# Chapter I – Urbanization Causes Shifts of Species' Trait State Frequencies – a Large Scale Analysis

## 1. Introduction

Cities differ from rural landscapes in many ways: Human densities peak in urbanized areas; pollutants, energy and nutrients concentrate there (Sukopp 1998); exotic species are more frequent and land use is more heterogeneous (Niemelä 1999; McKinney 2002; Kühn *et al.* 2004a); annual average air temperature is 0.5 to 1.5°C higher than in the non-urban surroundings and air moisture is reduced, at least in temperate and boreal zones (Sukopp 1998). In contrast to cities, many agricultural landscapes are homogeneous over large areas. They are often subjected to a highly industrialized agriculture, characterized by high pesticide and fertilizer input and water management aiming at the maintenance of favorable soil moisture conditions. Forested and semi-natural landscapes are often nutrient poor, like forests on siliceous rock or heathland, because many nutrient rich habitats were transformed to agricultural or urban habitats (cf. Pressey 1994).

Differences in land use lead to differences in species composition since functional traits (such as pollination) have different states (i.e. different classes of categorical traits, e.g. wind-pollination, insect-pollination, self-pollination) which respond differentially to environmental gradients and therefore show distinct biogeographic patterns (e.g. Kühn et al. 2006). In other words: Different environments filter for species with different trait states (Zobel 1997). An example is the study of Wittig and Durwen (1982) comparing the spectra of environmental indicator-values (Ellenberg et al. 2001) of spontaneous floras in four cities in the West of Germany with the floras of the cities' rural surroundings, showing a greater proportion of high indicator-values for e.g. light, temperature and nitrogen in the cities. Similar results were obtained for the Central German city of Halle (Klotz 1989) and the Czech city of Plzeň (Chocholoušková & Pyšek 2003). Therefore, shifts in land use, e.g. increasing urbanization accompanied by an increase in temperature (Landsberg 1981; Oke 1982; Sukopp 1998), might lead to shifts in trait state frequency and, in extreme cases, to the loss of plants with certain trait states (Díaz & Cabido 1997). Tamis et al. (2005) showed that recent changes in the frequency of occurrence of vascular plant species across the Netherlands are at least partly related to both urbanization and climate change. They did, however, not consider shifts in trait state frequency. If these shifts in trait spectra indeed occur, they might affect ecosystem functioning: Increased leaf dry matter content for example might decrease litter decomposability (Kazakou et al. 2006).

Today's differences in the trait state composition of urban and rural floras might point to potential future shifts with further urbanization. We compared the proportions of several trait states of vascular plants in urbanized, agricultural and semi-natural areas in Germany. We ask which trait states enable a plant to cope with the specifics of urban environments, e.g. the urban climate (Sukopp 1998), irregular disturbance, and spatial and temporal heterogeneity (Niemelä 1999). We chose traits that we expect to respond to these urban conditions: Leaf traits [leaf anatomy, leaf persistence, specific leaf area (SLA), leaf dry matter content (LDMC)] should respond to climate, because gas exchange and water storage make leaves key organs regarding the adaptation to air temperature and moisture (cf. Wright et al. 2005). Further, we chose type of reproduction, life span, and life form, as traits related to persistence and regeneration after disturbance (which is true for SLA and LDMC as well; Lavorel & Garnier 2002; Wittig 2002; Sudnik-Wójcikowska & Galera 2005). Both spatial and temporal heterogeneity call for the ability of plants to disperse in space, therefore we included dispersal type as another trait. Poschlod & Bonn (1998) already claimed shifts in dispersal processes in man-made landscapes, especially after land-use intensification which may cause the decrease or increase of species frequency (Römermann et al. 2008). Last, we chose pollination type and UV-reflection of flowers; both are related to a plant's fecundity and reflect the suitability of the environment for pollinating insects. We discuss possible urban and rural filters and consequences of shifts in trait expression.

# 2. Materials and Methods

## 2.1. Data Sources

Data on species' traits originate from BiolFlor, a database on biological and ecological traits of the German flora (Klotz *et al.* 2002; http://www.ufz.de/biolflor; Kühn *et al.* 2004b) and from LEDA, a database on life-history traits of the Northwest European flora (Kleyer *et al.* 2008; http://www.leda-traitbase.org; see Table A1 in the appendix for a complete overview and description of traits and trait states).

Plant species occurrences originate from the database on the German flora (FLORKART, http://www.floraweb.de), maintained by the German Center for Phytodiversity at the Federal Agency for Nature Conservation (Bundesamt für Naturschutz BfN). In FLORKART, Germany is divided into grid-cells of 10 minutes longitude × 6 minutes latitude (corresponding to *c.* 12 × 11 km or 130 km$^2$). The database contains more than 14 million records of plant occurrences, acquired by thousands of volunteers. We did not use cultivated occurrences and only referred to the spontaneous flora. This means that occurrences of cultivated alien species that escaped from cultivation and form self-sustaining populations were mapped when occurring spontaneously. This applies e.g. to *Robinia pseudoacacia* L. or *Ailanthus altissima* (Mill.) Swingle when growing spontaneously on e.g. railway sites. Occurrences that were apparently planted, e.g. in any kind of garden, urban park or on cemeteries, were not included in the analyses. All plant occurrences mapped by the volunteers were controlled for plausibility by specialists in floristic recording centers (see e.g. http://www.biologie.uni-regensburg.de/Botanik/Florkart/dbblber.htm). However, mapping intensity varies among grid-cells. Therefore, we only used grid-cells with at least 45 of 50 control species. These are the 45 most frequent species of the German flora according to Krause (1998) plus five generalists considered by the volunteers to be difficult to determine (Kühn *et al.* 2004a; Kühn *et al.* 2006). 136 out of 2995 grid-cells were excluded due to an insufficient number of control species.

Land-use data per grid-cell are based on Corine Land Cover data that are derived from satellite remote sensing images (Statistisches Bundesamt 1997; http://www.corine.dfd.dlr.de/intro_en.html). Corine data differentiate between artificial (i.e. urban), agricultural, and forested/semi-natural land use, wetlands and water bodies. These land-use classes again are subdivided; the artificial land-use class for example includes built-up residential, industrial, commercial and transport area, mines, dumps, and artificial non-agricultural vegetated areas, i.e. urban green space. However, we only used the main classes: We classified grid-cells with more than 33% of urban land use as urbanized grid-cells (n=59) (Kühn & Klotz 2006) and split the remaining grid-cells into agricultural ones with more than 50% agriculture (n=1365) and semi-natural ones with more than 50% forests or semi-natural land use (n=312; Fig. A2 in the appendix). Grid-cells not meeting the selection criteria were omitted (n=1259).

To account for effects of other environmental parameters than land use on the trait state proportions, we used co-variables calculated per grid-cell and known to act on species diversity (Kühn *et al.* 2003). Data on climate [mean annual, mean July and mean January temperature, mean difference between July and January temperature (all 1961-1990), mean annual precipitation (1951-1980), mean wind speed] were provided by the "Deutscher Wetterdienst Department Klima und Umwelt"; data on topography (mean altitude above sea level) were provided by ESRI (ARCDeutschland 500 dataset, 1: 500,000); data on soils (number of soil types, number of soil patches), and geology (number of geological types, number of geological patches) are based on the German soil survey map (Bundesanstalt für Geowissenschaften und Rohstoffe 1995) and the Geological survey map (Bundesanstalt für Geowissenschaften und Rohstoffe 1993) provided by the German Federal Agency for Nature Conservation. For an overview of differences in environmental parameters between urbanized and rural grid-cells in Germany see Fig. A1 in the appendix.

## 2.2. Data Analyses

### *2.2.1. Log-Ratios of Proportions*

We merged the matrices on species per grid-cell and trait state per species (by matrix multiplication) to a matrix on trait state frequency per grid-cell, from which we calculated the trait state proportions (for numbers of species analyzed per trait state see Table A2 in the appendix). Because the proportions add up to 100%, they depend on each other. To break this unit sum constraint, we used log-ratios of proportions (e.g. Aitchison 1982; Billheimer *et al.* 2001; Kühn *et al.* 2006). The log-ratio of two trait states a and b is log (a/b). For traits with more than two states the denominator should always be the same, without relevance which trait this is.

Zero values can neither be log-transformed nor used in the denominator. Therefore, we replaced each zero with the proportion one trait state would have if expressed by only one out of all species of a grid-cell, and reduced the respective non-zero values by a corresponding amount (Fry *et al.* 2000; Martin-Fernandez *et al.* 2000). Each log-ratio was used separately in the further analyses.

SLA and LDMC are the only continuous traits in our analysis, i.e. they were used directly as responses in the linear models without preceding log-transformation.

### *2.2.2. Linear Models*

To minimize the effects of climate, topography, soils and geology on the trait state composition, we explained each log-ratio in a multiple linear regression with the corresponding parameters. We included selected two-way interactions and reduced each model via backward selection until achieving its minimal adequate version (model selection by AIC; Mac Nally 2000). We calculated the mean of the minimal adequate models' residuals (i.e. the variation not explained by climate, topography, soils and geology) per grid-cell type. Since there are more agricultural (n=1365) and semi-natural (n=312) than urbanized (n=59) grid-cells, we resampled the former two separately by calculating the mean of 59 randomly chosen grid-cells 999 times. We tested for significant differences between the mean residuals of urbanized and agricultural and between urbanized and semi-natural grid-cells with the z-statistic (comparison of one mean value to a distribution of mean values).

We also calculated differences between urbanized and non-urbanized grid-cells with an alternative method, by including the three land-use types as a categorical predictor in a linear model together with the environmental parameters on climate, topography, soils and geology, and explaining each log-ratio with these predictors (Knapp *et al.* 2008b). This approach yielded the same results as the resampling-approach and is not presented here.

Choosing environmental variables to minimize non-land-use effects on log-ratios is problematic, because we might miss important variables. To corroborate the results of our first analysis, we additionally explained the log-ratios using linear mixed effect models that allow for random and fixed effects: We assigned the urbanized grid-cells to six regions that are reasonably homogeneous with respect to biogeography (Fig. 1.1). Within each region, we selected as many agricultural and semi-natural grid-cells as there were urbanized grid-cells to account for the differences in sample size of grid-cell types.

We explained the log-ratios (and SLA and LDMC) with the regions as random effects and land use as fixed effect. On this, we performed a variance components analysis.

We performed all analyses with the open source software R, Version 2.3.1 (R Development Core Team 2006), calculating the linear mixed-effect models with the R-function lme from the package nlme (Pinheiro *et al.* 2006), and variance components analysis with the R-function varcomp from the package ape (Paradis *et al.* 2006).

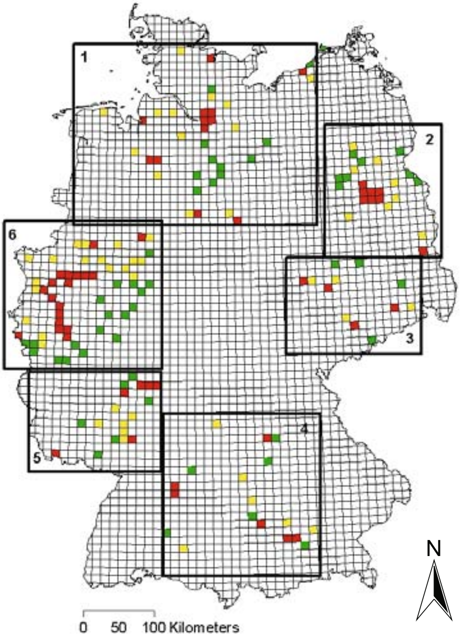

**Figure 1. 1** – Six regions in Germany selected for comparison of effects of biogeography and land use on the functional composition of plant species assemblages
(1) Northern Germany; (2) Berlin and Brandenburg; (3) Saxony and Saxony-Anhalt; (4) Southern Germany; (5) Rhine-Main region; (6) Rhine-Ruhr region. Red: urbanized grid-cells; yellow: agricultural grid-cells; green: semi-natural grid-cells. Figure taken from Preslia 80, 375-388 (2008), reprinted with permission of the Czech Botanical Society

# 3. Results

The models correcting for climate, topography, soils and geology were all significant and explained between 9% and 71% of the log-ratios (Table 1.1). Most differences in trait state composition between urbanized and non-urbanized grid-cells were significant (Fig. 1.2, Table 1.2): Plants dispersed by animals, humans or water had increased proportions in urbanized grid-cells at the expense of plants dispersed by wind, which were relatively more frequent in agricultural and semi-natural grid-cells (Fig. 1.2a, b). Proportions of plants with hygromorphic leaves were decreased in urbanized grid-cells in favor of plants with mesomorphic, scleromorphic or succulent leaves. (Fig. 1.2c, d). LDMC was lower in urbanized than in both types of non-urbanized grid-cells (Fig. 1.2e). Plants with overwintering green leaves were more frequent in urbanized than in agricultural and semi-natural grid-cells (Fig. 1.2f). There were relatively more therophytes in urbanized than in non-urbanized grid-cells but accordingly less chamaephytes, geophytes, hemicryptophytes and phanerophytes in proportion to therophytes in the urbanized grid-cells (Fig. 1.2g, h).

Plants in urbanized grid-cells were more often annual or biennial (Fig. 1.2i) than plants in agricultural and semi-natural grid-cells. Urbanized grid-cells had more wind-pollinated plants but less insect- and self-pollinated plants than agricultural grid-cells but showed no differences to semi-natural grid-cells (Fig. 1.2j, k). Plants in urbanized grid-cells had a higher SLA than plants in semi-natural grid-cells but showed no differences to plants in agricultural grid-cells (Fig. 1.2l). Plants in urbanized grid-cells reproduced more often by seeds than plants in non-urban grid-cells (Fig. 1.2m). Lastly, there were more plants with UV-reflecting flowers in urbanized than in agricultural and semi-natural grid-cells (Fig. 1.2n).

The linear mixed effect models correcting for biogeographic effects mainly corroborated these results. Land use explained more variance than the biogeographic differences between the six regions, throughout all tested trait state ratios (Table 1.3).

**Table 1. 1** – Variation of trait state ratios in urbanized, agricultural, and semi-natural grid-cells in Germany explained by climate, topography, soils, and geology in multiple linear models

$R^2$ shows the variation and is adjusted for the number of predictors. Asterisks mark significant *P*-values: *** = $P \leq 0.001$.

| **Trait** | **Trait state ratios** | **$R^2$** |
|---|---|---|
| Dispersal type | Dysochorous/Anemochorous | 0.45*** |
| | Endozoochorous/Anemochorous | 0.53*** |
| | Epizoochorous/Anemochorous | 0.56*** |
| | Hemerochorous/Anemochorous | 0.56*** |
| | Hydrochorous/Anemochorous | 0.63*** |
| Leaf anatomy | Helomorphic/Hygromorphic | 0.51*** |
| | Hydromorphic/Hygromorphic | 0.49*** |
| | Mesomorphic/Hygromorphic | 0.40*** |
| | Scleromorphic/Hygromorphic | 0.37*** |
| | Succulent/Hygromorphic | 0.22*** |
| LDMC | - | 0.18*** |
| Leaf persistence | Evergreen / overwintering green | 0.67*** |
| | Spring green / overwintering green | 0.29*** |
| | Summer green / overwintering green | 0.65*** |
| Life form | Chamaephyte/Therophyte | 0.71*** |
| | Geophyte/Therophyte | 0.59*** |
| | Hemicryptophyte/Therophyte | 0.70*** |
| | Hydrophyte/Therophyte | 0.30*** |
| | Phanerophyte/Therophyte | 0.45*** |
| Life span | Annual/pluriennial | 0.70*** |
| | Biennial/pluriennial | 0.46*** |
| Pollen vector | Insects/wind | 0.52*** |
| | Selfing/wind | 0.41*** |
| SLA | - | 0.24*** |
| Type of reproduction | Generatively only/vegetatively only | 0.48*** |
| | Generatively & vegettively/vegetatively only | 0.66*** |
| UV-reflection of flowers | No/yes | 0.09*** |

**Table 1. 2** – Differences between the functional composition of the flora in urbanized, agricultural, and semi-natural grid-cells in Germany

u = urbanized; a = agricultural; sn = semi-natural. *P*-values: $0.05 < P \le 0.1$+, $P \le 0.05$*, $P \le 0.01$**, $P \le 0.001$***, for non significant differences equal values are assumed.

| **Trait** | **Trait state** | **Urbanized – agricultural** | **Urbanized – semi-natural** |
|---|---|---|---|
| Dispersal type | Dysochorous/Anemochorous | u < a + | u < sn* |
| | Endozoochorous/Anemochorous | u > a** | u > sn** |
| | Epizoochorous/Anemochorous | u > a*** | u > sn*** |
| | Hemerochorous/Anemochorous | u > a*** | u > sn*** |
| | Hydrochorous/Anemochorous | u > a*** | u > sn*** |
| Leaf anatomy | Helomorphic/Hygromorphic | u > a** | u = sn |
| | Hydromorphic/Hygromorphic | u = a | u > sn** |
| | Mesomorphic/Hygromorphic | u > a*** | u > sn*** |
| | Scleromorphic/Hygromorphic | u > a*** | u > sn*** |
| | Succulent/Hygromorphic | u > a*** | u > sn*** |
| LDMC | - | u < a*** | u < sn*** |
| Leaf persistence | Evergreen / overwintering green | u < a*** | u < sn*** |
| | Spring green / overwintering green | u = a | u < sn* |
| | Summer green / overwintering green | u < a*** | u = sn |
| Life form | Chamaephyte/Therophyte | u < a*** | u < sn*** |
| | Geophyte/Therophyte | u < a*** | u < sn*** |
| | Hemicryptophyte/Therophyte | u < a*** | u < sn*** |
| | Hydrophyte/Therophyte | u < a*** | u < sn + |
| | Phanerophyte/Therophyte | u < a*** | u < sn*** |
| Life span | Annual/pluriennial | u > a*** | u > sn*** |
| | Biennial/pluriennial | u > a*** | u > sn*** |
| Pollen vector | Insects/wind | u < a* | u = sn |
| | Selfing/wind | u < a + | u = sn |
| SLA | - | u = a | u > sn** |
| Type of reproduction | Generatively only/vegetatively only | u > a*** | u > sn** |
| | Generatively & vegettively/vegetatively | u < a* | u = sn |
| UV-reflection of | No/yes | u < a** | u < sn*** |

**Table 1. 3** – Variation [%] of the flora's functional composition explained in linear mixed effect models by land use and differences in biogeography between six regions in Germany that are relatively homogeneous with respect to biogeography.
See below for further explanation.

| Trait | Trait state ratio | Land use | Biogeography | $Int_u$ | $Int_a$ | $Int_{sn}$ |
|---|---|---|---|---|---|---|
| Dispersal type | Dysochorous/Anemochorous | 80 | 20 | -0.67 | -0.62** | -0.67 n.s. |
| | Endozoochorous/Anemochorous | 63 | 37 | 0.05 | 0.04 n.s. | 0.01* |
| | Epizoochorous/Anemochorous | 78 | 22 | 0.60 | 0.51*** | 0.45*** |
| | Hemerochorous/Anemochorous | 88 | 12 | 0.37 | 0.32** | 0.24*** |
| | Hydrochorous/Anemochorous | 53 | 47 | -0.45 | -0.47 n.s. | -0.56*** |
| Leaf anatomy | Helomorphic/Hygromorphic | 62 | 38 | 0.29 | 0.25 n.s. | 0.16*** |
| | Hydromorphic/Hygromorphic | 83 | 17 | -1.25 | -1.30 n.s. | -1.65*** |
| | Mesomorphic/Hygromorphic | 94 | 6 | 1.58 | 1.44*** | 1.41*** |
| | Scleromorphic/Hygromorphic | 77 | 23 | 0.57 | 0.35*** | 0.34*** |
| | Succulent/Hygromorphic | 96 | 4 | -2.37 | -2.63*** | -2.72*** |
| LDMC | - | 68 | 32 | 211.62 | 218.70*** | 223.33*** |
| Leaf persistence | Evergreen / overwintering green | 89 | 11 | 0.82 | 0.93*** | 1.07*** |
| | Spring green / overwintering green | 91 | 9 | -1.78 | -1.74 n.s. | -1.94* |
| | Summer green / overwintering green | 81 | 19 | 1.51 | 1.55 n.s. | 1.59*** |
| Life form | Chamaephyte/Therophyte | 89 | 11 | -1.99 | -1.88*** | -1.60*** |
| | Geophyte/Therophyte | 89 | 11 | -0.84 | -0.68*** | -0.58*** |
| | Hemicryptophyte/Therophyte | 87 | 13 | 0.70 | 0.86*** | 0.97*** |
| | Hydrophyte/Therophyte | 78 | 22 | -1.74 | -1.53** | -1.75 n.s. |
| | Phanerophyte/Therophyte | 84 | 16 | -0.72 | -0.54*** | -0.42*** |
| Life span | Annual/pluriennial | 89 | 11 | 16.33 | 16.22*** | 16.13*** |
| | Biennial/pluriennial | 89 | 11 | 15.17 | 15.13** | 15.11*** |
| Pollen vector | Insects/wind | 55 | 45 | 1.02 | 1.03 n.s. | 1.04 n.s. |
| | Selfing/wind | 59 | 41 | 0.84 | 0.85 n.s. | 0.85 n.s. |
| SLA | - | 75 | 25 | 26.99 | 26.94 n.s. | 26.74* |
| Reproduction | Generatively only/vegetatively only | 61 | 39 | 2.27 | 2.16** | 2.17** |
| | Generatively & vegetatively/veg. only | 61 | 39 | 1.93 | 1.95 n.s. | 2.02*** |
| UV-reflection | No/yes | 96 | 4 | 0.45 | 0.46 n.s. | 0.48** |

Further explanation for table 1. 3: "Land use" and "Biogeography" show the percentage of variation explained by the respective parameters. Model intercepts for urbanized ($Int_u$), agricultural ($\text{Int}_a$) and semi-natural ($\text{Int}_{sn}$) grid-cells show whether there are significant differences between urbanized and agricultural (see $\text{Int}_a$) or between urbanized and semi-natural grid-cells (see $\text{Int}_{sn}$). Levels of significance are indicated as follows: n.s. = not significant, * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$.

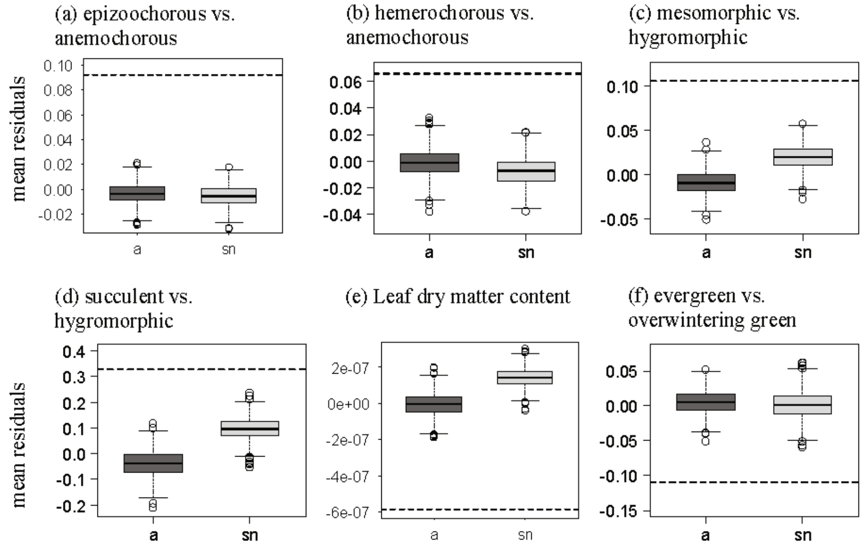

**Figure 1. 2** – Frequency of trait states in urbanized, agricultural and semi-natural grid-cells in Germany, corrected for specific environmental co-variables.

Shown are selected results: (a) epizoochorous vs. anemochorous; (b) hemerochorous vs. anemochorous; (c) mesomorphic vs. hygromorphic; (d) succulent vs. hygromorphic; (e) leaf dry matter content; (f) evergreen vs. overwintering green; (g) geophytes vs. therophytes; (h) phanerophytes vs. therophytes; (i) annuals vs. pluriennials; (j) insect-pollinated vs. wind-pollinated; (k) self-pollinated vs. wind-pollinated; (l) specific leaf area; (m) generative reproduction vs. vegetative reproduction; (n) flowers not reflecting UV vs. UV-reflecting flowers. Boxplots represent median (line), 25-75 % quartiles (boxes), ranges (whiskers) and extreme values (circles). Dark grey = agricultural grid-cells; light grey = semi-natural grid-cells; dashed line = urbanized grid-cells. Values for agricultural and semi-natural grid-cells are based on resampling. Shown are residuals (see Materials and Methods section of this chapter for details). *P*-values for differences between urbanized and agricultural/ urbanized and semi-natural grid-cells are shown in Table 1.2.

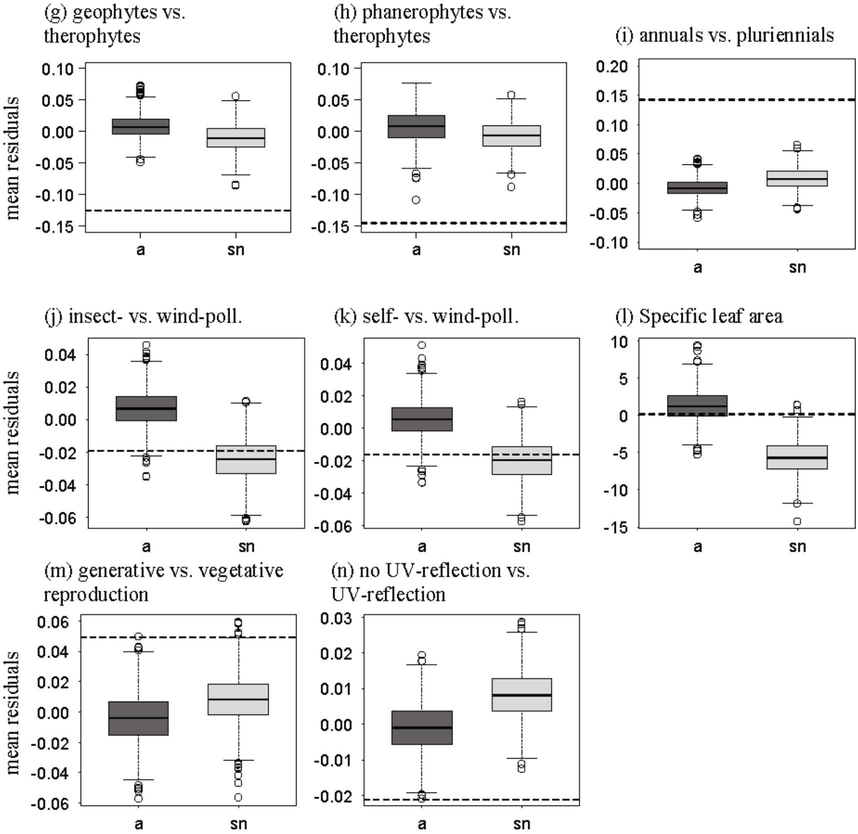

**Figure 1.2.** – continued

# 4. Discussion

The urban environment clearly favors plants with other trait states than agricultural or semi-natural environments. The trait state patterns we found are likely due to typical urban filters: First, the urban heat island (Landsberg 1981; Oke

1982) favors plants either able to cope with drought, e.g. plants with succulent or scleromorphic leaves, or to avoid drought, e.g. annuals that finish their life cycle in a temporal niche like springtime, when temperatures and drought stress are still low (Wittig 2002). High temperatures also promote plants with overwintering green leaves by decreasing the risk of frost, as already shown by Wittig & Ou (1993) for the *Hordeetum murini*, an association that is very typical for Central European cities. Furthermore, low air moisture promotes wind-pollination by increasing the probability of pollen to reach receptive surfaces (Culley *et al.* 2002). Secondly, the intensive and irregular disturbances in urbanized areas favor annuals and biennials (Kleyer 1999), leaves with high specific leaf area, low leaf dry matter content (Díaz *et al.* 1999), and plants with overwintering green leaves. The latter are often short-lived and use a temporal niche: In winter, disturbance in gardens, parks and cemeteries reaches a minimum. Thirdly, the spatial and temporal heterogeneity of cities should promote plants with high dispersal abilities. Although all dispersal types we compared potentially enable long-distance seed dispersal (Knevel *et al.* 2005), our results suggest that wind is less adequate for dispersal in urbanized areas: Wind gets channeled in streets and often follows the increasing temperatures towards the city center, thus seeds should end up more often on sealed surfaces. Moreover, calms are more frequent in than outside cities (Kuttler 1993) and seeds do not reach potential habitats in the lee of houses or walls. In contrast to wind-dispersal, animal-dispersal (endo- and epizoochory) seems to work as well in urbanized areas as dispersal by humans does. On the one hand, birds, cats, dogs, and some wild mammals like foxes (Gloor *et al.* 2001) are potential dispersers. However, birds are mainly relevant for the dispersal of fleshy fruits and hardly cover other types of seeds (Kollmann 1994). On the other hand, animal-dispersal and human-dispersal might overlap, with species with adhesive dispersal using humans or even cars as vehicles instead of animals (Hodkinson & Thompson 1997; von der Lippe & Kowarik 2007; 2008).

Fourthly, the high percentage of sealed surfaces increases the amount of surface runoff (Wessolek & Renger 1998), which in turn should be beneficial for plant species that disperse by water: Rain water that percolates immediately into the soil after reaching the earth surface cannot transport seeds; water running down a street can transport seeds over longer distances, e.g. to the next roadside ditch. Irrigation of urban green spaces might as well be advantageous for hydrochorous species.

Finally, cities have a high proportion of unstable habitats (e.g. urban brownfields) that favor annuals and biennials, reproduction by seeds and therophytes (Brandes & Oppermann 1995; Wittig 2002; Sudnik-Wójcikowska & Galera 2005). Note that therophytes are annual and reproduce by seeds (Table A1), thus, the results confirm each other since the trait states are correlated and partly depend on the same environmental factors. The same is true for specific leaf area and low leaf dry matter content, which are negatively correlated (Roche *et al.* 2004). Higher SLA and higher proportions of plants with scleromorphic leaves in urbanized areas seem contradictory but again point to the high heterogeneity of urbanized areas (Niemelä 1999) with dry, warm habitats like urban brownfields that support scleromorphic leaves, and nutrient rich watered habitats like urban parks, gardens and cemeteries (Sukopp 1998) that support high SLA (cf. Wright *et al.* 2005).The pattern for evergreen species seems contradictory as well: The high urban temperatures should not only promote plants with overwintering green leaves but also evergreen plants. However, the latter are more frequent in non-urban than in urbanized grid-cells. Thus, temperature is not the only restricting factor for evergreen species but land use is the main driving force: Evergreen species are normally long-lived and thus sensitive to disturbance.

The rural filters oppose the urban filters: Temperatures are lower, disturbances are more regular (in agricultural habitats) or less frequent (in semi-natural habitats), land use is more homogeneous (Lososová *et al.* 2006). Additionally, rural environments seem to be more suitable for insects than urban environments, due to less pollution and different land-use structure (e.g. less built-up area) and consequently favor insect-pollinated plants over wind-pollinated plants (Lososová *et al.* 2006). It seems contradictory having more wind-pollinated but less wind-dispersed species in urbanized grid-cells but pollinating insects might be more sensitive to urban land use than seed-dispersing animals, and animal-dispersed species might also be dispersed by humans (see above). A sensitivity of insects to urban land use can also explain the higher frequency of plants with UV-reflecting flowers in urbanized grid-cells: In BiolFlor, UV-reflection is mainly documented for insect-pollinated plants, which have to struggle harder in urbanized than in rural areas to attract their visitors. Nevertheless, we cannot tell from our data whether a low proportion of insect-pollinated species decreases pollinator richness or vice versa. It might be a parallel response to urbanization (Biesmeijer *et al.* 2006).

It seems surprising that self-pollinated species are less frequent in urbanized than in rural areas, although many urban habitats are quite young. Newly created habitats should be first invaded by plants that are independent of insects or other pollinating animals, since if pollinator availability is low, a successful reproduction is only possible by wind or self-pollination (Culley *et al.* 2002; Düring 2004). However, selfers are only more frequent in agricultural than in urbanized grid-cells but show no difference between semi-natural and urbanized grid-cells. Agricultural areas are tilled and harvested often several times a year. Therefore, many agricultural habitats are even younger than urban brownfields or industrial habitats. Furthermore, we did not include abundance data in our analysis, because these are not available for the total German flora. Including abundance data might clarify the pattern for self-pollinated species: Wittig (2002) showed that of the 20 plant species which are most common in the flora of Central European cities, 70% are self-pollinated.

Germany covers a range of biogeographic regions from the Alps in the South to the coasts in the North. There are more cities in the North and West of Germany but less in the South (Fig. A2); most cities are situated on rivers and below 300m a.s.l. (Kühn & Klotz 2006). Thus they have a biogeographically biased distribution (Kühn *et al.* 2004a). Therefore, the trait state patterns might not reflect differences between urban and rural land use but biogeographic gradients. Although we accounted for several parameters on climate, topography, soils and geology, there are of course more environmental parameters that might influence trait state patterns, such as variation in altitude, sunshine duration or length of vegetation period. To account for all these biogeographic effects, we applied the linear mixed effect models. Nevertheless, land use explains even more variation than differences in biogeography (Table 1.3).

Our results might be influenced by phylogenetic relatedness of species and spatial autocorrelation. Both can alter parameter estimates of linear models (Kühn 2007; Tremlová & Münzbergová 2007). Though we are aware of this, we neither corrected for phylogeny nor for spatial autocorrelation. We think that our results are yet reliable: Firstly, including or excluding phylogenetic relatedness produced similar results for most traits in an urban-rural comparison of plant trait patterns in the Czech Republic (Lososová *et al.* 2006). Secondly, analyses without phylogenetic correction are less problematic when dealing with large rather than small species groups (Tremlová & Münzbergová 2007). Besides, we are not aware of any method suitable to account for spatial as well as phylogenetic autocorrelation.

Our study clearly shows that on a coarse spatial scale shifts in land use can change the trait state composition of plant assemblages. This finding is remarkable, given the fact that grid-cells are rather heterogeneous – there is still 66% of non-urban land use in a grid-cell with 34% of urban land use. However, modern cities are not restricted to a few square kilometers bordered by city walls. They rather spread in the surroundings where they mingle with rural land use, creating urbanized landscapes. Given this spatial heterogeneity it can therefore be expected that, in addition to the effects of urban land use on coarse spatial scales, there are additional effects of urbanization on smaller spatial scales. There is, however, some evidence that the positive relation between urban land use and species richness (e.g. Hope *et al.* 2003; Araújo 2003; Kühn *et al.* 2004a) is especially strong at coarse scales (Pautasso 2007).

In conclusion, our study shows that shifts in land use can change the trait state composition of plant assemblages. Strong urbanization might consequently homogenize our flora with respect to trait state frequency.