RESEARCH ARTICLE

Alien aquatic plants in Slovakia over 130 years: historical overview, current distribution and future perspectives

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Abstract

Alien aquatic plants rank amongst the major threats to aquatic biodiversity and, since ongoing climate change is expected to facilitate their further spread, there is an urgent need for sound knowledge of their distribution and ecology. We collected published and unpublished data spanning the last ~130 years and performed the first comprehensive assessment of alien aquatic vascular plants in Slovakia with the following aims: (i) to prepare a national inventory, (ii) to assess the effects of climate and landscape on species diversity and (iii) to evaluate the habitat preferences of the species. The historical overview showed a strongly increasing trend in the number of alien species related to an increased amount of intensive research of aquatic vegetation over the last 30 years. Altogether, 20 neophyte alien aquatic plant taxa were recorded from 479 sampling sites. However, the species inventory seems to be far from complete and approximately 14 species are expected to remain undetected. *Elodea canadensis* and *E. nuttallii* are the most frequently occurring alien aquatic plants, while eight other species have been found at a single site only. The majority of alien plants were deliberately introduced as aquarium ornamentals or released through pond waste. The fragmented information on local habitat conditions did not allow us to draw firm conclusions about the habitat preferences of alien aquatic plants. However, artificial water bodies are more frequently colonised by alien species than natural habitats (95% of aliens were found in artificial water bodies and 60% of them

were recorded exclusively in these habitats) and many species have broad environmental tolerances (ability to colonise both standing and running waters, tolerances to a wide range of temperatures and water chemistry). Our results reaffirm the major role of increased temperatures and landscape modification in the distribution of alien aquatic plants and we can expect enhanced invasiveness and spreading of alien species into new habitats driven by climate change and land use intensification. Filling a main gap in the recognition of alien aquatic plant environmental preferences is a challenge for future research with the ultimate goal of maintaining natural aquatic plant diversity and ecosystem functioning.

Keywords
invasive species, macrophytes, aquatic weeds, distribution, climate change, land use

Introduction

Biological invasions by alien plants are generally recognised as an important component of human-induced environmental changes and they have a direct effect on the species diversity of various habitats (Manchester and Bullock 2000; Hulme 2003). Although water bodies have a relatively low level of invasion in Europe (Chytrý et al. 2009), these freshwater habitats are substantially influenced by alien plant species. Currently, almost 100 alien aquatic plants are recognised in Europe. However, the distribution pattern of this species in Europe is uneven; western, northern and central European countries, such as France, Italy, Germany or Hungary, are the most invaded, while some south-eastern European countries have a relatively low number of alien plants (Hussner 2012).

According to the Propagule, Abiotic, Biotic (PAB) framework (Catford et al. 2009), propagule pressure (e.g. the number of introduced individuals, seeds or propagules), abiotic (e.g. climatic or soil characteristics) and biotic (mutual relationships amongst species) variables are generally considered reasons for the presence, survival and success of alien species (Colangelo et al. 2017). While climate is important in setting the global range of alien species, factors related to human influence are of greater importance at regional scale (Kelly et al. 2014). Especially in the case of aquatic plants, trade and cultivation of aquatic ornamental plants are considered to be the main introduction routes for alien species (Duggan 2010; Hussner 2012). Moreover, the presence of alien aquatic species is usually positively correlated with shipping activity, tourism and human population size (Leuven et al. 2009; Panov et al. 2009; Hussner et al. 2010; O'Malia et al. 2018). Nunes et al. (2015) found that geographical patterns are related to some pathways of introduction of freshwater alien organisms in Europe: introductions through inland canals were concentrated in Central/North-eastern Europe, while introductions through pet/terrarium/aquarium trade were mainly observed in Central/Western Europe. In addition, thermal waters are key habitats for the establishment and survival of many alien aquatic plants. For example, approximately 80% of all detected non-indigenous aquatic plants in Hungary were found in thermal waters (Lukács et al. 2016).

Hussner (2012) reported only 6 alien aquatic plant species, namely, *Azolla filiculoides* Lam., *Crassula helmsii* (Kirk) Cockayne, *Elodea canadensis* Michx., *E. nuttallii* (Planch.) H. St. John, *Lemna minuta* Kunth and *Shinnersia rivularis* (A. Gray) R. M.

King & H. Rob. from Slovakia. The list was incomplete and information about the occurrence of *C. helmsii* was probably incorrect (Medvecká et al. 2012, http://dass.sav.sk/en/). Lukács et al. (2016) identified 48 alien aquatic plants from the Pannonian ecoregion including mainly Hungary and some parts of neighbouring countries, including Slovakia. The most recently published list of alien flora of Slovakia included the presence of 13 species (Medvecká et al. 2012). In addition to the species reported by Hussner (2012) and except for *C. helmsii*, eight additional species were included in the list (*Egeria densa* Planch., *Eichhornia crassipes* (Mart.) Solms, *Hydrilla verticillata* (L. f.) Royle, *Limnophila sessiliflora* Blume, *Najas guadalupensis* (Spreng.) Magnus, *Pistia stratiotes* L., *Sagittaria subulata* (L.) Buchenau and *Utricularia gibba* L.). Both sources pointed to a relatively low number of alien aquatic plants in freshwater habitats of Slovakia, which was also confirmed by a later study (Medvecká et al. 2014). During recent intensive limnological research, several new alien species were recorded and the volume of data on the distribution and ecology of alien aquatic plants in Slovakia increased substantially (e.g. Bubíková et al. 2016; Nobis et al. 2019). However, an exhaustive study on alien aquatic plants, their distribution and ecology was missing and the existing information remained scattered in various sources, many of them still unpublished.

Alien aquatic plants rank amongst the major threats to aquatic biodiversity (e.g. Strayer et al. 2010; Havel et al. 2015) and, since ongoing climate change is expected to facilitate the spread of these species (Lukács et al. 2016), there is an urgent need for sound knowledge of the distribution and ecology of alien aquatic species. Therefore, the aim of our study is to provide the first comprehensive examination of alien aquatic vascular plants in Slovakia, based on a critical review of all available data sources (published and unpublished). Our specific aims were to (i) prepare a national inventory of alien aquatic plants, (ii) assess the effect of climatic and landscape characteristics on alien species diversity and (iii) evaluate the habitat preferences of alien aquatic species. Subsequently, we discuss further trends in the distribution of alien aquatic plants and focus on the identification of research gaps.

Methods

Study area

The study covers two important Central European bioregions, the Alpine (Carpathians) and the Pannonian bioregions (Figure 1). The Pannonian bioregion is situated in the southern lowlands of Slovakia and is characterised by a relatively warm and dry climate with mean annual temperatures > 9 °C and relatively low total precipitation (< 600 mm). Conversely, a colder and more humid climate is typical for the Carpathians (mean annual temperatures 0–9 °C and total precipitation 600–1600 (2000) mm), which cover mainly large mountain ranges and inner-Carpathian basins in the central and northern parts. The area is very geologically heterogeneous and characterised by brackish and freshwater basin deposits in the south, flysch facies in the north and Mesozoic, marine and continental Triassic bedrocks in the central part (Miklós 2002).
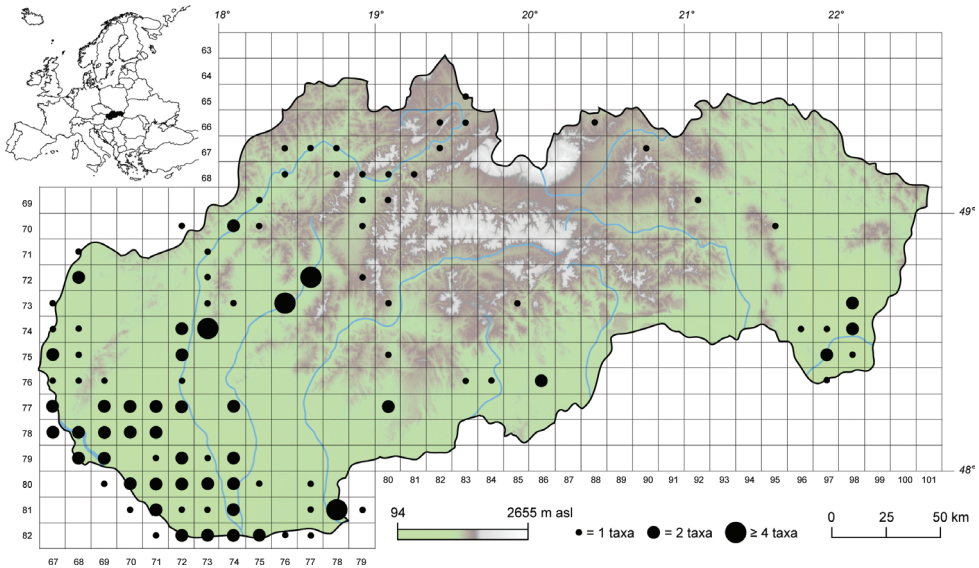
Figure 1. Spatial distribution of alien aquatic plants in Slovakia at the scale of the Central European Flora Mapping System.

The majority of water bodies in Slovakia belong to the catchment basin of the Danube River (Black Sea drainage area), while a small part (the Poprad River) flows to the catchment basin of the Vistula River (Baltic Sea drainage area). The majority of lotic water bodies in Slovakia have been heavily modified in the last century (Čiliak et al. 2014) and artificial canals and man-made lentic water bodies (e.g. gravel or sand ponds, water reservoir used for irrigation or recreation) have been constructed frequently. Therefore, together with thermal waters (small ponds or canals), artificial or human-modified water bodies create numerous habitats, potentially suitable for alien aquatic plants.

Data sources

We focused on alien aquatic vascular plant species using the definitions of alien species by Pyšek et al. (2004) and Blackburn et al. (2011). Aquatic plants were identified as those species that grow submerged or floating on the water surface for at least a part of their life history (Hussner 2012) and these included true aquatic plants (hydrophytes) and amphibious plants, adapted to both aquatic and terrestrial modes of life (cf. Janauer 2003, Janauer and Dokulil 2006). However, typical helophytes were excluded from the dataset.

We established a database of alien aquatic plants, based on data from the Database of non-native plant species of Slovakia (http://dass.sav.sk/en/) and a checklist of alien flora of Slovakia (Medvecká et al. 2012). After critical review, we added data from the Central database of phytocenological relevés of Slovakia (http://ibot.sav.sk/cdf/) up to 2016, scientific articles (Suppl. material 1), nature-based web sites (https://fotonet. sk/), (https://www.nahuby.sk/) and herbaria (BP, BRA, SAV, SLO, SMBB, OLM,

PMK, WU; for acronyms, see http://sweetgum.nybg.org/science/ih/ and Vozárová and Sútorý 2001). Last but not least, a large unpublished dataset, gathered by the authors during the intensive research of all types of water bodies from 2011–2017, was included in the database. We performed extensive floristic, phytosociological and ecological surveys of aquatic habitats in understudied parts of Slovakia (cf. Baláži et al. 2011). Besides native species, a large amount of data on alien aquatic plants was gathered during the research (e.g. Kochjarová et al. 2013, Bubíková et al. 2016, Nobis et al. 2019). Altogether, the database of alien aquatic plants in Slovakia contained 599 records. Collected data were further processed and multiple records for the same species in the same site over several years were reduced to a single oldest record. The database covered 512 unique records from 479 sampling sites. The records were arranged into grid cells according to the Central European Flora Mapping System (CEFMS, Niklfeld 1971). Whenever available, the plant data were supplemented by information on climate, landscape composition, habitat type and local physical and chemical conditions of water bodies.

Climate data (mean annual air temperature, January and July mean air temperatures and total annual precipitation) were calculated as mean values for the period 1981–2010. The data were extracted from raster layers provided by the Slovak Hydrometeorological Institute using the GRASS geographic information system (Grass Development Team 2010).

Composition of landscape was derived from CORINE Land Cover maps (Büttner and Kosztra 2017). We specifically focused on the coverage of road networks (thereafter also road networks), coverage of urban areas (urban areas) and on the proportion of forests, natural and semi-natural areas (natural areas) representing proxies for human-mediated vectors of dispersal, permanent human presence and intensity of land use, respectively, which are known to drive distribution of alien aquatic plants (e.g. Kelly et al. 2014; Tamayo and Olden 2014; Rodríguez-Merino et al. 2018). Land cover of those categories was calculated for each grid cell of the CEFMS in QGIS v. 3.6 (QGIS Development Team 2019).

Water bodies were classified according to their habitat type (lentic, lotic) and origin (natural: rivers, streams, river oxbows, watered terrain depression; artificial: drainage and irrigation canals, water reservoirs, sand or gravel pits). Local characteristics of water bodies, known to affect aquatic plant communities (Lacoul and Freedman 2006), were measured in the field as follows: the mean depth of water was calculated from 10 random measurements at each site; and water temperature, pH and conductivity were measured using a EUTECH Cyber Scan series 600 instrument. These local parameters were available only for 117 sites (103 sites with water depth, 68 with temperature, 75 with pH and 74 sites with conductivity values).

For each plant species, the first time of observation (FTO) and the following categories were evaluated: invasion status (IS), cas – casual, nat – naturalised, inv – invasive (Richardson et al. 2000); residence time (RT), arch – archaeophyte, neo – neophyte (Richardson et al. 2000); introduction mode (IM), d – deliberate, a – accidental, b – both means (Hulme et al. 2008, simplified according to Medvecká et al. 2012) and water type (WT), cold and thermal.

Data analysis

We constructed an analytical sample-based rarefaction curve with unconditional confidence intervals (Colwell et al. 2004) to assess the completeness of the inventory of alien aquatic plant species in Slovakia. The bias-corrected asymptotic species richness estimator Chao2-bc (Chao 2005) was used to estimate the total number of alien species, including those unobserved.

We evaluated the effects of climatic characteristics (mean annual air temperature, January and July mean air temperatures and total annual precipitation) and landscape characteristics (cover of road networks, urban areas and natural areas) on the diversity of alien aquatic plants using generalised linear models (GLMs, McCullagh and Nelder 1989). Prior to the analysis, we imposed a grid of the CEFMS over the studied area and pooled site-specific records for each grid cell. The grid cells were treated as sampling units in the GLMs to overcome possible problems with non-independence (e.g. sampling of several sites over a relatively short stretch of the same stream) and uncertainty in exact georeferencing of some historical records. Floristic records from thermal waters were excluded from this analysis since the occurrence of those species of (sub)tropical origin with higher temperature optima is mainly driven by locally-specific temperature regimes of water bodies without a direct link to regional climate or landscape features (cf. Vojtkó et al. 2017). Due to strong correlations amongst variables, we fitted separate GLMs for each predictor. The number of sampling sites in each grid cell was included as a covariate in the GLMs to account for differences in sampling effort amongst grids. Since the alien species counts showed lower variation than expected under the mean-variance relationship of the Poisson distribution (dispersion parameters of the Poisson GLMs $\varphi \sim 0.2$), we fitted GLMs with a Conway-Maxwell-Poisson distribution, a two-parameter generalised form of the Poisson distribution that is sufficiently flexible to describe count data with a wide range of dispersion levels (Shmueli et al. 2005). Diagnostic plots of residuals were inspected to assess the quality of the models and no violation of the assumptions was observed. The residuals were also screened for spatial autocorrelation using non-parametric spatial correlograms (Bjørnstad and Falck 2001) and any significant autocorrelation patterns were detected. Finally, a leave-one-out cross-validation procedure was employed to assess the predictive performance of the GLMs based on median absolute errors (MdAE).

Since the majority of records in the database stem from unstructured, opportunistic (presence-only) sampling lacking site-specific environmental information and since many species were found in only a few sites, we did not use inferential statistics to estimate species habitat preferences. Instead, we relied on exploratory data analysis and used a series of bar plots and boxplots to examine the environmental tolerances of alien aquatic plants in Slovakia. In particular, we focused on optima (median) and ranges (min-max) of species with a sufficient number of records.

The analyses were performed in Spade (Chao and Shen 2010) and R (R Development Core Team 2018) using the packages COMPoissonReg (Sellers et al. 2017), ggplot2 (Wickham 2016), iNEXT (Chao et al. 2014) and ncf (Bjørnstad 2018).

Results

Inventory of alien aquatic plant species in Slovakia

Altogether, twenty alien aquatic plant taxa were recorded in Slovakia (Table 1). The historical overview showed a strong increasing trend in the number of alien species over the last 30 years (Figure 2A). Indeed, the trend is parallel to the degree of scientific interest in alien plants mirrored in a number of published studies. However, the species inventory seems to be far from complete, as is apparent from the non-asymptotic rarefaction curve (Figure 2B). The expected total number of alien aquatic species calculated by the Chao2-bc estimator is 34 (95% conf. interval: 23–87), which means that 14 species are expected to remain undetected.

All of the recorded aliens belong to neophytes and a substantial proportion has naturalised invasion status (70%) and a deliberate introduction mode (60%) (Table 1). *Elodea canadensis* and *E. nuttallii* were the most widespread (55 and 41 grid cells, respectively) followed by a *Nymphaea* cultivar, *Pistia stratiotes*, *Azolla filiculoides*, *Eichhornia crassipes* and *Najas guadalupensis* (> 6 grid cells), while the remaining 65% of species occurred infrequently (≤ 3 cells).

The effect of climate and landscape characteristics on the diversity of aliens

Alien aquatic plants were recorded in 98 grid cells of the CEFMS (~23% of all cells), mainly in the lowlands and valleys of large rivers (Figure 1). This geographic pattern corresponds well with the results of GLMs. All studied climatic variables were significantly related to the number of alien species after accounting for sampling effort (Table 2). The diversity of alien species increased with temperature and decreased with precipitation. In addition, the number of aliens significantly increased with decreasing cover of natural and semi-natural areas. When we combined best climatic (mean annual temperature) and landscape (natural areas) predictors in a single model, predictive performance improved over those simple GLMs (MdAE = 0.30). However, there is still a lot of unexplained variance in the data (Figure 3).

Habitat preferences of aliens

A comparable number of species was found in cold and thermal waters (Table 1). All but one alien species (*Lemna turionifera*) were found in artificial water bodies and 60% of them were recorded exclusively in man-made habitats (Figure 4). Half of the species were able to colonise both lotic and lentic habitats, while 35% and 15% were found only in standing or running waters, respectively. Considering temperature preferences, *Hydrilla verticillata*, *Najas guadalupensis* and *Sagittaria subulata* prefer warm waters, while the other evaluated taxa (*Elodea canadensis*, *E. nuttallii*, *Nymphaea* sp. and *Pistia stratiotes*) were found in a relatively wide range of temperatures. Regarding water conductivity, the exam-

ined plants occurred in waters with an average to high mineral content (90–2790 μS/cm). *Elodea canadensis*, *Nymphaea* cultivar and *Najas guadalupensis* were the only taxa that were occasionally found in slightly acidic waters. Habitats of the other species showed neutral to alkaline pH. Amongst the five species with available water depth data, only *Elodea* species were also able to dwell in deeper waters (> 2 m). The remaining alien plants were recorded in shallow or even very shallow waters (< 0.4 m, *Sagittaria subulata*).

Table 1. List of the alien aquatic plants in Slovakia.

Species / family	FTO	Source of FTO	IS	RT	IM	WT	GO	CEFMS
Alisma subcordatum Raf. / Alismataceae	2017	Hrivnák observed & photo	cas	neo	d	Cold	Am	1
Azolla filiculoides Lam. / Salviniaceae	1951	Hejný (1958)	nat	neo	a	Cold	Am	9
Egeria densa Planch. / Hydrocharitaceae	1993	Somogyi (1995)	nat	neo	d	Therm	Am	1
Eichhornia crassipes (Mart.) Solms / Pontederiaceae	1999	Ružičková (2000)	nat	neo	d	Cold	Am	7
Elodea canadensis Michx. / Hydrocharitaceae	1883	Arpád Degen, BP	nat	neo	a	Cold	Am	58
Elodea nuttallii (Planch.) H. St. John / Hydrocharitaceae	1986	Helena Oťaheľová, SAV	nat	neo	a	Cold	Am	42
Hydrilla verticillata (L. f.) Royle / Hydrocharitaceae	1995	Májský and Rusko (1999)	nat	neo	d	Therm	As	2
Lemna minuta Kunth / Lemnaceae	1997	Feráková and Onderíková (1998)	nat	neo	a	Cold	Am	1
Lemna turionifera Landolt / Lemnaceae	2006	Helena Oťaheľová, CDPR	cas	neo	a	Cold	Am, As	1
Limnophila sessiliflora Blume / Plantaginaceae	1993	Somogyi (1995)	cas	neo	d	Therm	As	1
Ludwigia repens J. R. Forst. / Onagraceae	2017	Nobis et al. (2019)	nat	neo	d	Therm	Am	1
Najas guadalupensis (Spreng.) Magnus / Hydrocharitaceae	1986	Feráková and Kocianová (1997)	nat	neo	d	Both	Am, As	6
Nymphaea L. (cultivar) / Nymphaeaceae	1998	Májský and Rusko (1999)	nat	neo	d	Both	Unk	17
Pistia stratiotes L. / Araceae	2007	Tóthová et al. (2011)	nat	neo	b	Both	Am	10
Sagittaria latifolia Willd. / Alismataceae Vent.	2013	Nobis et al. (2019)	cas	neo	b	Cold	Am	3
Sagittaria subulata (L.) Buchenau / Alismataceae	1995	Májský and Rusko (1999)	nat	neo	d	Therm	Am	3
Shinnersia rivularis (A. Gray) R. M. King & H. Rob. / Asteraceae	1998	Májský and Rusko (1999)	nat	neo	d	Therm	Am	1
Utricularia gibba L. / Lentibulariaceae	1993	Somogyi (1995)	nat	neo	d	Therm	Am, As	1
Vallisneria spiralis L. / Hydrocharitaceae	2011	Košťál in Eliáš (2012)	cas	neo	d	Cold	Af, Am, As	1
Victoria amazonica Sowerby / Nymphaeaceae	1998	Májský and Rusko (1999)	nat	neo	d	Therm	Am	2

Legend: FTO – first time of observation; IS – invasion status, cas – casual, nat – naturalised, inv – invasive; RT – residence time; neo – neophyte; IM – introduction mode, d – deliberate, a – accidental, b – both means; WT – water types, Cold – freshwater, Therm – thermal water, Both – freshwater and thermal water; GO – geographical origin, Af – Africa, Am – America, As – Asia, Unk – unknown; BP – herbarium of the Hungarian Natural History Museum, CDPR – central database of phytocenological relevés of Slovakia, SAV – herbarium of the Institute of Botany, Slovak Academy of Sciences; CEFMS – number of Central European Flora Mapping System grid cells occupied by a species.
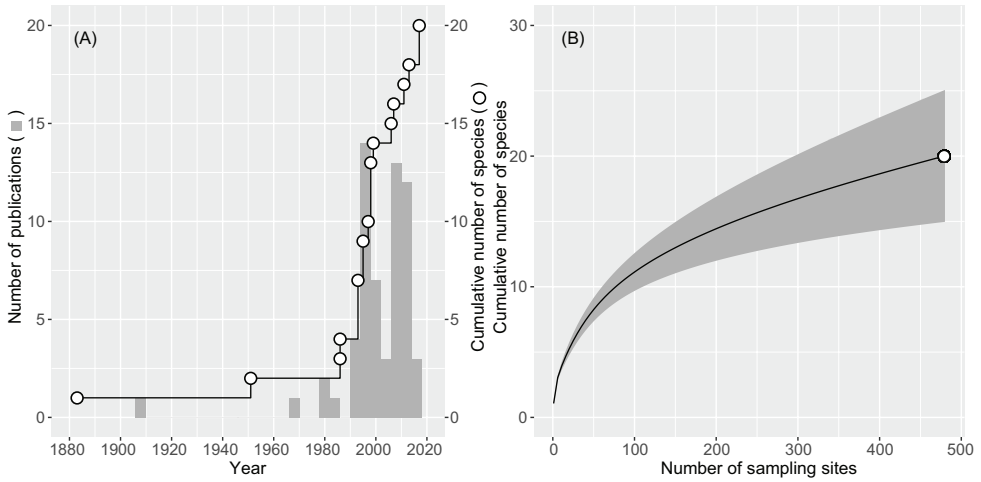
Figure 2. A Temporal trend in the number of studies involving alien aquatic plants (grey histogram) and cumulative number of alien aquatic plants recorded in Slovakia **B** Sample-based rarefaction curve of the number of alien aquatic plant species in Slovakia. The grey area represents the 95% confidence band of the diversity estimate. Full list of studies is given in Suppl. material 1.
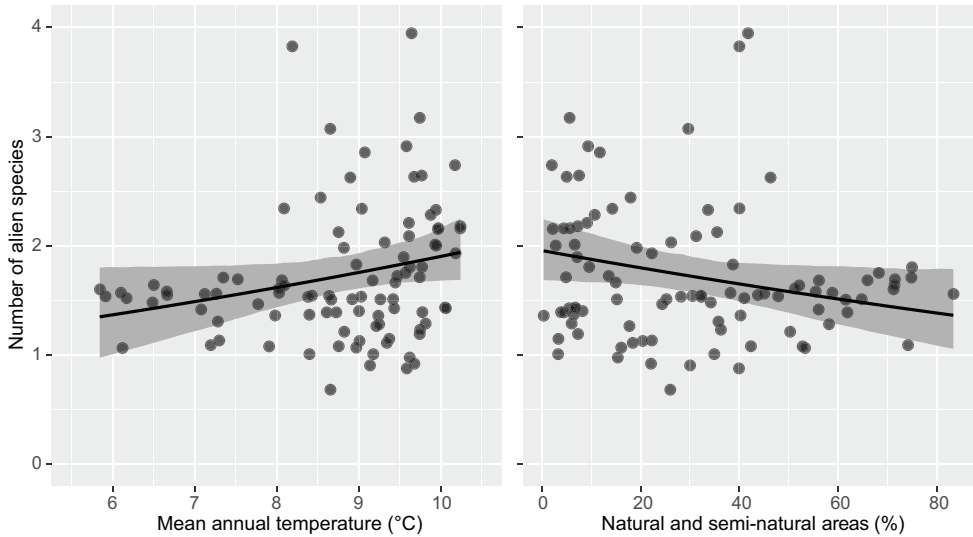

Figure 3. Conwell-Maxwell-Poisson GLM showing a partial relationship between mean annual air temperature, coverage of natural and semi-natural areas and the number of alien aquatic plant species recorded at the scale of the Central European Flora Mapping System with the sampling effort constant at a mean of 4.9 sites. The predicted number of species (line), 95% bootstrap confidence intervals (grey polygon) and partial residuals (points) are displayed.
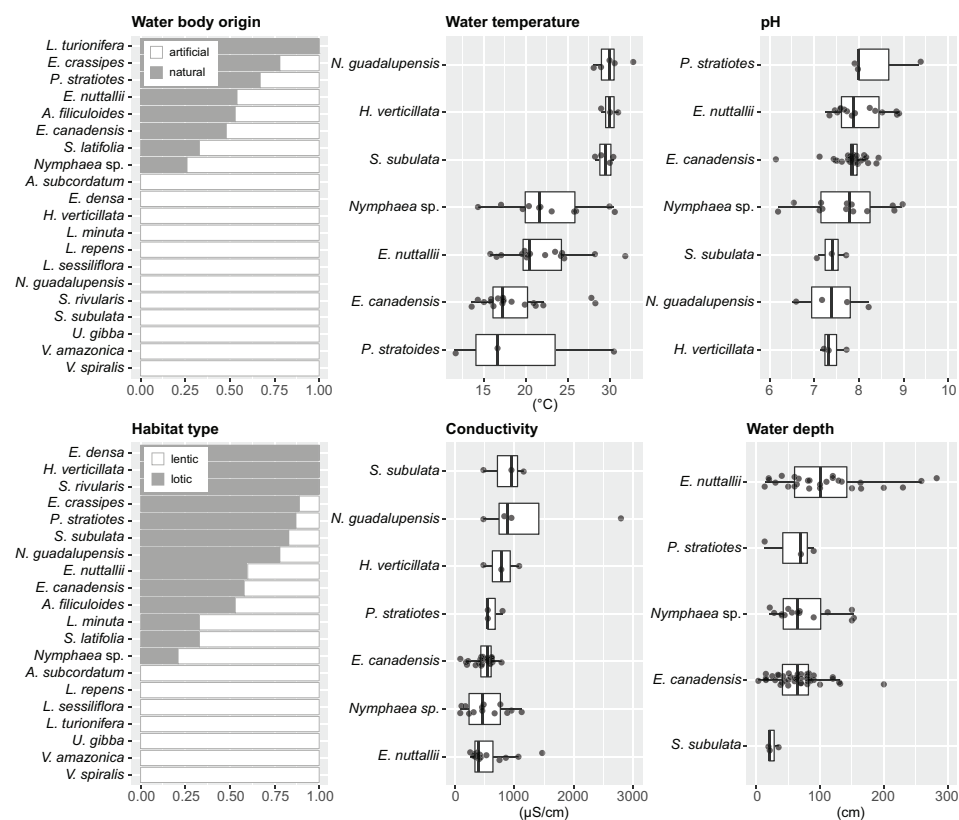
Figure 4. Environmental preferences of alien aquatic plants observed in Slovakia. Bar plots display the relative occupancy of water bodies according to the origin (artificial, natural) and habitat type (lotic, lentic). Boxplots show the occurrence of alien aquatic plants along environmental gradients of water temperature, conductivity, pH and water depth. Only species with at least 3 environmental measurements are plotted. Boxplots display median (line), interquartile range (box), range (whiskers) and observed values (jittered points). Full names of taxa are presented in Table 1.

Table 2. Results of Conway-Maxwell-Poisson GLMs for the effect of climatic and landscape characteristics on the number of alien aquatic plants in the grid cells of the Central European Flora Mapping System. Standardised regression coefficients (β) and dispersion parameters (ν) are displayed along with their 95% bootstrap confidence intervals (95%CI), test statistics (z, χ^2) and probabilities (p). The cross-validated median absolute error of prediction (MdAE) is shown for each model.

Environmental variables	Model coefficients			Dispersion parameters			MdAE
	β (95%CI)	z	p	ν (95%CI)	$\chi^2_{(1)}$	p	
Climate							
Mean annual temperature	0.83 (0.39–1.49)	3.22	0.0013	6.47 (5.12–9.17)	83.79	< 0.0001	0.332
Mean July temperature	0.81 (0.36–1.42)	3.19	0.0014	6.44 (5.02–9.03)	83.56	< 0.0001	0.333
Mean January temperature	0.81 (0.37–1.41)	3.17	0.0015	6.41 (5.10–9.08)	83.26	< 0.0001	0.337
Annual precipitation	-0.88 (-1.59– -0.45)	-3.32	0.0009	6.63 (5.29–9.49)	84.97	< 0.0001	0.381
Landscape							
Road networks	-0.25 (-0.57–0.19)	-0.62	0.5360	5.57 (4.45–7.92)	73.86	< 0.0001	0.421
Urban areas	0.44 (-0.10–0.70)	1.41	0.1579	5.68 (4.43–7.96)	75.15	< 0.0001	0.371
Natural areas	-0.79 (-1.34– -0.39)	-3.32	0.0009	6.48 (4.79–9.43)	84.51	< 0.0001	0.371

Discussion

Inventory of alien aquatic plant species in Slovakia

Our review of published and unpublished data revealed the presence of 20 alien aquatic plant species in Slovakia. The number of recorded species has steeply increased with scientific interest in recent decades (Figure 2). The spatial distribution of alien aquatic plants in Europe shows an uneven pattern (Hussner 2012), which does not fully correspond to the general picture of the climate-driven distribution of alien plants in Europe (Chytrý et al. 2009). Specifically, the highest number of species is known from Italy, France, Germany, Belgium, Hungary, Greece and the Netherlands (Hussner 2012; Brundu et al. 2013; Lansdown et al. 2016). This irregular pattern apparently relates to the intensity of aquatic vegetation research. For example, some southern European countries with Mediterranean climates, such as Albania, Bosnia or Montenegro, lack alien aquatic plant studies, which results in a seemingly low diversity of aliens in the waters (Hussner 2012; Lansdown et al. 2016). In contrast, comprehensive research can reveal surprising results. For example, Hungary hosts 48 species, which represents almost half of the known alien aquatic plants in Europe (Lukács et al. 2016). The high importance of sampling effort is obvious in the case of Slovakia. Intensive research in recent years has led to a steep increase in the number of alien aquatic plants on the national checklist and the last published inventories (Hussner 2012; Medvecká et al. 2012) are therefore outdated. In a broad context, high regional differences in the state of knowledge and research intensity may obscure or even preclude large-scale syntheses on the distribution of alien aquatic plants in Europe.

Given the occurrence of many rare species (singletons and doubletons) in Slovakia, the total number of alien aquatic plants is expected to be much higher (Chao2-bc = 34 species) than observed. We may reasonably assume the presence of several aliens, such as *Cabomba caroliniana* A. Gray, *Elodea callitrichoides* (Rich.) Casp., *Hydrocotyle ranunculoides* L. f., *Lagarosiphon major* (Ridl.) moss or *Pontederia cordata* L., reported from neighbouring countries. For example, *C. caroliniana* has been established for a long time in the Pannonian lowlands (Lukács et al. 2016) occurring along the main river course of the Danube River and along several canals in central Hungary (Király et al. 2008) as well as in a few isolated sites, including the Danube River at the Slovak-Hungary border (Bartha and Király 2015). Similarly, *L. major* and *P. cordata* are known from Hungary and the Czech Republic in the regions bordering Slovakia (Bartha and Király 2015; Kaplan et al. 2016). Other species that are frequent in Europe (e.g. *Crassula helmsii*, *Myriophyllum aquaticum* (Vell.) Verdc.) might also be overlooked or their presence may be limited by specific habitat requirements, which are rarely found in Slovakia (Dawson and Warman 1987; (https://www.cabi.org/ISC/datasheet/16463); (https://www.cabi.org/isc/datasheet/34939); Kasper and Krausch 2008).

Moreover, a broad number of alien aquatic species, mainly aquarium and ornamental plants, could be added to the list of alien aquatic plants in the future due to their potential release to thermal waters, such as small ponds and fountains in thermal spas, canals with thermal wastewater from spas and swimming pools and/or aquarium

waste. The list of these species depends on trade by aquarium and gardening shops. Generally, the pet/aquarium/terrarium trade is responsible for the introduction of numerous alien plants (Padilla and Williams 2004; Brunel 2009). This introduction mode is responsible for the spread of a substantial portion of alien aquatic plants in Europe and America (Maki and Galatovitsch 2004; Hussner et al. 2010; Peres et al. 2018) and was also a main mode of introduction in our study. Therefore, raising awareness about the harmful effects of dumping alien plant species to natural habitats is an important message to the public with the aim of preventing these activities.

Finally, it should be noted that some alien aquatic plants found in Slovakia are considered as invasive alien species of European Union concern (e.g. *Eichhornia crassipes*, *Elodea nuttallii*) and they require legislative attention and adequate prevention and management of their introduction and spread on a national level, as stated in EU Regulation no. 1143/2014.

The effect of climate and landscape characteristics on the diversity of aliens

We have shown that the diversity of alien aquatic plants is significantly linked with climatic conditions. In particular, the number of species increases along gradients of increasing air temperatures and decreasing precipitations. The geographic ranges of many alien aquatic plant species are strongly associated with climatic tolerances set by air temperatures (Kelly et al. 2014; Rodríguez-Merino et al. 2018) and a large number of studies have predicted alien species range shifts and expansions related to climate change (Bellard et al. 2018). In addition, the establishment of viable populations may be limited by temperature-controlled seed production and germination (Vojtkó et al. 2017).

The role of precipitation is less obvious since temperature characteristics and precipitation were strongly correlated in the studied area (Pearson r = -0.78 – -0.87). However, if we combined temperatures and precipitation in a single model or if we used some compound measures, such as climatic moisture index (Willmott and Feddema 1992), predictive performance would be comparable or even worse than in the case of simple temperature models. In other words, beside temperatures, precipitation did not contribute any additional information useful for predictions of alien species diversity. Since a vast majority of the investigated water bodies are permanent with a relatively stable water level, we believe that precipitation does not constrain distribution of alien aquatic plants in the region, as suggested from the grid-level data.

Our results also revealed that landscape with a higher proportion of natural and semi-natural areas supports lower diversity of aliens than intensively managed land. However, we have also shown that plain habitat accessibility to humans, as vectors of dispersal, is not sufficient to explain diversity patterns of aliens, since neither road network coverage nor the proportion of urban areas alone were significantly related with the alien species diversity. Human-mediated landscape effects are likely more complex, involving both accessibility and intensive land use. For example, extensive agricultural cultivation, associated with irrigation channels and elevated nutrient levels, may facili-

tate dispersal and establishment of alien aquatic plant populations (Téllez et al. 2008; Rodríguez-Merino et al. 2018). Similarly, Kelly et al. (2014) identified land use, nutrient levels and natural landscape as the most important factors associated with alien aquatic species ranges at the regional level. Tamayo and Olden (2014) also found that the probability of lake invasion by noxious submerged macrophytes is positively linked with the intensity of land use in the surrounding habitats. Apparently, the areas at greatest risk of invasions by aquatic plants in Europe are those experiencing considerable human pressure (Rodríguez-Merino et al. 2018).

In conclusion, our results reaffirmed the major role of climate and landscape modification in the distribution of alien aquatic plants. We may reasonably expect further increases in alien numbers under ongoing global climate change and land use intensification, especially in the lowlands of southern and eastern Slovakia. Moreover, since elevated temperatures and CO_2 levels are assumed to increase the performance of alien plants more steeply than that of native species (Sorte et al. 2013), aquatic systems may be particularly vulnerable to invasion as climate change proceeds and alien plant species may exert a stronger pressure on native biodiversity and ecosystem functioning than previously thought.

Habitat preferences of aliens

The lack of detailed information on local environmental conditions hampered our ability to draw broad conclusions about the habitat preferences of alien aquatic plant species in Slovakia. However, a few consistent patterns emerged. First, artificial water bodies were more often colonised by alien species than natural habitats and the majority of the species were found exclusively in man-made water bodies. Indeed, this seemingly higher preference of alien species for artificial habitats may partly stem from the fact that many (sub)tropical species are inevitably present only in artificial water bodies with thermal water (e.g. wastewater canals from thermal spas). However, our observations are in agreement with the patterns recorded in the terrestrial realm, where heavily modified and man-made habitats rank amongst the most invaded biotopes in Europe (Chytrý et al. 2009; Medvecká et al. 2014). Disturbed systems are generally more susceptible to invasions due to elevated fluctuations in resource availability (Davis et al. 2000; Hussner et al. 2017). Lower competition by native species in artificial habitats might also play a role (biotic resistance hypothesis, Levine et al. 2004), although evidence for this mechanism is rather weak in freshwaters (Alofs and Jackson 2014; Svitok et al. 2018).

Second, species with available environmental information showed relatively wide environmental tolerances (Figure 4), i.e. they were able to colonise both standing and running waters, tolerate a wide range of pH and conductivity values and, except for (sub)tropical species, span a large gradient of water temperatures. In general, environmental tolerance is a key parameter in the establishment success of introduced alien species (van Kleunen et al. 2015). Svitok et al. (2018) stated that alien aquatic plants

have broad niches, while invaded aquatic environments may not possess environmental constraints that are strong enough to filter alien macrophytes. Consequently, the presence and diversity of aliens may be difficult to predict using habitat properties.

Finally, our research revealed a serious gap in knowledge of alien aquatic plant habitat requirements; only a few species have sufficient records of local habitat quality necessary for sound examination of environmental niches. Therefore, further research should focus on estimating environmental niche breadths and subsequently identifying the potential invasiveness of alien aquatic plants.

Conclusions

Based on a thorough review of published and unpublished resources, 20 alien aquatic species were recorded in Slovakia. However, the presence of many other alien species might be reasonably expected considering (i) a high proportion of rare species (low detectability), (ii) the deliberate introduction of aquarium and ornamental plants and (iii) the positive effect of rising temperatures and intensively modified landscape on alien species diversity. Given ongoing climate change and land use intensification, one can reasonably assume enhanced invasiveness and spreading of alien species into new habitats.

Filling a gap in the recognition of alien aquatic plant environmental tolerances is a challenge for future research. There is also an urgent need for studies on population dynamics, reproductive output, seed-bank characteristics and functional traits of alien aquatic vascular plants, as well as their competitive ability and their interactions with native biota in freshwaters. Finally, raising public awareness and developing adequate management strategies are ultimate conservation goals for maintaining natural aquatic plant diversity and ecosystem functioning.

Acknowledgements

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Supplementary material 1

List of references used for the preparation of a database of alien aquatic plants in Slovakia

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