MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

„Rivers as dispersal corridors? Which factors are important for the spread of alien woody species along the Danube"

verfasst von / submitted by

Sabrina Wagner, BSc

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien, 2020 / Vienna, 2020

Studienkennzahl lt. Studienblatt / degree programme code as it appears on the student record sheet:	UA 066 879
Studienrichtung lt. Studienblatt / degree programme as it appears on the student record sheet:	Masterstudium Naturschutz und Biodiversitätsmanagement
Betreut von / Supervisor:	Ass.- Prof. Dr. Franz Essl

Acknowledgments

First and foremost, I would like to thank my supervisor Franz Essl for developing the topic of this thesis, his professional support, help in any part of the process and his supporting and motivating words.
I would also like to thank Dietmar Moser for his very helpful statistic skills, his patience and his professional expertise.
Above all, I would like to thank my family and friends, especially Georg, for their generous support in any way possible. Without them, I would not have been possible to finish this.

"The mind is everything. What you think you become." – Buddha

Abstract: Cities are hotspots of invasions, and this is particularly the case for urban rivers, which are known to serve as corridors for the spread of alien plant species to floodplain forests. Here, I present a case study on woody (shrubs, trees) species invasions across a gradient from a metropolis (Vienna) to rural regions along the Danube River in eastern Austria. In total, I identified 44 native and 25 alien woody species in 75 plots. Five alien woody species occur in at least 10 plots. The most wide-spread ones were species of floodplain forests (*Acer negundo, Fraxinus pennsylvanica, Populus x canadensis*), while *Ailanthus altissima* and *Robinia pseudoacacia* – which prefer dry sites – were recorded substantially less often. The average level of invasion – i.e. the relative proportion of alien to native woody species in plots – was high across all three study regions. Still, there was a moderate decline of alien woody species richness along the urban – peri-urban – rural gradient. Generalized Linear Mixed Models showed that population density and the proportion of urban habitats in the environs of the plots is significantly positively correlated with the presence of *Acer negundo* and *Ailanthus altissima*. Conversely, the occurrence of *Robinia pseudoacacia* is negatively correlated with surrounding population density and urban habitats. Occurrence of *Acer negundo* is positively correlated with urban habitats. For *Fraxinus pennsylvanica*, I found no significant relationships. Our results indicate that gallery forests at river banks are particularly susceptible to invasions. I argue that managing alien woody species in urban and peri-urban sites is not appropriate and useful, given that re-invasion is likely in most cases (from adjacent urban green spaces). I acknowledge that this recommendation entails the implicit recognition that gallery forests along urban sections of the Danube will contain a substantial – and likely further increasing – proportion of alien woody species.

Keywords: alien species; biological invasions; distribution; management; rivers; urban ecology; woody plants

Zusammenfassung: Städte agieren als “Hotspots“ für Invasionen. Hier wirken vor allem städtische Flüsse als Verbreitungskorridore für Neophyten in die umliegenden Gebiete. In meiner Arbeit untersuche ich die Verbreitung neophytischer Gehölze, am Gradienten „urban“ (Zentrum Wien, Donaukanal) zu „stadtfern“ (Tullner Becken) entlang der Donau in Österreich. In den drei Untersuchungsgebieten: Donaukanal, Donauinsel und Tullner Becken wurden dazu in je 25 plots zu 20x2 Metern die Zahl und Deckung der vorkommenden Gehölze aufgenommen und weitere Standortfaktoren wie Nutzungsintensität und Gehölzentnahme evaluiert. Um weitere Informationen zu dem Standort zu bekommen, wurde noch die Bevölkerungsdichte und die Habitattypen in einem 500m Umkreis pro plot dazu verschnitten. In diesen 75 plots konnte ich 44 heimische und 25 neophytische Gehölzarten identifizieren. Fünf dieser „Aliens“ kommen in mindestens 10 plots vor: *Acer negundo, Ailanthus altissima, Fraxinus pennsylvanica, Populus x canadensis and Robinia pseudoacacia.* Die häufigsten heimischen und neophytsichen Arten wurden am stark anthropogenen Gebiet, dem Donaukanal, gefunden. Generell war das durchschnittliche Invasionslevel – relative Anzahl von neophytisch zu heimischen Arten im plot – hoch, in allen Untersuchungsgebieten. Ein sinkender Artenreichtum an neophytischen Gehölzen und somit ein Gradient von urban – peri-urban – stadtfern zeigte sich hierbei. Generalized Linear Mixed Models bestätigten, dass die Bevölkerungsdichte und urbane Habitate, wie größere Straßen und Bauten, als Zeiger für „urban“, signifikant positiv korreliert sind mit dem Auftreten von *Acer negundo* und *Ailanthus altissima.* Im Gegensatz dazu, ist das Vorkommen von *Robinia pseudoacacia* negativ korreliert mit meinen urbanen Zeigern. Das Vorkommen von *Acer negundo* ist positiv korreliert mit den urbanen Habitaten und für *Fraxinus pennsylvanica* gab es keine signifikante Beziehung dazu. Meine Ergebnisse zeigen, das Galleriewald am Flussufer sehr anfällig für Invasionen ist. Ein Management für neophytische Gehölze im urbanen und peri-urbanen Raum ist meiner Meinung nach nicht sinnvoll, da es sehr wahrscheinlich ist, dass sich diese Arten in kürzester Zeit, aus benachbarten Parks, Gärten oder sonstigen Grünflächen, wieder ansiedeln werden. Somit komme ich abschließend zum Ergebnis, dass der Galleriewald entlang urbanen Flüssen weiterhin einen wesentlichen und weiter steigenden Anteil an neophytischen Gehölzen aufweist und aufweisen wird.

1. Introduction

Biological invasions have become a significant component of global environmental change [1]. While levels of invasions are highly uneven among habitats in Central Europe [2], they are particularly high in urban-industrial habitats, gardens and public green spaces [3]. Accordingly, due to high levels of anthropogenic disturbance and propagule pressure, urban environments have become a hotspot of biological invasions [4,5].

Humans are altering the biophysical world with unprecedented velocity, and one of the eminent drivers is increasing urbanization. Accordingly, cities have grown rapidly due to immigration from rural areas, and due to endogenous population growth. On average, 25% of the global population has moved from rural into urban settlements during the past six decades, and this trend is expected to continue [6]. Concomitantly, the number of alien plants and animals in urban regions has increased strongly [5].

It has been shown that alien – but also native – plant species richness is significantly higher in cities than in surrounding agricultural landscapes [4, 7]. The high urban plant diversity is caused by pronounced habitat heterogeneity linked to small-scale variations in land use, site conditions and disturbance, including often remnants of extensively used habitats from cultural landscapes in peri-urban regions [4, 7]. Further, ornamental horticulture in public spaces and private gardens is causing high levels of propagule pressure of alien plant species in urban settlements [9]. In addition, cities act as heat islands that facilitate the spread of thermophilic species. These effects combined increase in intensity from the periphery towards the centers of cities [10].

Dispersal corridors such as transport infrastructure (roads, railways) [11] and river networks play an important role for the spread of alien species [12,13]. Accordingly, running waters have been shown to be very effective conduits for the spread of some alien species [14,15]. The centers of large cities often encompass sections of rivers that serve as dispersal corridors for aquatic and riparian species [16] – particularly so for species which produce floating seeds or can be dispersed by floating rhizomes [15].

Woody species (trees, shrubs, lianas) contribute only a moderate proportion to the alien global flora. Currently, 0.5 % of the world's tree species and 0.7 % of the world's shrub species are invasive outside their native range [17]. This represents 622 species, of which 357 are trees and 265 shrubs. But in many parts of the world, alien woody species are among the most invasive species [12]. Cause once they are established, they are very difficult to eradicate [18]. Thus, it is argued that urban centers – and rivers in cities – may serve as a hub for the further spread of alien species into surrounding environments [19]. A better understanding of the factors that determine woody plant species invasions along rivers along an urban – peri-urban – rural gradient is highly important to improve alien species management strategies.

Here, I present a case study of woody plant invasions along the Danube River in eastern Austria and along a gradient from urban to rural areas. I selected three different sections of the Danube River in and near Vienna and sampled native and alien woody species composition in plots in these study regions. Specifically, I addressed the following research questions: 1) What is the proportion of alien woody species in different sections of the Danube River in eastern Austria? 2) Which alien woody species are the most common ones? 3) How does alien woody species abundance change along the urban-rural gradient? 4) Which factors explain the distribution of alien woody species? I hypothesized that richness of alien woody species decreases from urban to rural rivers sections and that this decline in alien woody species richness is related to anthropogenic disturbances (e.g. local population size, vicinity of major streets, and railways).

2. Materials and Methods

2.1 Study region and sites

The study region is located in eastern Austria in and near Vienna (Fig. 1). It consists of three sections located along the Danube River. With a total length of 2850 km and an average discharge of 7000 m^3/s at the river mouth, the Danube is the largest river of Central and Western Europe [20]. In eastern Austria, the Danube is characterized by spring and summer floods after snow melt and heavy precipitation events in the catchments of its alpine tributaries. The climate of Vienna is temperate Pannonian, with cool winters and warm summers, the average annual temperature is 10,4°C and annual precipitation is 500–650 mm (1981-2010) [21]. In Austria, the Danube is characterized by a substantial river slope of 40 cm/km, large amounts of gravel being transported, and thus it is classified as an alpine river. Until the 19th century, the Danube was characterized by a braided river system that was several kilometers wide in places [20]. The Danube had been channelized in the late 19th and early 20th century and protective dikes have been established, while several hydroelectric power plants have been built from the mid-20th century onwards. As a result, rarely flooded hardwood floodplain forests increased at the expanse of pioneer gravel banks and softwood floodplain forests that are adapted to regular flooding [22].

Vienna is the capital of Austria. It is a metropolis with c. 1.9 million inhabitants. It is located at the intersection of the eastern rim of the Alps – the Wienerwald – with the Pannonian plains to the east. The Danube River is running from northwest to southeast through Vienna.

I have selected three study regions along an urban – peri-urban – rural gradient, i.e. the Donaukanal (DK) in the city center of Vienna, the Donauinsel (DI) at the periphery of Vienna and a rural section of the Danube in the Tullner Becken (TB) west of Vienna (Figure S1). The "Donaukanal" is a branch of the Danube River which runs across a length of c. 15 km through the city of Vienna. It is a heavily modified water course running through densely populated areas, which is accompanied by narrow riverine groves [23]. The "Donauinsel" is a man-made island in the Danube north of the city center of Vienna that was created from 1972 to 1981 for flood protection [24]. The Danube River in the wide river basin section of the "Tullner Becken" is accompanied by wide floodplain forests that are located in an agriculturally dominated landscape. I selected a stretch of the Danube that extends from the western border of Vienna to the city Tulln located 25 km further west (Figure 1). The embankments of the Danube of all study regions are stabilized by rip-rap structures.

2.2 Plot selection, species and environmental data compilation

I randomly established 25 plots at the river embankments (above the mean water level) in each of the three study regions, i.e. 75 plots in total. In each plot, I collected alien – i.e. species introduced by human agency to Austria after c. 1500 CE [25] – and native woody species occurrence and abundance in each plot. Plots had a fixed size with a length of 20 meters along the river embankment and a width of 2 m to ensure that the narrow gallery groves along the Danube were adequately sampled; minimum distance between plots was set to be 300 m to reduce spatial auto-correlation. Every woody species was recorded within a plot, and its coverage was estimated (in %) separately for herb, shrub and tree layers. All field work was done in the growing season of 2018. Species nomenclature and taxonomy follow Fischer et al. [26].

For each plot, I estimated the level of anthropogenic disturbances (e.g. tree removal) in three classes ranging from 1 (low) to 3 (high). For analyzing the influence of adjacent human landscape transformation and local propagule pressure on woody species composition in the plots, I extracted the following data for a 500 m radius around the plots: human population density (extracted from Statistik Austria) [27], and the proportion of land cover types that contribute to high local propagule pressure. I used the habitat map of Kuttner et al. [28], which provides gridded high-resolution data (10 x 10 m) on habitat distribution in Austria. I combined all habitat types which are associated with planting of (alien) woody species in cities, i.e. parks and gardens, built up areas, roads and railways. The resulting proportion of urban habitat types (Table S1) was then used in the analyses.

2.3 Statistical analyses

Woody species were assigned as either native or alien according to the inventory of alien species in Austria [25]. In a first step, I analysed the level of invasion – i.e. proportion of woody alien species relative to native woody species numbers. For doing so, I merged woody species occurrences across all three vegetation layers and converted them to species presence / absence data per plot. Second, I plotted the distribution of native and alien woody species which were found in at least 10 plots to analyse differences between study regions.

To analyse the relationship between alien species occurrence and urbanization I calculated the amount of urban habitats and the human population density within a buffer of 500 m around every sampling point. Further, I used Generalized Linear Mixed Models (GLMMs) using the function glmmPQL from the MASS library [29], with presence/absence data from the most common alien species in plots as dependent variable and the level of disturbance, and proportion of urban habitats and human population density in the surroundings as predictors. To account for spatial non-independence of plots within the three study regions I included the study region as random factor. Adjacent population density and proportion of urban habitats were highly correlated (0.79) and thus the joint inclusion of both variables in a single model is inappropriate [30]. Therefore, I fitted separate single-predictor models with each of these three variables for each of the five most abundant alien woody species. The analyses were done in R Version 3.6.2 [31]. For the GLMM modelling I used the function *glmmPQL* from the MASS library [29].

3. Results

In total, I recorded 44 native and 25 alien woody species in the 75 plots (Table S2). The highest total woody species number in a plot was 16 (Donauinsel). The highest number of native woody species was 13 (Donaukanal), the highest number of alien woody species was 7 (Donaukanal).

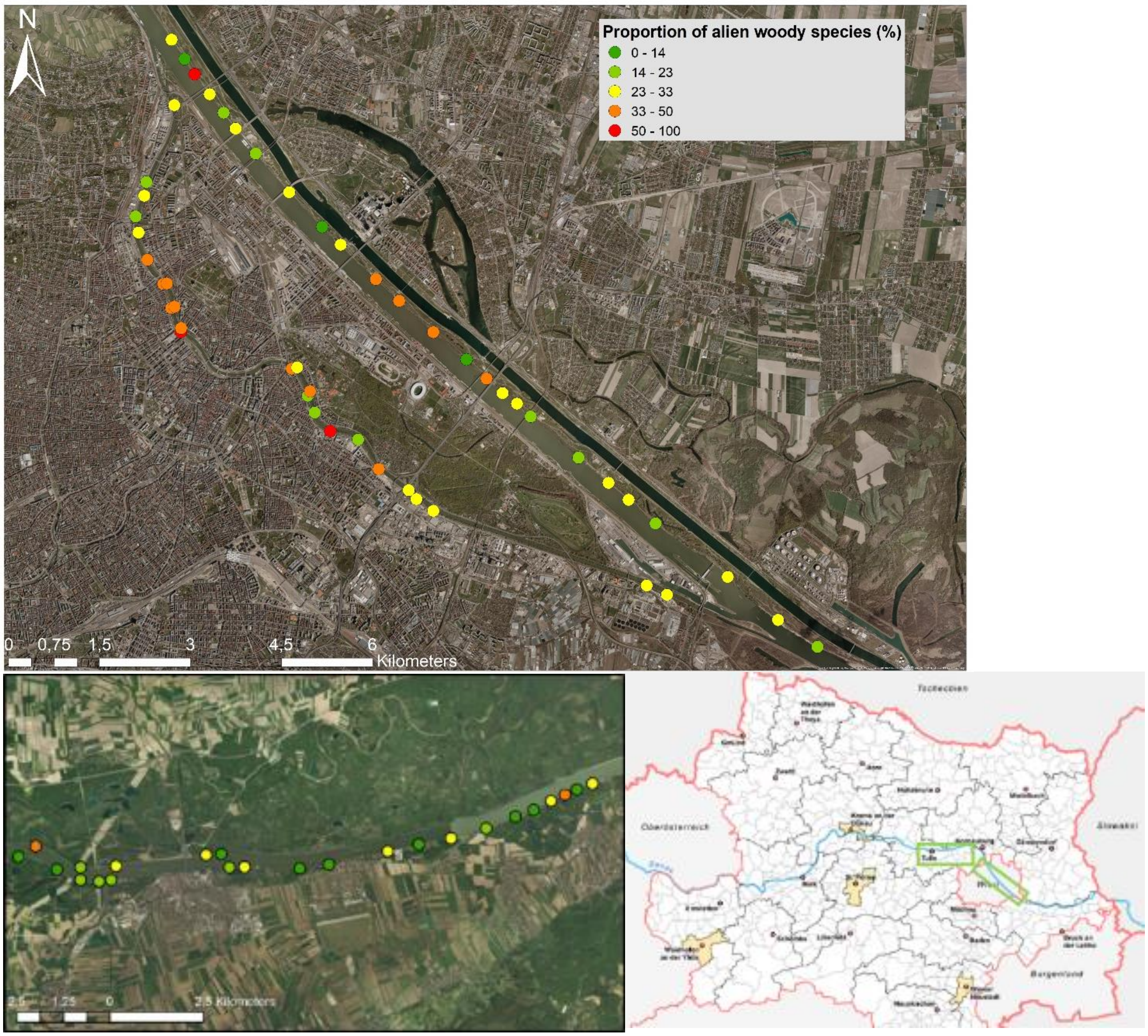

Fig. 1: Overview of the location of the study region in eastern Austria and the location of the study regions. Shown are the Donaukanal (top left), Donauinsel (top right), and the Tullner Becken (bottom). Plots are shown in different colours according to the proportion of alien woody species (i.e. number of alien species relative to number of native species per plot).

I found distinct differences in proportions of alien woody species among plots and among study regions (Fig. 1). Highest relative proportions of alien woody species Ire found at the Donaukanal and in several plots in the central section of the Donauinsel. In contrast, while plots in the Tullner Becken had much lower proportions of alien woody species.

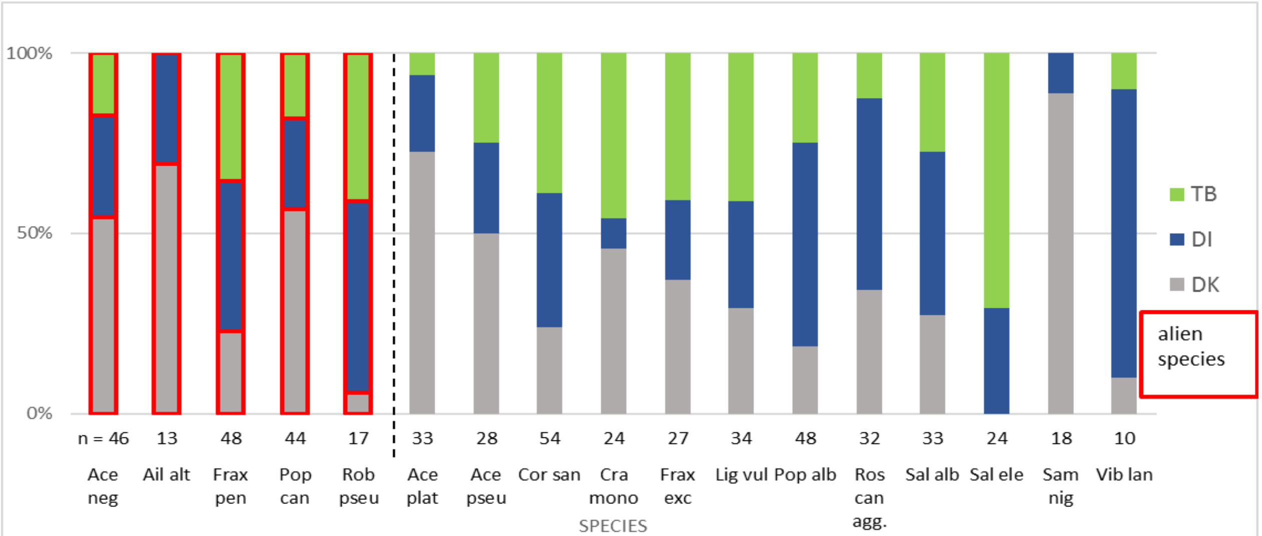

Fig. 2: Distribution of occurrences (presence / absence) of the 17 most widely distributed native and alien woody species (occurrences in at least 10 plots) between the three study regions. Occurrences are shown as proportion, i.e. total number of invaded plots = 100 %. Abbreviations: TB = Tullner Becken, DI = Donauinsel, DK = Donaukanal. Species abbreviations are as follows: Ace neg = *Acer negundo*, Ail alt = *Ailanthus altissima*, Frax pen = *Fraxinus pennsylvanica*, Pop can = *Populus x canadensis*, Rob pseu = *Robinia pseudoacacia*, Ace plat = *Acer platanoides*, Ace pseu = *Acer pseudoplatanus*, Cor san = *Cornus sanguinea*, Cra mono = *Crataegus monogyna*, Frax exc = *Fraxinus excelsior*, Lig vul = *Ligustrum vulgare*, Pop alb = *Populus alba*, Ros can agg. = *Rosa canina* agg., Sal alb = *Salix alba*, Sal ele = *Salix eleagnos*, Sam nig = *Sambucus nigra*, Vib lan = *Viburnum lantana.*

I found substantial differences in the distribution of the 17 woody species which occur in at least 10 plots (Fig. 2): *Cornus sanguinea* (n = 54), *Populus alba* (n = 48), *Fraxinus pennsylvanica* (n = 48) and *Populus x canadensis* (n = 44) are the most frequent native species. Five of the most common woody species are aliens: *Fraxinus pennsylvanica, Populus x canadensis, Acer negundo, Robinia pseudoacacia* and *Ailanthus altissima.* There are substantial differences in the distribution of alien woody species among the study regions. The majority of the species have more than 50 % of their occurrences at the Donaukanal, while *Fraxinus pennsylvanica* and *Robinia pseudoacacia* are more abundant in the other two study regions.

For most of the five most abundant alien woody species, I found rather little differences in the occurrence across vegetation layers (Tab. 1). *Populus x canadensis* was much more often found in the tree layer than in the shrub and herb layers, while for *Acer negundo* to some extent the opposite was the case.

Tab. 1: The number of invaded plots by the five most abundant alien woody species, shown separately for herb (h), shrub (s) and tree (t) layers.

Species	**Donaukanal**			**Donauinsel**			**Tullner Becken**			**Total**		
	h	s	t	h	s	t	h	s	t	h	s	t
Acer negundo	8	11	6	5	6	2	1	3	4	14	20	12
Ailanthus altissima	3	2	4	1	1	2	0	0	0	4	3	6

Fraxinus pennsylvanica	5	2	4	3	8	9	7	8	2	15	18	15
Populus x canadensis	4	1	20	2	2	7	2	0	6	8	3	33
Robinia pseudoacacia	0	0	1	5	4	0	1	2	4	6	6	5

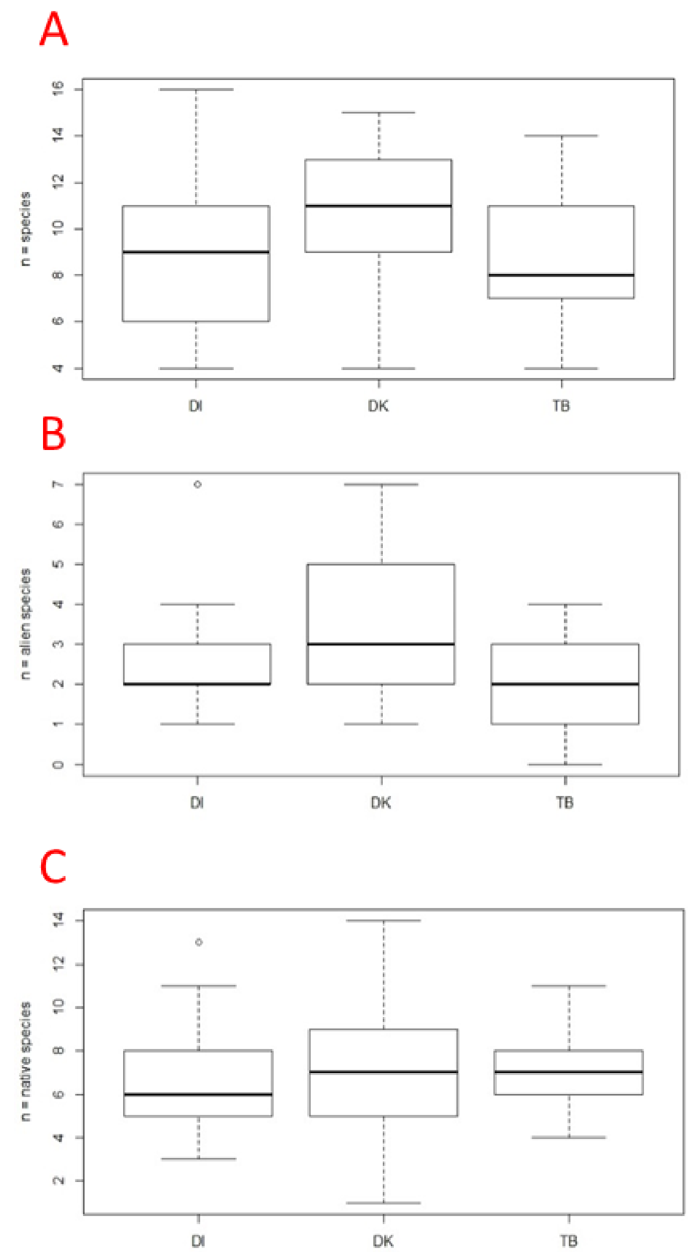

Fig. 3: Boxplots of total (A), alien (B) and native (C) woody species numbers per plot in the three study regions (DK = Donaukanal, DI = Donauinsel, TB = Tullner Becken). Data have been combined across all vegetation layers into presence/absence data.

Mean native woody species numbers per plot did not differ significantly between the three study regions (Fig. 3). Alien woody species numbers were somewhat higher at the Donaukanal (mean alien species number per plot 3.52) compared to the other two study regions: mean alien species number per plot was 2.37 (Donauinsel) and 1.75 (Tullner Becken).

Tab. 2: Generalized Linear Mixed Models of the occurrence (presence / absence) of the five most wide-spread alien woody species. As predictors I used level of disturbance in the plot, and human population density and the proportion of urban habitats in a radius of 500 m around each plot. Note that all models are single-predictor models of either variable as human population density and urban habitats are substantially correlated and their inclusion in one model is not appropriate. Significant predictors are shown in bold font. Given the rather low number of plots, I relaxed significance levels and considered P-values of $P \leq 0.1$ as significant. The study region the plots belonged to was included as random factor.

Alien woody species	Predictor	Intercept	Std.Error	P-value
Acer negundo	population	0.61	0.25	**0.02**
	urban	0.61	0.25	**0.02**
	disturbance	0.23	0.38	0.54
Ailanthus altissima	population	2.40	0.62	**<0.01**
	urban	1.49	0.47	**<0.01**
	disturbance	0.54	0.53	0.31
Fraxinus pennsylvanica	population	0.02	0.26	0.93
	urban	-0.18	0.27	0.51
	disturbance	-0.34	0.39	0.38
Populus x canadensis	population	-0.52	0.43	0.23
	urban	-1.51	0.83	0.07
	disturbance	-0.65	0.47	0.18
Robinia pseudoacacia	population	-1.58	0.32	**0.07**
	urban	-0.79	0.38	**0.04**
	disturbance	-0.01	0.49	0.98

The results from the GLMMs (Tab. 2) show that human population density in the environs of the plots is significantly positively correlated with the presence of *Acer negundo* and *Ailanthus altissima*. Conversely, the occurrence of *Robinia pseudoacacia* is negatively correlated with surrounding human population density. Further, the occurrence of *Acer negundo, Ailanthus altissima* and – although marginally so – of *Populus x canadensis* is positively associated with the proportion of urban habitats in the environs, while again, for *Robinia pseudoacacia* the opposite is the case. For *Fraxinus pennsylvanica*, I found no significant relationship. Finally, I found no evidence that the level of disturbance influenced the presence of any of the five most wide-spread alien woody species.

4. Discussion

4.1 The distribution of alien woody species in river corridors along an urban – peri-urban – rural gradient

Rivers and their adjacent habitats are known to be important corridors for the spread of a wide range of alien species [32,33]. For vascular plants, it has been shown that riverine habitats such as floodplain forests and tall-herb vegetation belong to the most heavily invaded habitats in Europe [1,2]. Our results show that woody plant species are an important component in gallery forests along the Danube in eastern Austria. The average level of invasion – i.e. the relative proportion of alien to native woody species in plots – was high across all three study regions. In several plots, there were more alien woody species than native ones, and average numbers of alien woody species per plot ranged from 1.75 (Tullner Becken) to 3.52 (Donaukanal). This high level of invasion is the more impressive as there was no evidence of planting of woody species in the plots, and it is most likely that all woody species have established themselves. This finding indicates that gallery forests directly established at riverbanks are particularly susceptible to invasions. Most likely, this is a result of the interactive effects of episodic disturbances (e.g. due to flooding) which facilitate the establishment of alien plants [34], and the high likelihood that propagules are transported and deposited by running water from sources that are located upriver [32].

Still, there was a moderate decline of alien woody species richness along the urban – peri-urban – rural gradient. However, given that human settlements in general and large cities in particular are known to be associated with high local propagule pressure and thus often serve as hub for the spread of alien species [35], the rather modest decline of alien species richness from urban to rural environments was rather surprising.

4.2 The distribution of widespread alien woody species across study regions and the underlying factors

Of the 17 woody species that were recorded in at least 10 plots, five were alien ones. *Fraxinus pennsylvanica, Acer negundo* and *Populus x canadensis* were particularly widespread with occurrences in more than 40 plots. *Fraxinus pennsylvanica*, which is native to eastern USA, is one of the most rapidly spreading woody alien species in Central Europe, and it is most abundant in hardwood floodplain forests of large lowland rivers [33,36]. In Austria, it is used as ornamental species in urban public spaces and sometimes it is planted for forestry purposes. Along the Danube, the species has spread considerably only since the 1990ies [37], and recently it has become managed in floodplain forests of the Danube National Park east of Vienna (G. Oitzinger pers. comm.). Due to its rapid ongoing spread, this species has been recorded with higher frequency in the herb (14 plots) and shrub layers (20 plots), but somewhat less in the tree layer (12 plots). *Acer negundo*, which is native to northeastern USA, has also spread considerably in Central Europe in recent decades. This species was solely introduced as ornamental tree, as its wood has no commercial value. It is most abundant in lowland softwood floodplain forests, where it can outcompete the native willow species (*Salix* spp.) as it is more shade-tolerant [37]. In the Danube National Park, there have been substantial recent eradication efforts (G. Oitzinger per. comm). *Acer negundo* is most widespread in the plots of the Donaukanal-study region, and high human population density and large proportion of urban habitats significantly explain its current distribution in the study plots. This finding indicates that spread from urban plantings seems to drive its invasion into more rural river sections. *Populus x canadensis* is a hybrid of a North American (*P. deltoides*) and European (*P. nigra*) parental species, which is widely cultivated for its fast growth mostly in floodplain forests [38]. Molecular studies revealed that up to 10 % of popular offspring in Europe consists of back crosses between *Populus x canadensis* and *P. nigra* threatening the native poplar species [38]. Interestingly, the majority of invaded plots is located in the Donaukanal study region, although this species is widely planted in floodplain forests along rural river sections such as the Tullner Feld.

With less than 20 plots invaded, *Ailanthus altissima* and *Robinia pseudoacacia* are both substantially less widely distributed than the above discussed species. Further, these two species differ also ecologically as they are tolerant to dry soils, can re-sprout by root suckers, and thus are tolerant to anthropogenic disturbance and most widespread in urban ruderal woodlands [27, 31]. *Ailanthus altissima*, which is native to East Asia, is limited to plots in an urban and peri-urban context and its occurrence is significantly explained by a high proportion of urban habitats and high population density. This species has been widely planted as ornamental tree in urban Vienna during the 19^{th} century [40,41]. In recent decades, it has spread strongly in Vienna and possibly has become the most characteristic alien urban woody species [42]. Surprisingly, the distribution of *Robinia pseudoacacia* differs strongly from the preceding species: it is most abundant in rural and peri-urban plots, but only rarely occurs in plots at the Donaukanal. Accordingly, human population density and proportion of urban habitats negatively affect its distribution. Possibly, this difference in distribution can be explained by the rather widespread distribution of *Robinia pseudoacacia* in floodplain forests of the Danube River [33,43], whereas this species is rather rarely planted or occurring as escaped tree in urban Vienna.

4.3 Implications for management and conclusions

Rivers and their accompanying habitats are highly important – yet increasingly threatened – corridors for biodiversity conservation. In cities, additional factors such as recreation further contribute to the high importance of rivers for urban ecology and human livelihoods alike. The high abundance of most alien woody species in herb and shrub layers indicate that species are still spreading.

Managing alien woody species in urban and peri-urban contexts has to weigh potential benefits (e.g. limiting impacts on native species, reducing or halting the spread to high conservation value areas such as protect areas such as the Danube National Park east of Vienna against the benefits that woody species bring about (e.g. providing shade, reducing microclimatic extremes). Therefore, management needs to be adapted and fine-tuned to specific situations [44].

I argue that while several of the alien woody species I have found are known to cause detrimental impacts in habitats of high conservation value [43, 45], management should be limited to rural sections of the Danube River. Currently, such management is on-going on a large scale in the Danube National Park [33]. However, I believe that managing alien woody species in urban and peri-urban sites is not appropriate and useful, given that re-invasion is likely in most cases (from planted trees in adjacent urban green spaces). I acknowledge that following this recommendation will entail the implicit recognition that gallery forests along the urban sections of the Danube will contain a substantial – and likely further increasing – proportion of alien woody species.

References

1. Chytrý, M.; Maskell, L.C.; Pino, J.; Pyšek, P.; Vilà, M.; Font, X.; Smart, S.M. Habitat invasions by alien plants: A quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *J. Appl. Ecol.* **2008**, *45*, 448–458.
2. Chytrý, M.; Pyšek, P.; Tichý, L.; Knollová, I.; Danihelka, J. Invasions by alien plants in the Czech Republic: A quantitative assessment across habitats. *Preslia* **2005**, *77*, 339–354.
3. Winter, M.; Schliger, O.; Klotz, S.; Nentwig, W.; Andriopoulos, P.; Arianoutsou, M.; Basnou, C.; Delipetrou, P.; Didžiulis, V.; Hejda, M.; et al. Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proc. Natl. Acad. Sci. U. S. A.* **2009**, *106*, 21721–21725.
4. Pyšek, P. Alien and native species in Central European urban floras: A quantitative comparison. *J. Biogeogr.* **1998**, *25*, 155–163.
5. Aronson, M.F.J.; La Sorte, F.A.; Nilon, C.H.; Katti, M.; Goddard, M.A.; Lepczyk, C.A.; Warren, P.S.; Williams, N.S.G.; Cilliers, S.; Clarkson, B.; et al. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proc. R. Soc. B Biol. Sci.* **2014**, *281,* 20133330.
6. Onandia, G.; Schittko, C.; Ryo, M.; Bernard-Verdier, M.; Heger, T.; Joshi, J.; Kowarik, I.; Gessler, A. *Ecosystem functioning in urban grasslands: The role of biodiversity, plant invasions and urbanization. PLoS One* **2019,** *14*, e0225438.
7. Kowarik, I. On the role of alien species in urban flora and vegetation. In: Marzloff, J.M.; Shulenberger, E.; Endlicher, W.; Alberti, M.; Bradley, G.; Ryan, C.; Simon, U.; ZumBrunnen, C. (eds.) *Urban Ecology.* **2008**, 321–338.
8. Kühn, I.; Brandl, R.; Klotz, S. The flora of German cities is naturally species rich. *Evol. Ecol. Res.* **2004**, *6*, 749–764.
9. Mayer, K.; Haeuser, E.; Dawson, W.; Essl, F.; Kreft, H.; Pergl, J.; Pyšek, P.; Iigelt, P.; Winter, M.; Lenzner, B.; et al. Naturalization of ornamental plant species in public green spaces and private gardens. *Biol. Invasions* **2017**, *19*, 3613–3627.
10. Pilsl, P.; Schröck, C.; Kaiser, R.; Gewolf, S.; Nowotny, G., Stöhr, O. *Neophytenflora der Stadt Salzburg*. Sauteria, **2008**, *17*, 1–608.
11. Von Der Lippe, M.; Kowarik, I. Do cities export biodiversity? Traffic as dispersal vector across urban-rural gradients. *Divers. Distrib.* **2008**, *14*, 18–25.
12. Williams, N.S.G.; Hahs, A.K.; Vesk, P.A. Urbanisation, plant traits and the composition of urban floras. Perspect. *Plant Ecol. Evol. Syst.* **2015**, *17*, 78–86.
13. Pyšek, P. On the terminology used in plant invasion studies. In: Pyšek, P.; Prach, K., Rejmanek, M.; Wade, M. (eds) Plant invasions – general aspects and special problems. SPB Adacemic Publishing **1994**, 71–81.
14. Pyšek, P.; Jarošik, V. Residence time determines the distribution of alien plants. In: Inderjit (Ed.) Invasive plants: Ecological and Agricultural Aspects. Springer **2005**, 77–96.
15. Säumel, I.; Kowarik, I. Urban rivers as dispersal corridors for primarily wind-dispersed invasive tree species. *Landsc. Urban Plan.* **2010**, *94*, 244–249.
16. Pyšek, P.; Richardson, D.. Traits associated with invasiveness in alien plants: where do I stand? In: Nentwig, W. (Ed.): Biological Invasions. Springer **2007**, 97–125.
17. Krumm, F.; Vitkova, L. (eds.) Introduced tree species in European forests: opportunities and challenges. European Forest Institute **2016**, 1–426.
18. Richardson, D.M.; Rejmánek, M. Trees and shrubs as invasive alien species - a global review. *Divers. Distrib.* **2011**, *17*, 788–809.

19. Botham, M.S.; Rothery, P.; Hulme, P.E.; Hill, M.O.; Preston, C.D.; Roy, D.B. Do urban areas act as foci for the spread of alien plant species? An assessment of temporal trends in the UK. *Divers. Distrib.* **2009**, *15*, 338–345.
20. Muhar, S.; Muhar, A.; Siegrist, D.; Egger, G. (eds.) Rivers of the Alps: Diversity in Nature and Culture. Haupt Verlag, **2019**, 1–480.
21. ZAMG (2010). Digitaler Klimaatlas Österreichs. Wien: Zentralanstalt für Meteorologie und Geodynamik.
22. Ließ, N.; Drescher, A. *Ailanthus altissima* spreading in the Danube National Park – possibilities of control. *Neobiota* **2008**, *7*, 84–95.
23. Buchmann, B.; Sterk, H; Schickl, R. Der Donaukanal. Geschichte – Planung – Ausführung. *Magistrat der Stadt Wien – Stadtentwicklung und Stadterneuerung (MA 19)* **1984**, ZDB-ID 263948-8.
24. Michlmayr, F. Die Grundzüge des Donauinsel-Projekts. *Denisia* **2002**, *3*, 11–25.
25. Essl, F.; Rabitsch, W. (eds.) *Neobiota in Österreich*. UmIltbundesamt, **2002**, 1–432.
26. Fischer, M., A.; Oswald, K.; Adler, W. Exkursionsflora für Österreich, Liechtenstein, Südtirol. Biologiezentrum der oö. Landesmuseen **2008**, 1–1392.
27. Statistik Austria. Regionalstatistische Rastereinheiten. http://www.statistik.at/Ib_de/klassifikationen/regionale_gliederungen/regionalstatistische_rastereinheiten/index.html (accessed on 12 December 2019).
28. Kuttner, M.; Essl, F.; Peterseil, J.; Dullinger, S.; Rabitsch, W.; Schindler, S.; Hülber, K.; Gattringer, A.; Moser, D. A new high-resolution habitat distribution map for Austria, Liechtenstein, southern Germany, South Tyrol and Switzerland. *Eco.mont* **2015**, *7*, 18–29.
29. Brian, A.; Venables, B.; Bates, D.M.; Firth, D.; Ripley, M.B. Package ‘ MASS .’ **2019**. Available online: https://cran.r-project.org/Ib/packages/MASS/MASS.pdf.(accessed on 12 December 2019).
30. Dormann, C.F.; Elith, J.; Bacher, S.; Buchmann, C.; Carl, G.; Carré, G.; Marquéz, J.R.G.; Gruber, B.; Lafourcade, B.; Leitão, P.J.; et al. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **2013**, *36*, 27–46.
31. R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
32. Rinaldo, A.; Gatto, M.; Rodriguez-Iturbe, I. River networks as ecological corridors: A coherent ecohydrological perspective. *Adv. Water Resour.* **2018**, *112*, 27–58.
33. Höfle, R.; Dullinger, S.; Essl, F. Different factors affect the local distribution, persistence and spread of alien tree species in floodplain forests. *Basic Appl. Ecol.* **2014**, *15*, 426–434.
34. Catford, J.A.; Daehler, C.C.; Murphy, H.T.; Sheppard, A.W.; Hardesty, B.D.; Istcott, D.A.; Rejmánek, M.; Bellingham, P.J.; Pergl, J.; Horvitz, C.C.; et al. The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. *Perspect. Plant Ecol. Evol. Syst.* **2012**, *14*, 231–241.
35. Essl, F.; Mang, T.; Moser, D. Ancient and recent alien species in temperate forests: Steady state and time lags. *Biol. Invasions* **2012**, *14*, 1331–1342.
36. Prots, B.; Drescher, A.; Vykhor, B. Invasion ecology of Green ash *Fraxinus pennsylvanica* Marsh. in the Transcarpathia (Ukraine). *Biol. Syst.* **2011**, *3*, 269–276.
37. Walter, J.; Essl, F.; Englisch, T.; Kiehn, M. Neophytes in Austria: habitat preferences and ecological effects. *Neobiota* **2005**, *6*, 13–25.
38. Smulders, M.J.M.; Beringen, R.; Volosyanchuk, R.; Vanden Broeck, A.; van der Schoot, J.; Arens, P.; Vosman, B. Natural hybridisation betIen *Populus nigra* L . and *P . x canadensis* Moench. Hybrid offspring competes for niches along the Rhine river in the Netherlands. *Tree Genet. Genom.* **2008**, 663–675.
39. Wickert, K.L.; O’Neal, E.S.; Davis, D.D.; Kasson, M.T. Seed production, viability, and reproductive limits of the invasive *Ailanthus altissima* (tree-of-heaven) within invaded environments. *Forests* **2017**, *8*.

40. Neilreich, A. *Flora von Wien. Eine Aufzählung der in den Umgebungen Wiens wild wachsenden oder im grossen gebauten Gefäßpflanzen, nebst einer pflanzengeografischen Übersicht*; F. Beck, **1849**.
41. Issely, J. Wiener Alleebäume. *Oesterr Monatsschr. ForstIs. 21* 1871, 417–420.
42. Kowarik, I.; Säumel, I. Biological Flora of Central Europe: *Ailanthus altissima* (Mill.) Swingle. *Perspect. Plant Ecol. Evol. Syst.* **2007**, *8*, 207–237.
43. Drescher, A..; Magnes, M. Anthropochoren im Nationalpark Donau-Auen - Ziel von Bekämpfungsmaßnahmen oder Bereicherung der Biodiversität? In: Wallner, R. (Ed.) Aliens. Neobiota in Österreich **2002**, 141–144.
44. Gaertner, M.; Novoa, A.; Fried, J.; Richardson, D.M. Managing invasive species in cities: a decision support framework applied to Cape Town. *Biol. Invasions* **2017**, *19*, 3707–3723.
45. Lapin, K.; Oettel, J.; Steiner, H.; Langmaier, M.; Sustic, D.; Starlinger, F.; Kindermann, G.; Frank, G. Invasive alien plant species in unmanaged forest reserves, Austria. *Neobiota* **2019**, *96*, 71–96.

Appendix A

Figure S1: Illustrative pictures of the study regions. Donaukanal study region in urban Vienna with the occurrence of *Ailanthus altissima* and *Populus x canadensis* (A, B). Donauinsel study region in peri-urban Vienna, with *Ailanthus altissima* growing in rip-rap structures (D). Sources: A: https://touren.labut.at/donaukanal/; B: https://www.wien.gv.at/stadtentwicklung/projekte/-zielgebiete/donaukanal/projekte/leitlinien.html; C: http://www.donauwanderIg.at/-neuedonaudonaustadt.html, D: http://www.oewav.at/home/Service/Neophyten.

Table S1: Survey data and explanatory variables used in the analyses. Given are plot number, study region (Donaukanal, Donauinsel, Tullner Becken), sampling date, level of disturbance (1 = low, 3 = high), proportion of urban habitats and human population density (in a radius of 500 m around the plot), and occurrence (presence / absence) of the five most wide-spread alien woody species in the study plots.

Study region	Plot ID	Sampling date	*Ailanthus altissima*	*Acer negundo*	*Fraxinus pennsylvannica*	*Populus x canadensis*	*Robinia pseudoacacia*	Proportion of urban habitat	Human population size	Disturbance
Donaukanal	DK1	17.04.2018	0	1	0	1	0	94%	52	2
Donaukanal	DK2	17.04.2018	0	1	0	1	0	94%	13	1
Donaukanal	DK3	28.07.2018	0	0	1	1	0	84%	7746	1
Donaukanal	DK4	21.08.2018	0	1	1	1	0	75%	7779	2
Donaukanal	DK5	21.08.2018	0	0	0	1	0	81%	9673	3
Donaukanal	DK6	23.08.2018	1	0	1	1	0	96%	11151	1
Donaukanal	DK7	23.08.2018	0	1	0	1	0	95%	12861	2
Donaukanal	DK8	17.04.2018	0	1	0	1	0	83%	1284	2
Donaukanal	DK9	17.04.2018	0	1	0	1	0	73%	970	2
Donaukanal	DK10	17.04.2018	0	0	0	0	0	89%	1205	2
Donaukanal	DK11	02.05.2018	1	1	0	1	0	96%	6983	3
Donaukanal	DK12	02.05.2018	1	0	1	1	0	68%	7396	3
Donaukanal	DK13	02.05.2018	0	0	0	1	0	84%	7821	3
Donaukanal	DK14	02.05.2018	0	0	0	0	0	83%	8498	3
Donaukanal	DK15	02.05.2018	0	1	0	1	0	85%	10832	3
Donaukanal	DK16	02.05.2018	1	1	0	1	0	96%	10843	2
Donaukanal	DK17	02.05.2018	1	1	0	1	0	96%	12822	3
Donaukanal	DK18	02.05.2018	0	1	1	1	0	95%	14330	2
Donaukanal	DK19	02.05.2018	0	0	0	0	0	96%	11975	3
Donaukanal	DK20	02.05.2018	1	1	1	0	1	96%	9018	3
Donaukanal	DK21	08.05.2018	0	1	0	1	0	94%	14197	3
Donaukanal	DK22	08.05.2018	1	1	0	1	0	96%	14496	3
Donaukanal	DK23	08.05.2018	1	1	1	1	0	97%	13605	2
Donaukanal	DK24	08.05.2018	0	0	0	1	0	96%	10329	3
Donaukanal	DK25	08.05.2018	0	0	0	1	0	89%	4770	2
Donauinsel	DI1	08.05.2018	0	0	0	1	1	38%	3091	2
Donauinsel	DI2	08.05.2018	0	1	0	0	0	39%	4255	2
Donauinsel	DI3	08.05.2018	0	0	0	0	0	45%	5173	2
Donauinsel	DI4	08.05.2018	0	0	1	0	0	40%	2976	1
Donauinsel	DI5	08.05.2018	0	1	0	0	0	40%	4130	2
Donauinsel	DI6	27.05.2018	0	0	0	0	1	32%	231	2
Donauinsel	DI7	27.05.2018	0	0	0	1	0	20%	23	1
Donauinsel	DI8	27.05.2018	1	1	0	0	0	29%	2192	1
Donauinsel	DI9	27.05.2018	0	1	1	0	0	34%	3951	2
Donauinsel	DI10	27.05.2018	1	1	0	0	0	38%	7877	2
Donauinsel	DI11	07.06.2018	0	1	0	0	0	32%	3751	1
Donauinsel	DI12	07.06.2018	0	0	0	0	1	41%	2550	2
Donauinsel	DI13	07.06.2018	0	1	0	0	0	38%	3239	2
Donauinsel	DI14	06.07.2018	0	0	1	0	0	27%	2835	2
Donauinsel	DI15	06.07.2018	0	1	0	1	0	24%	2114	2
Donauinsel	DI16	17.06.2018	0	0	0	0	1	35%	511	2
Donauinsel	DI17	17.06.2018	0	0	0	1	1	33%	406	1
Donauinsel	DI18	17.06.2018	0	0	0	0	0	32%	544	2
Donauinsel	DI19	17.06.2018	0	0	1	0	0	23%	55	2

Donauinsel	DI20	17.06.2018	0	1	1	0	1	22%	24	2
Donauinsel	DI21	17.06.2018	0	0	0	1	0	21%	25	2
Donauinsel	DI22	17.06.2018	0	0	0	0	1	21%	8	1
Donauinsel	DI23	17.06.2018	0	0	0	0	0	6%	52	1
Donauinsel	DI24	17.06.2018	0	1	1	1	0	11%	11	1
Donauinsel	DI25	08.05.2018	0	0	0	1	0	7%	3	1
Tullner Becken	TB1	20.07.2018	0	0	0	1	0	7%	74	2
Tullner Becken	TB2	20.07.2018	0	0	1	1	0	6%	2	1
Tullner Becken	TB3	20.07.2018	0	1	0	0	0	1%	0	1
Tullner Becken	TB4	20.07.2018	0	0	0	1	0	0%	0	1
Tullner Becken	TB5	20.07.2018	0	0	1	0	0	0%	0	1
Tullner Becken	TB6	20.07.2018	0	0	0	0	1	7%	76	2
Tullner Becken	TB7	20.07.2018	0	0	0	1	0	0%	0	1
Tullner Becken	TB8	20.07.2018	0	1	0	0	1	0%	406	1
Tullner Becken	TB9	20.07.2018	0	1	0	1	1	0%	0	1
Tullner Becken	TB10	20.07.2018	0	1	0	0	0	0%	0	1
Tullner Becken	TB11	20.07.2018	0	0	0	0	1	0%	20	1
Tullner Becken	TB12	20.07.2018	0	0	0	0	0	0%	17	1
Tullner Becken	TB13	20.07.2018	0	1	1	0	1	0%	12	2
Tullner Becken	TB14	20.07.2018	0	0	0	0	0	0%	2	2
Tullner Becken	TB15	20.07.2018	0	0	1	0	0	0%	0	1
Tullner Becken	TB16	20.07.2018	0	0	1	0	0	0%	5	1
Tullner Becken	TB17	20.07.2018	0	1	0	0	0	24%	79	2
Tullner Becken	TB18	20.07.2018	0	0	0	0	0	32%	149	2
Tullner Becken	TB19	20.07.2018	0	0	0	0	0	28%	94	2
Tullner Becken	TB20	20.07.2018	0	0	0	0	0	42%	27	2
Tullner Becken	TB21	20.07.2018	0	0	0	0	0	46%	401	2
Tullner Becken	TB22	20.07.2018	0	0	1	0	0	16%	221	2
Tullner Becken	TB23	20.07.2018	0	0	1	1	1	0%	78	2
Tullner Becken	TB24	20.07.2018	0	0	1	1	0	3%	347	2
Tullner Becken	TB25	20.07.2018	0	0	0	0	0	0%	241	1

Table S2: Overview on the recorded woody species in the 75 plots. Given are scientific name, and the biogeographic status (native / alien).

Species	**Biogeographic status**
Acer campestre	native
Acer negundo	alien
Acer platanoides	native
Acer pseudoplatanus	native
Acer pseudoplatanus f. *purpureum*	native
Acer saccharinum	alien
Aesculus hippocastanum	alien
Ailanthus altissima	alien
Alnus glutinosa	native
Amorpha fructicosa	alien
Betula pendula	native
Berberis thunbergii	alien
Buddleja davidii	alien
Celtis occidentalis	alien
Clematis vitalba	native
Cornus alba	alien
Cornus sanguinea	native
Corylus avellana	native
Corylus colurna	alien
Crataegus monogyna	native
Euonymus europaea	native
Ficus carica	alien
Frangula alnus	alien
Fraxinus excelsior	native
Fraxinus pennsylvanica	alien
Gleditsia triacanthos	alien
Hedera helix	native
Juglans nigra	alien
Juglans regia	alien
Koelreuteria paniculata	alien
Laburnum anagyroides	native
Ligustrum vulgare	native
Lonicera xylosteum	native
Mahonia aquifolium	alien
Malus domestica	alien
Morus alba	alien
Parthenocissus inserta	alien
Populus alba	native
Populus x canadensis	alien
Populus nigra	native
Prunus avium	native

Prunus cerasifera	native
Prunus cerasifera nigra	native
Prunus mahaleb	native
Prunus padus	native
Prunus spinosa	native
Pyrus pyraster	native
Quercus robur	native
Robinia pseudoacacia	alien
Rosa canina agg.	native
Rubus fruticosus	native
Salix alba	native
Salix cinerea	native
Salix eleagnos	native
Salix fragilis	native
Salix purpurea	native
Sambucus nigra	native
Sorbus domestica	native
Symphoricarpos albus	alien
Tilia cordata	native
Tilia platyphyllos	native
Ulmus campestris	native
Ulmus glabra	native
Ulmus laevis	native
Ulmus minor	native
Viburnum lantana	native
Viburnum rhytidophyllum	alien
Viscum album	native
Viburnum opulus	native