):69–81

Lososová Z, Chytrý M, Tichý L, Danihelka J, Fajmon K, Hájek O, Kintrová K, Kuehn I, Láníková D, Otýpková Z, Řehořek V (2012a) Native and alien floras in urban habitats: a comparison across 32 cities of central Europe. Global Ecology and Biogeography 21(5):545–555

Lososová Z, Chytrý M, Tichý L, Danihelka J, Fajmon K, Hájek O, Kintrová K, Láníková D, Otýpková Z, Řehořek V (2012b) Biotic homogenization of Central European urban floras depends on residence time of alien species and habitat types. Biological Conservation 145(1):179–184

Lososová Z, Horsák M, Chytrý M, Čejka T, Danihelka J, Fajmon K, Hájek O, Juřičková L, Kintrová K, Láníková D, Otýpková Z, Řehořek V, Tichý L (2011) Diversity of Central European urban biota: effects of human-made habitat types on plants and land snails. Journal of Biogeography 38(6):1152–1163

Lovett GM, Traynor MM, Pouyat RV, Carreiro MM, Zhu WX, Baxter JW (2000) Atmospheric deposition to oak forests along an urban-rural gradient. Environmental Science and Technology 34(20):4294–4300

Lowry WP (1977) Empirical estimation of urban effects on climate - problem analysis. Journal of Applied Meteorology 16(2):129–135

Lowry WP (1998) Urban effects on precipitation amount. Progress in Physical Geography 22(4):477–520

Luck GW, Smallbone LT, O’Brien R (2009) Socio-economics and vegetation change in urban ecosystems: patterns in space and time. Ecosystems 12(4):604–620

Luck M, Wu JG (2002) A gradient analysis of urban landscape pattern: a case study from the Phoenix metropolitan region, Arizona, USA. Landscape Ecology 17(4):327–339

Luo Z, Sun OJ, Ge Q, Xu W, Zheng J (2007) Phenological responses of plants to climate change in an urban environment. Ecological Research 22(3):507–514

Lu X, Siemann E, Shao X, Wei H, Ding J (2013) Climate warming affects biological invasions by shifting interactions of plants and herbivores. Global Change Biology 19(8):2339–2347

Magura T, Tóthmérész B, Molnár T (2004) Changes in carabid beetle assemblages along an urbanisation gradient in the city of Debrecen, Hungary. Landscape Ecology 19(7):747–759

Maron JL, Elmendorf SC, Vilà M (2007) Contrasting plant physiological adaptation to climate in the native and introduced range of *Hypericum perforatum*. Evolution 61(8):1912–1924

Maron JL, Vilà M, Bommarco R, Elmendorf S, Beardsley P (2004) Rapid evolution of an invasive plant. Ecological Monographs 74(2):261–280

Martilli A (2007) Current research and future challenges in urban mesoscale modelling. International Journal of Climatology. 27(14):1909–1918

Martín-Fernández JA, Barceló-Vidal C, Pawlowsky-Glahn V (2003) Dealing with zeros and missing values in compositional data sets using nonparametric imputation. Mathematical Geology 35(3):253–278

Mattocks AR (1967) Spectrophotometric determination of unsaturated pyrrolizidine alkaloids. Analytical Chemistry 39(4):443–447

Matzarakis A (2001) Die thermische Komponente des Stadtklimas. Berichte des Meteorologischen Institutes der Universität Freiburg 6, Freiburg

Maurel N, Salmon S, Ponge J, Machon N, Moret J, Muratet A (2010) Does the invasive species *Reynoutria japonica* have an impact on soil and flora in urban wastelands? Biological Invasions 12(6):1709–1719

Mayer H, Holst J, Dostal P, Imbery F, Schindler D (2008) Human thermal comfort in summer within an urban street canyon in Central Europe. Meteorologische Zeitschrift 17(3):241–250

McDonnell MJ, Hahs AK (2008) The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: current status and future directions. Landscape Ecology 23(10):1143–1155

McDonnell MJ, Hahs AK (2013) The future of urban biodiversity research: Moving beyond the 'low-hanging fruit'. Urban Ecosystems 16(3):397–409

McDonnell MJ, Pickett STA (1990) Ecosystem structure and function along urban rural gradients - an unexploited opportunity for ecology. Ecology 71(4):1232–1237

McDonnell MJ, Pickett STA, Groffman P, Bohlen P, Pouyat RV, Zipperer WC, Parmelee RW, Carreiro MM, Medley K (1997) Ecosystem processes along an urban-to-rural gradient. Urban Ecosystems 1:21–36

McIntire EJB, Fajardo A (2009) Beyond description: the active and effective way to infer processes from spatial patterns. Ecology 90(1):46–56

McIntyre NE, Knowles-Yánes K, Hope D (2000) Urban ecology as an interdisciplinary field: differences in the use of "urban" between the social and natural sciences. Urban Ecosystems 4:5–24

McKinney ML (2002) Urbanization, biodiversity, and conservation. BioScience 52(10):883–890

McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biological Conservation 127(3):247–260

McKinney ML (2008) Effects of urbanization on species richness: A review of plants and animals. Urban Ecosystems 11:161–1769

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecolog and Evolution 14(11):450–453

McLean E (1970) The toxic actions of pyrrolizidine (senecio) alkaloids. Pharmacological reviews 22(4):429–483

Meyer H (1955) Zur Adventivflora von Harburg, Wilhelmsburg und Umgebung. Harburger Jahrbuch:96–128

Miehlich G, Brandt I (2010) Natürliche Bodenformengesellschaften Hamburgs - Karte mit Erläuterungstext. Gutachten im Auftrag der Behörde für Stadtentwicklung und Umwelt, Hamburg

Mikulyuk A, Sharma S, van Egeren S, Erdmann E, Nault ME, Hauxwell J (2011) The relative role of environmental, spatial, and land-use patterns in explaining aquatic macrophyte community composition. Canadian Journal of Fisheries and Aquatic Sciences 68(10):1778–1789

Miller JR (2005) Biodiversity conservation and the extinction of experience. Trends in Ecology & Evolution 20(8):430–434

Mimet A, Pellissier V, Quenol H, Aguejdad R, Dubreuil V, Roze F (2009) Urbanisation induces early flowering: evidence from *Platanus acerifolia* and *Prunus cerasus*. International Journal of Biometeorology 53(3):287–298

Mitchell CE, Agrawal AA, Bever JD, Gilbert GS, Hufbauer RA, Klironomos JN, Maron JL, Morris WF, Im Parker, Power AG, Seabloom EW, Torchin ME, Vazquez DP (2006) Biotic interactions and plant invasions. Ecology Letters 9(6):726–740

Monty A, Bizoux J, Escarré J, Mahy G, Garcia de Leaniz C (2013) Rapid plant invasion in distinct climates involves different sources of phenotypic variation. PLOS ONE 8(1):e55627

Monty A, Lebeau J, Meerts P, Mahy G (2009) An explicit test for the contribution of environmental maternal effects to rapid clinal differentiation in an invasive plant. Journal of Evolutionary Biology 22(5):917–926

Monty A, Mahy G (2009) Clinal differentiation during invasion: *Senecio inaequidens* (Asteraceae) along altitudinal gradients in Europe. Oecologia 159(2):305–315

Monty A, Mahy G (2010) Evolution of dispersal traits along an invasion route in the wind-dispersed *Senecio inaequidens* (Asteraceae). Oikos 119(10):1563–1570

Monty A, Stainier C, Lebeau F, Pieret N, Mahy G (2008) Seed rain pattern of the invasive weed *Senecio inaequidens* (Asteraceae). Belgian Journal of Botany 141(1):51–63

Muratet A, Machon N, Jiguet F, Moret J, Porcher E (2007) The role of urban structures in the distribution of wasteland flora in the greater paris area, France. Ecosystems 10(4):661–671

Muratet A, Porcher E, Devictor V, Arnal G, Moret J, Wright S, Machon N (2008) Evaluation of floristic diversity in urban areas as a basis for habitat management. Applied Vegetation Science 11(4):451–460

Nichol JE, Fung WY, Lam K, Wong MS (2009) Urban heat island diagnosis using ASTER satellite images and ‘in situ’ air temperature. Atmospheric Research 94(2):276–284

Niemelä J (1999) Ecology and urban planning. Biodiversit and Conservation 8(1):119–131

Niziolek OK, Berenbaum MR, DeLucia EH (2013) Impact of elevated $CO_2$ and increased temperature on Japanese beetle herbivory. Insect Science 20(4):513–523

Nobis MP, Jaeger JAG, Zimmermann NE (2009) Neophyte species richness at the landscape scale under urban sprawl and climate warming. Diversity and Distributions 15(6):928–939

Nowak DJ (2010) Urban biodiversity and climate change. In: Müller N, Werner P, Kelcey JG (eds) Urban biodiversity and design. Wiley-Blackwell, Oxford [u.a.], pp 101–117

Nowak DJ, Crane DE (2002) Carbon storage and sequestration by urban trees in the USA. Environmental Pollution 116(3):381–389

O’Brien AM, Ettinger AK, HilleRisLambers J (2012) Conifer growth and reproduction in urban forest fragments: Predictors of future responses to global change? Urban Ecosystems 15(4):879–891

Oke TR (1973) City size and urban heat island. Atmospheric Environment 7(8):769–779

Oke TR (1982) The energetic basis of the urban heat island. Quarterly Journal of the Royal Meteorological Society 108:1–24

Oke TR (1988) The urban energy balance. Progress in Physical Geography 12(4):471–508

Oksanen J, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Simpson G, Solymos P, Stevens M, Wagner H (2012) vegan: Community Ecology Package. R package version 2.0-5. http://CRAN.R-project.org/package=vegan

Ossenbruegge J, Bechtel B (2010) Klimawandel und Stadt - der Faktor Klima als neue Determinante der Stadtentwicklung. In: Boehner J, Ratter B (eds) Klimawandel und Klimawirkung, Hamburger Symposium Geographie 2. Institut für Geographie der Universität Hamburg

Parker DE (2010) Urban heat island effects on estimates of observed climate change. Wiley Interdisciplinary Reviews-Climate Change 1(1):123–133

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637–669

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421(6918):37–42

Pataki DE, Xu T, Luo YQ, Ehleringer JR (2007) Inferring biogenic and anthropogenic carbon dioxide sources across an urban to rural gradient. Oecologia 152(2):307–322

Pauchard A, Aguayo M, Peña E, Urrutia R (2006) Multiple effects of urbanization on the biodiversity of developing countries: The case of a fast-growing metropolitan area (Concepción, Chile). Biological Conservation 127(3):272–281

Pautasso M (2007) Scale dependence of the correlation between human population presence and vertebrate and plant species richness. Ecology Letters 10(1):16–24

Pawlowsky-Glahn V, Egozcue JJ (2006) Compositional data and their analysis: an introduction. Geological Society, London, Special Publications 264(1):1–10

Pellissier V, Roze F, Aguejdad R, Quenol H, Clergeau P (2008) Relationships between soil seed bank, vegetation and soil fertility along an urbanisation gradient. Applied Vegetation Science 11(3):325–334

Peres-Neto PR, Legendre P (2010) Estimating and controlling for spatial structure in the study of ecological communities. Global Ecology and Biogeography 19(2):174–184

Petřík P, Wild J (2006) Environmental correlates of the patterns of plant distribution at the meso-scale: a case study from Northern Bohemia (Czech Republic). Preslia 78(2):211–234

Pickett STA, Cadenasso ML, Grove JM, Boone CG, Groffman P, Irwin E, Kaushal SS, Marshall V, McGrath BP, Nilon CH, Pouyat RV, Szlavecz K, Troy A, Warren P (2011) Urban ecological systems: Scientific foundations and a decade of progress. Journal of Environmental Management 92(3):331–362

Pickett STA, Cadenasso ML, Grove JM, Nilon CH, Pouyat RV, Zipperer WC, Costanza R (2001) Urban ecological systems: Linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. Annual Review of Ecology and Systematics 32:127–157

Pompe S, Berger S, Walther GR, Badeck F, Hanspach J, Sattler S, Klotz S, Kuehn I (2009) Mögliche Konsequenzen des Klimawandels für Pflanzenareale in Deutschland. Natur und Landschaft 84(1):2–7

Pompe S, Hanspach J, Badeck F, Klotz S, Thuiller W, Kuehn I (2008) Climate and land use change impacts on plant distributions in Germany. Biology Letters 4(5):564–567

Poppendieck HH, Bertram H, Brandt I, Engelschall E, v.Prondzinski J (eds) (2010) Der Hamburger Pflanzenatlas. von a bis z. Dölling und Galitz Verlag, München, Hamburg

Poppendieck HH, Brandt I, Prondzinski J von, Kreft KA (2002) Artenkataster Hamburg im Spannungsfeld von staatlicher Aufgabe und ehrenamtlichem Engagement. Schriftenreihe für Vegetationskunde 36:69–77

Pouyat RV, McDonnell MJ (1991) Heavy-metal accumulations in forest soils along an urban-rural gradient in Southeastern New York, USA. Water, Air and Soil Pollution 57-8:797–807

Prach K, Pyšek P, Bastl M (2001) Spontaneous vegetation succession in human-disturbed habitats: A pattern across seres. Applied Vegetation Science 4(1):83–88

Pyšek P (1993) Factors affecting the diversity of flora and vegetation in Central-European settlements. Vegetatio 106(1):89–100

Pyšek P (1998) Alien and native species in Central European urban floras: a quantitative comparison. Journal of Biogeography 25(1):155–163

Pyšek P, Chocholoušková Z, Pyšek A, Jarošík V, Chytrý M, Tichý L (2004) Trends in species diversity and composition of urban vegetation over three decades. Journal of Vegetation Science 15(6):781–788

Pyšek P, Jarošík V, Pergl J, Randall R, Chytrý M, Kuehn I, Tichý L, Danihelka J, Chrtek jun J, Sádlo J (2009) The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. Diversity and Distributions 15(5):891–903

Pyšek P, Richardson DM (2007) Traits associated with invasiveness in alien Plants: Where do we stand? In: Nentwig W (ed) Biological Invasions. Springer, Dordrecht, pp 97–126

R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0 , http://www.R-project.org/

R Development Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.R-project.org/

Rabinowitz D (1981) Seven forms of rarity. In: Synge H (ed) The Biological aspects of rare plant conservation. Wiley, Chichester [West Sussex], New York, pp 205–217

Raciti SM, Hutyra LR, Rao P, Finzi AC (2012) Inconsistent definitions of “urban” result in different conclusions about the size of urban carbon and nitrogen stocks. Ecological Applications 22(3):1015–1035

Ranta P, Viljanen V (2011) Vascular plants along an urban-rural gradient in the city of Tampere, Finland. Urban Ecosystems 14(3):361–376

Rebele F (1994) Urban ecology and special features of urban ecosystems. Global Ecology and Biogeography Letters 4(6):173–187

Reidat R (1971) Temperatur, Niederschlag, Staub. Deutscher Planungsatlas., Band VIII. Hamburg. Lieferung 7. Gebrüder Jaenecke, Hannover

Richardson DM, Pyšek P, Rejmanek M, Barbour M, Panetta FWC (2000) Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6(2):93–107

Roach DA, Wulff RD (1987) Maternal effects in plants. Annual Review of Ecology and Systematics 18:209–235

Robinson SL, Lundholm JT (2012) Ecosystem services provided by urban spontaneous vegetation. Urban Ecosystems 15(3):545–557

Rockel B, Will A, Hense A (2008) The Regional Climate Model COSMO-CLM (CCLM). Meteorologische Zeitschrift 17(4):347–348

Roetzer T, Wittenzeller M, Haeckel H, Nekovar J (2000) Phenology in central Europe - differences and trends of spring phenophases in urban and rural areas. International Journal Biometeorology 44(2):60–66

Rosenhagen G, Schatzmann M, Schrön A (2011) Das Klima der Metropolregion auf Grundlage meteorologischer Messungen und Beobachtungen. In: Storch H von, Claussen M (eds) Klimabericht für die Metropolregion Hamburg. Springer, Berlin, Heidelberg, pp 19–59

Roth M, Oke TR, Emery WJ (1989) Satellite-derived urban heat islands from 3 coastal cities and the utilization of such data in urban climatology. International Journal of Remote Sensing 10(11):1699–1720

Roumet C, Picon-Cochard C, Dawson LA, Joffre R, Mayes R, Blanchard A, Brewer MJ (2006) Quantifying species composition in root mixtures using two methods: near-infrared reflectance spectroscopy and plant wax markers. New Phytologist 170(3):631–638

Roy DB, Hill MO, Rothery P (1999) Effects of urban land cover on the local species pool in Britain. Ecography 22(5):507–515

Rudd H, Vala J, Schaefer V (2002) Importance of backyard habitat in a comprehensive biodiversity conservation strategy: A connectivity analysis of urban green spaces. Restoration Ecology 10(2):368–375

Rusterholz H, Wirz D, Baur B (2012) Garden waste deposits as a source for non-native plants in mixed deciduous forests. Applied Vegetion Science 15(3):329–337

Sadler JP, Small EC, Fiszpan H, Telfer MG, Niemelä J (2006) Investigating environmental variation and landscape characteristics of an urban-rural gradient using woodland carabid assemblages. Journal of Biogeography 33(6):1126–1138

Salisbury EJ (1943) The flora of bombed areas. Nature 151(3834):462–466

Santer BD, Wigley TM, Jones PD (1993) Correlation methods in fingerprint detection studies. Climate Dynamics 8(6):265–276

Sattler T, Borcard D, Arlettaz R, Bontadina F, Legendre P, Obrist MK, Moretti M (2010) Spider, bee, and bird communities in cities are shaped by environmental control and high stochasticity. Ecology 91(11):3343–3353

Schaffers AP, Sykora KV (2000) Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. Journal of Vegetation Science 11(2):225–244

Scheffer F (2008) Lehrbuch der Bodenkunde. Scheffer/Schachtschabel. Spektrum, Heidelberg

Scherber C, Crawley MJ, Porembski S (2003) The effects of herbivory and competition on the invasive alien plant *Senecio inaequidens* (Asteraceae). Diversity and Distributions 9(6):415–426

Schluenzen KH, Hoffmann P, Rosenhagen G, Riecke W (2010) Long-term changes and regional differences in temperature and precipitation in the metropolitan area of Hamburg. International Journal Climatology 30(8):1121–1136

Schmidt KJ, Poppendieck HH, Jensen K (2014) Effects of urban structure on plant species richness in a large European city. Urban Ecosystems 17(2):427–444

Schmidtlein S (2005) Imaging spectroscopy as a tool for mapping Ellenberg indicator values. Journal of Applied Ecology 42(5):966–974

Schubert K, Klein M (2011) Das Politiklexikon. Begriffe, Fakten, Zusammenhänge, 5th edn. Dietz, Bonn

Schulze D (2011) Einfluss von Herbivorie und Temperaturerhöhung auf den Neophyten *Senecio inaequidens* DC. entlang eines urban-ruralen Gradienten. BSc. thesis, Universität Hamburg

Schweiger O, Biesmeijer JC, Bommarco R, Hickler T, Hulme PE, Klotz S, Kuehn I, Moora M, Nielsen A, Ohlemüller R, Petanidou T, Potts SG, Pyšek P, Stout JC, Sykes MT, Tscheulin T, Vilà M, Walther GR, Westphal C, Winter M, Zobel M, Settele J (2010) Multiple stressors on biotic interactions: how climate change and alien species interact to affect pollination. Biological Reviews 85(4):777–795

Schweiger O, Heikkinen RK, Harpke A, Hickler T, Klotz S, Kudrna O, Kuehn I, Pöyry J, Settele J (2012) Increasing range mismatching of interacting species under global change is related to their ecological characteristics. Global Ecology and Biogeography 21(1):88–99

Sigmaplot for Windows Version 12.0 (2011) Systat Software, Inc.

Seto KC, Güneralp B, Hutyra LR (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proceedings of the National Academy of Sciences 109(40):16083–16088

Solecki W, Marcotullio P (2013) Climate Change and Urban Biodiversity Vulnerability. In: Elmquist T, Fragkias M, Goodness J, Güneralp B, Marcotullio PJ, Mcdonald RI, Parnell S, Schewenius M, Sendstad M, Seto KC, Wilkinson C (eds) Urbanization, Biodiversity and Ecosystem Services: Challenges and Opportunities. A Global Assessment. Springer Netherlands, Dordrecht, pp 485–504

Souch C, Grimmond S (2006) Applied climatology: urban climate. Progress in physical geography 30(2):270–279

SPSS Inc. (2009) PASW Statistics for Windows, Version 18.0. Chicago: SPSS Inc

Steinke J (2011) Pflanzliche Abwehrmechanismen in einem sich erwärmenden Klima: Konstitutive und induzierte Pyrrolizidinalkaloide in *Senecio inaequidens* DC. entlang eines Stadt-Land-Gradienten. BSc. thesis, Universität Hamburg

Stewart I, Oke TR (2009) Newly developed 'thermal climate zones' for defining and measuring urban heat island magnitude in the canopy layer. T.R. Oke Symposium & 8th Symposium on the Urban Environment, January 11-15, Phoenix, AZ

Stolter C, Julkunen-Tiitto R, Ganzhorn JU (2006) Application of near infrared reflectance spectroscopy (NIRS) to assess some properties of a sub-arctic ecosystem. Basic and Applied Ecology 7(2):167–187

Strohbach MW, Haase D (2012) Above-ground carbon storage by urban trees in Leipzig, Germany: Analysis of patterns in a European city. Landscape and Urban Planning 104(1):95–104

Sukopp H (2002) On the early history of urban ecology in Europe. Preslia 74:373–939

Sukopp H, Wurzel A (2003) The Effects of Climate Change on the Vegetation of Central European Cities. Urban Habitats 1(1):66–86

Susca T, Gaffin SR, Dell'Osso GR (2011) Positive effects of vegetation: Urban heat island and green roofs. Environmental Pollution 159(8-9):2119–2126

Sushinsky JR, Rhodes JR, Possingham HP, Gill TK, Fuller RA (2013) How should we grow cities to minimize their biodiversity impacts? Global Change Biology 19(2):401–410

Tait CJ, Daniels CB, Hill RS (2005) Changes in species assemblages within the Adelaide Metropolitan Area, Australia, 1836-2002. Ecological Applications 15(1):346–359

Tamis WL, Van't Zelfde M, van der Meijden R, Haes HA de (2005) Changes in vascular plant biodiversity in the Netherlands in the 20th century explained by their climatic and other environmental characteristics. Climatic Change 72(1-2):37–56

Ter Braak CJ, Barendregt LG (1986) Weighted averaging of species indicator values - its efficiency in environmental calibration. Mathematical Biosciences 78(1):57–72

Ter Braak C.J.F. & P. Smilauer (1997) Canoco for Windows Version 4.0. Centre for Biometry Wageningen, Wageningen.

The GIMP Development Team (2008) GNU Image Manipulation Program. GIMP 2.6.8

Thebault A, Stoll P, Buttler A (2012) Complex interactions between spatial pattern of resident species and invasiveness of newly arriving species affect invasibility. Oecologia 170(4):1133–1142

Thiele J, Kollmann J, Andersen UR (2009) Ecological and socioeconomic correlates of plant invasions in Denmark: The utility of environmental assessment data. Ambio 38(2):89–94

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, Siqueira MF de, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Townsend Peterson A, Phillips OL, Williams SE (2004) Extinction risk from climate change. Nature 427(6970):145–148

Thompson K, McCarthy MA (2008) Traits of British alien and native urban plants. Journal of Ecology 96(5):853–859

Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice I (2005) Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Science of the United States of America, PNAS 102(23):8245–8250

Titeux N, Dufrene M, Jacob JP, Paquay M, Defourny P (2004) Multivariate analysis of a fine-scale breeding bird atlas using a geographical information system and partial canonical correspondence analysis: environmental and spatial effects. Journal of Biogeography 31(11):1841–1856

Trammell TLE, Schneid BP, Carreiro MM (2011) Forest soils adjacent to urban interstates: Soil physical and chemical properties, heavy metals, disturbance legacies, and relationships with woody vegetation. Urban Ecosystems 14(4):525–552

Trenberth K, Jones P, Ambenje P, Bojariu R, Easterling D, Klein Tank A, Parker D, Rahimzadeh F, Renwick J, Rusticucci M, Soden B, Zhai P (2007) Observations: Surface and Atmospheric Climate Change. In: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambride University Press, Cambridge, United Kingdom and New York, NY, USA

Trentanovi G, von der Lippe M, Sitzia T, Ziechmann U, Kowarik I, Cierjacks A (2013) Biotic homogenization at the community scale: disentangling the roles of urbanization and plant invasion. Diversity and Distributions 19(7):738–748

United Nations Population Division (2011) World urbanization prospects. U.N. Department of Economic and Social Affairs, New York, New York, U.S.A.

Urban MC, Tewksbury JJ, Sheldon KS (2012) On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. Proceedings of the Royal Society B: Biological Science 279(1735):2072–2080

Vallet J, Daniel H, Beaujouan V, Roze F (2008) Plant species response to urbanization: comparison of isolated woodland patches in two cities of North-Western France. Landscape Ecology 23(10):1205–1217

van Dam NM, van der Meijden E, Verpoorte R (1993) Induced responses in 3 alkaloid-containing plant species. Oecologia 95(3):425–430

van den Boogaart K, Tolosana R, Bren M (2013) compositions: Compositional Data Analysis. R package version 1.30-1. http://CRAN.R-project.org/package=compositions

van der Meijden E (1996) Plant defence, an evolutionary dilemma: Contrasting effects of (specialist and generalist) herbivores and natural enemies. Entomologia Experimentalis et Applicata 80(1):307–310

van der Veken S, Verheyen K, Hermy M (2004) Plant species loss in an urban area (Turnhout, Belgium) from 1880 to 1999 and its environmental determinants. Flora 199(6):516–523

van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters 13(2):235–245

Vanparys V, Cawoy V, Mahaux O, Jacquemart A (2011) Comparative study of the reproductive ecology of two co-occurring related plant species: the invasive *Senecio inaequiden*s and the native *Jacobaea vulgaris*. Plant Ecology and Evolution 144(1):3–11

Verlinden M, Kerkhove A, Nijs I (2013) Effects of experimental climate warming and associated soil drought on the competition between three highly invasive West European alien plant species and native counterparts. Plant Ecology 214(2):243–254

Verlinden M, Nijs I (2010) Alien plant species favoured over congeneric natives under experimental climate warming in temperate Belgian climate. Biological Invasions 12(8):2777–2787

Vilà M, Weiner J (2004) Are invasive plant species better competitors than native plant species? Evidence from pair-wise experiments. Oikos 105(2):229–238

Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. Proceedings of the Royal Society B: Biological Science 272(1581):2561–2569

von der Lippe M, Kowarik I (2007) Long-distance dispersal of plants by vehicles as a driver of plant invasions. Conservation Biology 21(4):986–996

von der Lippe M, Kowarik I (2008) Do cities export biodiversity? Traffic as dispersal vector across urban-rural gradients. Diversity and Distributions 14(1):18–25

Voogt J, Oke TR (2003) Thermal remote sensing of urban climates. Remote Sensing of Environment 86(3):370–384

Vrieling K, Devos H, Van Wijk CA (1993) Genetic analysis of the concentrations of pyrrolizidine alkaloids in *Senecio jacobaea*. Phytochemistry 32(5):1141–1144

Walker JS, Grimm NB, Briggs JM, Gries C, Dugan L (2009) Effects of urbanization on plant species diversity in central Arizona. Frontiers in Ecology and the Environment 7(9):465–470

Walther G, Roques A, Hulme PE, Sykes MT, Pyšek P, Kuehn I, Zobel M, Bacher S, Botta-Dukát Z, Bugmann H, Czúcz B, Dauber J, Hickler T, Jarošík V, Kenis M, Klotz S, Minchin D, Moora M, Nentwig W, Ott J, Panov VE, Reineking B, Robinet C, Semenchenko V, Solarz W, Thuiller W, Vilà M, Vohland K, Settele J (2009) Alien species in a warmer world: risks and opportunities. Trends in Ecology and Evolution 24(12):686–693

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416(6879):389–395

Wang H, MacGregor-Fors I, Lopez-Pujol J (2012) Warm-temperate, immense, and sprawling: plant diversity drivers in urban Beijing, China. Plant Ecology 213(6):967–992

Wania A, Kuehn I, Klotz S (2006) Plant richness patterns in agricultural and urban landscapes in Central Germany - spatial gradients of species richness. Landscape and Urban Planning 75(1-2):97–110

Wasof S, Lenoir J, Gallet-Moron E, Jamoneau A, Brunet J, Cousins SAO, Frenne P de, Diekmann M, Hermy M, Kolb A, Liira J, Verheyen K, Wulf M, Decocq G (2013) Ecological niche shifts of understorey plants along a latitudinal gradient of temperate forests in north-western Europe. Global Ecology and Biogeography 22(10):1130-1140

Weller B, Ganzhorn JU (2004) Carabid beetle community composition, body size, and fluctuating asymmetry along an urban-rural gradient. Basic and Applied Ecology 5(2):193–201

Williams NS, Morgan JW, McDonnell MJ, McCarthy MA (2005) Plant traits and local extinctions in natural grasslands along an urban-rural gradient. Journal of Ecology 93(6):1203–1213

Williams NS, Schwartz MW, Vesk PA, McCarthy MA, Hahs AK, Clemants SE, Corlett RT, Duncan RP, Norton BA, Thompson K, McDonnell MJ (2009) A conceptual framework for predicting the effects of urban environments on floras. Journal of Ecology 97(1):4–9

Willis KJ, Bhagwat SA (2009) Biodiversity and Climate Change. Science 326(5954):806–807

Wilson JB, Peet RK, Dengler J, Paertel M (2012) Plant species richness: the world records. Journal of Vegetation Science 23(4):796–802

Wittig R (1991) Ökologie der Großstadtflora. Flora und Vegetation der Städte des nordwestlichen Mitteleuropas. Gustav Fischer Verlag, Stuttgart

Wittig R (2004) The origin and development of the urban flora of Central Europe. Urban Ecosystems 7:323–339

Wittig R, Becker U (2010) The spontaneous flora around street trees in cities-A striking example for the worldwide homogenization of the flora of urban habitats. Flora 205(10):704–709

Wittig R, Durwen KJ (1982) Ecological indicator-value spectra of spontaneous urban floras. In: Bornkamm R, Lee JA, Seaward MRD (eds) Urban ecology. The Second European Ecological Symposium Berlin, 8-12 September 1980. Blackwell, Oxford, pp 23–31

Wittig R, Kuttler W, Tackenberg O (2012) Urban-industrielle Lebensräume. In: Moosbrugger V, Brasseur G, Schaller M, Stribrny B (eds) Klimawandel und Biodiversität. Folgen für Deutschland, 1st edn. Wissenschaftliche Buchgesellschaft, Darmstadt, pp 290–307

Wong M, Nichol J, Kwok K (2009) The urban heat island in Hong Kong: causative factors and scenario analysis. Joint Urban Remote Sensing Event 2009. Proc IEEE Int:1–7

Yokobori T, Ohta S (2009) Effect of land cover on air temperatures involved in the development of an intra-urban heat island. Climate Research 39:61–73

Zangerl AR, Rutledge CE (1996) The probability of attack and patterns of constitutive and induced defense: A test of optimal defense theory. American Naturalist 147(4):599–608

Zeleny D, Schaffers AP (2012) Too good to be true: pitfalls of using mean Ellenberg indicator values in vegetation analyses. Journal of Vegetation Science 23(3):419–431

Zerbe S, Maurer U, Schmitz S, Sukopp H (2003) Biodiversity in Berlin and its potential for nature conservation. Landscape and Urban Planning 62(3):139–148

Ziska LH, Bunce JA, Goins EW (2004) Characterization of an urban-rural $CO_2$/temperature gradient and associated changes in initial plant productivity during secondary succession. Oecologia 139(3):454–458

Ziska LH, Gebhard DE, Frenz DA, Faulkner S, Singer BD, Straka JG (2003) Cities as harbingers of climate change: Common ragweed, urbanization, and public health. Journal of Allergy and Clinical Immunology 111(2):290–295

# DANKSAGUNG

Ohne die vielen Menschen, die mich im Laufe der letzten Jahre auf meinem Weg unterstützt haben, wäre diese Doktorarbeit nicht möglich gewesen. Bei ihnen allen möchte ich mich aufs herzlichste bedanken.

Zunächst möchte ich mich ganz besonders bei Kai Jensen für die engagierte Betreuung meiner Doktorarbeit bedanken, für die Unterstützung und die Motivation, zahlreiche Ratschläge, hilfreiche Kritik und kreative Ideen.

Hans-Helmut Poppendieck danke ich herzlich für die stadtökologische Betreuung und die vielen Informationen zur Hamburger Flora, außerdem für den Einsatz als ‚Co-Advisor' in meinem SICSS-Panel.

Bei Eva-Maria Pfeiffer möchte ich mich herzlich für die Übernahme des Zweitgutachtens, für ihren Einsatz als ‚Co-Advisor' und ‚Panel-Chair' und ihre hilfreichen Ratschläge bedanken.

Meinen KLIMZUG-Mitdoktorand_innen Christian, Kristin und Sebastian danke ich für die gemeinsame spannende Zeit und den intensiven Austausch. Besonders möchte ich mich bei Sebastian bedanken: für alles. Kristin danke ich sehr für die vielen inhaltlichen und statistischen Diskussionen sowie die Exkursionen in den Botanischen Garten und die gemeinsame Begeisterung für Pflanzenbestimmung. Außerdem möchte ich mich herzlich bei Wiebke für den vielseitigen Austausch und die koordinatorische Unterstützung bedanken.

Der gesamten AG Angewandte Pflanzenökologie und der AG Nutzpflanzenbiologie um Reinhard Lieberei danke ich ganz herzlich für das angenehme Arbeitsumfeld, den hilfreichen Austausch und die Unterstützung; ich bin froh, dass ich meine Doktorarbeit in dieser Umgebung durchführen konnte. Claudia danke ich ganz herzlich für zahlreiche Antworten auf zahlreiche Fragen und die organisatorische und logistische Unterstützung. Jens und Jessica möchte ich für den stadtökologischen Austausch danken.

Bei Nikola, Concha, Jonathan und Dennis bedanke ich mich für die gute Zusammenarbeit und ihre Begeisterung für die Stadtökologie während ihrer Abschlussarbeiten, die Betreuung der Arbeiten hat mir immer viel Spaß gemacht. Den Hiwis Nikola, Jonathan, Dennis, Peter, Katha, Anna R. und Anna S. sowie den BTA-Praktikanten Andreas, Anni, Lukas, Julian, Reinhild, Thomas und Tim danke ich für ihr Engagement und ihre Unterstützung im Feld, im Gewächshaus und im Labor. Marion und Sigrid danke ich für die Unterstützung in allen Gewächshausfragen, Jutta für ihre Hilfe bei der Samenbehandlung und den Keimungsversuchen. Weiterer Dank geht an Detlef und Thomas für ihre Hilfe bei den PA-Analysen. Ulrike und Andrea und den Mitarbeiterinnen der Bibliothek danke ich für die Unterstützung bei der Literaturrecherche und -beschaffung. Außerdem gilt mein Dank den Mitarbeitern des Botanischen Gartens. Ohne diese vielen Helfer und Helferinnen hätten meine Studien niemals so durchgeführt werden können.

Bei Benjamin Bechtel möchte ich mich für die produktive interdisziplinäre Zusammenarbeit, die mir einen spannenden Einblick in die Stadtklimatologie ermöglichte, bedanken. Ich danke Caroline Stolter für ihre Einführung in die NIRS-Analyse und die tolle Betreuung; die AG Dobler hat uns freundlicherweise intensiv zu Käfern für die Herbivorie-Experimente beraten.

Der SICSS-Graduiertenschule danke ich für die Möglichkeit, in zahlreichen Kursen meine statistischen, sprachlichen und methodischen Kenntnisse zu verbessern sowie für den Austausch mit anderen Doktorand_innen zahlreicher Fachrichtungen. Andrea Staudler danke ich für die Übernahme des ‚Panel-Chair‘ in der ersten Zeit und ihre hilfreichen Ratschläge.

Besonders bedanke ich mich beim Botanischen Verein zu Hamburg e.V und der Regionalstelle für Pflanzenartenschutz für die Bereitstellung der floristischen Kartierungsdaten. Ohne den umfangreichen ehrenamtlichen Einsatz der Vereinsmitglieder bei der Kartierung wäre die vorliegende Arbeit gar nicht möglich gewesen. Dabei möchte ich mich außerdem bei Ingo Brandt bedanken, der mir den Einstieg in diesen Datensatz erleichtert hat und mir weitere Daten zur Verfügung gestellt hat. Darüber hinaus möchte ich dem DWD, dem Statistikamt Nord, der BSU und dem Geologischen Landesamt für die Bereitstellung von Daten sowie der BSU, der Stiftung Naturschutz Schleswig-Holstein und der Stadt Ahrensburg für Betretungsgenehmigungen danken. Bei allen Flächenbesitzern und -besitzerinnen möchte ich mich für die Erlaubnis, auf ihren Grundstücken Vegetationsuntersuchungen durchzuführen, bedanken.

Diese Doktorarbeit wurde im Rahmen des Verbundprojektes KLIMZUG-Nord angefertigt und vom Bundesministerium für Bildung und Forschung (BMBF) gefördert (Fördernummer 01LR0805D). Ich danke allen Projektbeteiligten für die interessante Zeit und den vielseitigen Input. Besonders danke ich dem Team der KLIMZUG-Modellregion „Wandse“; die Zusammenarbeit mit so vielen anderen Fachrichtungen hat mir viele neue Sichtweisen und die Erfahrung interdisziplinärer Forschung ermöglicht. Elena Rottgardt möchte ich für die enge Zusammenarbeit im Rahmen des Projektes danken und dafür, dass alles immer so unkompliziert war.

Für das Korrekturlesen bedanke ich mich bei Marc, Martin, Uli, Jutta, Matthias und Claudia; bei Melissa Kostelecky für die Englischkorrekturen.

Meiner WG danke ich für das entspannte Zusammenleben, meinen Freundinnen und Freunden für Ablenkung und die Bereicherung meines Lebens neben der Ökologie. Marc danke ich für die liebe Unterstützung und freue mich, bald mehr Zeit zu haben.

Ganz besonders danke ich meinen Eltern Jutta und Ulrich Schmidt für die fortwährende Unterstützung bei allem, Ermutigung und Rückhalt und das starke Interesse an meiner Arbeit, ebenso gilt mein herzlichster Dank meinen Geschwistern Claudia und Martin, die immer für mich da waren.

# Eidesstattliche Versicherung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Hamburg, 13.12.2013 Katharina Schmidt