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BIODIVERSITY RESEARCH

# How species traits and affinity to urban land use control large-scale species frequency

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## ABSTRACT

**Aim** Although urban areas only occupy *c.* 2.8% of the earth's land surface, urbanization threatens biodiversity as areas of high human population density often coincide with high biodiversity. Therefore, nature conservation should concentrate on both remote areas and densely populated regions. Protecting rare plant species in rural and urban areas can contribute to the protection of biodiversity. We therefore need to understand why species are rare. Studies on causes of rarity often concentrate on either plant traits or extrinsic threats (such as habitat fragmentation or nitrogen enrichment). However, there are only a few studies that combine traits and extrinsic threats, although such analyses might clarify causes of rarity. We assessed how the affinity of vascular plant species to urban land use ('urbanity') interacts with plant traits in determining species frequency.

**Location** Germany, resolution *c.* 12 km × 11 km.

**Methods** Species with a low frequency may be rare because they occur in rare habitats or because of other reasons, although their habitat is frequent. Therefore, we calculated the frequency of species corrected for habitat frequency, i.e. relative species frequency. We explained relative species frequency by the interactions of species traits and species affinity to urban land use using generalized linear models. Simultaneous autoregressive error models controlled for phylogenetic relationships of species.

**Results** Relative species frequency depends on species affinity to urban land use, independent of the different interactions between traits and urbanity used as predictors. The higher the urbanity the higher is species frequency. Urbanity interacts with species preferences towards temperature and soil acidity. Moreover, dispersal, nitrogen preferences and origin explain relative species frequency, amongst others.

**Main conclusions** Many rare species, especially those preferring cool or acidic habitats might already have disappeared from urban areas. Analyses that combine species traits and environmental effects can explain the causes of rarity and help to derive better conservation strategies.

**Keywords**

**Functional traits, niche models, phylogenetic autocorrelation, plant rarity, species distribution models, urban ecology**

## INTRODUCTION

Urban areas only cover around 2.8% of the earth's land surface (Millennium Ecosystem Assessment, 2005) but more than 50% of the total world population lives in urban areas (United Nations, 2008). Urbanization will further intensify, as the urban world population is growing even faster than the total world population (United Nations, 2008). At the same time, there is an intensification of land use within existing urban areas.

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Land-use change, including urbanization, is the driving force of global change and the main driver for the loss of biological diversity (e.g. Vitousek *et al.*, 1997; Thuiller, 2007). Urban areas have a strong impact on biodiversity, as areas of dense human settlement and high biodiversity often coincide (e.g. Araújo, 2003), i.e. urban areas are often richer in plant species than their rural surroundings (e.g. Hope *et al.*, 2003; Kühn *et al.*, 2004a). This high species richness is based on both alien and native species (Kühn *et al.*, 2004a) and a few species-rich lineages (Knapp *et al.*, 2008a), at least in Germany. However, urban areas also contain many rare plant species (Kühn *et al.*, 2004a; Schwartz *et al.*, 2006). The high urban species richness is resulting partly from the fact that urban areas are very heterogeneous and often include habitat types that are rare or absent in the surrounding area (Sukopp & Starfinger, 1999; Godefroid & Koedam, 2007). Nevertheless, urbanization especially can cause the regional extinction of rare native species by altering or destroying natural and semi-natural habitats. We consequently need strategies for nature conservation in urban areas that sustain a high species diversity including rare and endangered species (Schwartz *et al.*, 2006). We then need to know why species are rare and how urban land use influences rarity.

Plant species frequency (or rarity) has become one of the most important parameters used in nature conservation when assessing the threat status of species and when making management and conservation decisions (Gaston, 1994; Dobson *et al.*, 1995). Generally, actual species distribution has been taken as an indicator for species frequency (e.g. Ellenberg *et al.*, 2001), and the determination of species rarity is mostly based on grid-based occupancy measures (e.g. Dony & Denholm, 1985; Kunin, 1998). This approach may, however, be too simple as species' distribution ranges are correlated to their niche width and specializations (Rabinowitz, 1981; Ehrlén & Eriksson, 2000). A species showing low absolute frequency may be rare because it occurs in rare habitats (Rabinowitz, 1981), or it may be rare for other reasons although its habitat is frequent (Römermann *et al.*, 2007). Hence, it is important to consider habitat frequencies as well, i.e. the number of grid cells where the respective habitat occurs, when using species frequencies to measure species rarity. Otherwise, the frequency of 'naturally rare species' *sensu* Rabinowitz (1981), i.e. species occurring only in rare habitats, would be underestimated. We illustrate this argument by using relative species frequencies as a measure for species rarity (Römermann, 2006).

Besides habitat availability, species rarity is influenced by the species' adaptability to environmental changes and hence by their life-history traits: Some traits make species more extinction prone, others less (Poschlod *et al.*, 2000; Cardillo *et al.*, 2004). Römermann *et al.* (2008), for example, showed that species of dry grasslands are mainly rare when preferring warm, dry, light and nutrient-poor conditions. Other studies identified species traits that are related to the rarity of insect visited forbs (Bekker & Kwak, 2005), to the regional frequency of forest herbs (Matlack, 2005) or arable weeds (Lososová *et al.*, 2008).

Species traits alone, however, seem insufficient to fully explain species rarity; interactions between species traits and environmental factors related to land-use change, e.g. elevated temperature or disturbance regimes, might yield more meaningful results (cf. Fréville *et al.*, 2007).

So far we are aware of only two studies that related species extinction risk to urban land use and species traits: Preston (2000) compared historical species extinctions in two British counties, one dominated by agriculture, the other by urban land use. He found that both land-use types preferably threaten small species of open, unfertile habitats. Williams *et al.* (2005) showed that urbanization increases the extinction risk of grassland species that were geophytes or hemicryptophytes with a flat rosette and dispersed by wind or ants.

We will go one step further by investigating whether species frequency is related to species traits whereas accounting for the affinity of plant species to urban land use (called 'urbanity' hereafter) without focusing on one specific habitat type. Specifically, we will explain the relative frequency of vascular plant species in Germany with species traits relevant for dispersal, persistence and reproduction and we will include the interactions of these traits with urbanity to assess whether a trait makes a species more or less frequent when having high urbanity. We will also account for the species' phylogenetic relationships. On the one hand, urbanization seems to cause increases in common native species but declines in rare native species (Kühn & Klotz, 2006), thus there should be a positive relation between species affinity to urban land use and species frequency. On the other hand, many alien species have been introduced into urban areas (Kent *et al.*, 1999), most of them being rare in their new area (Hulme, 2008), thus leading to differentiation among urban regions (Kühn & Klotz, 2006), at least at the beginning of their invasion process. Therefore, species affinity to urban land use might also be negatively related to species frequency. However, as there are far more native than alien species in the German flora, we suppose that species with a high affinity to urban land use are relatively frequent, whereas species with a low affinity to urban land use are less frequent.

## METHODS

### Data sources

#### *Species rarity*

Plant species occurrences are documented in FLORKART, the database of the German flora, maintained by the German Network for Phytodiversity (NetPhyD) at the Federal Agency for Nature Conservation (http://www.floraweb.de/). In FLORKART, species are recorded on the basis of grid cells, each *c.* 130 km$^2$ in size, corresponding to *c.* 12 km × 11 km (i.e. 10′ longitude × 6′ latitude). Because mapping intensity varies among grid cells, we only used those cells with at least 45 of 50 control species (Kühn *et al.*, 2006). These are the 45 most frequent species of the German flora according to Krause (1998), which should occur in nearly every grid cell plus five generalists that are difficult to determine (Kühn *et al.*, 2004a). The latter were chosen to ensure that only grid cells mapped with a sufficient knowledge of the flora were included in the analyses. Furthermore, we only used grid cells with at least 50% terrestrial area in Germany, resulting in 2709 grid cells for analyses.

We used all species (including the 50 control species) except those without phylogenetic classification and aquatic species (the latter as defined by Korneck *et al.*, 1998 according to their main habitat). In aquatic environments niche-based processes operate in a fundamentally different way as compared to terrestrial habitats (e.g. competition for nutrients is less severe, whereas the availability of inorganic carbon is more limiting). As a consequence, different 'environmental filters' operate on the assembly of local plant communities, and aquatic species often have to be treated separately in analyses (Roelofs *et al.*, 1996 for example developed a separate system of environmental indicator values for aquatic plant species in the Netherlands).

We further excluded all *Rubus* species but *Rubus caesius* L., *Rubus chamaemorus* L., *Rubus armeniacus* Focke, *Rubus laciniatus* Willd., *Rubus idaeus* L., *Rubus phoenicolasius* Maxim., *Rubus saxatilis* L. and *Rubus spectabilis* Pursh. All other 148 *Rubus* species in the original species list are apomictic microspecies, i.e. they are very similar to each other and can be seen as pseudo-replicates. In total, 1776 species were included in the analyses.

We used relative species frequency to measure species rarity, i.e. the grid-based actual occurrence of a species divided by its potential grid-based occurrence. As stated in the introduction, this approach measures the rarity of a species by accounting for the frequency of the species' habitat (Fig. 1; see Römermann, 2006). To obtain the relative frequency of a plant species, we first had to estimate its potential range. Therefore, we explained the actual occurrence of each species with several parameters on land use, climate, topography, soils, geology and the co-occurrence of habitat-specific species (Table 1) in an ecological niche modelling approach (Guisan & Thuiller, 2005) for two thirds of all grid cells, using generalized linear models (GLM).

Data on land use are based on Corine land cover data that are derived from satellite remote sensing images (Statistisches Bundesamt, 1997). Corine data differentiate between artificial (i.e., urban), agricultural and forested/semi-natural land-use classes, 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. We calculated the proportion of the main classes per grid cell except for water bodies, which we omitted according to the omission of aquatic species, and except for artificial land-use types which we omitted because we used them later to calculate the affinity of species to urban land use.

Data on climate, topography, soils and geology originate from various sources and were available per grid cell (see Table 1 and references therein). Additionally, we included some proxies for habitat conditions by calculating the probability of occurrence of habitat-specific species (Korneck *et al.*, 1998) following the approach described in Römermann *et al.* (2007). In short, it represents the probability that a group of species characteristic of one specific habitat occurs in a grid cell as estimated from specific species co-occurring in the grid cells. We avoided circularity by modelling each species separately and excluded the predicted species from its own model. Occurrence probabilities were calculated for three groups of species that were aggregated from the 24 groups of habitat-specific species used by Korneck *et al.* (1998). These groups represent (1) habitats defined climatically or edaphically (e.g., dry lawns or bogs), (2) habitats defined geographically (e.g. from coasts or high mountains), and (3) common habitats (e.g., arable fields or deciduous forests). The three groups were derived from the comparison of two alternatives of our modelling approach (not shown; Römermann *et al.* unpublished): One used land use, climate, topography, soils and geology to explain species actual occurrences, the other used the co-occurrence of habitat-specific species as explanatory variables. This comparison yielded three distinct groups of species; one estimated similarly in both approaches (species of habitats defined climatically or edaphically), one underestimated in the

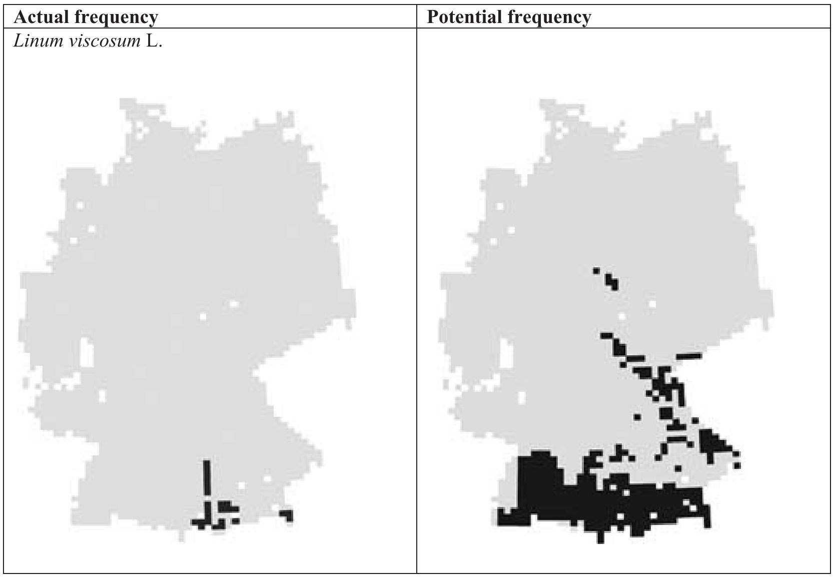

Figure 1 Comparison of actual frequency (occurrence per grid cell from FLORKART) and potential frequency (modelled with parameters on land use, climate, topography, soils, geology and the occurrence probability of habitat-specific species in BIOMOD; (Thuiller *et al.*, 2009), shown exemplarily for *Linum viscosum* L. The number of cells for actual frequency divided by the number of cells for potential frequency yields the relative frequency of the plant.

Table 1 Environmental parameters used to calculate the potential and relative frequency of vascular plant species in Germany. All climatic parameters have the reference period 1961–1990.

| Environmental parameter | Source |
|---|---|
| Mean temperature of the warmest month | Badeck *et al.*, 2008 |
| Mean temperature of the coldest month | Badeck *et al.*, 2008 |
| Temperature range per year | Badeck *et al.*, 2008 |
| Number of frost days per year | Badeck *et al.*, 2008 |
| Precipitation variability | Provided by the German Meteorological Service (Deutscher Wetterdienst, Department Klima und Umwelt); (cf. Kühn *et al.*, 2003) |
| Potential evapotranspiration | Badeck *et al.*, 2008 |
| Mean height above sea level | ARCDeutschland500 dataset, scale 1 : 500,000, provided by ESRI; (cf. Kühn *et al.*, 2003) |
| Mean wind speed | Provided by the German Meteorological Service (Deutscher Wetterdienst, Department Klima und Umwelt); (cf. Kühn *et al.*, 2006) |
| Number of soil patches | German soil survey map 1 : 1,000,000 (Bundesanstalt für Geowissenschaften und Rohstoffe, 1995) |
| Number of soil types | German soil survey map 1 : 1,000,000 (Bundesanstalt für Geowissenschaften und Rohstoffe, 1995) |
| Number of geological patches | German geological survey map 1 : 1,000,000 (Bundesanstalt für Geowissenschaften und Rohstoffe, 1993) |
| Number of geological types | German geological survey map 1 : 1,000,000 (Bundesanstalt für Geowissenschaften und Rohstoffe, 1993) |
| Proportion of agricultural land-use types | Corine land cover data (Statistisches Bundesamt, 1997) |
| Proportion of forested/semi-natural land-use types | Corine land cover data (Statistisches Bundesamt, 1997) |
| Proportion of wetlands | Corine land cover data (Statistisches Bundesamt, 1997) |
| Probability of occurrence of edaphically/climatically determined habitats* | Römermann *et al.*, 2007 using data from Korneck *et al.*, 1998; http://www.floraweb.de/ |
| Probability of occurrence of geographically determined habitats* | Römermann *et al.*, 2007 using data from Korneck *et al.*, 1998; http://www.floraweb.de/ |
| Probability of occurrence of common habitats* | Römermann *et al.*, 2007 using data from Korneck *et al.*, 1998; http://www.floraweb.de/ |

*see Methods for a more detailed description.

first approach (species of habitats defined geographically), and the third underestimated in the latter approach (species of common habitats). Based on this comparison, we used the parameters on land use, climate, topography, soils and geology together with the occurrence of the three groups of species as explanatory variables to reduce the risk of under- or overestimation of species occurrences.

The models that we used to explain the occurrence of species for two-thirds of grid cells were now validated by applying them to the same species but for the remaining third of grid cells. The agreement between the actual occurrence of a species and the potential occurrence of this species predicted by the models was evaluated by the area under the relative operating characteristic curve (AUC, Thuiller *et al.*, 2003). The more correctly a model classifies known species presences or absences, the higher is the AUC. The threshold to decide on the predicted presence or absence of species on the basis of occurrence probability was optimized based on AUC by maximizing the percentage of presence and absence correctly predicted for the evaluation data. We applied the models to all grid cells to calculate the potential frequency of each species for the whole study area. They mostly yielded good results with the AUC value showing fair to excellent prediction accuracy for 85% of all species.

We performed these calculations in BIOMOD (Thuiller *et al.*, 2009).

### *Species affinity to urban land use*

To investigate how species traits and affinity to urban land use jointly control relative species frequency, we calculated species affinity to urban land use (urbanity): This is Pearson's $r$ for the correlation of species' occurrence probability per grid cell (estimated from the species models; ranging from 0 to 1) and the intensity of urban land use per grid cell, according to the percentage of Corine artificial land-use types (for a similar approach see Thompson & McCarthy, 2008).

We divided urbanity into the categories low ($< 0$), medium ($> 0, \leq 0.1$) and high ($> 0.1$) urbanity, but these categories were not used for calculations but only in figures.

### *Species traits and phylogeny*

Species traits are documented in the BiolFlor database on biological and ecological traits of the German flora (Klotz *et al.*, 2002; Kühn *et al.*, 2004b), the LEDA database on life-history traits of the Northwest European flora (Kleyer *et al.*, 2008) and the Seed

Information Database (Flynn *et al.*, 2004). We chose species traits known to have different frequencies in urban and rural floras, respectively (e.g. Wittig & Durwen, 1982; Lososová *et al.*, 2006; Knapp *et al.*, 2008b). These were traits related to plant performance *in situ* (e.g. leaf traits), reproduction (e.g. pollination type), dispersal (e.g. dispersal type), persistence (e.g. seed mass), floristic origin (e.g. floristic status) and the realized niche of a species. For the latter we used Ellenberg indication values for moisture, nitrogen, reaction (soil acidity) and temperature, which range from 1–9 (or 1–12 for moisture) and estimate the optimum ecological occurrence of species along environmental gradients, reflecting habitat conditions (based on expert knowledge; Ellenberg *et al.*, 2001). Evidence for the accuracy of these indicator values has been provided by several studies reporting a close correlation between the indicator value and corresponding measurements of environmental variables (Schaffers & Sýkora, 2000; Diekmann, 2003). Ellenberg values behave as continuous variables for sample sizes exceeding 100 species and can be used as numerical variables (Ter Braak & Barendregt, 1986). Although floristic origin and Ellenberg values are no real traits (as defined by Violle *et al.*, 2007), we call them traits here for simplicity and refer to the different categories of a trait as 'states'.

In total, 8 continuous species traits and 10 categorical traits with totally 49 states were used to explain relative species frequency (see Table 2 for complete overview and definitions of species traits and their states).

The phylogenetic relationships of species are documented in BiolFlor. From the phylogenetic code, we determined the number of nodes separating one species from another but not the length of the branches of the respective phylogenetic tree. However, the number of nodes approximates the lengths of the branches that are set to unity (Faith, 1992).

### Data analyses

We explained relative species frequency for the 445 species for which all traits were available with the interactions between the species traits and urbanity in generalized linear models, then in simultaneous autoregressive error models (SARerr; see Dormann *et al.*, 2007; Kissling & Carl, 2008) to correct for phylogenetic relationships of species, if present. The latter two papers present methods for spatial autocorrelation but these can in principle be used for phylogenetic corrections as well (Sol *et al.*, 2008).

To assess the importance of each species trait we developed several full models; one model containing all traits, the others containing all but one of the traits, with each trait excluded in one of the models, plus one model excluding urbanity, containing the species traits without interactions, resulting in 20 different full models explaining relative species frequency. With this procedure, we excluded random effects caused by collinearities between species traits. We reduced each full model via backward selection of least significant variables, using the Akaike Information Criterion (AIC) for model comparison (MacNally, 2000).

In the course of model simplification, we partly had to group the states of species traits: If several states of one trait had similar effects on relative species frequency, they were grouped to simplify the model, provided this yielded a better AIC (see Table 3 for groupings).

To account for phylogenetic autocorrelation between species that might influence results, we calculated the Moran correlogram, which indicates autocorrelation for a model's residuals, in this case based on the phylogenetic distance between species. If the residuals of a minimal adequate model were autocorrelated, the model was included into a SARerr-model. In the SARerr-models, we included the topology of our phylogenetic tree instead of spatial information, defined species with up to 15 nodes distance to each other as neighbours, thus turning a spatial model into a phylogenetic model. For the SARerr-models again, the Moran correlogram was calculated, to check whether they fully accounted for phylogenetic autocorrelation.

We performed all calculations with the open source software R, version 2.6.0 (R Development Core Team, 2007). Moran correlograms were calculated with a modification of the function correlog by Ottar Bjørnstad (ncf package; see http://asi23.ent.psu.edu/onb1/). SARerr-models were computed in package spdep (Bivand *et al.*, 2007).

## RESULTS

### Species traits and relative frequencies

The species traits most influencing relative species frequency were the Ellenberg values for temperature and soil reaction, both with a negative effect; the Ellenberg value for nitrogen with a positive effect; the distribution of leaves along the stem of a species showing that species with rosettes or semirosettes are less frequent than species whose leaves are distributed regularly along the stem; long-distance dispersal showing that a species is more frequent the longer its potential dispersal distance; the floristic status showing that neophytes are generally less frequent than indigenous species and archaeophytes; the floristic origin of a species showing that species with an origin in all climatic zones are more frequent than species with a more restricted origin; life form showing that species that can express more than one life form type are more frequent than other species (all see Table 4).

Of minor importance (i.e. occurring in only a few of the 20 minimal adequate models) were canopy height, specific leaf area, dispersal type, leaf anatomy and leaf longevity (Table 4).

### Urbanity and relative frequencies

Urbanity itself was positively related to relative species frequency in every minimal adequate model, except for the model excluding Ellenberg temperature (where the effect of urbanity was negative).

### Effects of interactions between species traits and urbanity on relative frequencies

The interactions of Ellenberg soil reaction and Ellenberg temperature with urbanity were significant in most models: The former

**Table 2** Traits used to explain the relative frequency of vascular plant species in Germany; abbreviation of species traits, definitions and source database. LEDA = life-history traits of the Northwest European flora (Kleyer *et al.*, 2008; http://www.leda-traitbase.org/LEDAportal/), BiolFlor = biological and ecological traits of the German vascular flora (Klotz *et al.*, 2002; Kühn *et al.*, 2004b; http://www.ufz.de/biolflor), SID = Seed Information Database (Flynn *et al.*, 2004, http://www.kew.org/data/sid).

| Trait | Trait state | Abbreviation | Definition | Source |
|---|---|---|---|---|
| Canopy height | | | Distance between the highest photosynthetic tissue and the base of the plant [m] | LEDA |
| Dispersal type | Anemochory | | Dispersal by wind | LEDA |
| | Hemerochory | | Dispersal by man | LEDA |
| | Hydrochory | | Dispersal by water | LEDA |
| | Zoochory | | Dispersal by animals | LEDA |
| | Two types | | Plant can be dispersed by two of the four dispersal vectors | LEDA |
| | Three types | | Plant can be dispersed by three of the four dispersal vectors | LEDA |
| | Four types | | Plant can be dispersed by wind, humans, water or animals | LEDA |
| Leaf distribution along the stem | Regular | | Leaves distributed regularly along the stem | LEDA, BiolFlor |
| | Rosette | | Leaves concentrated near soil or water surface | LEDA, BiolFlor |
| | Semirosette | | Leaves arranged either scattered or tightly packed at the shoot | LEDA, BiolFlor |
| Leaf anatomy | Helomorphic | | With aeration tissue in the root as adaptation to oxygen deficiency in swampy soils | BiolFlor |
| | Hygromorphic | | Delicate plants of shade and semishade | BiolFlor |
| | Mesomorphic | | Without any characteristics, between scleromorphic and hydromorphic | BiolFlor |
| | Scleromorphic | | Firm and stiff leaves with thickened epidermis and cuticula but with mechanisms to promote water transport under beneficial conditions | BiolFlor |
| | Succulent | | With water storage tissue and thickened epidermis and cuticula | BiolFlor |
| | Two types | | Plant can have two of the five types of leaf anatomy | BiolFlor |
| Leaf longevity | Evergreen | | Leaves at all seasons often living more than one year | BiolFlor |
| | Spring-green | | Green from early spring to early summer; then usually decaying | BiolFlor |
| | Summer-green | | Green leaves only in the warm season | BiolFlor |
| | Winter-green | | Leaves developing in autumn, overwintering green and decaying in spring and summer | BiolFlor |
| Life form | Chamaephyte | | Resting buds are situated on herbaceous or only slightly lignified shoots some centimetres above the soil surface protected by parts of the plant itself and/or by a snow cover | BiolFlor |
| | Geophyte | | Resting buds are subterranean, often on storing organs protected within the soil | BiolFlor |
| | Hemicryptophyte | | Resting buds are situated on herbaceous shoots close to the soil surface, protected by foliage or dead leaves | BiolFlor |
| | Phanerophyte | | Resting buds are situated on (woody) shoots above the soil surface | BiolFlor |
| | Therophyte | | Summer annuals, which can only reproduce by means of generative diaspores | BiolFlor |
| | Two types | | Plant can have two of the five life form types | BiolFlor |
| | Three types | | Plant can have three of the five life form types | BiolFlor |
| Life span | Annual | | The individual cycle lasts for a maximum of one year | BiolFlor |
| | Biennial | | The plant grows for approx. one year vegetatively before reaching the generative phase after which it completes its life cycle | BiolFlor |
| | Perennial | | The plant has more than one generative phase in its life | BiolFlor |
| | Two types | | Plant can have two of the three life span types | BiolFlor |
| | Three types | | Plant can be annual, biennial or perennial | BiolFlor |

Table 2 *Continued*

| Trait | Trait state | Abbreviation | Definition | Source |
|---|---|---|---|---|
| Long-distance dispersal | | LDD | Ability to transport dispersal unit over long distances | LEDA |
| Pollination type | Insect-pollination | | Pollination by insects | BiolFlor |
| | Self-pollination | | Spontaneous pollination within a flower or by a flower from the same plant | BiolFlor |
| | Wind-pollination | | Pollination by wind | BiolFlor |
| | Two types | | Plant can be pollinated by two of the three pollination vectors | BiolFlor |
| | Three types | | Plant can be pollinated by insects, itself or wind | BiolFLor |
| Specific leaf area | | SLA | The ratio of fresh leaf area to leaf dry mass [$mm^2/mg$] | LEDA |
| Seed mass | | | The air dried weight of a dispersule [mg] | LEDA, SID |
| Type of reproduction | By seed | | Plant reproduces by seed or spore, rarely vegetatively | BiolFlor |
| | By seed and vegetatively | | Plant reproduces by seed or spore or vegetatively | |
| | Vegetatively | | Plant reproduces vegetatively | |
| Floristic status | Archaeophyte | | Taxon immigrated before the discovery of the Americas | BiolFlor |
| | Native | | Taxon native (i.e. indigenous) to Germany | BiolFlor |
| | Neophyte | | Taxon immigrated after the discovery of the Americas | BiolFlor |
| Floristic zone | Allrounder | | Origin in all climatic zones | BiolFlor |
| | Exratropical allrounder | FZ-extropical | Origin in every but the tropic zone | BiolFlor |
| | (Sub-)meridional | FZ-meridional | Origin in the zone of evergreen broad-leaved and coniferous forests, summer-green dry forests, steppes and deserts | BiolFlor |
| | Temperate | FZ-temperate | Origin in the temperate zone with summer green deciduous forests | BiolFlor |
| | Temperate and boreal/arctic | FZ-temperate-boreal/arctic | Origin in the temperate zone and the northern/southern taiga coniferous forests and/or tundras from the treelines polewards | BiolFlor |
| | Temperate-meridional | FZ-temperate-meridional | Origin in the temperate zone and the (sub-)meridional zone | BiolFlor |
| Ellenberg indicator values | Moisture value | Ellenberg_F | Showing the preferences of a plant with respect to moisture. Plants with low values can grow in extremely dry habitats; plants with high values can grow in extremely wet habitats. | Ellenberg *et al.*, 2001; |
| | Nitrogen value | Ellenberg_N | Showing the preferences of a plant with respect to nitrogen. Plants with low values can grow in nitrogen-poor habitats; plants with high values can grow in nitrogen-rich habitats. | Ellenberg *et al.*, 2001; |
| | Soil reaction value | Ellenberg_R | Showing the preferences of a plant with respect to soil pH. Plants with low values can grow in strongly acidic soils; plants with high values can grow in strongly alkaline soils. | Ellenberg *et al.*, 2001; |
| | Temperature value | Ellenberg_T | Showing the preferences of a plant with respect to temperature. Plants with low values can grow in cold habitats; plants with high values can grow in hot habitats. | Ellenberg *et al.*, 2001; |

Table 3 Traits used to explain the relative frequency of plant species in Germany with their original categories and the new categories derived from grouping of categories during model simplification (see Methods section for details).

| Trait | Original category | New category |
|---|---|---|
| Dispersal | Anemochory | – Anemo-, hemero- or zoochory |
| | Hemerochory | |
| | Hydrochory | – Hydrochory |
| | Zoochory | |
| | Two types | |
| | Three types | – More than one dispersal type |
| | Four types | |
| Leaf distribution | Regular | – Regular |
| | Rosette | |
| | Semirosette | – Rosettes or semirosettes |
| Leaf anatomy | Helomorphic | – One of the five leaf anatomy types |
| | Hygromorphic | |
| | Mesomorphic | |
| | Scleromorphic | – Two types |
| | Succulent | |
| | Two types | |
| Leaf longevity | Evergreen | – Evergreen |
| | Spring-green | – Summer-green |
| | Summer-green | – Green in spring or winter |
| | Winter-green | |
| Life form | Chamaephyte | – Non-therophyte (chamaephytes, geophytes, hemicryptophytes, phanerophytes) |
| | Geophyte | |
| | Hemikryptophyte | |
| | Phanerophyte | |
| | Therophyte | – Therophyte |
| | Two types | |
| | Three types | – More than one life form types |
| Life span | Annual | – Short-lived (annual or biennial) |
| | Biennial | |
| | Perennial | – Perennial or with more than one life span type |
| | Two types | |
| | Three types | |
| Status | Archaeophyte | – Non-neophyte* (archaeophytes or indigeneous species) |
| | Native | |
| | Neophyte | – Neophyte |
| Floristic zone | Allrounder | – Allrounder |
| | Exratropical allrounder | – 'southern dominated group': extratropical allrounder, (sub-)meridional, temperate-meridional |
| | (Sub-)meridional | |
| | Temperate | |
| | Temperate and boreal/arctic | |
| | Temperate-meridional | – 'northern dominated group': temperate, temperate-boreal/arctic |

*Archaeophytes and indigenous species were grouped in every model, except the one excluding Ellenberg temperature, where the grouping increased the AIC.

had a positive effect on relative species frequency, showing that species that grow in soils with medium to high reaction are most frequent when having high urbanity, whereas species that grow in soils with low pH are more frequent when having medium urbanity (Fig. 2a). The latter had a negative effect on relative species frequency, showing that species with high urbanity have high temperature requirements; but also that species are most frequent when having medium temperature requirements, independent from their degree of urbanity (Fig. 2b).

Further interactions that only occurred in one or two of the minimal adequate models were the interaction of urbanity with canopy height, leaf anatomy and leaf longevity, which were all negative, and the interaction of urbanity with life span, floristic status and the Ellenberg nitrogen values, which were all positive.

Only two of the minimal adequate models showed phylogenetic autocorrelation: the model excluding Ellenberg temperature and the model excluding Ellenberg nitrogen. The SARerr-models fully

**Table 4** Results of the linear models on relative plant species frequency in Germany. Given are importance and effects of traits and trait-urbanity interactions (URB = urbanity) for the relative frequency of plant species. Each predictor was excluded once (e.g. –Life form: interaction Life form:URB and the trait life form without interaction were excluded). '+' and '–' show whether a predictor was present in the minimal adequate model that resulted from backward model simplification by AIC, with '+' indicating a positive effect and '–' indicating a negative effect on the relative frequency of plant species. Model $R^2$ shows the $R^2$ adjusted for the number of predictors for each minimal adequate model. Model AIC shows Akaike's Information criterion for each minimal adequate model. Traits or their interaction with urbanity that are not listed in the table occurred in none of the minimal adequate models†. For categorical variables one category is represented by the model intercept (see Methods section for details). Levels of significance: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, (+) $P < 0.1$, n.s. not significant.

| | Σ positive sign. effects | Σ negative sign. effects | All‡ | –URB | –Leaf distribution | –Life form | –Long-distance dispersal | –Floristic status | –Floristic zone | –Ellenberg_N | –Ellenberg_R | –Ellenberg_T |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Model $R^2$ | | | 0.44 | 0.31 | 0.41 | 0.42 | 0.42 | 0.42 | 0.41 | 0.43 | 0.37 | 0.34 |
| Model AIC | | | –1084 | –989 | –1061 | –1070 | –1066 | –1060 | –1063 | –1075 | –1032 | –1005 |
| Model intercept | 19 | 0 | +*** | +*** | +*** | +*** | +*** | +*** | +*** | +*** | +*** | +*** |
| URB | 18 | 1 | +*** | | +*** | +*** | +*** | +*** | +*** | +*** | +*** | –*** |
| Log (canopy height) | 4 | 0 | | | +* | | | +* | | +* | | +(+) |
| Log (canopy height):URB | 0 | 2 | | | | | | –* | | | | –** |
| Hydrochory | 0 | 1 | | | | | –(+) | | | | | |
| More than one dispersal type | 1 | 0 | | | | | +*** | | | | | |
| Rosettes or semirosettes | 0 | 19 | –*** | –*** | | –*** | –*** | –** | –** | –*** | –*** | –** |
| Two-leaf anatomy types | 0 | 1 | | | | | | | | | | –(+) |
| Two-leaf anatomy types:URB | 0 | 1 | | | | | | | | | | –(+) |
| Spring or winter-green | 1 | 0 | | | | | | +** | | | | |
| Spring or winter-green:URB | 0 | 1 | | | | | | –* | | | | |
| Summer-green | 0 | 0 | | | | | | n.s. | | | | |
| Summer-green:URB | 0 | 0 | | | | | | n.s. | | | | |
| Therophyte | 0 | 16 | –* | –** | | | –* | –* | | –(+) | n.s. | –** |
| More than one life form type | 16 | 0 | +** | +* | | | +** | +* | | +** | +*** | n.s. |
| Perennial or more than one life span type | 0 | 0 | | | | | | | | | | n.s. |
| Perennial or more than one life span type:URB | 1 | 0 | | | | | | | | | | +(+) |
| Long-distance dispersal | 19 | 0 | +*** | +*** | +*** | +*** | | +*** | +*** | +*** | +*** | +*** |
| Specific leaf area | 3 | 0 | | | +(+) | | | | +(+) | +** | | |
| Indigeneous | 0 | 1 | | | | | | | | | | –** |
| Indigeneous:URB | 1 | 0 | | | | | | | | | | +*** |
| Neopyte | 0 | 19 | –*** | –*** | –*** | –*** | –*** | | –*** | –*** | –*** | –** |
| Neophyte:URB | 0 | 0 | | | | | | | | | | n.s. |
| FZ-extropical, meridional or temperate-meridional | 0 | 19 | –** | –* | –** | –** | –*** | –* | | –*** | –** | –* |
| FZ-temperate or temperate-boreal/arctic | 0 | 19 | –*** | –*** | –*** | –*** | –*** | –*** | | –*** | –*** | –*** |
| Ellenberg_F | 0 | 1 | | –(+) | n.s. | | | | | | | |
| Ellenberg_N | 19 | 0 | +*** | +*** | +** | +*** | +*** | +** | +*** | | +** | +* |
| Ellenberg_N:URB | 1 | 0 | | | | | | | | | | +** |
| Ellenberg_R | 0 | 19 | –*** | –*** | –*** | –*** | –*** | –*** | –*** | –*** | | –*** |
| Ellenberg_R:URB | 17 | 0 | +** | | +** | +* | +** | +** | +* | +** | | |
| Ellenberg_T | 0 | 19 | –* | –* | –* | –* | –* | –** | –(+) | –* | –** | |
| Ellenberg_T:URB | 0 | 18 | –*** | | –*** | –*** | –*** | –*** | –*** | –*** | –*** | |

†These are: the interactions of dispersal types with urbanity (URB), of leaf distribution with URB, of leaf anatomy with URB, of life forms with URB, of LDD with URB, of pollination types with URB, of SLA with URB, of floristic zones with URB, of Ellenberg_F with URB, seed mass and its interaction with URB, all types of reproduction and their interactions with URB.

‡The models that excluded the following traits yielded the same minimal adequate model as the starting model with all traits and are thus not shown here: canopy height, dispersal type, leaf anatomy, leaf longevity, life span, pollination type, SLA, seed mass, type of reproduction, Ellenberg_F.

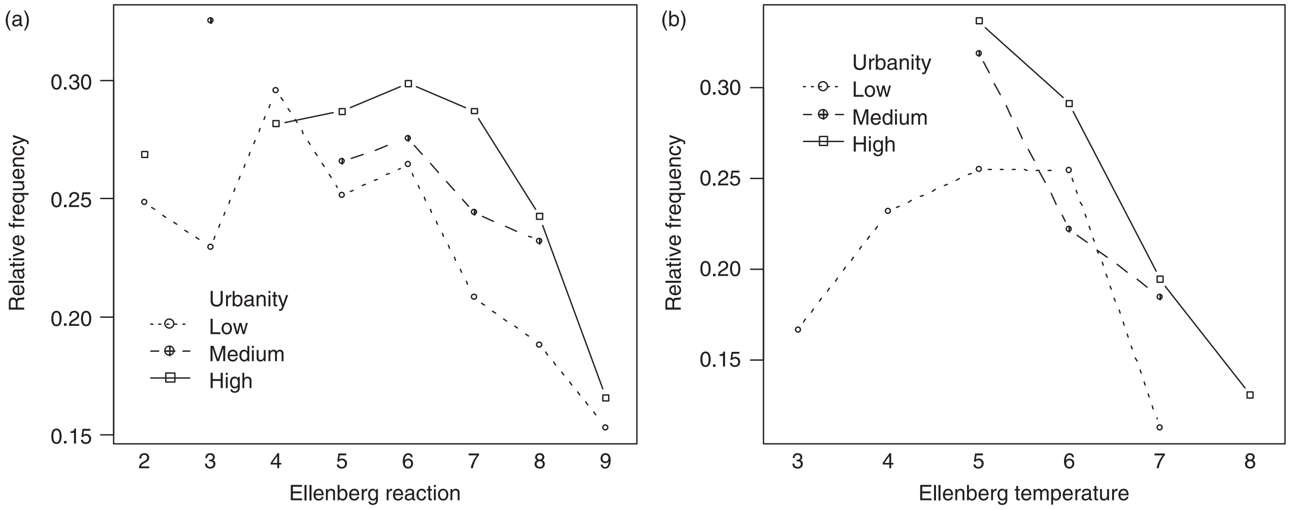

Figure 2 Interactions between urbanity and (a) Ellenberg soil reaction with values 1–9 corresponding to acidic – alkaline habitats; (b) Ellenberg temperature with values 1–8 corresponding to cold–hot habitats. Lines were included for clear illustration, but only when no value in-between two other values was missing. Urbanity was divided in three classes with low: urbanity ≤ 0; medium: 0 < urbanity ≤ 0.1; high: 0.1 < urbanity ≤ 0.5. Relative frequency was arc-sin transformed. Points based on < 5 species were excluded.

accounted for this autocorrelation; still they did not change results (not shown).

## DISCUSSION

Our study clearly shows that species frequency is influenced by both species traits and urbanization. As expected, the higher the affinity of a plant species to urban land use, the higher is its relative frequency. Besides, urbanization mainly interacts with the species' general habitat preferences for temperature and soil reaction.

### Species traits and relative frequencies

The following species traits influence relative species frequency independent of the species' degree of urbanity: the type of dispersal, leaf distribution along the stem, long-distance dispersal, specific leaf area, the floristic zone of origin and requirements towards soil moisture (Table 4). Species dispersed by wind, humans or animals are capable of long-distance dispersal and less restricted by fragmentation. Moreover, human-dispersed plants profit from human activities, which are not restricted to urban areas. Vice versa, hydrochorous species are slightly less frequent than species with other dispersal types, which is probably resulting from the fact that they are restricted by the occurrence of water. Similarly, Ozinga *et al.* (2008) showed that hydrochorous species are overrepresented among declining species in Northwest Europe, whereas wind- or bird-dispersed species were under-represented.Moreover, our analyses show that a species is more frequent if it is dispersed by several dispersal vectors, as compared to species limited to a single dispersal vector. However, the different models illustrate that it is mainly the ability of long-distance dispersal that increases a species' frequency and to a minor degree the type of dispersal: The type of dispersal is only significant in the model that excluded the variable 'long-distance dispersal'.

Species with rosettes or semirosettes are generally less frequent than species whose leaves are distributed regularly along the stem, probably because the number of species with semirosettes decreased in many agricultural areas of Germany as a result of the abandonment (MacDonald *et al.*, 2000) or intensification of grasslands and pasture lands. A similar effect might decrease the frequency of rosette species.

Species are also more frequent the higher their SLA: Large leaves can be beneficial in competition as they shade smaller plants with smaller leaves. Besides, high soil nitrogen contents favour a high SLA as there is no need for the plant to store large concentrations of nitrogen in the leaves (cf. Wright *et al.*, 2005). Thus, they profit from the high loads of nitrogen from agriculture, traffic, and industries in European landscapes (Franzaring & Fangmeier, 2006). This relation becomes obvious in the model that excludes the Ellenberg indicator value for nitrogen, where the effect of SLA is especially strong.

The floristic zone of origin shows that species with an 'all-round' global origin are the most frequent, whereas species with a more restricted origin should be more strongly restricted to special environmental conditions than 'all-rounders' and are thus less frequent.

The negative effect of Ellenberg moisture on species relative frequency is only weak but indicates that species with medium moisture requirements find more habitats in Germany than those that mainly occur in wet habitats.

### Urbanity and relative frequencies

Plant species with a high urbanity are relatively frequent, as urbanized areas are characterized by a set of common native species (Kühn & Klotz, 2006). Many rare species may already have disappeared from urbanized areas. Removing urbanity and its interactions from the model decreased model performance by about one fourth compared to most models (Table 4). Thus, the adaptation to urban land use is clearly important for plant species in Germany, a country with a high settlement density.

## Effects of interactions between species traits and urbanity on relative frequencies

The interaction of Ellenberg temperature with urbanity indicates that plant species are most frequent when preferring moderately warm habitats (Fig. 2b), whereas species preferring very warm habitats are less frequent than species preferring cool habitats (as also shown by Korneck *et al.*, 1998; Römermann *et al.*, 2008). However, the higher the urbanity of warmth-preferring species, the more frequent they are, because urban landscapes provide many suitable habitats (e.g. warm railway or industrial sites) and generally have higher temperatures than surrounding rural areas (Oke, 1982). The interaction also shows that species occurring in cool habitats hardly occur in urbanized areas whereas species occurring in very warm habitats (Ellenberg temperature = 8) hardly occur in the least urbanized areas. This clearly illustrates the temperature gradient along urban-to-rural gradients.

The interaction of Ellenberg soil reaction with urbanity indicates that many urban habitats have quite alkaline soils, as species that occur in alkaline habitats (high soil-reaction values) are more frequent with a high or medium than low urbanity, respectively (corresponding to results from, e.g. Wittig & Durwen, 1982). The high alkalinity of many urban habitats is resulting partly from the use of alkaline building materials such as concrete, cement and mortar that are also deposited in urban soils (Sukopp *et al.*, 1979). Accordingly, species with medium urbanity have higher frequencies than species with high urbanity for low soil reaction values, i.e. low pH.

The negative interaction of canopy height and urbanity indicates that taller species are less frequent the higher their urbanity. This is probably because urban floras consist of many short-lived (Knapp *et al.*, 2008b) and ruderal plant species, most of which do not grow very tall.

Spring and winter-green species are less frequent the higher their urbanity, but this is only significant when the floristic status is excluded. Therefore, this is mainly an effect of neophytes, which are generally rarer: Around 25% of the neophytes in our analysis are winter-green species, but only *c.* 8% of indigenous species are winter-green. Generally, there are much more winter-green than spring-green species in the German flora, thus, the former dominate the effect of both together.

Surprisingly, neophytes do not interact with urbanity, although cities are the places where alien plants are transported to (via trade and traffic) and where aliens from warmer climates find temperatures high enough to persist (Sukopp *et al.*, 1979). This effect is masked by the strong effect of the Ellenberg temperature value. However, when plotting only the floristic status against relative species frequency (Fig. 3), we see that neophytes are indeed less frequent with a medium than high urbanity (neophytes with low urbanity do not occur). The missing interaction of neophytes and urbanity in our models also shows that neophytic species generally have a low relative frequency, independent in which land-use type they occur, confirming that most neophytes are not invasive but rather rare, at least at the beginning of their invasion process (Williamson & Fitter, 1996).

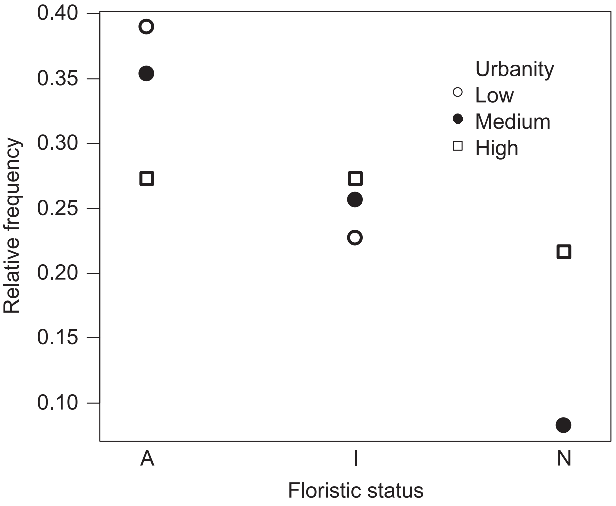

Figure 3 Interaction between urbanity and the floristic status of species with A, archaeophytes; I, indigenous species; N, neophytes. Urbanity was divided in three classes with low: urbanity ≤ 0; medium: 0 < urbanity ≤ 0.1; high: 0.1 < urbanity ≤ 0.5.

The positive interaction of Ellenberg nitrogen and urbanity in the model where Ellenberg temperature was excluded again shows the high availability of nutrients in urban soils.

## Applicability and conclusions

Modelling the potential frequencies of vascular plant species in Germany with environmental niche models implies some uncertainties that might have influenced our results: Within its geographical range (reflected by its actual frequency), a species is affected by a variety of local factors (e.g. biotic interactions such as predation, competition and mutualism; Hampe, 2004), which could not be included in our analyses. Small-scale abiotic factors such as disturbance intensity and soil nutrients could also not be included in the niche models. Therefore, although the models to calculate species potential frequency yielded good results, they still over- or underestimate species potential occurrences. Because small-scale habitat conditions are often crucial for plant performance (Korneck *et al.*, 1998) but large-scale climate influences species' ranges (Hampe, 2004), future studies should include effects acting on different spatial scales. Our approach of including large-scale climate, topography, soils, and geology as well as the co-occurrence of habitat-specific species reflecting small-scale habitat conditions is a first step in this direction. For instance, habitat-specific species could be proxies for disturbance intensity and soil nutrients.

Many rare species might have already gone extinct as a result of urbanization and are thus not included in our analyses. Hence, our study shows the current state of the German flora and we cannot make statements about formerly rare but now extinct species, which might add valuable information about the causes of rarity.

Our study showed that species occurring in cool habitats or on acidic soils are especially threatened by urbanization. Consequently, remnants of semi-natural landscape within urbanized areas, such as alluvial habitats along rivers or forests that have lower temperatures than typical urban habitats, might improve living conditions for these species within cities. The same should be true for habitats on sandy or rocky soils with low pH. Accordingly, results might look different when applying this study to cities with a high percentage of semi-natural habitats. Vice versa, effects of urban land use on rare species might be even more pronounced in countries, which do not have such a long history of human land use as the European countries, and where plant species thus had less time to adapt to human land use.

Generally, it is hard to grasp why species are rare. Our results, however, emphasize the need to concentrate on both species traits and effects of different land-use types to assess species rarity (cf. Fréville *et al.*, 2007). Such analyses might enlighten our understanding of rarity and help to derive better conservation strategies, such as creating and protecting habitats that especially support rare species, also within urban areas.

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