

# Is there an urban effect in alien plant invasions?

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**Abstract** Cities are known to be extraordinarily rich in alien plant species compared to rural environments. This is related to specific attributes of urban areas including the availability of natural resources and habitats (namely geological substrates and land cover), the dispersal pathways and associated propagule pressure due to trade and traffic, and the proximity many urban hubs have to rivers. Here we explored how richness and proportions of alien species introduced after the discovery of the Americas (so-called neophytes), can be explained by environmental covariates along the urbanization gradient from very rural to very urbanized grid cells. We tested whether there is a specific urban effect, either as an interaction effect of

urbanized areas that changes these general relationships, or if there is an effect due to specific urban conditions. We found that the environmental covariates explaining richness as well as proportions of neophytes remain largely the same across the rural–urban gradient. There is, however, an effect of urbanized area on neophyte species richness and proportions, which also incorporates strictly urban conditions. Rivers, roads and railroads contribute disproportionately less to the increase of neophyte species diversity in more urbanized areas, which might be due to the already higher number of neophytes in cities. We argue that the conditions determining neophyte richness in cities are not fundamentally different from those in rural environments, but extend on the same environmental axis, i.e. having different positions along the gradient towards the upper end.

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## Introduction

Compared to non-urban areas, urban areas are extraordinarily rich in plant species in general, and are hot-spots of alien plant species, richness in particular (e.g. Haeupler 1974; Klotz and Il'minskich 1988; Pyšek 1993; Kuhn et al. 2004; Kühn and Klotz 2006; Aronson et al. 2014). This occurs for several reasons: cities, at least in central Europe, are not randomly located but thrive specifically in naturally resource-rich regions, as indicated by the richness of different geological substrates (Kuhn et al. 2004). This means that large cities are usually located close to a river, and are often associated with the exploitation of mineral resources. In addition, cities have a variety of different soil types that support different agricultural practices, which in turn supported the population during the initial time of city growth. Also these urban settings are often topographically heterogeneous areas. Both alien and native plant species occur in higher numbers when resources are rich (Stohlgren et al. 2003), hence the natural resource richness of cities promote both species groups. In principle, this richness is independent from the city. However, not only the heterogeneity but also the identity of specific bedrock influences species occurrences in such areas. Calcareous regions, for example, are particular species rich (Ewald 2003; Kühn et al. 2003). Likewise sandy bedrock can have differential effects on species richness, in turn loess promotes agriculture (Kühn et al. 2003), but because loess is very fertile and calcareous, it can also promote other plant species. Further, alien species are promoted by trade and traffic and hence are more frequent at traffic hubs and increase with the density of traffic lines (Kopecký 1988; Vilà and Pujadas 2001; von der Lippe and Kowarik 2012; von der Lippe et al. 2013). Harbours (and potentially airports) can also serve as entry points for alien plant species (Hulme 2009; Essl et al. 2015; Seebens et al. 2015; Padayachee et al. 2017). Rivers (passing through the cities) promote alien species spread and establishment (Planty-Tabacchi et al. 2001; Deutschewitz et al. 2003; Burton et al. 2005). Urban gardens and parks are an important source for escaped and naturalized alien species (Kowarik 2005; Hanspach et al. 2008; Hulme 2011; McLean et al. 2017). All of these features, which are typical for a city, promote propagule pressure, a key driver of alien plant species richness (Lockwood et al. 2005; Pyšek et al. 2015; Maurel et al. 2016). In

addition, plant species numbers (in general) increase with increasing temperature (Francis and Currie 2003; Nobis et al. 2009) and are influenced by precipitation (Kühn et al. 2003; Pino et al. 2005). Locally, habitat diversity is an important driver of native and alien species richness (Deutschewitz et al. 2003) and specifically former industrial urban brown fields are known to host many alien plant species (Schadek et al. 2009). All these different features (see Table 1 for proxies of the above mentioned features) can be used to model alien plant species richness.

In our analysis, we do not only want to model plant species in general or native (indigenous) species in particular, but we want to specifically focus on alien plant species. Traditionally, in many parts of Europe botanists divide alien plants into archaeophytes (being introduced prior to the discovery of the Americas, c. 1500) and neophytes (introduced after the discovery of the Americas) (Schroeder 1969; Pyšek et al. 2004). While archaeophytes are mostly associated with agriculture, neophytes are predominantly found in urban areas (Wania et al. 2006; Botham et al. 2009; Knapp and Kühn 2012). Hence we are interested in the richness of neophytes rather than that of archaeophytes in relation to environmental drivers (Table 1) in a rural–urban gradient. Since it is known that alien and native plant species richness are highly correlated at larger scales, e.g. in the US (Stohlgren et al. 2003) and in Germany (Kühn et al. 2003), one might argue for using native plant species richness as additional predictor of neophyte species richness. Due to the positive correlation between neophytes and native species, it is also likely that alien and native species respond to similar environmental drivers (at least in part) (Ricotta et al. 2014). This collinearity may potentially result in problems when modelling species richness (Dormann et al. 2013), especially masking the effect of particular environmental drivers, because the richness patterns of neophytes might be explained by environmental drivers similar to those of native plant species richness. We therefore put a second focus on modelling the proportion of neophytes in relation to native plant species in addition to a simple model of neophyte richness. This second model aims to identify environmental conditions promoting the increase in neophytes more strongly than that in native species richness.

Statistical relationships modelled across space, though, can potentially suffer from spatial

**Table 1** Environmental data and sources used for the analysis of neophyte species richness in Germany, known to be related to species richness in general, and alien species richness, in particular

Variable	Description of variable	Source
tmpJul	Average temperature of July	Fronzek et al. (2012), observations period 1961–2000
sanye	Range of annual temperature, i.e. average difference between January and July temperature	
supre	Average summer precipitation (June, July, August)	
supre_sqr	Squared average summer precipitation (June, July, August)	
geo_p_n	Number of geological patches	Bundesanstalt für Geowissenschaften und Rohstoffe (1993)
geo_t_n	Number of geological types	
g_loess	Area geologically covered by loess	
g_sand	Area geologically covered by sand	
g_calc	Area geologically covered by limestone	
clc_t_n	Number of land cover types	CLC10 (CORINE Land Cover 10 ha), LBM-DE2012: (Bundesamt für Kartographie und Geodäsie 2012)
clc_p_n	Number of land cover patches	
Indust	Area covered by industrial facilities	
Harbour	Area covered by harbours	
Airport	Area covered by airports	
Rivers	Area covered by rivers	
URBAN	Urbanized area (> 50% covered by houses)	
length_roads	Total length of roads	Open Street Map Project (OSM) <a href="http://www.mapcruzin.com/free-germany-arcgis-maps-shapefiles.htm">http://www.mapcruzin.com/free-germany-arcgis-maps-shapefiles.htm</a>
length_railw	Total length of railways	

autocorrelation (SAC) (Dormann et al. 2007). This can be problematic when the residuals of a statistical model of locations close by are more similar than those further away from each other, because it can have severe impacts on error probabilities as well as parameter estimates—even resulting in a change of the direction of an relationship (Kühn 2007). Among the most versatile and least biased modelling approaches to account for spatial autocorrelation are Generalized Estimating Equations (GEE) (Carl and Kühn 2007; Dormann et al. 2007). They enable to correct for spatial autocorrelation by including a spatial correlation structure into the model. They do not, contrary to some misconception, remove spatial trends or important spatially structured variables from a model (Kühn and Dormann 2012).

Our specific question is whether neophyte richness and proportions in more urbanized areas follows the same general trend as that in less urbanized areas or whether the urban alien flora is different from non-urban flora (Kowarik 1995). Under the latter assumption one could expect changes in the relationship between neophyte richness (or proportions) and

environmental covariates along the rural–urban gradient. This is what we understand as ‘urban effect’. In the absence of such an urban effect, cities are simply more species rich because they have more favourable (or less unfavourable) resources and better (or less bad) conditions for alien plant species, or factors promoting propagule pressure are more widely available in cities compared to rural areas. In contrast, there might be a specific urban effect. This would mean that in addition to the usual drivers of species richness, other drivers typical for urban areas, which so far were not incorporated in statistical models or for which no proper data would be available, mediate the general relationships between environmental drivers and alien species richness. Therefore, taking into account the known drivers of species richness and those of biological invasions typical for urban areas, we asked the following question:

- Is there an additional effect of urban areas explaining the extraordinary species richness and higher proportions of neophytes in cities compared to less urbanized areas?

The way to investigate this is to test whether there is a statistical interaction between environmental (non-urban) correlates of alien species richness and proportions with urbanized areas (as a gradient from rural to urban). If there is an interactive effect, this would mean that the relationship between environmental drivers and neophyte diversity is different in urban compared to non-urban area, or more general, it changes with the degree of urbanization. Using Generalized Estimating Equations, we hence investigate whether there is an interaction between non-urban drivers of neophyte diversity and the degree of urbanization in Germany.

## Materials and methods

### Data sources

Species richness was calculated based on the most recent (2013) version of FlorKart ([www.floraweb.de](http://www.floraweb.de)) as published by the Netzwerk Phytodiversität Deutschlands and Bundesamt für Naturschutz (2013) with a resolution of  $10' \times 6'$  (arc minutes, i.e. c.  $130 \text{ km}^2$ ). This database is maintained by the Federal Agency for Nature Conservation (Germany) and has currently more than 14 million datasets resulting from several mapping schemes of the German federal provinces and other regionally coordinated citizen science activities of thousands of volunteers. To account for mapping bias, we only used those grid cells with at least 45 ‘control species’, i.e. species expected to occur in every grid cell in Germany (Kühn et al. 2006). Additionally, we only used those grid cells that have more than  $117 \text{ km}^2$  land area in Germany (i.e. removing border grid cells and those with large proportions of sea), rendering 2599 grid cells for analyses. Alien status of species was retrieved from BiolFlor (Kühn and Klotz 2002). Synonymies between these two different sources were manually matched. We only counted those species that are naturalized in Germany outside cultivation (so-called spontaneous species occurrences) after 1950 (in fact, more than 80% of the observations were after 1980).

Environmental data covers climate, geology, and land cover and stems from different sources (Table 1).

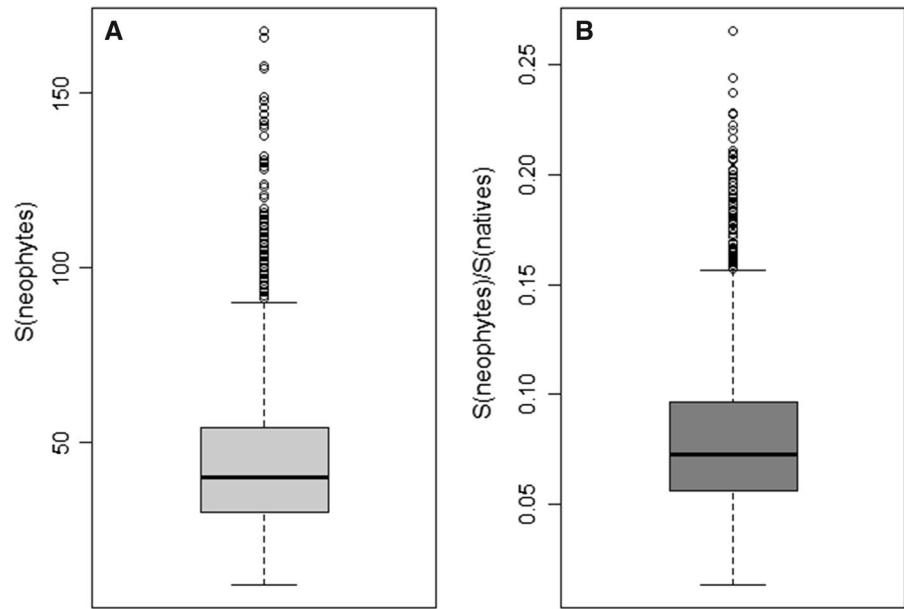
Land cover data and especially the system of roads and railroads had to be intersected with the lattice used for the floristic mapping to calculate areas and lengths.

For this purpose, further processing and visualisation, geographical information systems (GIS) ArcGIS 10.5 (ESRI) and QGIS 2.18 (QGIS Development Team 2015) were used.

### Analyses

We first modelled species richness of neophyte species (square root transformed to achieve normality) in response to environmental covariates. We used all environmental covariates of Table 1 as initial predictors plus the interaction of each of the variables with URBAN (i.e. the area of urbanized land cover, hereafter called ‘urbanized area’) to detect the ‘urban effect’. We also tested simple regression models with having either lengths of roads, lengths of railroad or their log-transforms as single predictors to account for non-linear effects of decreasing species additions with increasing length of traffic infrastructure. In all cases, the models with non-transformed predictors were superior to the ones with log-transformed predictors. The residuals of the minimum adequate model (after backward selection) showed significant amount of autocorrelation (tested with ‘`correlog()`’ in R package `ncf`; Bjornstad 2013) (see electronic supplement, figure S1). We therefore used Generalized Estimating Equations (GEE) which are an extremely efficient means to remove SAC in a generalized regression framework (Carl and Kühn 2007). Generalized estimating equations developed by Zeger and Liang (1986) are an extension of generalized linear models (GLM) and allow for correlated responses (Diggle et al. 1995). Mathematically, the variance of the response is replaced by a variance–covariance matrix which takes into account that observations are not independent, by adding a matrix that incorporates the correlation structure. Unlike GLMs (which in principle work with an identity matrix, i.e. the diagonals are 1 and all off-diagonals are 0), this matrix has non-zero values as off-diagonals which correspond to the spatial correlation among observations (grid cells). Originally, the approach has been developed for analysing longitudinal data. We modified this approach to use GEE models for spatial, two-dimensional datasets sampled in rectangular grids (Carl and Kühn 2007). We used a spatial Gaussian correlation structure and performed backward selection based on error probabilities. The GEE function is available in the recently

**Fig. 1** Number of neophyte species (a) and ratio of neophyte species/native species (b) in 2599 grid cells of the floristic mapping of Germany.  $S$  means species richness. Bold black lines represent medians, boxes 25–75% interquartiles, whiskers samples with less than 1.5 times of the interquartile range and dots are outliers



revised version of the R package *spind* (Carl and Kühn 2017).

Since it is known that native species richness begets alien species richness (Stohlgren et al. 2003), we performed an additional analysis accounting for native species richness but without risking that native species covariance with environmental predictors would corrupt the model. In a second model we therefore used GEE with a binomial error structure, having a two column response matrix, i.e. number of neophyte species as first and number of native species as second column, which effectively models the proportion of neophyte of native species. Summer precipitation was also squared as predictor to account for unimodal responses. Correlation structure was set to ‘fixed’ in both analyses. Both times, SAC was largely removed (see electronic supplement, figure S1). All analyses were done in R 3.3.2 (R Core Team 2016).

## Results

In total, we had 516 neophyte species in the analyses, with species numbers ranging between 9 and 168 per grid cell (median 40; see Fig. 1a). The ratio of neophyte/native species richness ranged from 0.013 to 0.265 (median 0.073, Fig. 1b). Urbanized area, as central environmental covariate, ranges from 0 to

79.7 km<sup>2</sup> with a median of 6.7 km<sup>2</sup> and a 25–75% interquartile ranging from 4.3 to 11 km<sup>2</sup>.

Neophyte species richness was mainly positively related to lengths of railroads, rivers, range of annual temperature, urbanized area, length of roads, the numbers of different land cover types and geological types, and negatively to summer precipitation (see Table 2a for details). Lengths of railroads and roads, rivers and area of sandy bedrock had significant interactions with urbanized area. In all cases, neophyte species richness increase with these covariates is less in more urbanized areas, but still positive.

Taking native species richness into account, i.e. recognizing proportions of neophyte species resulted in an only slightly different picture: Most important positively related predictors were still urbanized area, length of railroads, rivers, length of roads (to a lesser degree) and negatively related summer precipitation (see Table 2b for details). Important new positively related covariates were now area of loess bedrock, industrial areas, and mean July temperature, small negative influence had number of geological patches and number of land cover patches. Except for the interaction of urban land cover with sandy bedrock the interactions remained the same, only the orders of magnitude differed.

**Table 2** Summaries of modelling the log-transformed neophyte species richness (a) and the binomial response of neophyte species richness versus native species richness (b) in response to environmental covariates and their interaction with URBAN land cover in Germany using Generalized Estimating Equations (GEE) with fixed correlation structure

Predictors	(a) Neophyte richness	(b) Neophyte proportions
Intercept	2.508	− 2.685***
tmpJul		0.038*
ranye	0.153**	
supre	− 0.007***	− 0.002***
geo_p_n		− 0.002**
geo_t_n	0.021**	
g_loess		0.001***
g_sand	0.002*	
clc_t_n	0.048***	0.004*
clc_p_n		− 0.0003*
Indust		0.006**
Airport	− 0.035*	
Rivers	0.250***	0.045***
length_roads	0.053***	0.007*
length_railw	0.658***	0.116***
URBAN	0.054***	0.011***
g_sand:URBAN	− 0.0001*	
rivers:URBAN	− 0.003**	− 0.0007**
length_roads:URBAN	− 0.001**	− 0.0003**
length_railw:URBAN	− 0.007*	− 0.001*

Asterisks represent error probabilities: \* $0.05 > p \geq 0.01$ ; \*\* $0.01 > p \geq 0.001$ , \*\*\*  $0.001 > p$ . For the abbreviations of predictors see Table 1

## Discussion

Most predictors of neophyte species richness or proportions were not unexpected, since they match the expectations formulated in the introduction. Surprisingly, though, the negative impact of precipitation is more important than the positive one of temperature, although many alien plant species originate from regions with similar or warmer climates (Walther et al. 2009). Also, as expected, natural heterogeneity (different geological bedrock types) as well as mostly human-made habitat heterogeneity (different types of land cover), which can be interpreted as proxies for resource and habitat diversity, increased number or proportions of neophytes, respectively (Deutschewitz et al. 2003; Kühn et al. 2004). The negative

relationship of the ratio neophyte/native species richness with the patch numbers of geological bedrock types and land cover types needs a second thought. At first it seems counterintuitive that increased landscape heterogeneity or resource availability should decrease the proportion of neophyte species. This, however, is due to an increase in the denominator: native plant species increase disproportionately more in these heterogeneous landscapes compared to neophyte species, given that all other environmental covariates remain constant.

Previous studies showed that rivers, roads and railroads are associated with a high number of alien species (reviewed by Kowarik 2010). Also from adjacent countries, the importance of specific bedrock types was documented. Moser et al. (2005), for example, showed that in Austria, the importance of calcareous bedrock, temperature, variance in geological bedrock and land cover, but unfortunately they provided no sign of the relationship between these variables.

Interestingly, harbour areas were in none of the models significant although being recognized as source for neophyte species in Germany (see Brandes 2002 for an overview). Most harbours, though, are located at large rivers (except some of the Baltic Sea harbours) and all are associated to large cities. Hence river and urbanized area might have already accounted for this effect and therefore it is possible that there is no additional “harbour” effect.

We were mostly interested in finding interactions of other predictors with urbanized areas. Most surprisingly, all observed interactions showed unexpected directions, i.e. they are negative rather than positive. In particular, they diminish the positive relationship found in less urbanized areas, but they do not substantially change the general direction. This means that although we have an increase in traffic lines and rivers in cities, the increase in neophyte species is *less* than to be expected. Using log-transformed lengths of road and railroads, respectively, did not improve the models. Therefore many of the traffic routes cannot be interpreted as being introduction pathways of alien species into the cities, or they did not contribute as much to the introduction as they could by their sheer amount. On the other hand, roads and rivers might even contribute to export propagules (von der Lippe and Kowarik 2008; Sämel and Kowarik 2010).

We did not find an interaction of urbanized area with habitat related variables, nor (except for sandy bedrock) with ‘natural’ environmental conditions (those related to climate or geology). Thus there does not seem to be a special effect of urbanized areas modifying the relationship of variables representing general conditions of neophyte species richness. In preliminary analyses, this was different, because we found interactions of urbanized area with summer precipitation and the number of land cover types. These interactions vanished once we introduced lengths of roads and railroads, respectively, into the model. Hence, it seems that the relationship with proxy variables for habitat was especially spurious and should be replaced by variables more closely related to dispersal corridors.

Lastly, we found that urbanized area was an extremely important covariate of both neophyte richness and proportions. The urban area incorporates various urban drivers on alien species richness that were not included in the environmental predictors (e.g. garden area). The effect of ‘urbanized area’ might therefore partially compensate for those typical urban structures that play an important role in rural environments and might even explain that the positive effects of typical urban structures diminish with increasing urbanized area. At local scale, for example, Štajerová et al. (2017) found that cover of invasive species increased towards the city centre and likewise increased with habitat richness as well as increased with the proportion of specific habitats such as road margins, ruderal sites, and railway sites. Unfortunately, due to data deficiency, typical land cover types associated with urban invasions are not incorporated in our model since our class ‘urbanized area’ summarized CLC classes 111 and 112 (i.e. house cover > 50%). Hence our analyses could not have been as detailed as the one of Štajerová et al. (2017).

The vast majority of neophytes was deliberately introduced for ornamental reasons (Lambdon et al. 2008). Furthermore, it was shown that planting intensity is an important correlate of invasion success of tree species (Pyšek et al. 2009). Escapes from botanic gardens (Hanspach et al. 2008; Hulme 2011) and garden centres (Dehnen-Schmutz et al. 2007) may also contribute to spread of alien species into cities. Unfortunately, neither the areas of gardens and parks, nor planting frequency or selling frequency are available at the scale and resolution we need. We

believe, though, that ‘urbanized area’ can serve as proxy for associated gardens and urban greens. Hence it would need to be explored in the future which specific processes that are not explicitly considered here (e.g. dispersal pathways associated to roads, railroads, rivers) contribute further to the extraordinary neophyte species richness of cities. Still, it seems that there is not a specific ‘urban effect’ that modifies the relationships generally found for environmental covariates and species richness of alien plant species in a positive way, i.e. increasing alien species richness disproportionately, e.g. due to synergistic effects. Future research on this topic therefore would need to consider mechanisms typical for cities and not those modifying relationships along the rural–urban gradient.

Kowarik (1995) argued that changes in environmental factors of the urban–rural gradient may provide specific ‘urban niches’ realized by alien plant species. And indeed, not only are environmental conditions in cities different from those of rural environments but also the realized niches between successful alien and native plant species differ (Knapp et al. 2008; Knapp and Kühn 2012). Still, this does not explain the differences in species richness. To do so, the heterogeneity as well as the amount of resources and the availability of conditions related to niche properties of alien species in the urban–rural gradient would need to be assessed as well as the corresponding requirements (niche properties) of the plant species.

In summary, the current analysis is a first step towards a macroecological perspective (in the sense of Guisan and Rahbek 2011) on species richness in the urban–rural gradient. Following our results, we can argue that the conditions determining neophyte plant species richness (and hence summarize the respective plants’ niche properties) in cities are not fundamentally different from those in rural environments. They extend, though, on the same environmental axis, i.e. have different positions along the same gradient, especially when taking into account that our ‘urbanized area’ is a continuous variable, where grid cells with less urbanized areas are much more abundant than highly urbanized grid cells.

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