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Long-Term Changes of Softwood Floodplain Forests—Did the Disappearance of Wet Vegetation Accelerate the Invasion Process?

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Abstract: *Objectives:* We followed the long-term changes of softwood floodplain forests strongly altered by water regime changes and examine the behaviour of neophytes in this environment. Here we ask: (1) How did the composition of neophyte and native species change? (2) How did the presence of species that prefer wetter conditions change? (3) What traditionally distinguished type of softwood floodplain forests (a wetter one or a more mesophilous one) do neophytes prefer? (4) What environmental factors affect the native species richness and the occurrence and cover of neophytes? *Materials and Methods:* Historical and recent phytosociological relevés of the association *Salicetum albae* of the Slovak part of the inland delta of the Danube River were used (177 plots together). For each plot, the number and cover of neophytes and number of native species were measured, and the Shannon-Wiener diversity index, the stand structure (cover of tree, shrub and herb layer) and the mean of Ellenberg indicator values were calculated and compared among time periods. Temporal trends of the soil moisture characterized by indicator values calculated for each plot were determined using a Linear Model. The synoptic table of traditional vegetation types was done to show preferences of neophytes for particular softwood forest types. The effect of site conditions on native species richness and occurrence of neophytes was determined using the Generalized Linear Model. *Results:* The relative number and cover of neophyte species increased and the absolute number of native species decreased over time; the vegetation of the area has changed from variable hygrophilous and mesophilous to homogenised mesophilous; most non-native species prefer the mesophilous vegetation of the floodplain forests; the wetter parts of the floodplain more successfully resisted invasions. *Conclusions:* The vegetation of the researched area has considerably changed over time to become less diverse and less hygrophilous, and has more invasive species. To preserve floodplain forests, natural hydrological and connectivity patterns should be adequately protected.

Keywords: alien species; biodiversity; Danube; floodplain forest; long-term change; neophyte; *Salicion albae*

1. Introduction

The floodplains of large rivers create space for the development of various riparian ecosystems [1]. Although these ecosystems previously covered wide stretches along rivers, today only a fraction of them remain. The floodplain vegetation fulfils various ecological functions, including provision of food and habitats for aquatic and terrestrial organisms, moderation of stream water temperature via evapotranspiration and shading, provision of a corridor for biota movements and human-related ecosystem services such as reducing flood risks, recreation and providing a source of wood [2].

The spatiotemporal dynamics of vegetation structure and composition in floodplains reflects the unique hydrological connectivity and patterns of inundation [3]. The physical processes play a substantial role in diaspore dispersal, the creation of new ecotopes and the establishment of the cottonwood and willow tree stands [4,5]. However, these processes are often disrupted by intensive human activities concentrated along rivers [4]. Melioration and damming cause direct alteration of river channels, changes in the water regime and groundwater table and changes in the natural patterns of floods. Agriculture near alluvial plains increases the deposition of nutrients and pesticides, and thus, eutrophication. Intensive forestry, water extraction and recreational activities significantly contribute to reducing the stability of river ecosystems as well [4].

The invasion of non-native plant species (as per [6]) is considered as one of the major threats to the diversity of natural ecosystems [7,8]. Among semi-natural and natural habitats, floodplain forests are strongly invaded by alien plants [9–14], and among European forests, softwood floodplain forests exhibit the highest level of invasion [15]. Additionally, in Slovakia, floodplain forests have the highest number and cover of neophytes [16] among the natural forests [17]; moreover, they show the highest cover of neophyte species among all natural habitats [18].

The assessment of vegetation change over time is important to better understand the effects of the different drivers of vegetation changes [19], as well as invasions [13,20,21]. In habitats with long-lived species, e.g., forests, such studies are important to monitor the long-term changes of vegetation, though vegetation dynamics in these habitats are often inherently slow [19]. The floodplain forests of the Danube inland delta have been in focus of scientists since the 1950s. This interest has been present not only because of the uniqueness of this area but also thanks to the assessment of the impact of the Gabčíkovo water dam and the constant threat of other dams being built.

The large amount of data gives us the great opportunity to follow the long-term changes of softwood floodplain forests strongly altered by water regime changes and examine the behaviour of neophytes in this environment. Here we ask: (1) How did the composition of neophyte and native species change? (2) How did the presence of species that prefer wetter conditions change? (3) What traditionally distinguished type of softwood floodplain forests (a wetter one or a more mesophilous one) do neophytes prefer? (4) What environmental factors affect the native species richness and the occurrence and cover of neophytes?

2. Materials and Methods

2.1. Study Area

The study area is situated in Central Europe—Slovakia, in the northwest part of the Pannonian basin. In this region—the Danubian Flat—the largest European inland delta extends. As the river Danube passes the Devín Gate, it slows down and forms intricate meanders, channels, oxbow lakes and other alluvial forms. From Bratislava to Sap, marine clays form an impermeable base at which alluvial sediments lie and are currently up to 500 m deep. Thanks to these geological conditions, the largest reservoir of drinking water in Europe has evolved [22].

The climate of the study area is temperate, with the effect of both continental and temperate air masses. Summers are warm and dry with an average July temperature of 18 to 21 °C. January average temperatures decrease to −1 to −2 °C. Precipitation is approximately 500 mm per year. The Danubian Flat is protected against the western winds by the foreland of the Alps and the Malé Karpaty Mts. [23]. As the Danube drainage basin is influenced by the Alps, its water regime depends on snow melting in these mountains. Therefore, in the middle stream, where the Slovak part of the river is, the maximum flow rates are recorded from April to August [24].

Environmental conditions of the study area give rise to the extensive azonal floodplain forests and other river and alluvial ecosystems. The softwood willow-poplar floodplain forests of the alliance *Salicion albae* Soó 1930, the association *Salicetum albae* Issler 1926 occupy the alluvia of great rivers, situated on typical fluvisols and gleysols in the inundated area. The tree layer is dominated by *Populus alba*, *P. nigra*, *P.* × *canescens*, *Salix alba*, *S. fragilis* and *S.* × *rubens.* The shrub layer has higher cover only in less waterlogged places. Nitrophilous and hygrophilous taxa dominate in species composition [25,26]. The association *Salicetum albae* is traditionally divided along the soil moisture gradient to two types—the wetter type with a high presence of hygrophilous taxa (e.g., *Alisma plantago-aquatica*, *Carex acutiformis*, *C. riparia*, *Galium palustre*, *Iris pseudacorus*, *Lythrum salicaria*, *Lysimachia vulgaris*, *Mentha aquatica*, *Myosotis scorpioides*, *Phragmites australis*, *Rorippa amphibia* and *Stachys palustris*) and the more mesophilous type with a higher presence of shrubs (*Sambucus nigra* and *Swida sanguinea*), climbing plants (*Clematis vitalba* and *Humulus lupulus*) and more mesophilous herbs (e.g., *Angelica sylvestris*, *Aegopodium podagraria*, *Galium aparine*, *Glechoma hederacea* and *Lamium maculatum*).

The area is strongly influenced by human activities. The Danube River, as an important transport route, has been gradually adjusted for navigation even at a low water level. Due to the dense settlement, a system of embankments was constructed as a protection against floods, which was finished in the 19th century. Upstream dams in Germany and Austria retain sediments, leading to undercutting of the riverbed and decline of the groundwater levels in the Danubian Flat. In recent decades, the construction of the Gabčíkovo dam (finished in October 1992) has been the most significant intervention to the Danube inland delta. The management of water levels for the original channel system is insufficient, almost completely lacking floods, and consequently, forests are degrading continuously [21].

The Danubian Flat is the most fertile area in Slovakia with very intensive agriculture and forestry. In most areas, the floodplain forests have been changed into agricultural landscape. The remaining forests were mostly replaced by hybrid poplar plantations—circa 80% of forest area [27].

2.2. Data Collection

In 1956, extensive syntaxonomic research was done by Jurko [25]. We use phytosociological plots classified within the association *Salicetum albae* (45 relevés) as the original state of willow-poplar forests of the Danube inland delta. The plots were distributed equally within the study area along the whole ecological gradient of softwood floodplain forests. For the same purposes—of the syntaxonomic revision of the association *Salicetum albae*—we sampled 20 plots in the study area during the growing seasons of the years 2013 and 2014. Plot sampling was done across the entire area in leftover fragments of willow-poplar forests [26]. The dataset was enlarged by all available plots sampled in this area and ordered within the association *Salicetum albae* using the Slovak vegetation database [28]. The final dataset comprised 177 plots. The location of the plots is shown in Figure 1.

All of the plots contain a list of plant species with their cover recorded using the old or new Braun-Blanquet cover-abundance scale [29]. The area of used plots was mostly 400 m^2 (117 plots), followed by 200–300 m^2 (56 plots), 100–150 m^2 (3 plots) and 600 m^2 (1 plot).

2.3. Data Analyses

Data were computerized using the TURBOVEG database program [30]. Further adjustments were carried out using JUICE software [31]. Statistical analyses were conducted using R Project (version 3.2.4, R Foundation for Statistical Computing, Vienna, Austria, https://www.r-project.org/). Non-vascular plants including algae were excluded from the dataset because of unequal determination by the authors. For the purpose of analyses, all species occurring in different vertical layers were merged using standard methods implemented in JUICE software (species in more layers were substituted by one species with cover of three layers together). Neophytes were identified according to the Slovak list of non-native species [32]. The relative number and total cover of recorded neophytes and the absolute number of native species were calculated for each plot. To calculate the cover of neophytes, we converted the cover-abundance scales to percentage numbers: Br.-Bl. values "r" was converted to 0.01%, "+" to 0.05%, "1" to 3%, "2m" to 5%, "2a" to 8%, "2" to 13%, "2b" to 18%, "3" to 33%, "4" to 68% and "5" to 88%, while ordinal value "1" was converted to 0.01%, "2" to 0.05%, "3" to 3%, "4" to 5%, "5" to 8%, "6" to 18%, "7" to 33%, "8" to 68% and "9" to 88%. For each relevé, the Shannon-Wiener diversity index, the information about stand structure (cover of tree, shrub and herb layer) and the unweighted arithmetic mean of the Ellenberg indicator values (EIV) [33], namely, light, soil moisture, nutrients, temperature and soil reaction of native species only were calculated using JUICE software [31]. Unweighted EIV were chosen to eliminate the effect of species facies typical for floodplain forests and to support the indicator values of important hydrophilous species with lower cover values. Weighted EIV will accentuate these expansive species at the expense of other indicative species. Neophytes and species that were absent or not assigned to a particular indicator value in the Ellenberg tables were omitted.

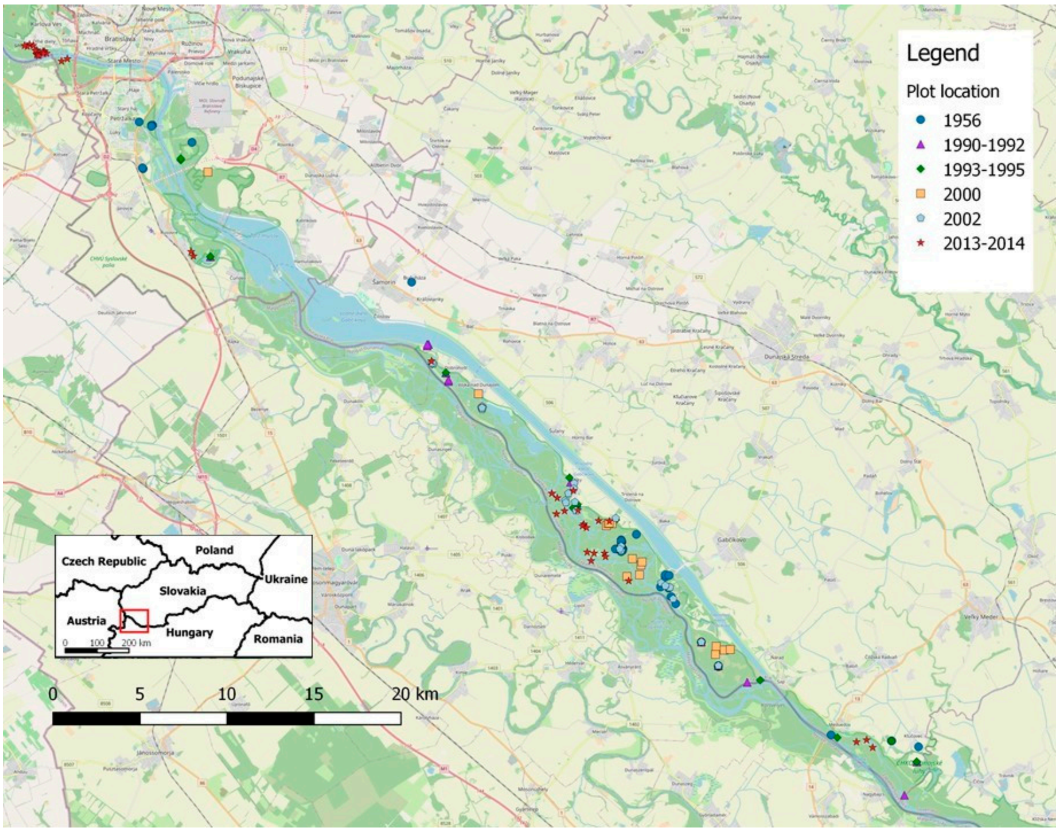


Figure 1. The localities of plots used. The map was made using QGIS (version 2.18.26, https://www.qgis.org), base map© OpenStreetMap Contributors.

The dataset was divided into the following time periods (phases): plots measured in 1956 (45 plots), plots measured during the Gabčíkovo dam construction from the years 1990–1992 (20 plots), plots measured a short time after the Gabčíkovo dam began operation from the years 1993–1995 (32 plots), plots measured in the period after a decade without floods from the year 2000 (15 plots), plots measured with floods in 2002 (26 plots) and plots measured 20 years after the building of the Gabčíkovo dam in the years 2013–2014 (39 plots).

2.3.1. The Long-Term Changes in Presence of Neophyte and Native Species

The relative number and cover of neophytes and the absolute number of native species among analyzed periods were compared using the Generalized Linear Model, with periods as the explanatory variable and quasibinomial distribution family in case of relative numbers and quasi-Poisson in case of total numbers. All models were tested for heteroskedasticity and normality in raw residuals and for zero-inflation. Model selection was based on significance testing between nested models. The results are presented as graphs using R package ggplot2 [34].

2.3.2. The Long-Term Changes in Presence of Soil Moisture Preferring Species

The changes in presence of soil moisture preferring species over time were determined using the Ellenberg soil moisture indicator values. Time patterns of the soil moisture indicator values of plots were determined using the Linear (Mixed Effect) Model, where the time period was used as a fixed variable. The results are presented using R package ggplot2 [34].

2.3.3. The Preferences of Non-Native Species between the Two Types of Softwood Floodplain Forests

To find non-native species preferences for soil moisture, we divided the used plots into the traditionally distinguished types—wet and mesophilous softwood floodplain forests. The break value of Ellenberg soil moisture indicator value (7.75) of relevés was selected according to the Twinspan division of original plots from the year 1956 conducted in JUICE [31]. A synoptic table of non-native species with frequency and fidelity measure [35] has been created using the percentage frequency and fidelity values [36].

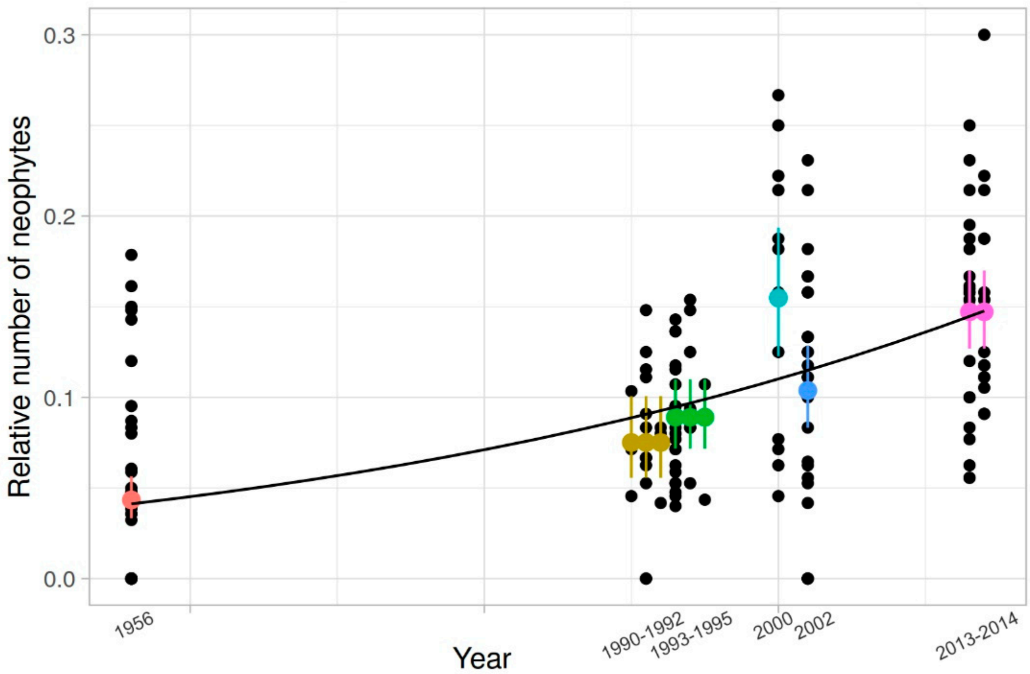
2.3.4. The Effect of the Site Conditions on the Native Species Richness and Occurrence of Neophytes

The relationship between the composition of native and neophyte species in plots (the relative number and cover of neophytes and the absolute number of native species) and site conditions (the Shannon-Wiener diversity index, the cover of tree, shrub and herb layer and the unweighted arithmetic mean of Ellenberg indicator values of native species) was determined using the Generalized Linear Model (with a quasi-Poisson distribution family for the number of species and the quasibinomial family for cover). The final model was chosen according to F test. Analyses were conducted separately for historical plots made in the year 1956 and plots sampled after the construction of the Gabčíkovo dam.

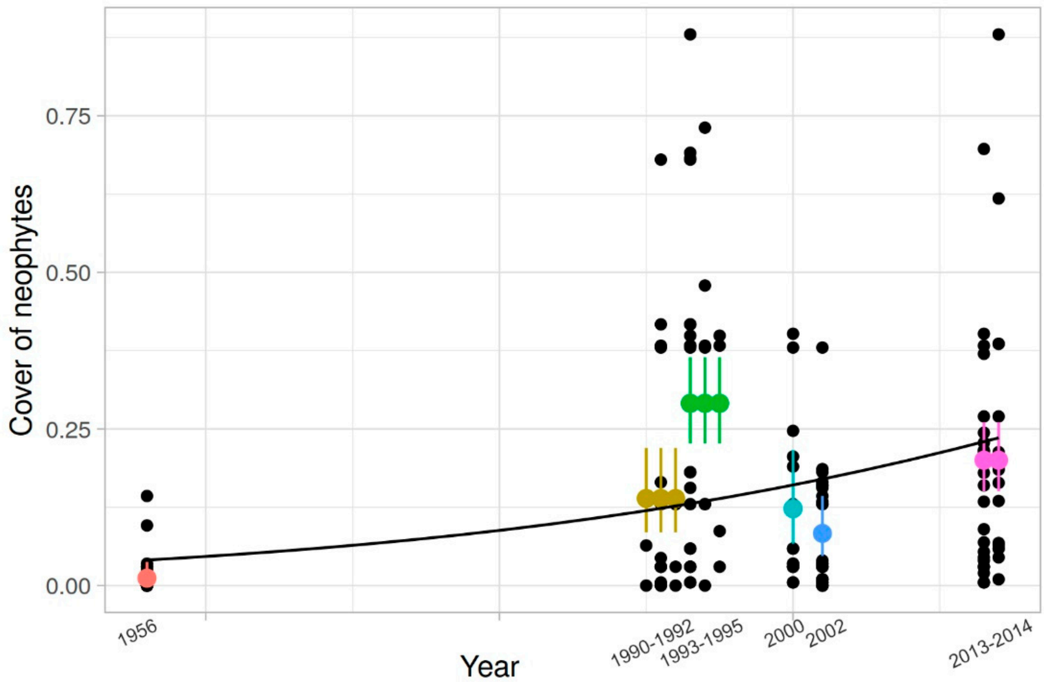
3. Results

3.1. The Long-Term Changes in Presence of Neophyte and Native Species

The species composition of the softwood floodplain forests of the Danube inland delta significantly changed over time (Figure 2). In the absolute number of native species, a declining linear trend was found. In 1956, the mean number of native species was almost 23 per plot. Until the year 1990, the mean number of native species declined to 17 species per plot. In contrast, the relative number and cover of neophyte species increased over time. In case of the neophytes cover, a significant piece-wise trend was observed. While in 1956, the mean relative number of neophyte species was 4% (one neophyte species per plot on average) with a mean cover of approximately 1%, after the construction of the Gabčíkovo dam, it was above 9% (two neophytes per plot on average) with a mean cover of up to 18%. Although the model of the trend alone is significant, the variance between time periods is too heterogeneous to be captured by trend; most likely there is some other factor than time influencing the appearance of neophytes in the plots, which could be the subject of further research. For instance, in the heavily flooded year 2002, there was a notable decline in the number of neophytes (Figure 2), despite the increasing trend.

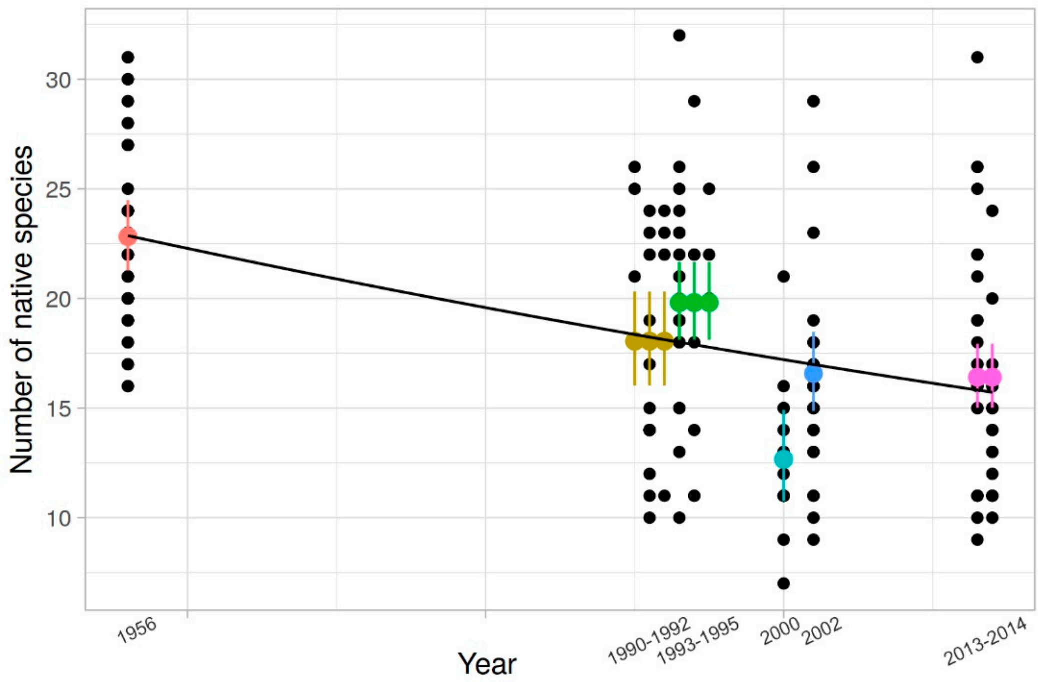


(**a**)



(**b**)

Figure 2. *Cont*.



(**c**)

Figure 2. The changes in species composition of the softwood floodplain forests of the Slovak part of the Danube inland delta. (**a**) relative number and (**b**) cover of neophytes, (**c**) number of native species. Black dots represent observations, colored points (accompanied by segments) represent the mean value (point and interval) estimates for the analyzed periods and the trend line follows the model without effect of the observation phases.

3.2. The Long-Term Changes in Presence of Soil Moisture Preferring Species

The Ellenberg soil moisture indicator value of used plots decreased over time, there is significant downward trend since 1990 (at about 0.4 per decade, Figure 3). The effect of the time periods along the trend is rather faint (statistical tests were ambiguous to conclude at the standard significance level 5%, the most conservative being the one that treats the time periods as random effects). The plots recorded in 2002, when strong floods occurred, have a higher soil moisture indicator value compared to the fourth and last time periods (Figure 3). Hygrophilous species commonly present in the past, such as *Alisma lanceolatum*, *A. plantago-aquatica*, *Alnus incana*, *Carex acuta*, *C. acutiformis*, *Cardamine amara*, *Galium palustre*, *Leucojum aestivum*, *Lysimachia vulgaris*, *Lythrum salicaria*, *Mentha* × *verticillata*, *M. aquatica*, *Myosotis scorpioides* or *Persicaria hydropiper*, are no longer common nowadays.

3.3. The Preferences of Non-Native Species between the Two Types of Softwood Floodplain Forests

In the dataset used, 17 neophytes were identified. Ten of them have an invasive status (Table 1). The most common non-native species occurring in the dataset is *Aster lanceolatus* agg. (49% of relevés). The second most commonly occurring neophyte—*Negundo aceroides* was found in 36% of all relevés bounding to the more mesophilous type of floodplain forest. The same applies for *Impatiens glandulifera*, *I. parviflora* and *Solidago gigantea*, occurring in more than 20% of all relevés. *Bidens frondosa* and *Populus* × *canadensis* are the only species occurring more often in the wet type of softwood floodplain forests (Table 1).

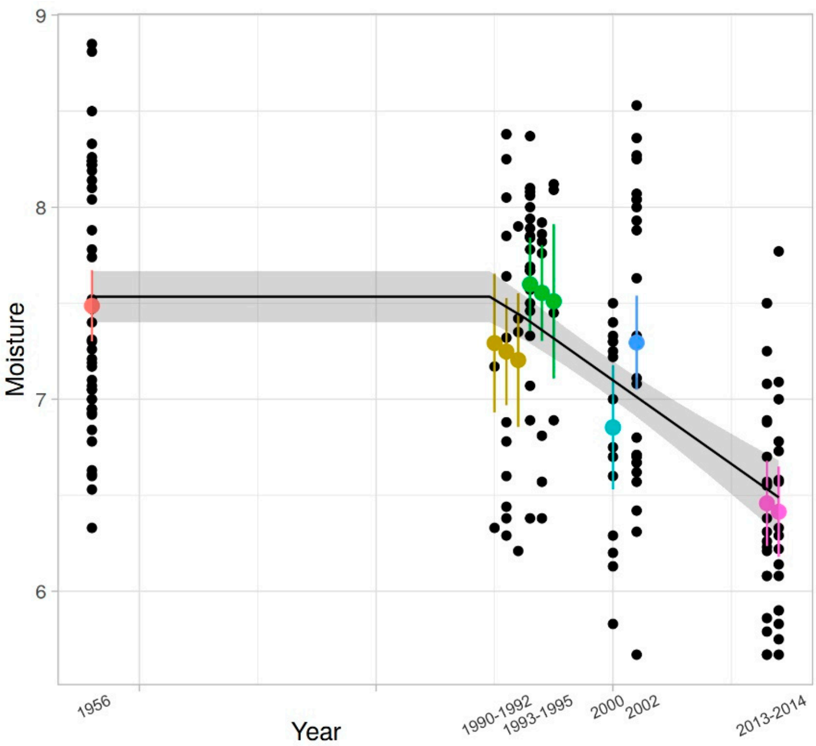


Figure 3. Changes of the Ellenberg moisture indicator value for plots of softwood floodplain forests of the Slovak part of the Danube inland delta. A partially constant and linear trend clearly dominates, while the effect of observation phases (periods) is questionable.

Table 1. Synoptic table of frequency and fidelity (coefficient phi × 100) of neophyte species of two traditional types of softwood floodplain forests. Neophyte species with frequencies identified in the whole dataset and groups divided according to the Ellenberg soil moisture indicator value into the mesophilous type and wet type of softwood floodplain forest with the percentage of frequency and fidelity of species. Species with invasive status are in bold.

	Whole Dataset	**Mesophilous Type**		**Wet Type**	
Soil moisture indicator value	5.67–8.85	more than 7.75		less than 7.75	
No. of relevés	177	129		49	
	Freq.	**Freq.**	**Fidelity**	**Freq.**	**Fidelity**
***Aster lanceolatus* agg.**	49	47	—	53	5
Negundo aceroides	36	44	32	14	—
Solidago gigantea	28	32	18	16	—
Impatiens glandulifera	23	29	26	8	—
Impatiens parviflora	21	28	36	2	—
Bidens frondosa	8	5	—	14	14
Fraxinus pennsylvanica	6	7	11	2	—
Populus × canadensis	6	4	—	12	15
Robinia pseudoacacia	4	6	17		—
Erigeron annuus	2	3	12	.	—
Morus alba	2	2	10		—
Helianthus tuberosus	1	2	8		—
Oxalis fontana	1	2	8		—
Aesculus hippocastanum	1	1	6		—
Conyza canadensis	1	1	6		—
Juglans nigra	1	1	6		—
Physocarpus opulifolius	1	1	6		—

3.4. The Effect of Site Conditions on Native Species Richness and Occurrence of Neophytes

The analyses of historical plots [25] showed that in localities with a lower soil moisture indicator value, the relative number (F = 31.646, $p < 0.001$) and cover (F = 11.110, $p = 0.001$) of neophyte species was higher. The cover of neophytes increased in places with a higher nutrient indicator value (F = 7.822, $p = 0.008$). In contrast, the number of native species decreased with a higher nutrient indicator value (F = 27.386, $p < 0.001$). The cover of neophyte species was higher in plots with a higher temperature indicator value (F = 16.305, $p < 0.001$). The relative number of neophytes decreased with increasing coverage of the shrub layer (F = 9.192, $p = 0.004$). In plots with a higher Shannon-Wiener index, the cover of neophytes is higher (F = 9.257, $p = 0.004$). Other factors had non-significant effects (Table 2).

Table 2. The effect of site conditions on native and neophyte species. Site conditions affecting the relative number and cover of neophytes and absolute number of native species in the Danube inland delta of Slovakia for the reference state (year 1956) and after Gabčíkovo dam construction. The results were calculated using a Generalized Linear Model. The minimal adequate model for the relative number and the cover of neophytes was fitted with a quasibinomial family and for the number of native species quasi-Poisson family with a log link function. Models were tested using F statistics. Estimates, their standard errors and significance marks/stars (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) are presented.

	Reference State—the Year 1956			**After Gabčíkovo Waterworks Construction**		
	Relative Number of Neophytes	**Cover of Neophytes**	**Absolute Number of Native Species**	**Relative Number of Neophytes**	**Cover of Neophytes**	**Absolute Number of Native Species**
Moisture	−1.387 ± 0.25 ***	−1.644 ± 0.53 **				
Nutrients		1.444 ± 0.54 **	−0.267 ± 0.05 ***	0.384 ± 0.09 ***		−0.285 ± 0.05 ***
Soil reaction						−0.349 ± 0.13 **
Temperature		5.764 ± 1.5 ***				
Cover of shrub layer	−0.034 ± 0.01 **	-			-	0.003 ± 0.00 *
Cover of herb layer		-			-	0.003 ± 0.00 ***
Shannon-Wiener index		2.724 ± 0.98 **	-			-
Time	-	-	-	0.023 ± 0.01 ***		

After the construction of the Gabčíkovo dam, the nutrient indicator value had a significant effect. With a higher nutrient indicator value, the relative number of neophytes increases (F = 14.768, $p < 0.001$) and the number of native species decreases (F = 27.337, $p < 0.001$). The number of native species declined with a higher soil reaction indicator value (F = 10.257, $p = 0.002$). With a higher cover of shrub (F = 4.234, $p = 0.042$) and herb layer (F = 11.781, $p < 0.001$), the number of native species increased. The relative number of neophytes significantly increased in this time period (F = 15.737, $p < 0.001$). Other factors had non-significant effects (Table 2).

4. Discussion

4.1. The Long-Term Changes in Presence of Neophyte and Native Species

The assessment of the long-term vegetation change showed interesting patterns in the occurrence and cover of neophytes and species composition of the softwood floodplain forests of the Slovak Danube inland delta. The number of non-native species increased over time, which corresponds to findings from other floodplain biotopes [13,20]. Alluvial plains are considered to be susceptible to invasions because they are in a close contact with rivers, which are the important migratory corridors for the non-native species [37,38]. Moreover, the dynamic water regime causes the regular natural disturbance of floodplain ecosystems, which intensifies the spread and establishment of invasive species [37]. However, natural disturbance has not occurred at the study area since 1992, except for the heavy floods in 2002 when there was an observable decline in the number of neophytes.

On the other hand, the area is under the pressure of various anthropogenic disturbances. Human activities such as agriculture, forestry, transportation, recreation and building cause fragmentation of natural alluvial ecosystems, including riparian forests [39], spreading invasive species and lowering the resilience of natural ecosystems [11]. The building of the Gabčíkovo dam was the strongest intervention to the water regime of the area, which led to a decline in the resilience of alluvial ecosystems. The increase in the relative number of non-native species in the study area is visible primarily ten years after the building of the Gabčíkovo dam. In contrast, the absolute number of native species declined. The delayed effect of water regime change in forests was expected due to the relatively slow vegetation dynamics of forests [19]. Crucial elements of resilience in riverine systems are linkages: lateral linkage—between the floodplain and channel, longitudinal linkage—upstream and downstream river channel and vertical linkage—between channel and riverbed [40]. The building of the Gabčíkovo dam limited all linkages and caused the cut-off sedimentation, the deepening of the riverbed and thus the decline of groundwater tables and restricted the recruitment of indigenous species, which potentiates the incursion of alien species [21,41].

4.2. The Long-Term Changes in Presence of Soil Moisture Preferring Species

The analyses show the gradual transformation of hygrophilous to mesophilous vegetation, and thus, its homogenization. The changes in the water regime and groundwater table and associated vegetation changes are typical consequences of intensive rivers exploitation and water management, especially dam constructions [41]. The retention of sediments in dams causes downstream riverbed deepening and the decline of groundwater tables along a river. This effect caused almost the complete loss of the wet type of softwood floodplain forests and associated species. Such drainage of the land will become even worse in the future due to the consequences of the recent climate changes in forests and will manifest mainly through drought- and heat-induced tree mortality [42]. Moreover, in long-term waterlogged soils, the availability of nutrients due to slower decomposition is lower. When the area is drying out, decomposition accelerates, the amount of nutrients increases and favorable conditions for excessive development of invasive plants are created. For the recruitment of willows, poplars and other plants typical for floodplains, floods and water table changes are crucial [5]. Better development of hygrophilous plants was seen in the year 2002, when a strong flood occurred.

4.3. The Preferences of Non-Native Species between the Two Types of Softwood Floodplain Forests

According to our analysis, the wetter parts of the floodplain forests were more resistant to invasions. Invasive species are often generalists, and it seems that in wet conditions, the upper soil moisture threshold for most invasive species is exceeded, so they are unable to deal with such extreme conditions. This applies to the woody species *Negundo aceroides* and for herbaceous species *Impatiens glandulifera*, *I. parviflora* and *Solidago gigantea. Robinia pseudoacacia*, one of the most invasive species in the world [42], showed this pattern even more. In the study of Petrášová, Jarolímek and Medvecká [20], it is the most frequently recorded neophyte species (22%) of hardwood floodplain forests of selected area of Slovakia and Hungary, while in the used softwood floodplain forest dataset, it occurs only in the more mesophilous type with a frequency of only 6% of relevés. The woody species *Robinia pseudoacacia* prefers rather mesophilous habitats [43]; therefore, it does not deal with conditions of softwood floodplain forests as successfully as in hardwood floodplain forests. *Bidens frondosa* is the only species (except of *Populus* × *canadensis* that is planted and therefor its occurrence is directly caused by human) that seems to be better adapted to wet rather than to mesophilous conditions. The most common neophyte species, *Aster lanceolatus* agg., grows along the whole gradient of soil moisture conditions of softwood floodplain forests. Following the results of Jurko [25] and Petrášová, Jarolímek and Medvecká [20], non-native species more easily penetrated to the less flooded habitats of floodplain forests. Jurko [25] even described a subassociation with *Solidago gigantea* within hardwood floodplain forests.

4.4. The Effect of Site Conditions on Native Species Richness and Occurrence of Neophytes

According to the analyses of data from the 1950s, when the water regime of the Danube River was less affected by humans, plots with higher soil moisture and lower nutrient indicator value were less invaded. Not only lower availability of nutrients but also extremely wet conditions in long-term waterlogged soils does not allow excessive development of invasive plants. The higher cover of neophytes was associated with the warmer environment, which is known from other studies as well, e.g., [9]. Occurrence of neophytes was positively driven by soil pH gradient in alder-dominated forests in Pannonian region, where neutral and more alkalic sites were more invaded [44], but this variable was non-significant in case of willow-poplar forests. This could be caused by shorter gradient in softwood floodplains in comparison with alder dominated forests along smaller rivers. Soil reaction affected only number on native species in the period after building the Gabčíkovo water dam. Higher evaporation in wetter environments causes cooling of the microclimate and thus enhanced the resilience of wet biotopes. Places shaded by shrubs were less invaded. Localities with a higher Shannon-Wiener diversity index were more invaded in the past. It could be an effect of invasive species occurrence with small cover in the past (before rapid spreading) without negative effect on native species diversity. Additionally, the diversity of native species has no significant effect presently. This is in agreement with recent studies [20,45,46].

After the construction of the Gabčíkovo dam, the number of neophytes increased. The effect of these factors is not significant anymore, probably because of the homogenization of environmental conditions and vegetation. Only the availability of nutrients has the same effect. A nutrient-rich environment is more vulnerable to invasions, as confirmed by other studies, e.g., [9,20,47].

The restoration of the natural water regimes on rivers raises concerns about supporting the spread and establishment of non-native species. However, floodplain ecosystem restoration first requires the restoration of the hydrological regime [48,49], since it is, among other things, critical for riparian species [49]. It can also directly affect the performance of native and alien species [50]. High water levels and long-term waterlogging limit plant invasion [51–53]. Additionally, our results show that only in years when the branch system of the old riverbed is filled with a large amount of water, at least some indications of restoration of floodplain habitats can occur. Strong floods in the spring and summer of 2002 are an example of such a case. Plots sampled that year showed a significant increase in the number of hygrophilous species, while the relative number and cover of neophytes decreased. According to our results, the maintenance and the support of the development of the wet communities is an effective tool against invasions of non-native species in softwood floodplain forests. However, in the Danube inland delta, it is just the opposite situation when the area is drying out. Thus, we cannot expect the decrease in the presence of neophytes and the improvement of the natural regeneration of riparian species, unless there is at least some restoration of the water regime.

Complete ecological restoration to historic species assemblages in human-affected areas is not possible. However, restoration of alluvial processes provides the desired ecosystem structure, function and services. Introduced species may not be a restraint in ecosystem functioning; however, they may be understood as a type of ecosystem adaptation to the altered conditions. Some non-native species, termed “transformers” [6], may cause irreversible changes in the composition and structure of plant communities and in ecosystem functions. In such cases, or when a sufficient water regime is not possible to access, alien-removing efforts are appropriate, of course on the basis of sufficient knowledge of alien species and floodplain ecology. According to the theoretical framework of fluctuating resources [46], the timing of the disturbance event and the phenological events of invader and native species (e.g., timing of seed production and release) should be considered as well.

5. Conclusions

In the last 60 years, the vegetation of softwood floodplain forests of the Slovak part of the largest inland delta of the Danube River has considerably changed. (1) The relative number and cover of neophyte species increased and the absolute number of native species decreased over time; (2) the vegetation of the area has changed from variable hygrophilous and mesophilous to homogenized mesophilous; (3) most non-native species prefer mesophilous vegetation of the floodplain forests, only *Aster lanceolatus* and *Bidens frondosa* seem to adapt to wet conditions successfully; (4) the moister parts with slower decomposition and better evapotranspiration cooling more successfully resisted invasions.

Human interventions to the river continuum resulted in drying up of the land, and thus increased presence of neophytes in previously diverse floodplains, and should be absolutely avoided. In the context of recent climate change, restoration of the river continuum and thus floodplain ecosystems are especially important and, in many countries, is already common (e.g., http://damremoval.eu; accessed 5 October 2020). Possibilities for the improvement of the conditions of the Danube inland delta are currently present by increasing the amount of water supplied to the "old" channel system. Floodplain forests as unique ecosystems should be adequately protected, ensuring natural hydrological and connectivity patterns.

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