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Using relevé-based metrics to explain invasion patterns of alien trees in temperate forests

Die Verwendung von Vegetations-Indikatoren zur Erklärung der Ausbreitung gebietsfremder Baumarten in temperaten Wäldern

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Abstract

Central European temperate forests are – with the exception of floodplain forests – relatively little invaded by alien plants. However, despite substantial recent progress, there is still a lack of using vegetation plot data for analyzing spatio-temporal patterns of alien tree species invasions.

We calculated relevé-based metrics of tree species' ecological preferences using 19,413 phytosociological forest relevés of the Austrian vegetation database. We focused on the five most widely distributed alien trees, i.e. two archaeophytes (*Castanea sativa*, *Juglans regia*) and three neophytes (*Acer negundo*, *Ailanthus altissima*, *Robinia pseudoacacia*). For each of these species we analyzed the mean cover in the tree layer and the occurrence in the herb and shrub layers in relevés colonized by adult trees as a measure for persistence. Further, we evaluated the inter-generational ecological plasticity (= the ability of young trees to grow under different site conditions than adults) for the tree species, and the mean relevé indicator values for light, nutrients, moisture and hemeroby. We then compared these alien and native tree species metrics.

We found that *A. altissima* and *R. pseudoacacia* build up high mean cover values in invaded forests, but this was not the case for the other alien trees. Thus, both species strongly affected forest communities of invaded sites. Similarly, the two species were common in the lower vegetation layers indicating recruitment under the canopy of adult conspecifics; this was facilitated by their ability to produce root suckers. Highest values of inter-generational ecological plasticity occurred in native pioneer trees and species of softwood floodplain forests, while alien trees had moderately high (*A. negundo*, *A. altissima*, *J. regia*) to low values (*C. sativa*, *R. pseudoacacia*).With the exception of *C. sativa*, all alien species showed high mean Ellenberg indicator values for light and nutrients, and were more common in sites with high hemeroby and high mean Ellenberg indicator values for temperature. Distinct from the ecological preferences of alien trees, and thus rarely invaded, were montane beech forests, coniferous mountain forests and forests at extremely dry sites, as well as swamp and bog forests dominated by willows and ash.

We conclude that relevé-based metrics of the behavior of alien tree species allow new insights into the spatio-temporal dynamics of invasion of woody species in forests. Future work should expand this approach, e.g., by considering the role of life history traits and actual site conditions.

Keywords: archaeophytes, co-occurrence metrics, Ellenberg indicator values, invasiveness, neophytes, relevés, spread, succession

Erweiterte deutsche Zusammenfassung am Ende des Artikels

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1. Introduction

The spread of alien plant species has become a rapidly increasing global phenomenon (VAN KLEUNEN et al. 2015, SEEBENS et al. 2017), and negative impacts on biodiversity (e.g., via competition, hybridization) are increasingly reported (VILÀ et al. 2010). In Central Europe, temperate forests are rather resistant to plant invasions (CHYTRÝ et al. 2008). Important exceptions are forests that are shaped by frequent natural disturbance (e.g., floodplain forests; SCHNITZLER et al. 2007, VILÀ et al. 2007), forest plantations, and open forests at the ecological limits of tree vegetation, e.g., transitions to steppe vegetation like in the Pannonian region of Hungary, where zonal forests are the fourth-most invaded habitat type (BOTTA-DUKÁT 2008). Plant invasions into forests in Central Europe is a lowland phenomenon und sharply decreases with altitude (CHYTRÝ et al. 2009, BERG et al. 2016). Higher density of the forest canopy and more natural site conditions are negatively correlated with plant invasions (PYŠEK et al. 2003, FLORY & CLAY 2009, BERG et al. 2016), while human impact such as forest fragmentation, intensive management or eutrophication increase the susceptibility of forests to invasions (DAVIS et al. 2000, MARTIN et al. 2009). Disturbances may create gaps in the canopy that offer suitable microsites for the initial establishment of alien tree species. Dispersal limitations may hinder or delay further spread (ESSL et al. 2011a). If local conditions are suitable, alien tree species may establish persistent populations in canopy gaps or otherwise disturbed forests that may result in increased propagule pressure on surrounding forests (LOCKWOOD et al. 2005). Finally, habitat suitability of forests adjacent to the initial points of establishment is decisive for a long-term invasion success (CHYTRÝ et al. 2008). Repeated introduction and recurring disturbances facilitate invasion (KOWARIK 2003).

Similarly to the spread of alien species in other habitats, the invasion of alien trees into Central European forests can be summarized as a multi-stage process (ESSL et al. 2011a, CARBRA-RIVAS et al. 2016, OBIDZINSKI et al. 2016): First, alien trees are introduced mostly via plantations that are established for a range of purposes. Second, disturbances facilitate escape and subsequent establishment of alien trees in forest gaps and at forest margins. Thirdly, the final invasion success of alien trees depends on their ability to invade and survive in temperate forests.

In recent decades, the abundance of alien tree species has increased considerably in lowland forests of Central Europe (e.g., ESSL et al. 2011b, HÖFLE et al. 2014, BERG et al. 2016). Some of these act as transformers by radically changing species composition, structure and ecological functioning (RICHARDSON et al. 2000). For Central European forests, ZERBE (2007) reported 29 naturalized alien woody species. In Austria, the five most wide-spread alien tree species are three neophytes, i.e. alien species introduced after 1500 [*Robinia pseudoacacia* (KLEINBAUER et al. 2010, CIERJACKS et al. 2013), *Acer negundo* (HÖFLE et al. 2014) and *Ailanthus altissima* (KOWARIK & SÄUMEL 2007)], and two archaeophytes (*Castanea sativa* and *Juglans regia*), most probably introduced by the Romans.

It is well-known that young and old trees of the same species may have different preferences for light conditions (ELLENBERG et al. 1991: 13). The ability of young trees to grow under different site conditions than adults (as indicated by the co-occurrence of light-demanding species) indicates the potential to spread beyond the site conditions where adults occur. Vice versa, the co-occurrence of young growth with adult individuals of the same tree species in a relevé indicates the ability to persist and reproduce in temperate forests.

Here, we study the ecological preferences of native and alien tree species in different vegetation layers (herb, shrub, tree) of forest relevés by means of co-occurrence analysis.

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We used a large dataset of Austrian forest relevés that comprises all phytosociological forest classes, and ask the following questions: (1) What are the differences in co-occurrence of native and alien tree species in the herb, shrub layer tree layers in terms of alien tree species' dominance, persistence and plasticity? (2) What are the phytosociological and ecological preferences of alien tree species in temperate forests?

2. Material and Methods

2.1 Relevé data selection

We used the Austrian Vegetation Database (WILLNER et al. 2012), which contains more than 50,000 relevés from a large number of primary sources (e.g., phytosociological literature, master theses, unpublished relevés provided by vegetation ecologists). We filtered for relevés that contained herb, shrub and tree layers. We excluded relevés from outside Austria, and with insufficient layer differentiation. For the analysis, we selected the 34 most abundant tree species including archaeophytes and neophytes, which have more than 100 occurrences in every layer of the relevés (Table 1). For analysis, we excluded rare tree species (i.e. those with an absolute frequency < 100 occurrences of the relevés, or with missing occurrences in at least one layer), and we excluded species of some forest communities that are rare in Austria, like *Fraxinus ornus*, *Ostrya carpinifolia*, *Quercus cerris*, *Pinus cembra*, *Pinus uncinata, Betula pubescens*, *Sorbus aria*, *Sorbus aucuparia* and *Taxus baccata*. Finally, we excluded 828 relevés that did not contain any tree species given in Table 1. The final dataset used for analyses contained 19,413 relevés.

Differing species delineations due to different taxonomic concepts (e.g., different subsp. or s.str) were merged to the species level. The TURBOVEG Austrian Vegetation Database (WILLNER et al. 2012) allowed for distinguishing three tree layers, two shrub layers, one herb layer, and a seedling and juvenile layer. These layers have not been consistently distinguished, so we merged the layer information to one tree, one shrub and one herb layer, respectively.

2.2 Data analyses

We analyzed species co-occurrence using differences in community composition as a measure of differences in ecological preferences of tree species. For each tree species, we calculated the mean cover value in the tree layer of all the relevés with an occurrence of the respective tree species as an estimate for its dominance of the canopy. For each relevé, we calculated (1) mean hemeroby, (2) frequency-weighted means of Ellenberg indicator values for light, nutrients, moisture and temperature for every tree species (ELLENBERG et al.1991), based on mean unweighted indicator values of the single relevés, and (3) mean values for the life form strategies competitors (C), stress tolerators (S) and ruderals (R; GRIME 2001), using the method of HUNT et al. (2004). For hemeroby, we used the classification of KLOTZ & KÜHN (2002) and transformed the data into numeric values in an ordinal scale (see BERG et al. 2016). All calculations were performed with the program JUICE (TICHÝ 2002), using the function for importing external species-specific data.

For analyzing differences in species co-occurrence between vegetation layers, we performed a Detrended Correspondence Analysis (DCA) with 15,989 data plots (relevés with only one or two occurrences of tree species included in Table 1 were omitted) using the software Canoco 4.5 (TER BRAAK & ŠMILAUER 2002). We kept the layer information; therefore, tree species can occur at most three times in the DCA plot.

We used the "species co-occurrence" function in JUICE to calculate the relative occurrence of tree species in the shrub and herb layers of relevés with occurrences of the respective tree species in the tree layer as a measure for natural regeneration (hereafter referred to as "persistence"). For every tree species, we calculated the Euclidian distance in the three-dimensional DCA-space between the species scores in different layers. This distance indicates differences in community composition between occurrences of the tree species in herb, shrub and tree layers. Thus, larger distances in a DCA indicate higher

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species turn over and larger compositional differences between vegetation layers, and are therefore indicative of the ability of young trees to grow under different site conditions than adults (hereafter referred to as "inter-generational ecological plasticity").

Finally, to determine differences in species occurrences between vegetation layers, we calculated the weighted mean of the mean indicator values for light and nutrients of each relevé and for each layer with occurrences of the respective tree species (Fig. 2, 3).

Species nomenclature followed FISCHER et al. (2008), nomenclature of syntaxa MUCINA et al. (2016).

3. Results

3.1 Tree cover values

Mean values in the upper quartile (i.e. mean cover values > 25%) represented the most important tree species in the canopies of Central European forests, i.e. *Fagus sylvatica* (32%), the dominant species in temperate beech forest of the class *Carpino-Fagetea sylvaticae* Jakucs ex Passarge 1968, *Quercus petraea* (30%) in oak-hornbeam forests of the *Quercetea robori-petraeae* Br.-Bl. et Tx. ex Oberd. 1957, and *Quercus pubescens* (25%) in thermophilous forests of the class *Quercetea pubescentis* Doing-Kraft ex Scamoni et Passarge 1959. *Picea abies* (30%) was the most abundant species in the canopy of *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 forests. The azonal phytosociological class *Alnetea glutinosae* Br.-Bl. et Tx. ex Westhoff et al. 1946 was dominated by *Alnus glutinosa* (40%), softwood floodplain forests of the *Salicetea purpureae* Moor 1958 were dominated by *Salix alba* (25%), and hardwood floodplain forests *Alno glutinosae-Populetea albae* P. Fukarek et Fabijanić 1968 by *Alnus incana* (38%). Among alien trees, the two archaeophytes and the neophyte *Acer negundo* had much lower mean cover values (< 15%). In contrast, the neophytes *Ailanthus altissima* (30%) and *Robinia pseudoacacia* (29%) had high mean cover values (*Robinietea* Jurko ex Hadač et Sofron 1980).

3.2 Persistence and inter-generational ecological plasticity

Among native tree species, *Fagus sylvatica, Tilia cordata* and *Acer campestre* were the most persistent tree species with low inter-generational ecological plasticity between occurrences in different vegetation layers (Table 1). Similar, but less pronounced values characterized *Abies alba*, *Carpinus betulus*, *Quercus robur*, *Q. petraea* and *Sorbus torminalis*. In contrast, *Salix alba*, *S. fragilis*, *Populus nigra*, *P. tremula*, *Betula pendula*, *Alnus glutinosa*, *Ulmus glabra*, and the conifers *Larix decidua* and *Pinus sylvestris* were characterized by low persistence and high inter-generational ecological plasticity. These were pioneer species in early stages of forest succession, or species of forests with high rates of natural disturbances (e.g., floodplain forests). The remaining native tree species showed divergent results. While *Acer platanoides*, *A. pseudoplatanus*, *Picea abies*, *Fraxinus excelsior*, *Quercus pubescens, Tilia platyphyllos* and *Prunus padus* had high values for persistence and inter-generational ecological plasticity, *Populus alba* and *Ulmus laevis* showed low values for both parameters. The values of *Alnus incana* were intermediate for both parameters.

Among the neophytes, *Ailanthus altissima,* followed by *Acer negundo,* showed high persistence and moderately high inter-generational ecological plasticity (similar to *Acer platanoides* and *Picea abies*). *Robinia pseudoacacia* resembled mostly *Quercus robur*, with high persistence, and low inter-generational ecological plasticity. Among the archaeophytes, the

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Table 1. Results of the co-occurrence analysis across vegetation layers (herb, shrub, tree) of native and alien tree species in 19,413 relevés of Austrian forest vegetation. Persistence = proportion of tree layer relevés with the same tree species in the shrub and herb layers. Ecological plasticity = Euclidean distance of species' centroids in the herb and shrub layers from those in the tree layer with respect to DCA space of the first three axes. *n* = number of relevés, Cov = mean percentage cover, tree, shrub, herb = tree, shrub and herb layers. Abbr. = species name abbreviations, (A) = archaeophytes, (N) = neophytes. All values are divided into quartiles, grey shaded cells with bold numbers indicate the uppermost quartile, cells with bold numbers the second, cells with normal font the third, and cells with numbers in italics the lowermost quartile.

Table 1. Ergebnisse der Vorkommensanalyse in der Kraut-, Strauch- und Baumschicht von einheimischen und gebietsfremden Baumarten in 19.413 Vegetationsaufnahmen österreichischer Wälder. Persistence = Prozentualer Anteil von Aufnahmen einer Art in der Baumschicht mit der gleichen Art in der Strauch- oder Krautschicht. Ecological plasticity = Euklidischer Abstand der Strauch- und Krautschicht von der Baumschicht der gleichen Art im DCA-Raum der ersten drei Achsen. *n* = Anzahl Aufnahmen, Cov = mittlere prozentuale Deckung, tree l, shrub l, herb l = Baum-, Strauch- und Krautschicht. Abbr. = Abkürzungen der Artennamen, (A) = Archäophyten, (N) = Neophyten. Alle Werte werden in Quartile aufgeteilt, grau schattiert Zellen mit fetten Zahlen geben das oberste Quartil an, Zellen mit fetten Zahlen die zweite, Zellen mit normaler Schrift die dritte und Zellen mit Zahlen in Kursivschrift das unterste Quartil.

						persistence		ecological plasticity	
Name	Abbr.	*n* tree	*n* shrub	*n* herb	Cov tree	with shrub	with herb	shrub	herb
Abies alba	Aalb	3523	1556	2569	12.9	**30.9**	**52.0**	*0.462*	*0.359*
Acer campestre	Acam	736	928	1475	9.2	**49.6**	**71.1**	*0.296*	*0.468*
Acer negundo (N)	Aneg	97	114	98	14.2	**33.0**	**33.0**	**1.077**	0.834
Acer platanoides	Apla	390	329	839	7.9	**30.0**	**54.4**	**0.919**	0.832
Acer pseudoplatanus	Apse	3343	1901	4854	11.3	24.2	**58.1**	**1.317**	**1.881**
Ailanthus altissima (N)	Aalt	85	109	126	29.6	**71.8**	**78.8**	**0.923**	0.644
Alnus glutinosa	Aglu	1366	314	127	39.8	*17.8*	*7.0*	**1.230**	**1.652**
Alnus incana	Ainc	1543	1062	529	37.8	**40.8**	*21.7*	**1.035**	**2.130**
Betula pendula	Bpen	997	467	432	6.7	*17.2*	*11.6*	**0.939**	**1.121**
Carpinus betulus	Cbet	1884	1280	1399	24.4	**43.7**	**44.3**	0.503	0.590
Castanea sativa (A)	Csat	87	65	180	7.7	28.7	**65.5**	0.614	0.704
Fagus sylvatica	Fsyl	5622	3404	3859	31.6	**46.9**	**52.7**	*0.209*	*0.344*
Fraxinus excelsior	Fexc	3206	2147	4018	21.2	**36.2**	**56.8**	*0.472*	**1.115**
Juglans regia (A)	Jreg	177	242	323	12.0	24.3	26	**1.190**	**1.618**
Larix decidua	Ldec	3418	824	711	8.9	*14.7*	*11.8*	**0.954**	0.594
Picea abies	Pabi	9705	5838	5292	30.1	**45.1**	**44.1**	**1.490**	*0.481*
Pinus sylvestris	Psyl	3011	601	587	21.7	*15.2*	*14.5*	**1.147**	*0.249*
Populus alba	Palb	250	60	91	22.3	*14.0*	*21.2*	*0.361*	*0.232*
Populus nigra	Pnig	292	68	32	8.4	*4.1*	*2.7*	**2.672**	0.687
Populus tremula	Ptre	229	195	256	6.7	*18.8*	24.0	**1.133**	**1.019**
Prunus padus	Ppad	517	1365	662	7.8	**51.6**	29.4	**1.440**	**1.170**
Quercus petraea	Qpet	1692	576	1275	30.3	28.1	**53.2**	*0.154*	*0.494*
Quercus pubescens	Qpub	348	151	245	25.1	**31.3**	**43.7**	0.605	**1.061**
Quercus robur	Qrob	1307	517	1311	18.2	*13.8*	**35.1**	0.617	0.564
Robinia pseudacacia (N)	Ppse	388	223	211	28.9	**37.4**	**33.8**	0.571	0.676
Salix alba	Salb	537	182	20	25.0	*4.5*	*1.1*	**1.882**	**2.921**

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						persistence		ecological plasticity	
Name	Abbr.	*n* tree	*n* shrub	*n* herb	Cov tree	with shrub	with herb	shrub	herb
Salix fragilis	Sfra	284	101	15	19.2	*8.8*	*2.8*	**1.427**	**2.574**
Sorbus torminalis	Stor	199	278	446	3.8	**31.2**	**38.2**	*0.159*	*0.134*
Tilia cordata	Tcor	933	709	551	14.0	**51.7**	**35.7**	0.563	0.618
Tilia platyphyllos	Tpla	456	322	354	16.0	**43.6**	**34.4**	0.695	**1.427**
Ulmus glabra	Ugla	1111	674	891	8.5	27.4	**32.9**	**1.315**	**1.701**
Ulmus laevis	Ulae	215	125	94	9.2	25.1	27.9	*0.184*	*0.347*

values of *Castanea sativa* were similar to the native *Acer pseudoplatanus*, with persistence and inter-generational ecological plasticity being moderately high. *Juglans regia* resembled *Ulmus glabra* with moderate persistence and high inter-generational ecological plasticity.

3.3 Results of Detrended Correspondence Analysis

The first axis of the DCA (Fig. 1) explained 21.8% of the variance of species-environment relationship and was most strongly influenced by the variables of human impact (hemeroby), climate (Ellenberg indicator values for temperature and altitude), and the proportion of stress-tolerant species. Accordingly, tree species that are characteristic for spruce, larch and beech forests of higher altitudes were found on the right side of the DCA plot, while tree species typical for warm lowland forests (e.g., *Tilia cordata*, *Carpinus betulus*, *Quercus robur*, *Acer platanoides*) were located on the left side, and *Fagus sylvatica* showed intermediate behavior. Tree species that are indicative for disturbances, like *Betula pendula* and *Populus tremula,* were also found there, as well as *Castanea sativa*. On the left side of the first axis, and closely associated with high hemeroby, were *Salix fragilis*, *S. alba* and *Populus nigra*, species of softwood floodplain forests (Salicetea purpureae). *Acer negundo* was closely associated with high indicator values for temperature and hemeroby, and its optimum was most similar with native trees of hardwood floodplain forests (e.g., *Ulmus laevis, Populus alba*). *Vaccinio-Piceetea*, with the orders *Pinetalia sylvestris* Oberd. 1957 (associated with low moisture) and *Piceetalia excelsae* Pawłowski et al. 1928 (associated with high altitude), showed the lowest indicator values for hemeroby and the highest proportion of stress tolerators.

The second DCA axis explained 15.1% of the variance of species-environment relation and was closely associated with mean Ellenberg indicator values for moisture and light, and with the proportion of species with ruderal life form strategy. The wettest sites were covered by swamp forests of the Alnetea glutinosae, whereas the thermophilous oak forests of the class Quercetea pubescentis were associated with dry sites and high Ellenberg light indicator values. The five alien study species showed a preference for high mean Ellenberg values of light and for a high proportion of species with ruderal life form strategies.

The DCA showed that *Ailanthus altissima* and *Robinia pseudoacacia*, the two alien tree species with highest mean cover values in the tree layer (Table 1), were closely associated with mean Ellenberg indicator values for temperature. Both species were most common in lowlands as observed for Quercetea pubescentis communities, but on more humid sites, and with a substantially higher rate of disturbance, outside the ecological spectrum of native Central European temperate forests.

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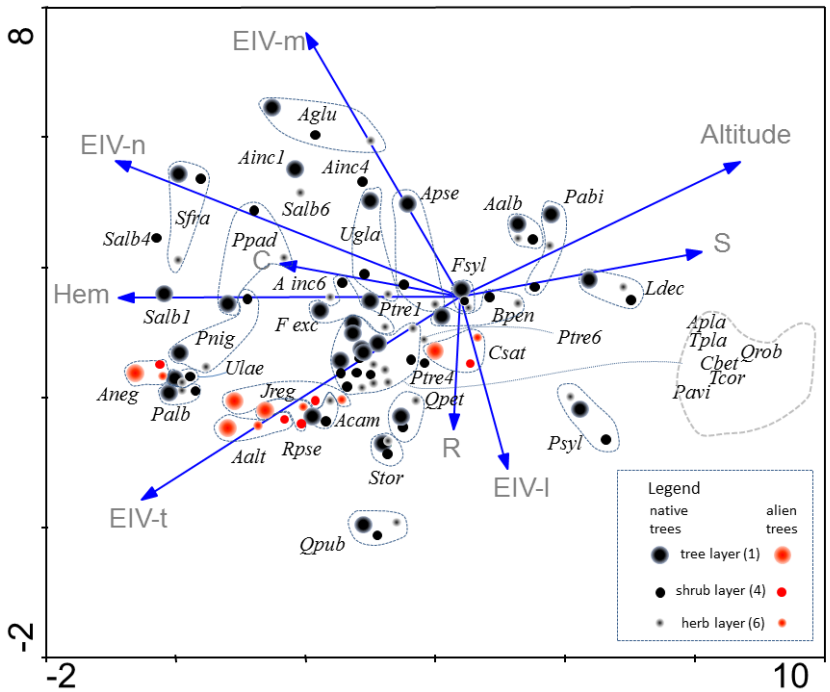

Fig. 1. The first two axes of a Detrended Correspondence Analysis (DCA) with tree species occurrences and environmental variables of Austrian forest relevès (*n* = 15,989). Lengths of gradient of first axis 8.1, sum of all eigenvalues 42.6. Hem = Hemeroby; EIV = mean Ellenberg's indicator values for moisture (m), nutrients (n), temperature (t) and light (l); C, S, R = strategy types (GRIME 2001); only tree species of Table 1 are shown. 1 = tree layer; 4 = shrub layer, 6 = herb layer. For abbreviations of tree species, see Table 1.

Abb. 1. Die ersten beiden Achsen einer Detrended Correspondence Analysis (DCA) mit Baumarten und Umweltvariablen der österreichischen Waldaufnahmen (*n* = 15.989). Länge des Gradienten der ersten Achse 8.1, Summe aller Eigenwerte 42.6. Hem = Hemeroby; EIV = mittlere Ellenberg-Indikatorwerte für Feuchtigkeit (m), Nährstoffe (n), Temperatur (t) und Licht (l); C, S, R = Strategie-Typen (GRIME 2001). Es werden nur die Baumarten der Tabelle 1 gezeigt; 1 = Baumschicht; 4 = Strauchschicht, 6 = Krautschicht; Abkürzung der Artnamen nach Tabelle 1.

3.4 Mean Ellenberg indicator values of relevés

Two mean indicator value plots were particularly relevant. The first plot shows the occurrences of the tree species in different vegetation layers in relationship to mean hemeroby and the Ellenberg indicator values for moisture (Fig. 2).

The three neophyte tree species were most common in relevés with a mean hemeroby value > 2.05. Among native trees, only the softwood species *Salix alba* showed a preference for similarly high mean hemeroby values, and the younger stages of *S. fragilis*, *Populus alba* and *P. nigra* as well. The archaeophyte *Juglans regia* was also correlated with high mean hemeroby in the tree and shrub layers, but this was less the case for occurrences in the herb layer. Tree species of hardwood floodplain forests showed intermediate values of mean hemeroby, followed by tree species of oak-hornbeam forests. The lowest mean hemeroby values revealed *Fagus sylvatica*, *Picea abies*, *Abies alba*, *Larix decidua*, *Pinus sylvestris*,

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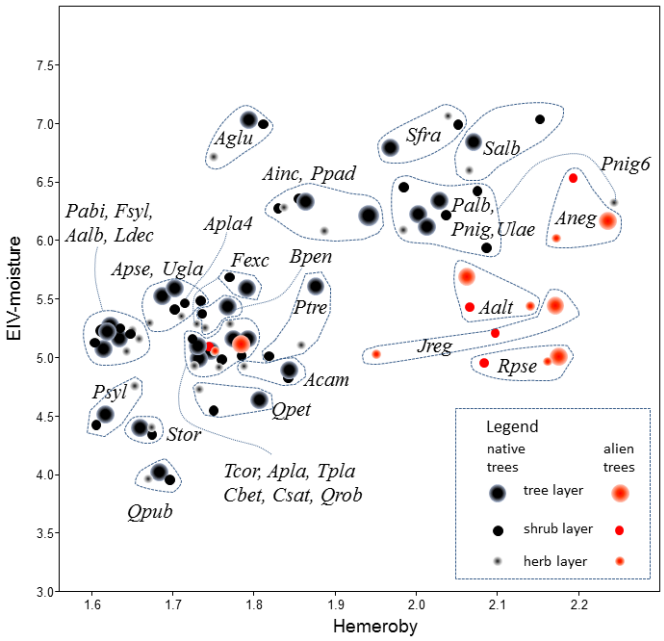

Fig. 2. The occurrences of tree species in different vegetation layers (herb, shrub, tree) in relationship to mean hemeroby and Ellenberg indicator values for moisture of 19,413 relevés from Austrian forests. For abbreviations of tree species, see Table 1.

Abb. 2. Das Vorkommen von Baumarten in der Kraut-, Strauch- und Baumschicht im Verhältnis von Kultureinfluss (hemeroby) und Ellenbergs Zeigerwerten für Feuchtigkeit (EIV-moisture) von 19.413 Aufnahmen österreichischer Wälder. Abkürzungen der Artnamen siehe Tabelle 1.

Sorbus torminalis and *Quercus pubescens*. The mean Ellenberg indicator values for moisture of *Robinia pseudoacacia* and *Ailanthus altissima* were similar to native trees of zonal Central European deciduous forests (e.g., *Fagus sylvatica*, *Fraxinus excelsior*, *Quercus robur*), while *Acer negundo* was more moisture demanding, similar to *Prunus padus*, *Ulmus laevis* and *Populus* spp.

In relation to mean Ellenberg indicator values for light and nutrients (Fig. 3), four of the alien tree species (*Acer negundo*, *Ailanthus altissima*, *Juglans regia*, *Robinia pseudoacacia*) showed a clear preference for sites characterized by species that are more light-demanding and prefer nutrient-rich sites. The number of native tree species that co-occurred with light demanding species is rather low in the Central European flora. *Pinus sylvestris*, *Quercus pubescens* and again younger stages of the softwood floodplain species *Salix alba*, *S. fragilis*, *Populus alba* and *P. nigra* are the most conspicuous in this regard. The mean light indicator values of these alien trees were similar to the indicator values of *Betula pendula*, *Larix decidua*, *Alnus incana* and *Populus tremula*. The archaeophyte *Castanea sativa* occurred in relevés with intermediate mean Ellenberg indicator value for light. *Fagus sylvatica* was found in communities with the lowest light indicator value, together with *Acer platanoides*, *Acer pseudoplatanus* and *Ulmus glabra*.

The mean nutrient Ellenberg indicator values in relevés with neophytic trees and *Juglans regia* were among the highest of the Austrian forest vegetation (> 6.0). In contrast, relevés with *Castanea sativa* had low mean nutrient indicator values (< 5.0).

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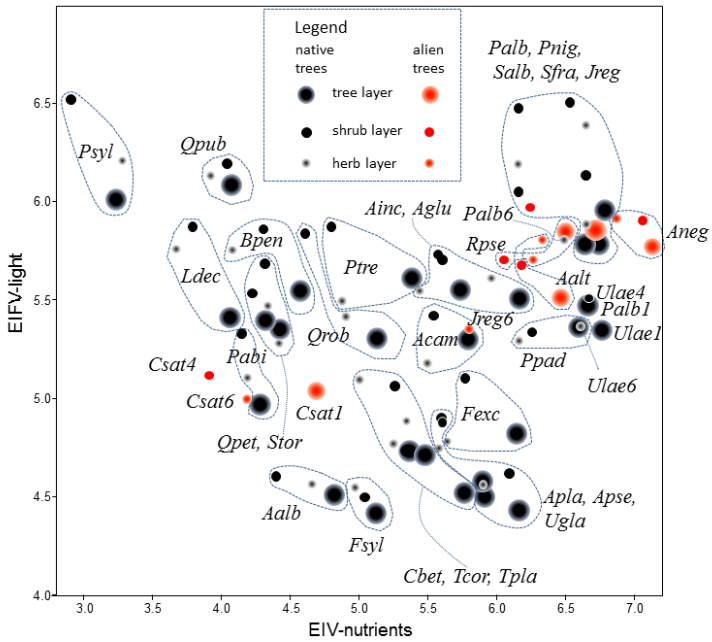

Fig. 3. The occurrences of tree species in different vegetation layers (herb, shrub, tree) in relationship to mean Ellenberg indicator values for light and nutrients of 19,413 relevés of Austrian forests. For abbreviations of tree species see Table 1.

Abb. 3. Das Vorkommen von Baumarten in der Kraut-, Strauch- und Baumschicht im Verhältnis von Ellenbergs Zeigerwerten für Licht (EIV-light) und Nährstoffe (EIV-nutrients) von 19.413 Aufnahmen aus österreichischen Wäldern. Abkürzungen der Artnamen siehe Tabelle 1.

4. Discussion

4.1 The ecological preferences of tree species

The mean cover value in the tree layer of relevés is as a metric that assesses the ability of tree species to dominate the canopy of forest types in Austria (Table 1). Of the five alien tree species considered here, *Ailanthus altissima* and *Robinia pseudoacacia* had the highest mean tree layer cover values, similar to some dominant native species. However, the high level of hemeroby separates these types from other forests. Stands dominated by the two alien tree species mostly result from the succession of open habitats (e.g., abandoned fields, fallow grasslands, ruderal habitats, scrub; SÎRBU & OPREA 2011). Also in their native ranges, both species prefer disturbed sites with open canopy (ALBRIGHT et al. 2009), and often occur in early forest successional stages (BORING & SWANK 1984, CALL & NILSEN 2005). The most similar species in the DCA (Fig. 1), *Acer campestre* and *Juglans regia,* were characteristic for agricultural landscapes close to human settlements (BERG et al. 2016). The persistence of *A. altissima* and *R. pseudoacacia* across vegetation layers was high (Table 1). Persistence of both species is strongly supported by clonal reproduction via root-suckers (KOWARIK 1995), a trait that is rare in the native tree flora. In addition, inter-generational ecological plasticity is also high for both aliens, in particular for *A. altissima*, facilitating the spread by sexual reproduction into sites that differ from those with occurrences of adult trees.

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Mean weighted Ellenberg relevé light indicator values indicate that *A. altissima* is a light-demanding species similar to *Populus tremula* (Fig. 3; CALL & NILSEN 2005). Thus, forest gaps are essential for forest colonization by this species (KNAPP & CANHAM 2000). MARTIN et al. (2010) found that the ability of seedlings to survive under low-light conditions is crucial for invasion into natural forests. Currently, *A. altissima* is absent in dense, shaded forests in Austria, but under the warmer climate of the southern Alps, it also invades dense forest stands (KNÜSEL et al. 2017). *Ailanthus altissima* has the closest affinity to mean Ellenberg temperature indicator value of all trees studied here (Fig. 1). Further spread will therefore be promoted by global warming (STEVENS et al. 2015), that may lead to increased drought stress and more open canopies of many forests types (KNÜSEL et al. 2015).

The low inter-generational ecological plasticity of *Robinia pseudoacacia* resembles that of native trees of zonal lowland climax forests (e.g., *Fraxinus excelsior*, *Carpinus betulus*, *Quercus robur*). This likely is an indication that *R. pseudoacacia* rarely reproduces via seeds, but mostly clonal growth. VÍTKOVÁ et al. (2017) argue that in case that forest management would be reduced, *R. pseudoacacia* abundance should decrease because of competitive exclusion by shade-tolerant species. However, climate change will facilitate further spread of the species in Central Europe (KLEINBAUER et al. 2010).

The other three alien species studied here have lower cover values of the tree layer, i.e. they do not perform as a co-dominant species in the canopy of Austrian forests. Thus, their ability to transform natural forests into alien-dominated stands is rather low. *Acer negundo* is most closely adapted to floodplain forest of the alien tree species considered here, and its ecological preferences are, thus, similar to native floodplain species, i.e. *Populus alba*, *P. nigra* and *Ulmus laevis*. BERG et al. (2016) showed that the spread of *A. negundo* into floodplain forests did replace native tree species, but led to more closed canopies of floodplain forests during the past decades. A study from the Danube floodplains in eastern Austria showed that the proportion of alien trees like *A. negundo* decreases with stand age and absence of forest management (HÖFLE et al. 2014). The presence of a closed canopy of native tree species hinders the invasion of *A. negundo* (SACCONE et al. 2013). This species prefers intermediate conditions within floodplain forests (SCHNITZLER et al. 2007), and thus moderate floods are beneficial for its spread and establishment (DEWINE & COOPER 2007), while it does not tolerate prolonged flooding (FRIEDMAN & AUBLE 1999), and highly dynamic and wet conditions of softwood floodplain forests with *Salix alba* (see Fig. 2).

Juglans regia shows a preference for high levels of anthropogenic disturbance, as indicated by high mean hemeroby values of the relevés (Fig. 2). Persistence is low, while inter-generational ecological plasticity is high. *Juglans regia* prefers early stages of forest succession (LENDA et al. 2012). The remarkable spread of *J. regia* in the past decades throughout Europe was facilitated by the increase of rook (*Corvus frugilegus*) that act as seed disperser, by land abandonment (LENDA et al. 2012), and climate warming (LOACKER et al. 2007).

Castanaea sativa is the only alien tree species studied here that has spread into beech and oak-hornbeam forests, where it shows high persistence and moderate inter-generational ecological plasticity. Its Ellenberg moisture, light and hemeroby values are similar to native tree species of oak-hornbeam forests, while its nutrient preference is the lowest of the alien tree species considered here.

In general, mean hemeroby values of the herb and shrub layers of relevés with alien tree species are lower compared to those of the tree layer. This may indicate a preferential spread into sites with lower mean hemeroby, or that mean hemeroby of invaded relevés increases with time spread of the tree species into the forest stand (e.g., STASKA et al. 2014).

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4.2 Differences in invasibility of different forest types

Floodplain forests are known to be vulnerable to the invasion of alien species (e.g., RICHARDSON et al. 2007, SCHNITZLER et al. 2007, VILÀ et al. 2007, CHYTRÝ et al. 2009). It is assumed that intermediate disturbance rates from flooding, high nutrient input and human reduction of river dynamics (e.g., river channelization, hydropower use) facilitate alien species invasion. In Austria, one of the studied species (*Acer negundo*) is widely naturalized in floodplain forests (HÖFLE et al. 2014), while the other alien trees are restricted to the driest (or drained or regulated) parts of floodplains. Non-floodplain forest types are less affected by invasions of alien trees (CHYTRÝ et al. 2009). The archaeophyte *Castanea sativa* is restricted to lowland and submontane forests, and occurs in moderate densities, without substantial impact on community composition. The transformer species *Ailanthus altissima* and *Robinia pseudoacacia* form distinct forest types related to hardwood floodplain, oak-hornbeam and thermophilous oak forests, characterized by considerable human disturbance. Far away from the ecological preferences of the studied alien trees, and thus rarely invaded, are montane beech forests, coniferous mountain forests and forests at extremely dry sites as well as swamp and bog forests dominated by willows and ash.

4.3 Relevance of persistence and inter-generational plasticity for understanding tree invasions in forests

The indicator for persistence characterizes the ability of tree species to reproduce under closed canopies of the same species. Softwood floodplain species have very low persistence values because the high light-requirements for young growth are not met under the canopy of adult conspecifics and because their habitats are rapidly changing, while species of beech forests show highest persistence. Generally, persistence values calculated for the shrub or herb layers are similar, with only few exceptions. In particular, for tree species that do not form a soil seed bank, seedlings in the herb layer often show higher persistence values compared to the shrub layer (e.g., *Castanea sativa*, *Acer pseudoplatanus*, *Quercus petraea*, *Q. robur*). Seedlings of wetland species like *Alnus incana* or *Prunus padus,* or pioneer tree species as *Salix* spp. or *Populus* spp., grow fast and thus stay only for a short time period in the herb layer. For such species, relevés with occurrences in the herb layer are rare while in the shrub layer they occur more frequently.

Inter-generational ecological plasticity describes the ability of species to establish in sites, and, thus plant communities that differ from sites already invaded by adult trees. Differences in ecological preferences may be substantial between young growth and adult trees of the same species (e.g., in light requirements). This parameter captures an important aspect for invasion success of alien trees in forests.

Mean cover in the tree layer, persistence, inter-generational plasticity and mean Ellenberg indicator values of relevés in combination provide interesting insights in the invasion process of alien trees. 'Mean cover in the tree layer' is an indicator for behaving as transformer (RICHARDSON et al. 2000), 'persistence' indicates the ability to reproduce within forest stands once a site is invaded, while 'inter-generational ecological plasticity' describes the ability to colonize new ecologically different habitats. Finally, mean indicator values of relevés across vegetation layers provide insights into the ecological preferences of tree species, how these change between different vegetation layers. Additionally, they allow to identify which native tree species are most similar in this respect. We conclude that relevé-based metrics of tree species behavior are able to deliver new insights into the spatio-temporal

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dynamics of biological invasions in forests. Future work should expand this approach (e.g., by considering the role of life history traits and measured environmental conditions), and by identifying the limitations of these metrics.

Erweiterte deutsche Zusammenfassung

Einleitung – In Mitteleuropa gelten die zonalen Waldgesellschaften als relativ resistent gegen Invasionen durch fremdländische Baumarten. In der vorliegenden Arbeit werden das ökologische Verhalten der in Österreich am weitesten verbreiteten baumförmigen Neophyten (*Robinia pseudacacia*, *Acer negundo*, *Ailanthus altissima*) sowie der Archäophyten *Castanea sativa* und *Juglans regia* untersucht. Ziel der Arbeit war es, an Hand der Artenzusammensetzung der Vorkommen in der Kraut-, Strauch- und Baum-Schicht herauszufinden, in wie weit die betreffenden Arten bereits erfolgreich in vorhandene natürliche Waldgesellschaften eingedrungen sind.

Material und Methoden – Aus der österreichischen Vegetationsdatenbank (WILLNER et al. 2012) wurden 19.413 Vegetationsaufnahmen mit den 34 häufig vorkommenden Baumarten (> 100 Vorkommen in einer der drei Vegetationsschichten, siehe Tab. 1) selektiert, die eine Baumschicht aufwiesen.

Für die Analyse wurde eine unterschiedliche Artzusammensetzung (co-occurence) in den verschiedenen Vegetationsschichten als Indikator für unterschiedliche ökologische Schwerpunkte der Artvorkommen in den einzelnen Schichten verwendet. Für die Berechnungen wurden die Dominanz (mittlere Deckungswerte für die einzelnen Arten in der Baumschicht), eine Detrended Correspondence Analysis (DCA), mittlere Zeigerwerte der Einzelaufnahmen nach Ellenberg für die Größen Licht, Nährstoff, Feuchte und Temperatur sowie mittlere Hemerobiestufen der Einzelaufnahmen unter Verwendung von KLOTZ & KÜHN (2002), deren Angaben in eine Ordinalskala überführt wurden, herangezogen. Für die Beurteilung der Art des Eindringens in vorhandene Waldbestände nutzten wir das Konzept von GRIME (2001) mit den Grundtypen C-, S- und R-Strategie. Als Maß, inwieweit eine Baumart ihren einmal eroberten Standort behauptet (wir nennen es hier "Persistenz"), haben wir den Anteil jener Aufnahmen berechnet, in denen die Art in der Kraut- oder Strauchschicht zusammen mit Exemplaren der eigenen Art in der Baumschicht vorkommt. Als Maß, inwieweit eine Art als Sämling oder Jungpflanze sich in neuen Lebensräumen etablieren kann (wie nennen es hier "ökologische Plastizität"), haben wir den Abstand zwischen den Zentroiden der Arten in einzelnen Schichten innerhalb des dreidimensionalen DCA-Raumes verwendet.

Ökologische Preferenzen einzelner Arten stellen wir in Zeigerwert-Diagrammen, separat für die einzelnen Vegetationsschichten, dar. Für alle Berechnungen wurde das Programmpaket JUICE (TICHÝ 2002) verwendet, für die Detrended Correspondence Analysis das Programmpaket Canoco 4.5 (TER BRAAK & ŠMILAUER 2002). Die Nomenklatur der Arten folgt FISCHER et al. (2008), die für Syntaxa MUCINA et al. (2016).

Ergebnisse – Die mittleren Deckungswerte (Tab. 1) als Maß für die Dominanz einzelner Arten zeigten, dass nur die beiden Neophyten *Ailanthus altissima* und *Robinia pseudoacacia* hohe Deckungswerte über 25 % aufweisen, was zur Beschreibung eigener Waldgesellschaften innerhalb einer eigenen Klasse *Robinietea* geführt hat. *Acer negundo* und die beiden Archäophyten erreichten hingegen nur Werte unter 15 %. *Ailanthus altissima* wiesen den höchsten Persistenz-Wert unter allen untersuchten Baumarten auf, vergleichbar mit Buche oder Fichte. Auch die ökologische Plastizität war eher hoch. In der Performance ähnlich, wenn auch mit geringeren Werten, verhielt sich *Acer negundo*. *Robinia pseudoacacia* war am ehesten mit den Eigenschaften der heimischen Stiel-Eiche vergleichbar. Die Werte von *Castanea sativa* waren denen des Berg-Ahorn ähnlich mit eher hohen Werten für Persistenz und ökologische Plastizität, die von *Juglans regia* denen der Berg-Ulme mit mittleren Persistenzwerten und hoher ökologischer Plastizität.

Die DCA (Abb. 1) zeigt mit der ersten Achse, dass der anthropogene Einfluss den wichtigsten Faktor darstellt. Weitere Faktoren, die gut mit der ersten Achse korrelierten, waren (positiv) Temperatur sowie (negativ) Meereshöhe und der Anteil der Stress-Strategen. Die zweite Achse war mit den Zei-

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gerwerten Feuchte und Licht, sowie mit dem Anteil an Ruderal-Strategen korreliert. Trägt man die mittleren Zeigerwerte für Feuchte gegen den Hemerobiegrad der einzelnen Arten in ein Diagram ein (Abb. 2), so zeigten die drei Neophyten *Acer negundo, Ailanthus altissima* und *Robinia pseudoacacia* sowie *Juglans regia* hohe Hemerobiewerte > 2,0, vergleichbar nur mit den störungstoleranten Bäumen der Weichholzaue, während sich *Castanea sativa* näher bei den Laubmischwaldarten *Tilia cordata, T. platyphyllos, Acer platanoides, Carpinus betulus* und *Quercus robur* positionierte. Auch Unterschiede zwischen den Vorkommen von Arten in verschiedenen Schichten traten hervor: deutlich unterschiedlich etwa bei den störungstoleranten Arten *Acer negundo, Salix alba* und *Juglans regia*, kaum unterschiedlich bei Arten der (extra-)zonalen Schlusswaldgesellschaften wie *Fagus sylvatica, Quercus pubescens, Abies alba* oder *Picea abies*.

Das Diagram der mittleren Zeigerwerte für Licht gegen Nährstoffe (Abb. 3) zeigt deutlich, dass – abgesehen von *Castanea sativa* – alle fremdländischen Baumarten relativ häufig mit lichtliebenden Arten vorkamen, vergleichbar mit *Betula pendula, Larix decidua, Alnus incana* und *Populus tremula* als Vertretern der mitteleuropäischen Gehölzflora. Nur Jugendstadien von Weichhölzern aus Flussauen (Baumweiden und Pappeln), *Pinus sylvestris* und *Quercus pubescens* wuchsen zusammen mit noch höheren Anteilen von Lichtzeigern. Wiederum mit Ausnahme von *Castanea sativa* kamen alle gebietsfremden Baumarten in stark von Nährstoffzeigern dominierten Gesellschaften vor.

Diskussion – Die mittleren Deckungswerte der Baumschicht als Maß der Häufigkeit der dominanten Baumarten in den Waldgesellschaften Mitteleuropas spiegeln sich gut in der pflanzensoziologischen Klassifikation. Nur die Neophyten *Ailanthus altissima* und *Robinia pseudoacacia* zeigen ähnlich hohe mittlere Deckungswerte wie dominante Arten heimischer Waldgesellschaften, sind aber durch hohe Hemerobiewerte deutlich von diesen separiert. Klonales Wachstum (Wurzelschösslinge) von *Ailanthus altissima* und *Robinia pseudoacacia* schlagen sich in hohen Persistenzwerten nieder, bei *Ailanthus* sorgt die weite ökologische Amplitude für hohe Werte der ökologischen Plastizität. Alle anderen fremdländischen Arten weisen niedrigere mittlere Deckungswerte auf und sind zurzeit nicht in der Lage, Waldbestände in Neophyten- bzw. Archäophytenbestände umzuwandeln. *Acer negundo*, in seinen ökologischen Anprüchen ähnlich den Auenarten *Populus alba, P. nigra, Ulmus laevis*, kann zwar in Auwaldbestände erfolgreich einwandern, bevorzugt aber wie die anderen beiden Neophyten, und auch *Juglans regia,* anthropogen gestörte Standorte. *Castanea sativa* ist die einzige der untersuchten Arten, die in temperate Buchenbestände einwandern konnte, was auf die ähnlichen ökologischen Ansprüche wie die Baumarten der Buchen- und Eichen-Hainbuchen-Wälder zurückzuführen ist. Ihre Nährstoffansprüche sind ähnlich gering wie die von *Betula pendula* und *Populus tremula*.

Die hohen Lichtansprüche der untersuchten gebietsfremden Arten, mit Ausnahme von *Castanea sativa*, führen dazu, dass Bestandslücken oder Waldränder benötigt werden, um sich in Waldnähe ansiedeln zu können (KNAPP & CANHAM 2000). Die Auswertung der Temperaturzeigerwerte zeigt, dass alle vier Arten vom Klimawandel begünstigt werden.

Die Gefährdung heimischer Waldgesellschaften durch Invasion ist unterschiedlich ausgeprägt. Auenwälder sind wegen ihrer standortsbedingten Dynamik besonders empfindlich gegenüber invasiven Arten. Hier kann *Acer negundo* als voll etabliert gelten, bevorzugt aber entwässerte, anthropogen überformte Standorte und fehlt insbesondere in den hoch-dynamischen, natürlichen Weichholzauen der *Salicetea purpureae*. Außerhalb der Auwälder konnte sich bisher nur *Castanea sativa* in temperaten Laubwäldern Mitteleuropas etablieren, während *Ailanthus altissima, Robinia pseudoacacia* und *Juglans regia* bisher eher in eigenen Beständen außerhalb des ökologischen Spektrums des mitteleuropäischen Waldes vorkommen. Weit weg von den ökologischen Präferenzen der gebietsfremden Bäume, und somit kaum betroffen von deren Invasion, sind montane Buchenwälder, Gebirgsnadelwälder, Wälder an extrem trockenen Standorten sowie nasse Weiden- und Erlenwälder.

Die Kombination der Daten von Dominanz, Persistenz, ökologischer Plastizität und ökologischen Anprüchen liefern gute Einblicke in das Verhalten und die Strategie der fremdländischen Arten. Die mittlere Deckung in der Baumschicht ist ein Indikator für das Verhalten als Ökosystem-Umwandler („transformer", RICHARDSON et al. 2000). Persistenz zeigt die Fähigkeit, einen Wuchsort zu behaupten, während die ökologische Plastizität die Fähigkeit beschreibt, verschiedene Lebensräume zu kolonisieren. Schließlich liefern Analysen mittlerer Zeigerwerte Einblicke in die ökologischen Präferenzen von

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Baumarten in verschiedenen Schichten, und erlauben den Vergleich mit heimischen Baumarten und bekannten Pflanzengesellschaften. Wir schließen daraus, dass eine Analyse von Vegetationsaufnahmen aus vegetationskundlichen Datenbanken in der Lage ist, neue Einblicke in die räumlich-zeitliche Dynamik biologischer Invasionen in Wäldern zu liefern. Der Ansatz kann beispielsweise unter Berücksichtigung von funktionell-ökologischen Parametern oder von Standort-Messungen weiterentwickelt werden.

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References

ALBRIGHT, T.P., CHEN, H., CHEN, L. & GUO, Q. (2009): The ecological niche and reciprocal prediction of the disjunct distribution of an invasive species: the example of *Ailanthus altissima*. – Biol. Invasions 12: 2413–2427.

BERG, C., DRESCHER, A., WAGNER, V. & ESSL, F. (2016): Temporal trends in the invasions of Austrian woodlands by alien trees. – Preslia 88: 185–200.

BORING, L. & SWANK, W. (1984): The role of black locust (*Robinia pseudo-acacia*) in forest succession. – J. Ecol. 72: 749–766.

BOTTA-DUKÁT, Z. (2008): Invasion of alien species to Hungarian (semi-)natural habitats. – Acta Bot. Hung. 50: 219–227.

CABRA-RIVAS, I., SALDAÑA, A., CASTRO-DÍEZ, P. & GALLIEN, L. (2016): A multi-scale approach to identify invasion drivers and invaders' future dynamics. – Biol. Invasions 18: 411–426.

CALL, L.J. & NILSEN, E.T. (2005): Analysis of interactions between the invasive tree-of-heaven (*Ailanthus altissima*) and the native black locust (*Robinia pseudoacacia*). – Plant Ecol. 176: 275–285.

CHYTRÝ, M., JAROŠÍK, V., PYŠEK, P., HÁJEK, O., KNOLLOVÁ, I., TICHÝ, L. & DANIHELKA, J. (2008): Separating habitat invasibility by alien plants from the actual level of invasion. – Ecology 89: 1541–1553.

CHYTRÝ, M., PYŠEK, P., WILD, J., PINO, J., MASKELL, L.C. & VILÀ, M. (2009): European map of alien plant invasions based on the quantitative assessment across habitats. – Divers. Distrib. 15: 98–107.

CIERJACKS, A., KOWARIK, I., JOSHI, J., HEMPEL, S., RISTOW, M., VON DER LIPPE, M. & WEBER, E. (2013): Biological flora of the British Isles: *Robinia pseudoacacia*. – J. Ecol. 101: 1623–1640.

DAVIS, M.A., GRIME, J.P. & THOMPSON, K. (2000): Fluctuating resources in plant communities: a general theory of invasibility. – J. Ecol. 88: 528–534.

DEWINE, J.M. & COOPER, D.J. (2007): Effects of river regulation on riparian box elder (*Acer negundo*) forests in Canyons of the upper Colorado River Basin, USA. – Wetlands 27: 278–289.

ELLENBERG, H., WEBER, H.E., DÜLL, R., WIRTH, V., WERNER, W. & PAULIßEN, D. (1991): Zeigerwerte von Pflanzen in Mitteleuropa. 2. Aufl. – Scr. Geobot. 18: 1–258.

ESSL, F., MANG, T. & MOSER, D. (2011a): Ancient and recent alien species in temperate forests: steady state and time lags. – Biol. Invasions 14: 1331–1342.

ESSL, F., MILASOWSZKY, N. & DIRNBÖCK, T. (2011b): Plant invasions in temperate forests: Resistance or ephemeral phenomenon? – Basic Appl. Ecol. 12: 1–9.

FISCHER, M.A., ADLER, W. & OSWALD, K. (2008): Exkursionsflora für Österreich, Liechtenstein und Südtirol. 3. Aufl. – Land Oberösterreich, Biologiezentrum der OÖ Landesmuseen, Linz: 1392 pp.

FLORY, S.L. & CLAY, K. (2009): Effects of roads and forest successional age on experimental plant invasions. – Biol. Conserv. 142: 2531–2537.

FRIEDMAN, J.M. & AUBLE, G.T. (1999): Mortality of riparian box elder from sediment mobilization and extended inundation. – Regulated Rivers: Res. Manag. 15: 463–476.

GRIME J.P. (2001): Plant strategies, vegetation processes and ecosystem properties. 2nd ed. – Wiley & Sons, Chischester: 456 pp.

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HÖFLE, R., DULLINGER, S. & ESSL, F. (2014): Different factors affect the local distribution, persistence and spread of alien tree species in floodplain forests. – Basic Appl. Ecol. 15: 426–434.

HUNT, R., HODGSON, J., THOMPSON, K., BUNGERER, P., DUNNETT, N. & ASKEW, A. (2004): A new practical tool for deriving a functional signature for herbaceous vegetation. – Appl. Veg. Sci. 7: 163–170.

KLEINBAUER, I., DULLINGER, S., PETERSEIL, J. & ESSL, F. (2010): Climate change might drive the invasive tree *Robinia pseudacacia* into nature reserves and endangered habitats. – Biol. Conserv. 143: 382–390.

KLOTZ, S. & KÜHN, I. (2002): Indikatoren des anthropogenen Einflusses auf die Vegetation. – Schriftenr. Vegetationskd. 38: 241–246.

KNAPP, L. & CANHAM, C. (2000): Invasion of an old-growth forest in New York by *Ailanthus altissima*: sapling growth and recruitment in canopy gaps. – J. Torrey Bot. Soc. 127: 307–315.

KNÜSEL, S., CONEDERA, M., RIGLING, A., FONTI, P. & WUNDER, J. (2015): A tree-ring perspective on the invasion of *Ailanthus altissima* in protection forests. – For. Ecol. Manag. 354: 334–343.

KNÜSEL, S., DE BONI, A., CONEDERA, M., SCHLEPPI, P., THORMANN, J.J., FREHNER, M. & WUNDER, J. (2017): Shade tolerance of *Ailanthus altissima* revisited: novel insights from southern Switzerland. – Biol. Invasions 19: 455–461.

KOWARIK, I. (1995): Clonal growth in *Ailanthus altissima* on a natural site in West Virginia. – J. Veg. Sci. 6: 853–856.

KOWARIK, I. (2003): Human agency in biological invasions: Secondary releases foster naturalisation and population expansion of alien plant species. – Biol. Invasions 5: 281–300.

KOWARIK, I. & SÄUMEL, I. (2007): Biological flora of Central Europe: *Ailanthus altissima* (Mill.) Swingle. – Perspect. Plant Ecol., Evol. Syst. 8: 207–237.

LENDA, M., SKÓRKA, P., KNOPS, J., MORON, D., TWOREK, S. & WOYCIECHOWSKI, M. (2012): Plant establishment and invasions: an increase in a seed disperser combined with land abandonment causes an invasion of the non-native walnut in Europe. – Proc. R. Soc. Ser. B 279: 1491–1497.

LOACKER, K., KOFLER, W., PAGITZ, K. & OBERHUBER, W. (2007): Spread of Walnut (*Juglans regia* L.) in an Alpine valley is correlated with global warming. – Flora 202: 70–78.

LOCKWOOD, J.L., CASSEY, P. & BLACKBURN, T. (2005): The role of propagule pressure in explaining species invasions. – Trends Ecol. Evol. 20: 223–228.

MARTIN, P.H., CANHAM, C.D. & MARKS, P.L. (2009): Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. – Front. Ecol. Environ. 7: 142–149.

MARTIN, P.H., CANHAM, C.D. & KOBE, R.K. (2010): Divergence from the growth-survival trade-off and extreme high growth rates drive patterns of exotic tree invasions in closed-canopy forests. – J. Ecol. 98: 778–789.

MUCINA, L., BÜLTMANN, H., DIERßEN, K. et al. (2016): Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. – Appl. Veg. Sci. 19, Suppl. 1: 3–264.

OBIDZINSKI, A., MEDRZYCKI, P., KOLACZKOWSKA, E., CIURZYCKI, W. & MARCISZEWSKA, K. (2016): Do David and Goliath play the same game? Explanation of the abundance of rare and frequent invasive alien plants in urban woodlands in Warsaw, Poland. – PLoS One 11 (12): 1–28.

PYŠEK, P., JAROŠÍK, V. & KUČERA, T. (2003): Inclusion of native and alien species in temperate nature reserves: an historical study from Central Europe. – Conserv. Biol. 17: 1414–1424.

RICHARDSON, D., PYŠEK, P., REJMÁNEK, M., BARBOUR, M., PANETTA, F. & WEST, C. (2000): Naturalization and invasion of alien plants: concepts and definitions. – Divers. Distrib. 6: 93–107.

RICHARDSON, D.M., HOLMES, P.M., ESLER, K.J., GALATOWITSCH, S.M., STROMBERG, J.C., KIRKMAN, S.P., PYSEK, P. & HOBBS, R.J. (2007): Riparian vegetation: degradation, alien plant invasions, and restoration prospects. – Divers. Distrib. 13: 126–139.

SACCONE, P., GIREL, J., PAGES, J. P., BRUN, J.J. & MICHALET, R. (2013): Ecological resistance to Acer negundo invasion in a European riparian forest: Relative importance of environmental and biotic drivers. – Appl. Veg. Sci. 16: 184–192.

SCHNITZLER, A., HALE, B.W. & ALSUM, E.M. (2007): Examining native and exotic species diversity in European riparian forests. – Biol. Conserv. 138: 146–156.

SEEBENS, H., BLACKBURN, T.M., DYER, E. et al. (2017): No saturation in the accumulation of alien species worldwide. – Nat. Commun.: doi 10.1038/ncomms14435.

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SÎRBU, C. & OPREA, A. (2011): Contribution to the study of plant communities dominated by *Ailanthus altissima* (Mill.) Swingle, in the eastern Romania (Moldavia). – Cercet. Agron. Mold. 44: 51–74.

STASKA, B., ESSL, F. & SAMIMI, C. (2014): Density and age of invasive *Robinia pseudoacacia* modulate its impact on floodplain forests. – Basic Appl. Ecol. 15: 551–558.

STEVENS, J.T., SAFFORD, H.D., HARRISON, S. & LATIMER, A.M. (2015): Forest disturbance accelerates thermophilization of understory plant communities. – J. Ecol. 103: 1253–1263.

TER BRAAK, C.J.F. & ŠMILAUER, P. (2002): CANOCO reference manual and CanoDraw for Windows: Software for canonical community ordination (version 4.5). – Microcomputer Power, Ithaca. NY, US.

TICHÝ, L. (2002): JUICE, software for vegetation classification. – J. Veg. Sci. 13: 451–453.

VAN KLEUNEN, M., DAWSON, W., ESSL, F. et al. (2015): Global exchange and accumulation of non-native plants. – Nature 525: 100–103.

VILÀ, M., BASNOU, C., PYŠEK, P. et al. (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European cross-taxa assessment. – Front. Ecol. Environ. 8: 135–144.

VILÀ, M., PINO, J. & FONT, X. (2007): Regional assessment of plant invasions across different habitat types. – J. Veg. Sci. 18: 35–42.

VÍTKOVÁ, M., MÜLLEROVÁ, J., SÁDLO, J., PERGL, J. & PYŠEK, P. (2017): Black locust (*Robinia pseudoacacia*) beloved and despised: A story of an invasive tree in Central Europe. – For. Ecol. Manag. 384: 287–302.

WILLNER, W., BERG, C. & HEISELMAYER, P. (2012): Austrian Vegetation Database. – Biodivers. Ecol. 4: 333.

ZERBE, V.S. (2007): Neophyten in mitteleuropäischen Wäldern. – Naturschutz Landschaftsplan. 39: 361–368.

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