Temporal trends in the invasions of Austrian woodlands by alien trees

Průběh invaze nepůvodních druhů stromů v rakouských lesích

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Invasion of different habitats differs greatly with that of temperate woodlands being characterized by relatively low levels of invasion. However, evidence is accumulating that alien species of trees are increasingly colonizing woodlands, in particular floodplain woodlands. Here, we used 346 stratified relevés (154 plots in floodplain and 192 in non-floodplain woodlands) sampled between 1950–2014, combined with a control dataset of 369 uninvaded plots (97 plots in floodplain and 272 in non-floodplain woodlands), to analyse the invasion over time of Austrian woodlands by alien species of trees. The most frequent alien species of trees were *Robinia pseudoacacia*, *Acer negundo* and *Ailanthus altissima*. In addition, eight species of alien trees were recorded infrequently at the end of the study period. The average cover of alien trees has steadily increased since 1950. While the proportions of alien trees in floodplain relevés were significantly higher in 1950 than in non-floodplain relevés, the spread of alien trees was more pronounced in the latter. Average cover of native trees in the tree layer decreased over time in non-floodplain relevés, while for floodplain woodlands there was no temporal trend. Since 1950, indicators of human impact (mean levels of hemeroby and urbanophily) increased in both habitats, particularly in non-floodplain woodland, but remained stable in the control dataset. The frequency of nitrophilous and drought-tolerating species increased in non-floodplain and floodplain woodland, respectively, but both trends were also recorded in the control dataset. Further, changes in altitude and proportion of thermophilous species over time could indicate an effect of global warming. Our results point to anthropogenic habitat destruction, climate change, propagule pressure and deliberate planting of alien trees as the main drivers of alien tree invasions in the region studied.

Keywords: Ellenberg indicator values, floodplains, global warming, naturalization, neophytes, non-native plants, relevés, spread, time, vegetation

Introduction

In Europe, the level of invasion of different habitats differs greatly (Chytrý et al. 2008b, Botham et al. 2009), which indicates that some habitats are more susceptible to invasion than others. In particular, forests in temperate regions are relatively little affected by invasions (Chytrý et al. 2008b). However, evidence is accumulating that alien species, in particular trees, are spreading in central-European forests (e.g. Botta-Dukát 2008, Essl et al. 2011b, Höfle et al. 2014) and worldwide (Lamarque et al. 2011).

A suite of different alien species of trees is involved in this process, including those that have been present and established in central Europe for many decades or even several hundred years, such as *Robinia pseudoacacia* (Kleinbauer et al. 2010, Cierjacks et al. 2013), *Acer negundo* (Höfle et al. 2014) and *Ailanthus altissima* (Kowarik & Säumel

2007). In addition, there is anecdotal evidence that over the last few decades several species of alien trees such as *Aesculus hippocastanum*, *Fraxinus pennsylvanica*, *Juglans nigra* and *Rhus typhina* have started to spread. Recently, this trend was reinforced by other species of alien trees such as *Aralia elata* (Berg et al. 2009), *Catalpa bignonioides* (Schrammel 2013) and *Paulownia tomentosa* (Essl 2007).

It is well-known that invasions of forests are facilitated by disturbances (e.g. clear cuts, forest roads, windfalls), which create gaps for the establishment of seedlings, and by planting of alien trees for forestry or ornamental purposes, which increases propagule pressure (Davis et al. 2000, Chytrý et al. 2008a, Martin et al. 2009). In Europe and elsewhere, riparian floodplain forests are characterized by particularly high and increasing levels of invasion by alien species of plants (Rabitsch & Essl 2006, Richardson et al. 2007, Schnitzler et al. 2007, Vilà et al. 2007, Chytrý et al. 2008b, Petrášová, et al. 2013). High nutrient levels and periodic disturbances due to flooding (Richardson et al. 2007, Chytrý et al. 2008a) are assumed to facilitate invasions in riparian areas. In addition, rivers may transport propagules very effectively and thus may serve as important invasion corridors for alien species (Pyšek & Prach 1993, Chytrý et al. 2009).

Recent studies have revealed that the current distributions of alien species are often in disequilibrium (Essl et al. 2011a). This is particularly true for habitats dominated by long-lived species, and, accordingly, biological inertia and time lags may mask the ultimate level of invasions of forests (Von Holle et al. 2003, Essl et al. 2011b, Petrášová et al. 2013, Höfle et al. 2014). Consequently, long-term studies are necessary to gain deeper insights into alien tree invasions.

Here, we reconstruct the invasion by alien species of trees in Austria from 1950 onwards based on relevés in the Austrian Vegetation Database (Willner et al. 2012). In particular, we ask the following questions: (i) Are there temporal trends in the invasions of alien species of trees? (ii) Which changes in community structure and composition (changes in weighted hemeroby, urbanophily and mean Ellenberg indicator values) are associated with the spread of alien trees? (iii) What are the differences in the invasions by alien species of trees of non-floodplain and floodplain forests and what are the underlying factors determining these differences?

Material and methods

Data selection and stratification

We obtained data from the Austrian Vegetation Database, which contains 43,000 relevés, sampled from 1926 onwards (Willner et al. 2012). We searched relevés containing at least one of the following neophytic species of trees (i.e. recorded > 1492 for the first time in the wild in Austria; Aliens Austria 2014) in any layer: *Acer negundo, Aesculus hippocastanum, Ailanthus altissima, Aralia elata, Catalpa bignonioides, Fraxinus pennsylvanica, Juglans nigra, Paulownia tomentosa, Rhus typhina* and *Robinia pseudoacacia* (hence: the species studied). Relevé data do not differentiate between planted and escaped trees, and thus it is possible that some of the stands included in the analyses were planted. However, the majority of these species of trees are not or only rarely planted for forestry purposes in Austria. *Robinia pseudoacacia* is only rarely planted in forests, but widely established in the Pannonian lowlands in eastern Austria, while *Fraxinus*

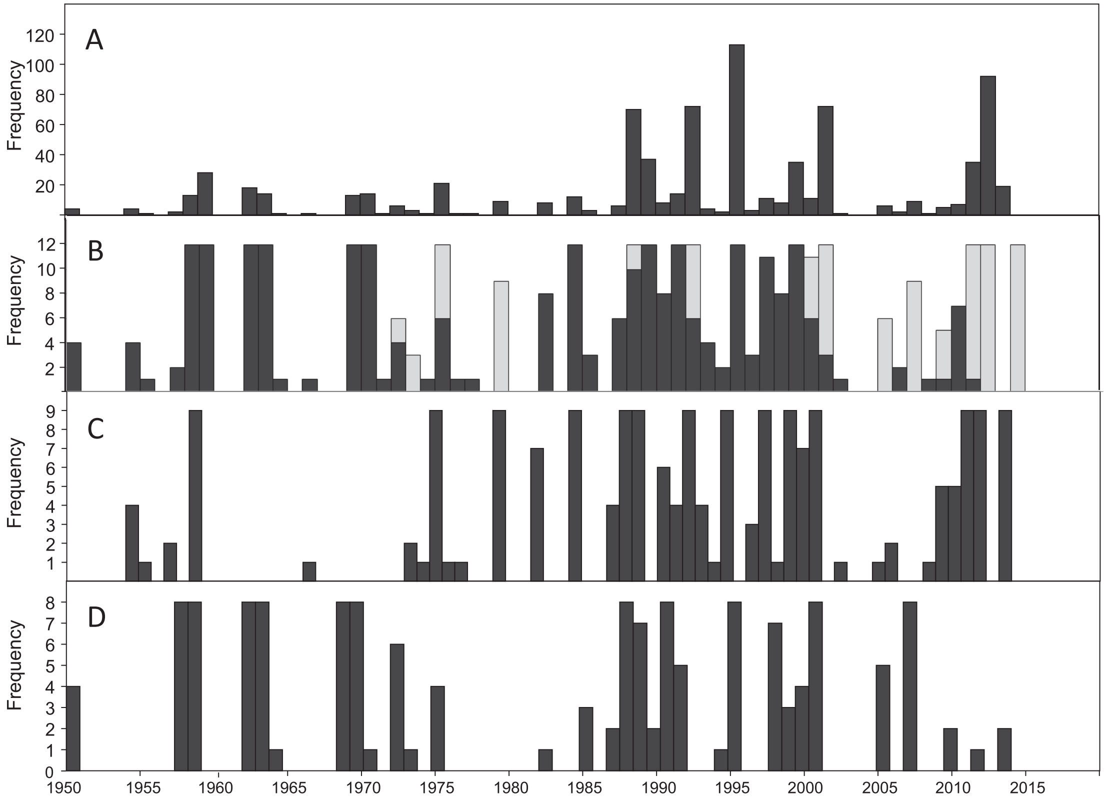


Fig. 1. – Number of relevés for the time period studied from (A) the entire dataset (n = 822), (B) after stratification with a maximum number of 12 relevés per year (n = 346), divided into those without (black) and with (grey) a special focus on ruderal woody habitats, (C) non-floodplain woodlands (max. no. of relevés per year = 9, n = 192) and (D) floodplain woodlands (max. no. of relevés per year = 8, n = 154).

pennsylvanica and *Juglans nigra* are planted in forests, there are also many populations that have become established in floodplain forests (see e.g. Höfle et al. 2014). To conclude, most of the populations included consist of escaped individuals. In contrast, the alien tree species *Quercus rubra* and *Populus ×canadensis* were excluded from the analyses, as most of their stands are planted. *Castanaea sativa* and *Juglans regia* were excluded because they are considered to be archaeophytes (i.e. alien species introduced < 1492) in Austria (Aliens Austria 2014). We included only relevés with a shrub or tree layer cover of > 25%, thus our dataset also contains scrubland and pioneer woodland relevés. These search criteria yielded 936 relevés collected from 1950 onwards, including 822 relevés with information on the year of collection (Fig. 1A).

We divided this dataset into floodplain (n = 370) and non-floodplain stands (n = 452) based on information provided in the original data sources and the phytosociological assignments of the relevés. Relevés of the following phytosociological alliances were assigned to floodplain forests: *Salicion albae*, *Salicion triandrae*, *Alnion incanae*

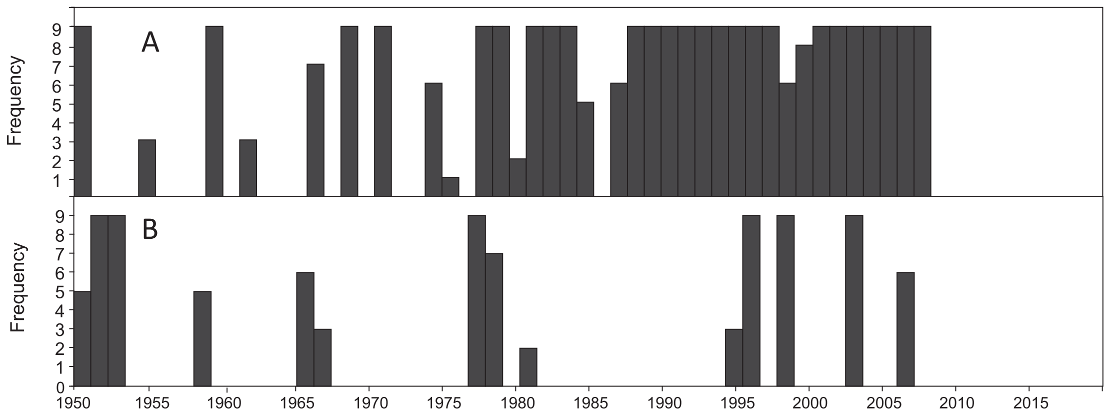


Fig. 2. – Number of relevés for the time period studied from the control dataset (max. no. of relevés per year = 9) (A) non-floodplain woodlands (n = 272), and (B) floodplain woodlands (n = 97).

(Willner & Grabherr 2007). Floodplain stands are defined in a broad topographical sense, and include not only the area inside the embankment for flood protection, but also the historical floodplain prior to river channelization, with at least episodic flooding and a periodically high groundwater table (Demek et al. 2008). Non-floodplain relevés belonged mostly to zonal colline forests or degraded forests (e.g. *Carpinion betuli*, *Arctio-Sambucion nigrae*; Willner & Grabherr 2007).

Large vegetation databases are unique data repositories for the analyses of vegetation composition and changes in vegetation composition over time (Jandt et al. 2011), but they also have specific limitations and biases (Chytrý et al. 2014). In particular, preferences of the data contributors could have introduced spatio-temporal biases. We used two methods to avoid this problem. First, we stratified our dataset by randomly selecting a maximum number of 12 relevés per biblioreference or author (Fig. 1B), or of nine relevés after division into non-floodplain and floodplain relevés, respectively (Fig. 1C, D). These values were chosen as they are close to the median number of relevés per biblioreference or author. This resulted in 346 stratified relevés (154 plots in floodplain and 192 in non-floodplain woodlands). All analyses were performed using this stratified dataset.

Another problem that can bias our data is changes in sampling preferences during our assessment period (Jandt et al. 2011). As shown in Fig. 1B, the interest in ruderal woody vegetation increased over time. To account for that, we performed a test using 246 relevés in our stratified dataset that were collected in studies that did not focus on ruderal woody vegetation. Subsequently, we repeated all analysis with this dataset. We only present those results that show the same trends and significance for the slope ($P < 0.01$) as the original dataset.

In addition, we used the same approach as described above and extracted a control dataset of comparable forest plots (same phytosociological alliances) not invaded by alien species (except for floodplain vegetation for which we allow the occurrence of one herbal neophyte species per relevé), and repeated all analyses using this data (henceforth the “control dataset”). This yielded 974 relevés for non-floodplain forests, and

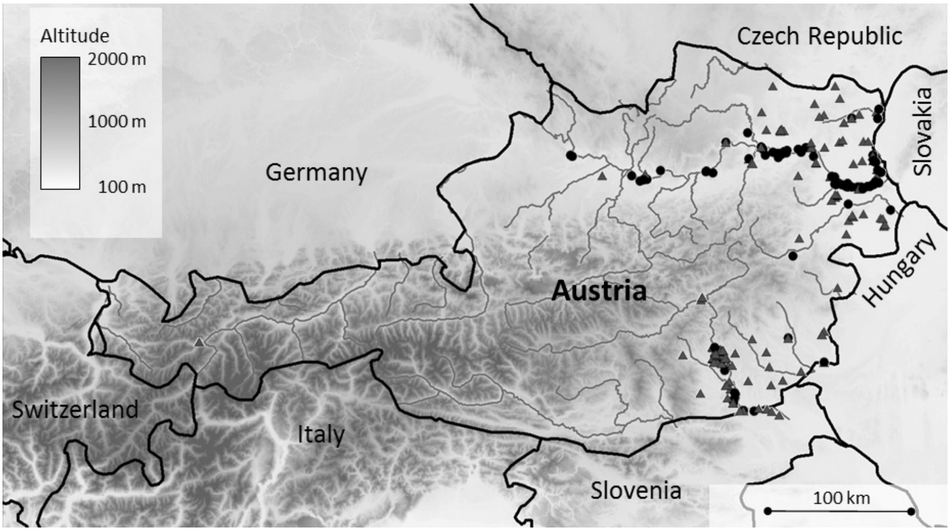


Fig. 3. – Location of georeferenced relevés of woodlands with alien species of trees in Austria. Black dots indicate floodplain relevés (n = 246), grey triangles non-floodplain relevés (n = 318, overlapping data not shown).

371 relevés for floodplain forests. We used the same stratification (randomly selecting a maximum number of nine relevés per year) resulting in 369 non-invaded plots (272 for non-floodplain and 97 relevés for floodplain forests; Fig. 2). Species nomenclature follows Fischer et al. (2008).

Geographical distribution

In our dataset, 566 relevés contained information on their geographical position (Fig. 3). The vast majority of relevés selected were collected in eastern and southern Austria, whereas only a few relevés were sampled in the more mountainous western Austria. Relevés for floodplain woodlands were mostly sampled along large Austrian rivers (Danube, March, Mur).

Plant indicator values

For all species in our dataset, we obtained information on hemeroby and urbanophily from the BIOLFLOR-Database (Klotz et al. 2002), and indicator values for nutrients, moisture and temperature (Ellenberg et al. 1991). Hemeroby is an indicator of human impact on ecosystems, first introduced by Sukopp (1972) for different types of vegetation and further developed for plant species by Kowarik (1988). Urbanophily is the affiliation of a plant species with urban environments, as used by Wittig et al. (1985). For every relevé and layer, we calculated the relative cover and relative numbers of alien and native species, altitude, mean hemeroby and urbanophily, and mean Ellenberg indicator values for nutrients, moisture and temperature. To test for changes in the composition of species with different temperature requirements we calculated cover-weighted mean Ellenberg temperature values for each relevé (Ellenberg et al. 1991).

We transformed ordinal data, such as hemeroby and urbanophily, into numeric values in the same manner as Ellenberg indicator values (Ellenberg et al. 1991). Hemeroby values given by Klotz & Kühn (2002) for each plant species were transformed in the following way: ahemerob = 0; oligohemerob = 1; mesohemerob = 2; β-euhemerob = 3; α-euhemerob = 4; and polyhemerob = 5. Hemeroby ranges were considered as means following Klotz & Kühn (2002). Urbanophily ranged from 1 (urbanophob) to 5 (urbanophil). For every relevé, we then calculated cover-weighted means of hemeroby and urbanophily.

Data analysis

We calculated relative alien species richness (= proportion of alien species of trees in relation to total number of species) and abundance (= relative cover of alien trees) for every relevé. We used generalized linear models (GLM) with a binominal error distribution and a log-link function (Nelder & McCullagh 1989) to analyse temporal changes in alien species richness and cover. Plant cover and species proportion data were skewed and zero-inflated. Consequently, we transformed these values to a categorical scale, corresponding to values below or above the centered threshold at the median. In addition, we analysed temporal changes in native tree richness and cover using the same approach. To analyse the effects of global warming on alien tree species invasions, we analysed temporal changes in the altitude of relevés. In addition, we used ANCOVA to analyse the temporal change in hemeroby, urbanophily and Ellenberg indicator values, with habitat (floodplain vs non-floodplain stands) and level of invasion (invaded vs uninvaded control stands) as a factor. Finally, we contrasted relative alien species richness and relative alien species abundance per relevé using linear regression, similar to the approach of Catford et al. (2012). Vegetation data was prepared using JUICE (Tichý 2002) and statistical analyses performed using PAST (Hammer et al. 2001).

Results

Changes in the level of invasion

We found a strong increase in the level of invasion in recent decades (Fig. 4). While for the decade 1950, on average ~6% of the tree species and 3% of total cover consisted of alien trees, for the decade 2010 (2005–2014) these values had increased to 16% of the species and 38% of the total cover.

Changes in the percentages of alien and native species of trees over time

The most frequent alien species of trees in the Austrian Vegetation Database were *Robinia pseudoacacia*, followed by *Acer negundo* and *Ailanthus altissima* (Table 1). Whereas *Acer negundo, Fraxinus pennsylvanica* and *Juglans nigra* were mostly recorded in floodplain woodlands, *Robinia pseudoacacia, Ailanthus altissima* and all rare species of alien trees were mainly recorded in non-floodplain woodlands.

The average cover of alien species in the relevés selected has steadily increased since 1950. This is true for both total cover (= all vegetation layers combined, Fig. 5A, B) and cover in the tree layer (Fig. 5C, D). The increase in the cover of alien species was more

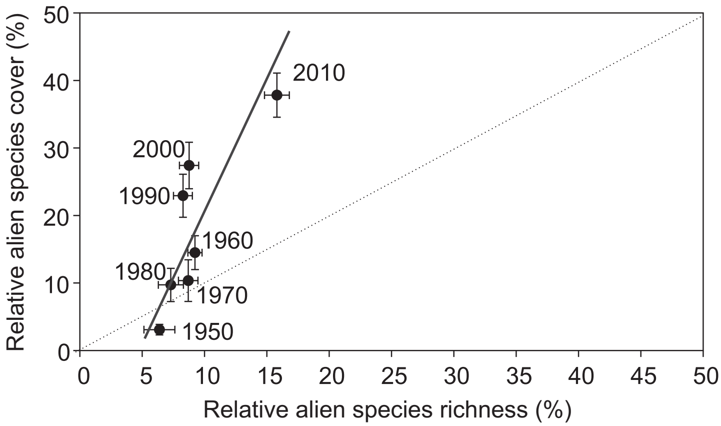


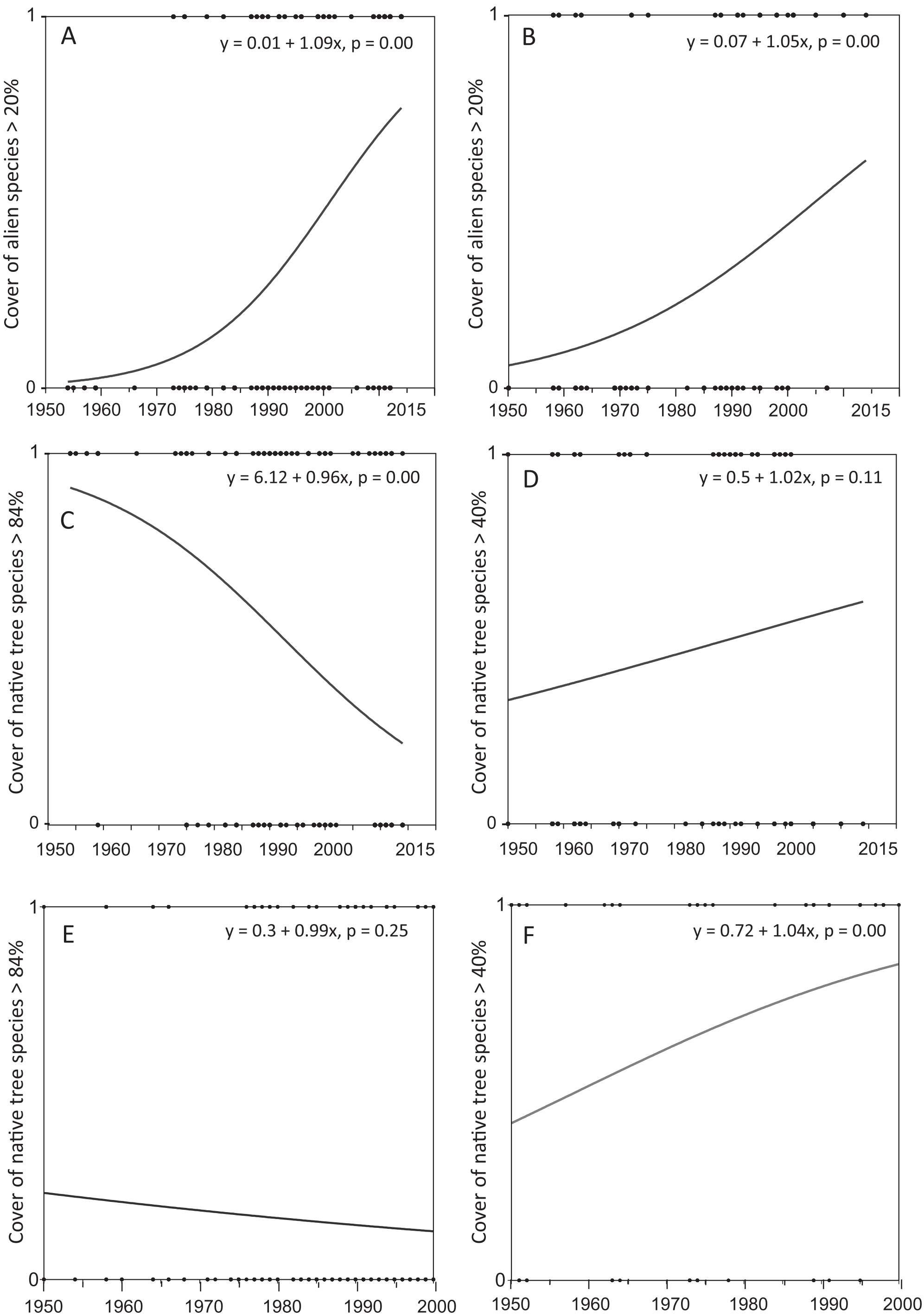
Fig. 4. – Relationship between mean relative alien species richness and mean relative alien species cover of woodland for relevés invaded by at least one alien species of tree from 1950 to 2010 (span –4 and +5 years, n = 346, y = 3.25x – 11.9, $R_{\llcorner}$ = 0.69, P = 0.01). Relevés were divided into decades. The solid line shows the best fit to the given equation, the unity line is dotted.

pronounced in non-floodplain woodland (Fig. 5A) than in floodplain woodland (Fig. 5B), but the percentages of alien species in floodplain relevés were significantly higher than in non-floodplain relevés in 1950 (Mann-Whitney permutation test, P = 0.023).

The average percentage of native tree species in the tree layer decreased over time in non-floodplain relevés (P < 0.001, Fig. 5C), while in the uninvaded control dataset no change in the cover of native tree species over time was detected (P = 0.25, Fig. 5E). For floodplains we found no temporal trend in invaded stands (P = 0.1, Fig. 5D), while in the uninvaded control dataset we found a significant increase in native species of trees (P = 0.002, Fig. 5F).

Table 1. – Alien species of trees in the dataset (n = 822, 30% of the relevés contain more than one alien species of tree), their frequency of occurrence (number of relevés with invaded vegetation), their frequency in floodplain and non-floodplain woodlands (in %), their first record in Austria (Aliens Austria 2014) and in a relevé in the Austrian Vegetation Database (Willner et al. 2012).

Species	Number of relevés	Frequency in floodplain relevés (%)	Frequency in non-floodplain relevés (%)	First record in Austria	First record in the Austrian Vegetation Database
Robinia pseudoacacia	495	21	79	1849	1950
Acer negundo	224	94	6	1900	1950
Ailanthus altissima	159	32	68	1890	1963
Fraxinus pennsylvanica	39	95	5	1958	1958
Juglans nigra	37	92	8	1971	1962
Aesculus hippocastanum	23	13	87	1795	1959
Paulownia tomentosa	16	0	100	1965	2011
Rhus typhina	5	0	100	1859	1989
Aralia elata	4	0	100	1909	2009
Catalpa bignonioides	2	0	100	1990	2014


A
y = 0.01 + 1.09x, p = 0.00
Cover of alien species > 20%
B
y = 0.07 + 1.05x, p = 0.00
Cover of alien species > 20%
C
y = 6.12 + 0.96x, p = 0.00
Cover of native tree species > 84%
D
y = 0.5 + 1.02x, p = 0.11
Cover of native tree species > 40%
E
y = 0.3 + 0.99x, p = 0.25
Cover of native tree species > 84%
F
y = 0.72 + 1.04x, p = 0.00
Cover of native tree species > 40%
1
0
1950
1960
1970
1980
1990
2000
2015

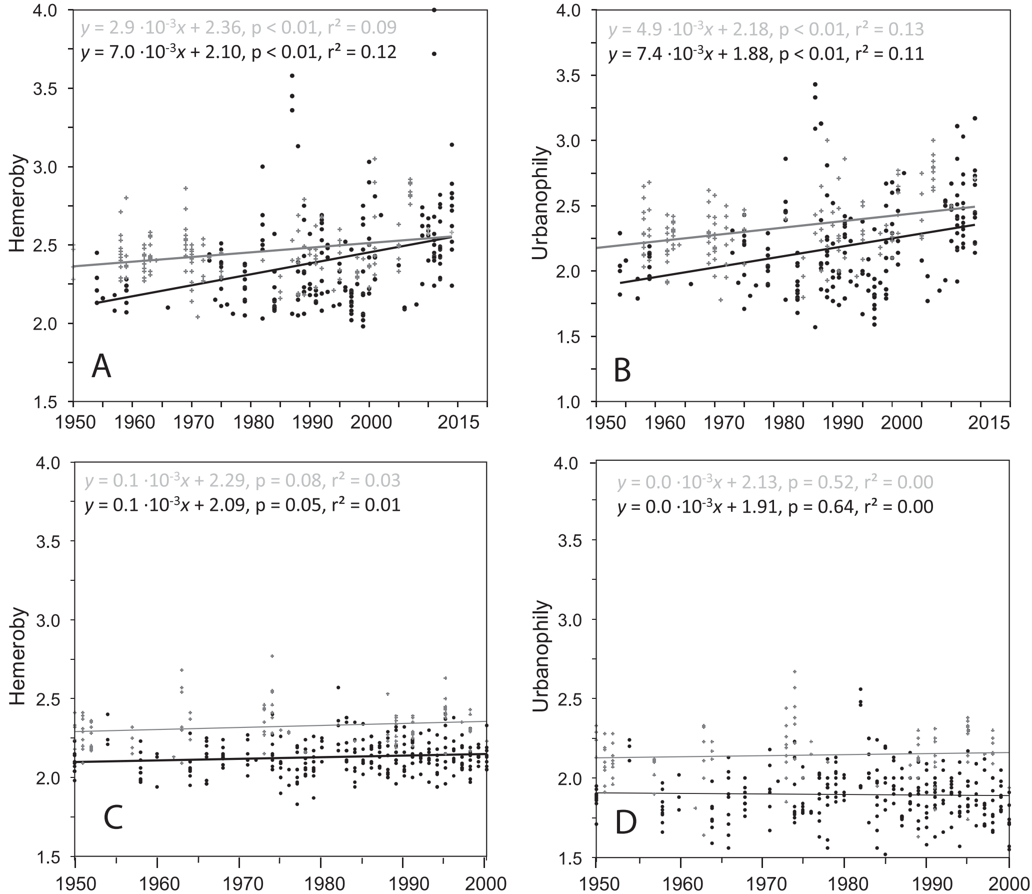


Fig. 6. – Linear model (ANCOVA) of temporal changes in mean hemeroby and urbanophily plot indices between relevés invaded by alien tree species at non-floodplain (black dots, n = 192) and floodplain sites (grey crosses, n = 154) (A, B), and in a control dataset of plots uninvaded by alien species: non-floodplain (black dots, n = 272) and floodplain sites (grey crosses, n = 97) (C, D).

◀ Fig. 5. – Time series of the probability of changes in relevé cover values. (A) Changes in alien species in total cover of non-floodplain relevés. GLM with cover ≤ 20% = 0 and > 20% = 1 (n = 192). (B) Changes in alien species in total cover of floodplain relevés. GLM with cover ≤ 20% = 0 and > 20% = 1 (n = 154). (C) Changes in the cover of the tree layer of non-floodplain relevés. GLM with cover ≤ 84% = 0 and > 84% = 1 (n = 161). (D) Changes in the proportion of native trees in the tree cover for floodplain relevés. GLM with cover ≤ 40% = 0 and > 40% = 1 (n = 128). (E) Changes in the native tree species in an uninvaded control dataset of non-floodplain forests with cover < 84% = 0 and > 84% = 1 (n = 272). (F) Changes in the native tree species in the uninvaded control dataset of floodplain forests with cover < 40% = 0 and cover > 40% = 1 (n = 97). For D, E, and F, relevés without a tree layer were omitted. Estimates are shown as odd-ratios.

Human impact: hemeroby and urbanophily

Average mean hemeroby and urbanophily indices provide an indication of the level of human impact on vegetation plots. We found slight increases in the mean hemeroby and urbanophily indices over time (Fig. 6A, B) in the invaded, but not in the control dataset (Fig. 6C, D); the trend was similar for both floodplain and non-floodplain habitats. In a comparison of invaded and uninvaded plots, we identified a strong and significant level of invasion × time interaction for hemeroby (non-floodplain woodland: $F_{1, 461} = 116.4$, $P < 0.001$; floodplain woodland: $F_{1, 248} = 33.0$, $P < 0.001$) and urbanophily (level of invasion × time interaction, non-floodplain woodland: $F_{1, 461} = 110.9$, $P < 0.001$; floodplain woodland $F_{1, 248} = 35.6$, $P < 0.001$). Furthermore, these two response variables showed different trends in the two habitats (Fig. 6A, B). At the beginning of the time period, the level of both hemeroby and urbanophily was higher in floodplain woodlands. While urbanophily increased in floodplain and non-floodplain woodlands in a similar manner (habitat × time interaction: $F_{1, 344} = 1.8$, $P = 0.181$), hemeroby values of non-floodplain woodland showed a significantly stronger increase (habitat × time interaction: $F_{1, 344} = 6.0$, $P = 0.014$, Fig. 6A).

Changes in community indicator values for moisture and nutrients

Changes in Ellenberg community indicator values show that soil moisture and nutrient availability were substantially higher for relevés of floodplains in the mid-20th century (Fig. 7A, B). While the moisture indicator level remained constant for non-floodplain woodland over the time period studied, the percentage of species with high demands on moisture decreased significantly for floodplain woodlands (habitat × time interaction: $F_{1, 344} = 21.6$, $P > 0.01$, Fig. 7A). On the other hand, there was no significant change in nutrient levels for floodplain relevés, while for non-floodplain relevés the percentage of nutrient demanding species increased (habitat × time interaction: $F_{1, 344} = 4.8$, $P = 0.029$, Fig. 7B). This was accompanied by a significant increase in the density of the canopy in floodplain woodlands (Fig. 5F). In contrast, we found no significant changes over time in mean soil moisture and nutrient indicator values, and no habitat × time interaction in the control dataset of plots uninvaded by alien species (Fig. 7C, D). When we compared invaded and control plots, we did not detect any level of invasion × time interaction, except for the Ellenberg moisture indicator for non-floodplain woodland ($F_{1, 457} = 37.0$, $P < 0.001$, Fig. 7A, C).

Changes in altitude and percentage of thermophilous species of trees

Since 1950, the average altitude of relevés in non-floodplain woodland invaded by alien trees increased significantly; for uninvaded relevés the effect was weak (Fig. 8A). Invaded plots showed a significantly stronger increase in altitude than control plots (level of invasion × time interaction $F_{1, 416} = 55.2$, $P < 0.001$). For floodplain relevés there was no significant change (data not shown).

In plots invaded by alien trees, the percentage of thermophilous species remained stable for non-floodplain relevés while it increased for floodplain relevés (habitat × time interaction: $F_{1, 344} = 6.4$, $P = 0.01$, Fig. 8B). In the uninvaded control dataset, there was no change over time in the percentage of thermophilous species and no habitat × time interaction (Fig. 8C).

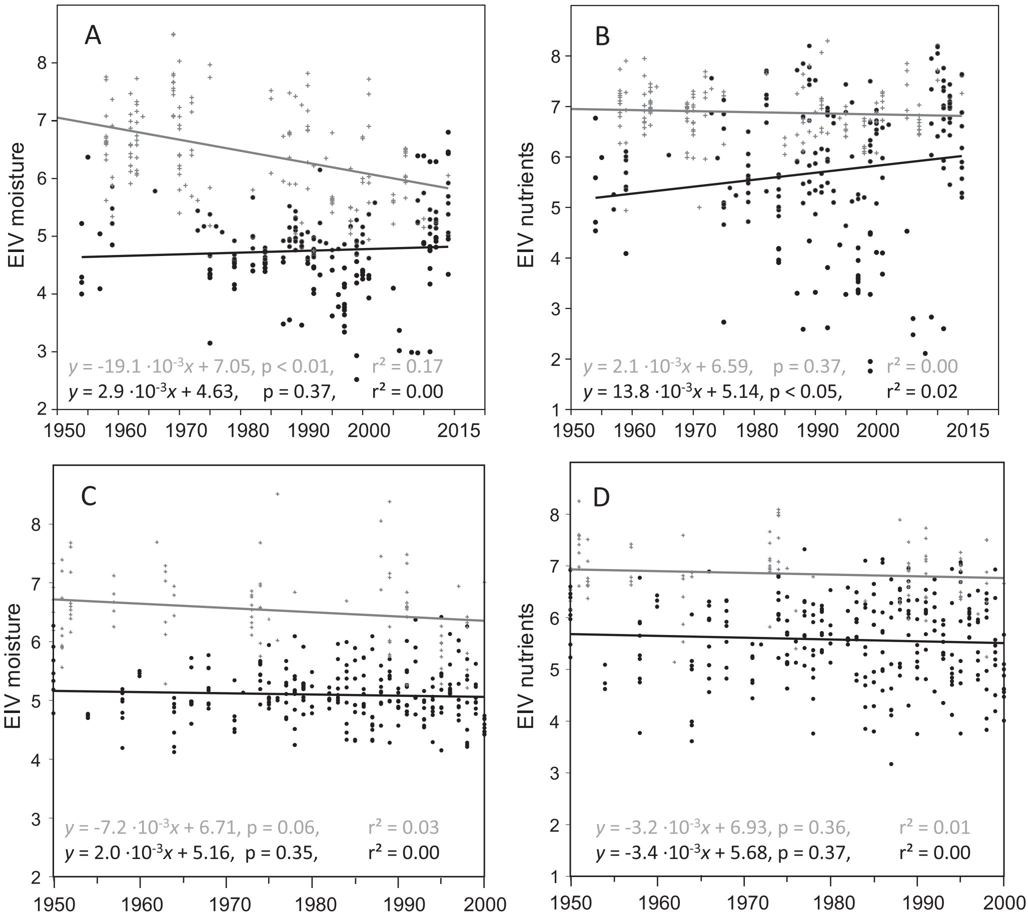


Fig. 7. – Linear model (ANCOVA) of temporal changes in weighted mean Ellenberg indicator values for moisture and nutrients in relevés invaded by alien species of trees (A) at non-floodplain (black dots, n = 192) and (B) floodplain sites (grey crosses, n = 154), and for the control dataset of plots uninvaded by alien species: (C) non-floodplain (black dots, n = 272) and (D) floodplain sites (grey crosses, n = 97).

Discussion

Temporal trends in alien tree species invasions

The forests invaded by alien tree species are currently mainly in the lowlands of southern and eastern Austria (Kleinbauer et al. 2010). This supports previous findings that alien tree species in central Europe are confined to low altitudes (e.g. Becker et al. 2005, Medvecká et al 2014), reflecting these species' preferences for low altitude habitats, time-lags in colonization, higher propagule pressure in the lowlands and lack of disturbance at high-altitudes.

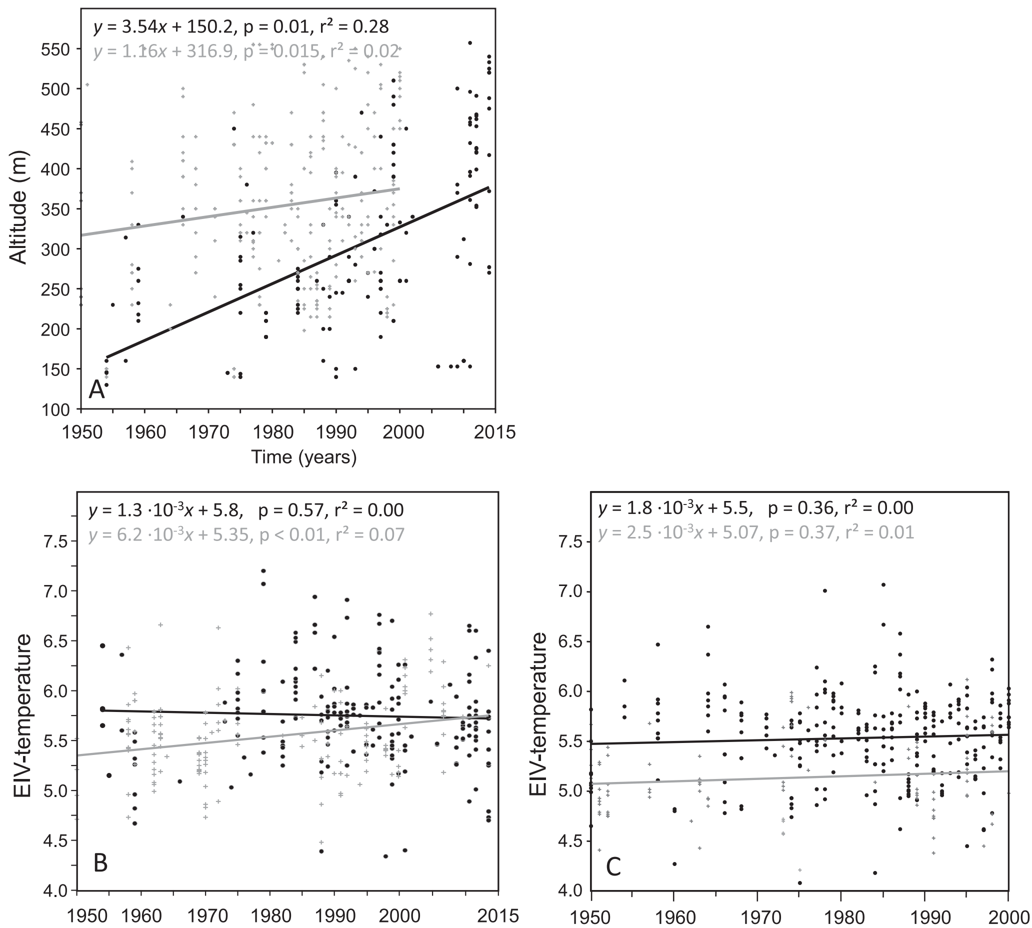


Fig. 8. – Linear model (ANCOVA) of temporal changes in (A) altitude for invaded relevés (black dots, n = 162) and the uninvaded control dataset (grey crosses, n = 257). (B) weighted Ellenberg temperature community indices for non-floodplain (black dots, n = 192) and floodplain relevés (grey crosses, n = 154). (C) weighted Ellenberg temperature community indices for an uninvaded control dataset in non-floodplain (black dots, n = 272) and floodplain relevés (grey crosses, n = 97).

This study has shown that the relative richness and cover of alien trees has steadily increased in Austrian woodlands since the 1950s. This spread of alien species of trees was mainly driven by *Robinia pseudoacacia* and *Ailanthus altissima* in non-floodplain forests, while *Acer negundo* and *Fraxinus pennsylvanica* are by far the most wide-spread species in floodplain forests. These findings confirm the results of Petrášová et al. (2013) for hardwood floodplain forests in neighbouring Hungary and Slovakia. Despite this temporal trend, our data show that the current level of invasion is similar to the situation in the Czech Republic (Chytrý et al. 2005) and not yet particularly high in Austria's invaded woodlands, compared to the extreme example of Berlin's city forests, where

56% of all the species of plants and 55–95% of all plant individuals are aliens (Kowarik et al. 2013). The steep rise in the regression line (Fig. 4) indicates the dominance of one or few invaders, although relative alien tree species richness increased as well, it did not increase as much as alien species abundance. In non-floodplain stands, natural disturbances, like forest fires and wind throw are rare in central Europe, but anthropogenic disturbance caused by forestry, airborne eutrophication and waste deposition are common. In any case, the increase in mean hemeroby over time in non-floodplain relevés indicates that anthropogenic disturbance could be a driving factor for the alien tree invasion of this type of stand.

Furthermore, this study points to human impact as a crucial factor in the spread of alien tree species in Austrian woodland. The results for urbanophily corroborate the finding of previous studies, which have shown that alien tree invasions often start in or close to human settlements, as they are widely planted for ornamental purposes (e.g. *Ailanthus altissima, Paulownia tomentosa, Robinia pseudoacacia*; Pyšek 1998, Essl 2007, Godefroid & Koedam 2007, Kowarik & Säumel 2007).

The observed increases in mean altitude of the invaded relevés over time indicate that global warming might have promoted the invasion of alien tree species into areas at higher altitudes (Becker et al. 2005). A substantial increase in thermophilous species is only detectable in the more open floodplain woodlands. However, a causal relationship with climate change is not mandatory. Spread of thermophilous species can be also facilitated by drier conditions in the drained floodplains as well as by increasing hemeroby (Stevens et al. 2015). In non-floodplain woodland, the denser tree canopy possibly buffers species against the effects of climate warming (De Frenne et al. 2013), or the shift to higher altitudes is not yet followed by thermophilous species.

The importance of global warming in facilitating alien tree invasions of Austrian woodlands is difficult to assess given other confounding factors. However, its importance will likely increase in the near future (Walther 2002, Kleinbauer et al. 2010). In addition, changes in precipitation might be important in influencing the future spread of alien species of trees. If summer precipitation decreases, as predicted by IPCC (2013) for the area studied, increasing tree mortality at dry sites will lead to more open forests. Combined, these effects might enhance the spread of alien species of trees, as indicated by the high level of invasion of dry pannonian forests in eastern Austria and Hungary (Rabitsch & Essl 2006, Botta-Dukát 2008).

Differences between tree invasions of floodplain and non-floodplain woodlands

While several features of the invasion of alien tree species are similar for floodplain and non-floodplain woodlands, there are also some striking differences. We argue that a range of differences in natural site conditions, as well as their trajectories of change in the second half of the 20th century account for the observed differences between floodplain and non-floodplain forests. While in floodplain woodland the community level of hemeroby and urbanophily was higher in the mid-20th century, their increase in recent decades was less pronounced. The percentage of moisture indicating species remained the same in invaded and uninvaded non-floodplain woodland (Fig. 7A, C) but has decreased remarkably in invaded floodplain woodland (Fig. 7A), while in the floodplain control dataset no significant decrease in the percentage of moisture indicating species is visible (Fig. 7C, P = 0.06, r^2 = 0.03). Meanwhile, canopy cover in uninvaded floodplain forests increased (Fig. 5F). These results could indicate a general decline in natural floodplain dynamics due to the decoupling of hydromorphological river processes in the second half of the 20th century. In addition, alien tree species prefer stands disturbed by humans (where no increase in cover of native tree species is recorded, Fig. 5C) and falling ground water levels due to river channelization and protective dike construction (Fig. 7A). Several of the most widespread alien tree species (*Ailanthus altissima, Robinia pseudoacacia*) nearly only invade rather dry floodplain areas (Petrášová et al. 2013, Höfle et al. 2014).

We conclude that the interplay of anthropogenic habitat modification (i.e. human disturbance and eutrophication of non-floodplain forests, hydromorphological changes leading to denser canopies in floodplain woodlands), climate change and increased propagule pressure due to increase in planting and uncontrolled spread of alien species of trees were likely the main drivers of tree invasion in the second half of the 20th century in Austria.

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Souhrn

Mezi mírou invaze jednotlivých habitatů jsou velké rozdíly, temperátní lesy jsou však obecně zasaženy relativně málo. Přibývá však dokladů o tom, že podíl nepůvodních druhů stromů postupně stoupá i v lesních společenstvech, zejména pak v lužních lesích. V této práci jsme analyzovali 346 vegetačních snímků z let 1950–2014 (z toho 154 z lužních lesů a 192 z jiných typů lesa) spolu s kontrolním datovým souborem, pocházejícím z neinvadovaných lesů; ten tvořilo celkem 369 snímků (97 lužní lesy, 272 ostatní). Vedle nejčastěji se vyskytujících druhů, *Robinia pseudoacacia*, *Acer negundo* a *Ailanthus altissima*, se dalších osm na konci studovaného období objevovalo s malou frekvencí. Průměrná pokryvnost nepůvodních druhů od roku 1950 trvale stoupala. Podíl nepůvodních druhů ve snímcích z lužních lesů byl na začátku studovaného období průkazně vyšší než v lesích z jiných stanovišť, jejich nárůst mimo lužní lesy byl však výraznější. Průměrná pokryvnost původních druhů ve stromovém patře se v lužních lesích neměnila, v ostatních typech lesů klesala. Od roku 1950 stoupalo zastoupení hemerobních a urbanofilních druhů v invadovaných lesích, v kontrolním datovém souboru zůstávalo beze změny. Frekvence druhů tolerantních vůči suchu stoupala v lužních lesích, zatímco v ostatních lesích se zvyšovala frekvence druhů nitrofilních; oba tyto trendy byly zachyceny i v kontrolních neinvadovaných lesích. Další zaznamenané změny, jako je vazba na nadmořskou výšku a zastoupení termofilních druhů, mohou být důsledkem globálního oteplování. Antropogenní změny stanovišť, změny klimatu, přísun diaspor a úmyslné pěstování nepůvodních stromů lze na základě našich výsledků považovat za hlavní příčiny invaze ve studovaném regionu.

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