FOLIA OECOLOGICA – vol. 43, no. 1 (2016). ISSN 1336-5266

Assessment of ornithochory in the north-western part of the Podunajská nížina Lowland (SW Slovakia)

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Abstract

Ružičková, J., Lehotská, B., Kalivodová, E., 2016. Assessment of ornithochory in the north-western part of the Podunajská nížina Lowland (SW Slovakia). *Folia Oecologica*, 43 (Special Issue: A tribute to FJT): 50–63.

Plant seeds and fruits can be dispersed in several ways; diaspore dispersal by ornithochory is common to many plant species. The aim of the study was to assess the birds' potential in dispersal of woody species which are present in the riparian vegetation of two streams with tributaries in the lowland of SW Slovakia. We examined three hypotheses related to riparian woody vegetation: (1) ornithochory plays an important role in the formation of riparian vegetation, (2) riparian vegetation serves as a food source for bird species in highly deforested lowland landscape, (3) there are differences among selected indication groups of woody plant species by types of diaspore dispersal. Four indication groups represent natural alluvial woody vegetation, adjacent forests, other autochtonous woody species and non-native species. Characteristics, such as diaspore type, weight, maturity, and dispersal patterns within four indication groups of woody species were analysed. The occurrence of bird species, feeding strategy and weight categories of birds were assessed. In addition to field research, the data were obtained from the work of Turček "Ecological relationships of birds and woody plants" and from the D^3 Dispersal and Diaspore Database. The results show a high proportion (53%) of plants with fleshy fruits, consequently endozoochory (including ornithochory) appears to be the dominant pattern of diaspore dispersal of riparian woody species of the study area, and the second is anemochory. Evident differences in diaspore dispersal patterns were found within the indication groups. Five bird species participate in dispersal of more than 50% of the assessed woody plants. The analyses showed that a significant share of small-size birds (50–100 g) and large-size birds (500–1,000 g) spread riparian vegetation woody species.

Keywords

birds, diaspore, maturity, riparian vegetation, woody species

Introduction

Plants are usually not able to move from place to place and their seed dispersal depends on external factors (wind, water, animals). Therefore, the course of seed movement after release from the parent plant is so important. Regarding animals, most seeds are dispersed by three classes of vertebrates: birds, mammals (including humans) and reptiles (Traveset et al., 2014). Birds play a significant role in this process, as they are able in their digestive tract or at body surface (e.g. feathers, legs) to carry plant diaspores, even over long distances (Cain et al., 2000; Vittoz and Engler 2007; Nathan et al., 2008). The transfer of fruits and seeds by birds,

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so-called ornithochory, is indeed known, however, this phenomenon should still be examined (Pijl, 1972; Snow and Snow, 1988; Cousens et al., 2008; Pejchar et al., 2008; Traveset and Rodriguez-Perez, 2008; Garcia et al., 2010). As already mentioned by Morellato and Leitão-Filho (1996), numerous ecological factors may contribute to dispersal phenology. Ideally, seed maturation and dispersal would be timed to match the seasonal availability of good dispersal agents (where required) and the availability of good germination conditions. According to Kollmann (2000), the processes associated with the dispersal of fleshy-fruit species include fruit removal, seed rain, seed predation, seed bank dynamics, germination and establishment. In several studies, ornithochory was studied in the context of dispersal phenology (Snow and Snow, 1988; Debussche and Isenmann, 1992; Fuentes, 1992; Guitián, 1998; Hanya, 2005), wintering resources for European frugivores (Jordano and Herrera 1981; Tellería et al., 2005), nature conservation and natural restoration of disturbed areas (e.g. Bengtsson et al., 2003; Howe and Miriti, 2004; Tellería et al., 2005; Hilje et al., 2015). Riparian vegetation along rivers and streams represents an important natural or semi-natural element in the agricultural and urbanised areas of lowlands, but it is also accompanied by non-native species. In the context of riparian vegetation, several studies are aimed at hydrochory but stressed the importance of anemochory and ornithochory (e.g. Merrit and Wohl, 2002; Leyer, 2006; Nilsson et al., 1991, 2010, Parolin et al., 2013).

The aim of the study was to assess the potential of bird species as dispersal agents of woody plants, growing in study sites, representing the riparian vegetation of Stoličný potok and Gidra streams (regional bio-corridors) within the scope of indication woody species groups. As indication groups, native species of riparian vegetation, species of adjacent forests, other native woody species and non-native species were chosen. The mentioned theme has become important due to the disappearance of a large number of trees from the landscape, particularly on agricultural land after the elimination of small hedges and streamside vegetation (Kopecká, 2011; Tóth and Supuka, 2014) and the spread of built-up areas in Slovakia (Šveda and Vigašová, 2010; Ružičková et al., 2011, 2015; Kopecká et al., 2015). According to Supuka et al. (2013), agricultural land covers in Slovakia 50% of the overall territory. In this type of landscape, there is an ongoing intensive anthropogenic activity. One of the partial problems with a significant negative biotic and ecological impact is the rapid decrease in scattered non-forest woody vegetation. Landscape change along the studied streams, monitored over the period 2006–2014 expressed, in particular, at the expense of arable land in favour of built-up areas, indicating a dominant urbanization process (Ružičková et al., 2015). The analyses at the base of the target and other selected indication groups should be used for land-use management and nature protection. As stated by Kontrišová (2006), indication groups of plant species were often used in bio-monitoring for obtaining information on the state of soil and vegetation. According to Burley and Gauld (1995), it is necessary to determine which groups are sensitive to environmental and managerial change. The indication groups of species seem to be a suitable methodological approach for the assessment of forest fragments biodiversity (Reháčková and Ružičková, 2003; Ružičková, 2004); the groups of endangered, protected and forest species as the most sensitive to fragmentation, and on the other hand, synanthropic, invasive and non-native species as indicators of biotope disturbance. Turček (1961a) presented an ecological comparison of riparian vegetation of selected Slovak rivers on the basis of birds and woody species relations. Research of bird communities in riparian stand habitats of two rivers and four streams from the viewpoint of bioindication elaborated Kaňuch (2000). Bird assemblages of linear wood stands in the agricultural landscape of the Podunajská nížina Lowland was studied by Bohuš (2011). Bird diversity of two streams of the Trnavská pahorkatina Upland was elaborated by Kalivodová et al. (2010). In the assessment of ornithochory we applied i.e. the synthetic work of Turček (1961b) "Ecological relationships of birds and woody plants", where the author, a significant Slovak zoologist and ecologist (1915–1977), listed woody plants consumed and transmitted by bird species, and also a list of bird species that feed on various seeds and fruits of plants, and thus contribute to the dissemination and reproduction of various woody species. Turček's work is still cited by several authors who deal with the importance of birds for dissemination of the fruits and seeds of plants in different levels (e.g. Jordano and Herrera, 1981; Snow and Snow, 1988; Barnea et al., 1991; Cramp et al., 1994; Matthysen, 1998; Saniga, 2003; Schaefer and Ruxton, 2011).

In the study area, we examined three hypotheses related to riparian woody vegetation: (1) ornithochory plays an important role in the formation of riparian vegetation, (2) riparian vegetation serves as a food source for bird species in highly deforested lowland landscapes, (3) there are differences among selected indication groups of woody plant species by types of diaspore dispersal. Four indication groups represented natural alluvial woody vegetation, adjacent forests, other autochtonous woody species and non-native species.

Material and methods

Study area

The study area is located in SW Slovakia, in the Trnavská pahorkatina Upland, the north-western part of the Podunajská nížina Lowland (Fig. 1). It represents riparian vegetation of Stoličný potok stream with its

tributaries (the streams Trniansky potok and Vištucký potok) and Gidra stream (with the tributaries of Štefanovský potok and Ronava streams), stemming in the Malé Karpaty Mts, flowing through the Trnavská pahorkatina Upland to the Podunajská nížina Lowland where the Stoličný potok stream flows into the Čierna voda river and Gidra to Dudváh river. The Stoličný potok (38.9 km) and Gidra (38.5 km) streams represent hydric bio-corridors at a regional level (Ružičková et al., 2015). Riparian vegetation of the studied streams (width about 7–15 m) is dominated by Black alder (*Alnus glutinosa*) and Common ash (*Fraxinus excelsior*). Upstream stands were classified as association *Stellario-Alnetum glutinosae* Lohmeyer 1957. Association *Carici remotae-Fraxinetum* Koch in 1926 occurs in bank growths almost at the entire length of the flows at the Trnavská pahorkatina Upland. Locally, stands of non-native tree species of *Robinia pseudoacacia*, added to the association *Chelidonio-Robinietum pseudoacacie* Jurko 1963, were recorded.

Data collection and analysis

An assessment of potential ornithochory was made according to the synthetic floristic and ornithological field research along the streams of the study area. The floristic research of riparian flora and vegetation along the studied streams was realized in 2008–2015. Data collection from the alluvial communities was done by Zürrich-Montpellier phytosociological method (Braun-Blanquet, 1964; Westhoff and Maarel, 1978). Recorded woody plants were analysed within the following four indication groups of woody species: (1) alluvial forests natural woody species; (2) forest species of adjacent forest communities, including characteristic species of oak-hornbeam forests and thermophilous Turkey oak – Sessile oak forests with Lady's mantle (Stanová and Valachovič, 2002; Jarolímek and Šibík, 2008); (3) other autochthonous woody species; (4) alien introduced and invasive species (Benčať, 1982; Medvecká et al., 2012). The periods of fruit maturity and remaining at mother plants were assessed according to field survey and published data (Pagan and Randuška, 1987, 1988; Snow and Snow, 1988; Úradníček et al., 2009). The scientific names of plants were listed by Marhold and Hindák (1998).

The mapping of birds along the studied streams took place from 2008–2015. The occurrence of bird species was assessed according to field research and our own published data (e.g. Kalivodová et al., 2010; Ružičková et al., 2015). During the breeding and migratory seasons, we investigated birds along the Stoličný potok and Gidra streams on selected line transects with a length of 500 or 1,000 m. Transects were determined by the landform, especially near water bodies and in stream parts with riparian vegetation. In total, we established nine transects with a length of 500 m and six transects with a length of 1,000 m (Fig. 1). From 2008–2010, we made these observations on the mentioned transects regularly in the spring (at the time 05:00–09:30 and 16:00–20:00 CET) and autumn migration period (07:00–11:00 and 14:00–18:00 CET). In the other months of the year, we conducted a stationary observation (at least once a month) between water bodies. For bird species, characteristics such as occurrence, weight and prevailing diet were added (Ferianc, 1977, 1979; Kalivodová and Feriancová-Masárová, 1993, 1999; Zuna-Kratky et al., 2000; Danko et al., 2002). The scientific names of birds were listed in accordance with Kovalik et al. (2010).

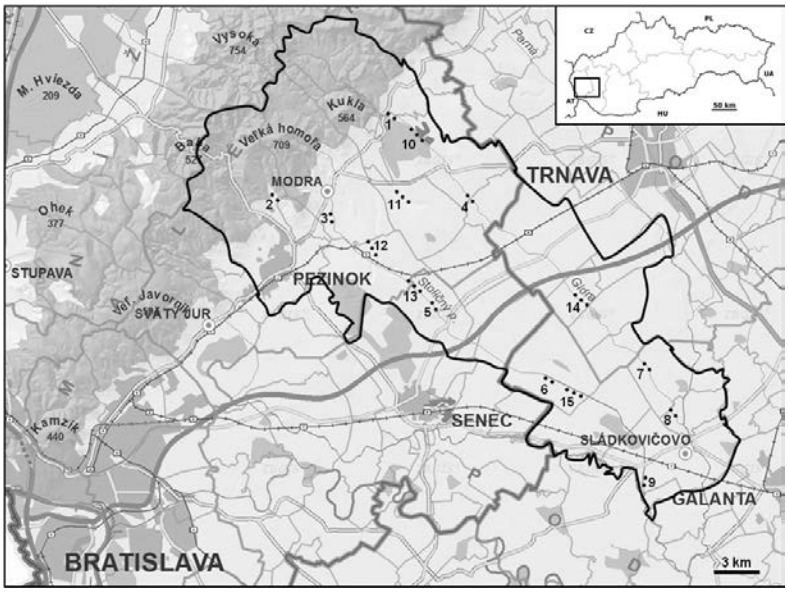

Fig. 1. Study area.

Data from Turček (1961b) were used for identification of bird species spreading the seeds and fruits of recorded woody plant species. Analyses focused on bird species, which potentially transport a minimum of 10% of recorded plant species. The ways of plants' diaspore dispersal were assigned according to Jurko (1990). The author introduced nine types of diaspore dispersal: anemochory, autochory, boleochory, endozoochory, epizoochory, hemerochory, hydrochory, myrmecochory and ombrochory and their combinations for about 2,500 plant species. For each plant species, one or a combination of two or four types of diaspore dispersal and vegetative reproduction is listed. In quantification, all types of diaspore dispersal were counted. Diaspores of the selected plant species were divided into the criteria as diaspore type (fleshy fruit, dry fruit and seed), the amount of nutrients, weight categories and number of seeds per diaspore. Data about diaspore characteristics such as weight and types of fruits were obtained from the D^3 Dispersal and Diaspore Database (Hintze et al., 2013) and from Bojňanský and Fargašová (2007).

Results

Diaspores maturing, availability and dispersal

Riparian vegetation of the study area plays an important function as a habitat and also as a food source for birds. As shown in Fig. 2, woody plants of stream-side vegetation in the studied streams provide seeds, dry and fleshy fruits, which are available as food for birds throughout the year. Fleshy fruits of *Hedera helix* are available year-round. In spring, seeds of *Salix* spp. and dry fruits of *Ulmus* spp. predominate. From June, the maturity of fleshy fruits begins; the most important among them are species with high coverage, abundance and production of fruits such as *Cerasus avium* and *Padus avium*. From August, fleshy fruits of the most abundant shrubs *Sambucus nigra* and *Swida sanguinea* are available. In September, the mature fruits of *Crataegus monogyna, Viburnum opulus, Rhamnus catharticus, Rosa canina* agg. and others predominate. Dry fruits of *Acer* spp., *Corylus avellana* and more are also available. In autumn, seeds of *A. glutinosa* and *R. pseudoacacia* are also accessible. At the edge of riparian vegetation, *C. monogyna, Ligustrum vulgare* and *Prunus spinosa* dominate. In winter, the fleshy fruits of *Viscum album*, found in tree-tops are available.

Endozoochory (including ornithochory) was the dominant pattern of diaspore dispersal of riparian woody species of the study area (Fig. 3). The second most important was anemochory. The other significant type of dispersal was hemerochory which is probably due to anthropogenic influence. Myrmecochory, ombrochory and epizoochory (including ornithochory) appeared to accompany them. In riparian vegetation, a significant presence of hydrochory could be expected for *A. glutinosa*.

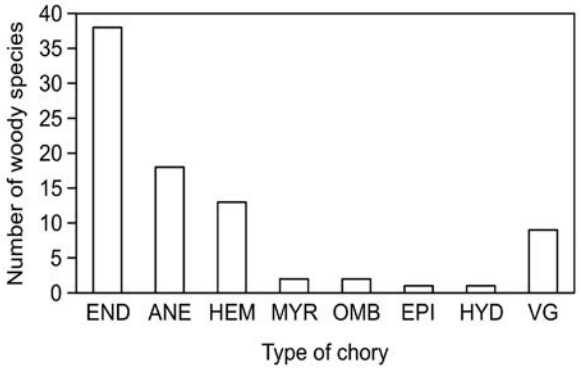

Fig. 3. Presence of diaspore dispersal types (END – endozoochory, including ornithochory, ANE – anemochory, HEM – hemerochory, MYR – myrmecochory, OMB – ombrochory, EPI – epizoochory, including ornithochory, HYD – hydrochory and VG – vegetative reproduction).

Characteristics of the diaspores of the studied woody species

The analyses of diaspore types showed a high proportion (53%) of plants with fleshy fruits (27 of 51). Most of the fleshy fruits had weight over 100 mg (Table 1). Each fleshy fruit and half of the dry fruits are rich of nutrients. Most of the dried fruits had weight less than 100 mg. Diaspores of *Salix* spp. form seeds had weigh less than 0.1 mg. For fleshy fruits, it is common that a higher number of seeds (55%) are present in the fruit. Dry fruits and seeds are mostly monospermous.

Birds' community and species feeding strategies

In the riparian vegetation, we registered 61 woody species, from that 44 tree species, 15 shrub species and two species of lianas, from which seven species were not listed in Turček (1961b). During mapping of the birds, we recorded 64 species of birds in the study area. Analyses were focused on 34 bird species (53%) which potentially transport a minimum of five plant species each of them (Table 3). In terms of the occurrence of bird species in the study area, 17 (50%) bird species were sedentary, of these 12 were breeding in riparian vegetation in the study area and five bird species reach riparian vegetation from the surrounding area. The other 17 bird species (from 34 above-mentioned) belong to migratory species; of these 13 were breeding in riparian vegetation in the study area.

The most preferred types of food of the analysed bird species were categorised like so: 18 species (53%) belonged to insectivorous, 11 species (32%) to omnivorous and five species (15%) to granivorous (Table 3).

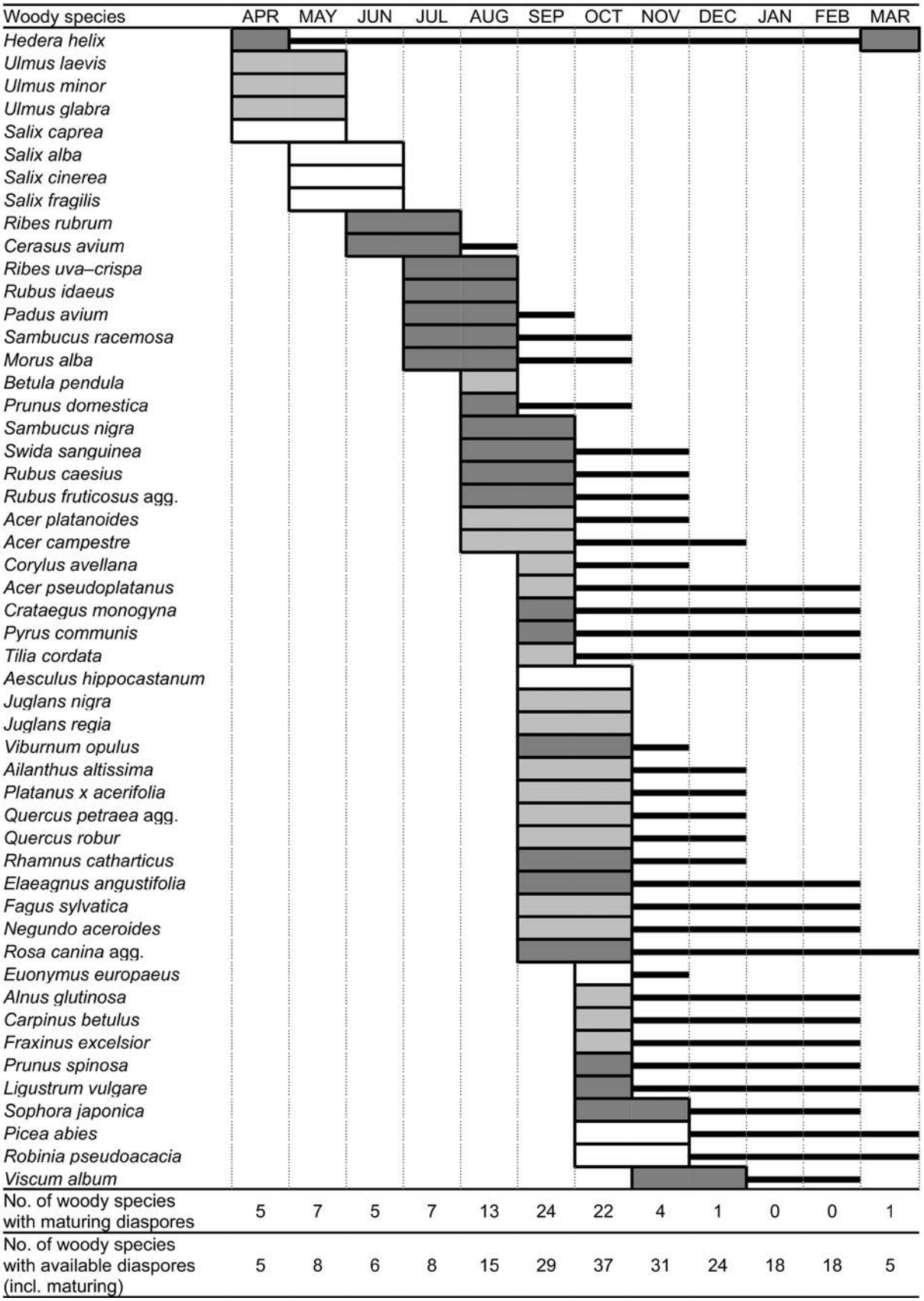

Fig. 2. Schedule of maturing and accessibility of woody species diaspores during the year (white – seeds, light grey – dry fruits, dark grey – fleshy fruits).

Table 1. Characteristics of the diaspores of evaluated woody species.

Diaspore type	Fleshy fruits	Dry fruits	Seeds	Sum
Total number of woody species	27	19	5	51
Number of woody species with significant amount of nutrients	27	11	0	38
Number of woody species without significant amount of nutrients	0	8	5	13
Number of woody species in weight categories of diaspores				
≤0.1 mg	0	0	4	4
0.1–1 mg	0	2	0	2
1–10 mg	0	4	1	5
10–100 mg	2	7	0	9
100–1,000 mg	19	3	0	22
>1,000 mg	6	3	0	9
Number of woody species according to the seeds amount				
1 seed per diaspore	12	18	5	35
2–10 seeds per diaspore	9	1	0	10
11–100 seeds per diaspore	6	0	0	6

Within the categories of most preferred foods, we noticed slight differences between sedentary and migratory species. Among sedentary insectivorous species were species which in the breeding season feed mainly on insects (on various development stages). This group included species such as *Parus major*, *Cyanistes caeruleus*, *Poecile palustris*, *Dendrocopos major*, *Dendrocopos medius*, *Dendrocopos syriacus* and *Sitta europaea*. Omnivorous species living in the study area feed on plant and animal food during the year. In spring, animal food (insects, molluscs, spiders etc.) are predominant, later, the green parts of plants; in winter, fruits and seeds.

The majority of migratory species in the study area (11 of 17) were insectivorous (e.g. *Erithacus rubecula*, *Oriolus oriolus*, *Sylvia* sp.). Most of them arrive when they can already find different stages of insects and depart when the insects are less abundant. Omnivorous migrants comprised four species of thrushes (*Turdus merula*, *Turdus philomelos*, *Turdus pilaris*, *Turdus viscivorus*), which consume a diversity of animal foods (earthworms, insects, larvae, pupae, molluscs, spiders etc.) and a variety of fruits, especially berries. Granivorous species comprised two of the identified migratory birds *Columba palumbus* and *Carduelis spinus*. Although they consume insects, they also prefer vegetable ingredients of food, mostly different seeds mainly in winter period.

Birds' size and diaspore dispersal

More than half of the studied 34 bird species (68%) were small-sized, weigh up to 100 grams (50% weigh up to 50 grams and 18% 50–100 g). Medium-sized birds (100–500 g) represented 20%. Bigger birds made up only 12% (6% weighing 500–1,000 g and 6% more than 1,000 g). In the study area, small-sized birds up to 50 g (17.5%) contributed to the transfer of 45 woody species (88%). In this category, there was a high difference between the minimal (5) and maximal (33) number of plants, dispersed by one bird, while the average number was 17 (Fig. 4). Birds in the weight categories of 50–100 g and 500–1,000 g made up a significant share of diaspore dispersal.

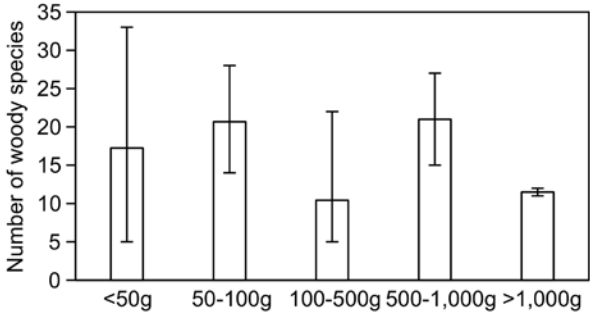

Fig. 4. Average number of woody plants dispersed by one bird species (with marked minimum and maximum values) in the selected bird's weight categories.

Indication groups of woody plant species

Woody species composition follows the character of landscape through which the streams flow. In the riparian vegetation, typical alluvial species occurred in addition to forest species, typical of oak-hornbeam forests, especially in the Malé Karpaty Mts, where the streams

begin. The Gidra and Vištuk streams overflow near the turkey oak-sessile oak forest fragment Lindava. The Stoličný potok stream flows near the forest fragments Šenkvický háj and Martinský les, representing Euro-Siberian steppe oak woods. Streams in the long section run down the intensively used agricultural landscape with the current trend of settlement growth, which is reflected in the appearance of introduced non-native and invasive woody plants. The analyses showed well-marked differences in diaspore dispersal type and strategy among four selected indication groups (IG1–IG4) of woody species (Table 2) as follows.

Table 2. The selected indication groups of woody plants

Indicator groups of woody species	Characteristics	Woody plant species	No. of species
IG1 – alluvial forests woody species	Ash-alder alluvial forests natural plant species	*Alnus glutinosa*, *Fraxinus excelsior*, *Padus avium*, *Salix alba*, *S. caprea*, *S. cinerea*, *S. fragilis*, *Ulmus laevis*, *Viburnum opulus*	9
IG2 – characteristic species of adjacent forest communities	Oak-hornbeam forests species	*Acer platanoides*, *A. pseudoplatanus*, *Carpinus betulus*, *Cerasus avium*, *Corylus avellana*, *Euonymus europaeus*, *Fagus sylvatica*, *Swida sanguinea*, *Tilia cordata*	16
	Thermophilous turkey oak-sessile oak forests and forest mantle species	*Acer campestre*, *Crataegus monogyna*, *Prunus spinosa*, *Quercus petraea* agg., *Q. robur*, *Rhamnus catharticus*, *Ulmus minor*	
IG3 – other autochthonous woody species	Other native woody species	*Betula pendula*, *Hedera helix*, *Ligustrum vulgare*, *Picea abies*, *Prunus domestica*, *Pyrus communis*, *Ribes rubrum*, *R. uva–crispa*, *Rosa canina* agg., *Rubus caesius*, *R. fruticosus* agg., *R. idaeus*, *Sambucus nigra*, *S. racemosa*, *Ulmus glabra*, *Viscum album*	16
IG4 – non-native introduced and invasive species	Introduced species	*Aesculus hippocastanum*, *Elaeagnus angustifolia*, *Juglans nigra*, *J. regia*, *Morus alba*, *Platanus x acerifolia*, *Sophora japonica*	10
	Non-native invasive species	*Ailanthus altissima*, *Negundo aceroides*, *Robinia pseudoacacia*	

IG1) alluvial forests woody species (18%) – The group IG1 included nine tree and shrub species, typical for ash-alder alluvial forests. The riparian vegetation of the studied streams is dominated by *A. glutinosa*, in which dry diaspores are distributed by anemochory, combined with endozoochory, hydrochory and myrmecochory. Species with dry fruits are also present, such as *F. excelsior* and *Ulmus laevis* and several species of *Salix* spp. (Table 2) with lightweight seeds, well-adapted to anemochory. Fleshy fruits are typical for two species – *P. avium*, in which stone fruits mature in July, and *V. opulus* with fruits mature in September. In comparison with the other indication groups, seeds and dry fruits (Fig. 5) dominated among diaspores of IG1, resulting in the highest presence of anemochory (78%). The share of endozoochory (including a combination with anemochory) is about 50% (Fig. 6). In relation to ornithochory (including endozoochory and epizoochory), 28 bird species foraged and dispersed diaspores of nine woody species of riparian vegetation. Amongst the birds, 82% were breeding species, 71% represented small species in weight categories < 100 g. In spite of this, a very important distributor in the group IG1 was the large-sized bird *Anas platyrhynchos*, which spreads five of nine plant species (*A. glutinosa* and *Salix* spp.). The other considerable diaspore distributors were four bird species (Table 3): *Phasianus colchicus* (weight category > 1,000 g), *T. merula*, *Pica pica* (100–500 g) and small-size *Carduelis chloris* (<50 g).

IG2) forest species of adjacent forest communities (31%) – The group IG2 consisted of 16 species, typical for adjacent oak-hornbeam and Turkey oak – Sessile oak forests. Dry fruits such as acorns, nuts, nutlets and samaras are characteristic for forest species.

As is shown in Fig. 5, stream banks mainly reach species with dry fruits such as *Acer platanoides*, *A. pseudoplatanus*, *C. betulus*, *Fagus sylvatica*, *Quercus petraea* agg., *Q. robur* and *C. avellana* (Table 2). Species with fleshy fruits were also recorded, among them the shrubs *Euonymus europaeus*, *S. sanguinea* and *R. catharticus* prevailed. *E. rubecula*, *Turdus* spp. and *Sylvia borin* prefer fleshy fruits. A high share of endozoochory (87.5%), in combination with anemochory (Fig. 6), was characteristic for species in IG2. In the distribution of 16 woody plants of IG2, 32 bird species were involved, of which 75% bred there. In the distribution of trees and shrubs, small-sized birds (66%) potentially participated, but also large and medium-sized bird species (34%). The five most important distributors in the group IG2, which distributed 10–13 plant species from 16, were represented by different weight categories; the large-sized bird *Phasianus colchicus* (weight category > 1,000 g), the medium-sized bird species *G. glandarius* (100–500 g) and the small-sized species *D. major*, *P. major* and *S. europaea* (<100 g). All of them were sedentary species (Table 3). All five of the above

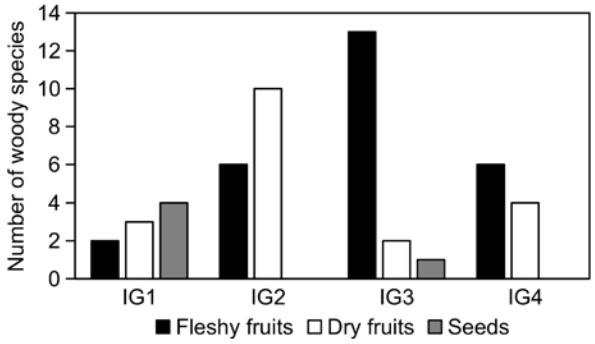

Fig. 5. Types of fruits within the indication groups of plants (IG1 – alluvial forests woody species, IG2 – forest species of adjacent forest communities, IG3 – other autochthonous woody species, IG4 – non-native introduced and invasive species).

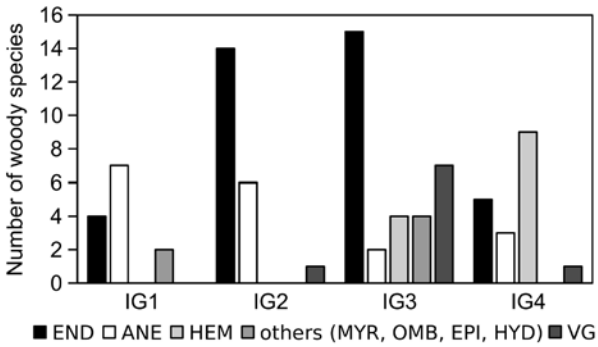

Fig. 6. Diaspore dispersal types within the indication groups (IG1–IG4, see Fig. 5) of plants (END – endozoochory, including ornithochory, ANE – anemochory, HEM – hemerochory, MYR – myrmecochory, OMB – ombrochory, EPI – epizoochory, including ornithochory, HYD – hydrochory and VG – vegetative reproduction).

mentioned bird species were involved in distribution of the following eight plant species: *C. avellana*, *Tilia cordata*, *Q. petraea* agg., *Q. robur*, *A. pseudoplatanus*, *C. betulus*, *C. avium* and *F. sylvatica*. From migratory birds significant are *Ficedula coelebs*, *Sylvia atricapilla*, *T. pilaris*, *T. philomelos*, *T. viscivorus* and *C. palumbus*, participating in the distribution of six–nine plant species from 32.

IG3) other autochthonous woody species (31%) – The group IG3 consisted of 16 widespread native woody species, of which all the 34 bird species participated in the distribution (Table 2, 3). Fleshy fruits such as drupes and berries are typical for the majority of the plant species (81%). In lower proportions, dry fruits and seeds (Fig. 5) are present. In terms of diaspore dispersion in IG3, endozoochory dominated in combination with a wider range of diaspore dispersal patterns, including epizoochory and anemochory (Fig. 6). Compared with the other indication groups in IG3, there is a high proportion of vegetative reproduction which is typical especially for shrubs as *L. vulgare*, *Rubus* spp. and *S. nigra*. In the group IG3, the most important distributors (10) which contributed to the spread of 9–12 plant species from 16, were medium-sized birds (weight category 100–500 g) such as *G. glandarius*, *P. pica*, *T. merula*, *T. pilaris* and *C. palumbus*. Among small-sized species (<100 g), *E. rubecula*, *P. major*, *S. atricapilla* and *T. philomelos* contributed significantly (Table 3). All 10 bird species participated in the distribution of the following five plant species: *L. vulgare*, *Rubus caesius*, *R. idaeus*, *S. nigra* and *S. racemosa*.

IG4) non-native introduced and invasive species (20%) – The group IG4 included 10 non-native tree species, introduced as ornamental and fruit trees, three of them are also invasive (Table 2). Diaspore dispersal patterns respond to outlandish origins and types of fruits (Fig. 5). Plant species were primarily introduced by people; therefore hemerochory dominated. Fleshy fruits slightly prevail over dry fruits; consequently, endozoochory is more frequent in the group than anemochory (Fig. 6). 30 bird species from IG4 foraged and dispersed diaspores of ten non-native woody species. Altogether, six woody species (from 10) were potentially transported by two medium-sized bird species, *G. glandarius* and *T. merula*. Significant dispersal agents were also birds which transport three woody species such as *P. pica* and *C. palumbus* and small-sized birds such as *D. major*, *F. coelebs*, *P. major*, *S. atricapilla* and *Sturnus vulgaris* (Table 3).

Discussion

In the context of riparian vegetation, several studies are aimed at hydrochory but stressed the importance of anemochory and ornithochory (e.g. Nilsson et al., 1991, 2010; Merrit and Wohl 2002; Leyer, 2006). Our results showed that woody species in the studied

Table 3. Characteristics of analysed bird species and their potential of diaspores dispersal within the indication groups of plants

Bird species	Occurrence	Breeding	Prevailed food type	Weight (g)	No. of woody species spread by birds				
					IG1	IG2	IG3	IG4	Sum
Garrulus glandarius	S	N	O	100–500	1	13	12	6	33
Phasianus colchicus	S	B	O	>1,000	3	13	12	2	31
Parus major	S	B	I	<50	1	13	11	3	29
Turdus merula	M	B	O	100–500	3	8	12	4	28
Pica pica	S	B	O	100–500	3	8	12	3	27
Fringilla coelebs	M	B	I	<50	2	9	8	3	23
Sitta europaea	S	B	I	<50	2	13	6	2	23
Sylvia atricapilla	M	B	I	<50	2	6	10	3	23
Turdus philomelos	M	B	O	50–100	1	6	12	3	22
Turdus pilaris	M	N	O	100–500	2	6	11	1	22
Columba palumbus	M	B	G	100–500	1	6	9	3	21
Dendrocopos major	S	B	I	50–100	1	10	7	3	21
Cyanistes caeruleus	S	B	I	<50	1	9	8	1	20
Erithacus rubecula	M	B	I	<50	2	6	9	2	20
Poecile palustris	S	B	I	<50	2	8	6	1	17
Sturnus vulgaris	M	B	I	50–100	–	6	7	3	17
Turdus viscivorus	M	N	O	100–500	1	5	8	1	17
Carduelis chloris	S	B	G	<50	3	7	4	2	16
Corvus frugilegus	S	N	O	500–1,000	–	7	5	3	15
Sylvia borin	M	B	I	<50	1	4	8	1	14
Corvus cornix	S	N	O	500–1,000	–	4	6	2	12
Oriolus oriolus	M	B	I	50–100	1	1	8	2	12
Coloeus monedula	S	N	O	100–500	–	5	5	1	11
Dendrocopos medius	S	B	I	50–100	–	7	3	–	10
Sylvia curruca	M	B	I	<50	1	2	5	2	10
Sylvia communis	M	B	I	<50	1	2	6	–	9
Anas platyrhynchos	S	B	O	>1,000	5	2	1	–	8
Hippolais icterina	M	B	I	<50	1	2	4	1	8
Passer montanus	S	B	G	<50	1	2	2	2	8
Muscicapa striata	M	B	I	<50	1	1	3	2	7
Carduelis spinus	M	N	G	<50	1	1	3	1	6
Carduelis carduelis	S	B	G	<50	2	–	2	1	5
Dendrocopos syriacus	S	N	I	50–100	–	2	1	2	5
Phoenicurus phoenicurus	M	N	I	<50	1	–	4	–	5

S, sedentary (year-long) species; M, migratory species; B, species breeding in the study area; N, species non-breeding in the study area; I, insectivorous species; G, granivorous species; O, omnivorous species; IG1–4, indication groups of woody species 1–4.

riparian vegetation benefit from different types of diaspore dispersal, dominated by endozoochory (including ornithochory). The second most important is anemochory, especially in the indication group of alluvial plant species. For the five assessed woody species in which diaspore are dispersed primarily by anemochory and endozochory (Jurko, 1990), anemochory's and hydrochory's ranking index is listed in D³ Database

(Hintze et al., 2013). Diaspores of *Betula pendula*, *Salix fragilis* and *Acer pseudoplatanus* are well-adapted for anemochory and hydrochory, lower ranking index values for anemochory and especially for hydrochory were given for *Carpinus betulus* and *F. excelsior*. As stated by Drezner et al. (2001), wind-dispersed species are proportionally more abundant in the pioneer *Populus-Salix* community. According to Fér (2013), seeds dispersal patterns (by water or wind) and their ability to float play an important role in the migration of aquatic and coastal plants in rivers and strongly influence the genetic variability on the landscape level. Plant species diaspores which are distributed by water float mainly in a one-way direction along a flow. On other hand, plant diaspores, which are dispersed by wind, are transfered along river corridors, but more common is dispersion among streams or river basins. After Hampe (2004), the influence of water dispersal decreases upstream, and birds remain the most reliable dispersal agents in the uppermost reaches. They are also indispensable for any seed dispersal upstream or between different streams.

In the study area, more than half of the bird species were small-sized, weighing up to 100 grams. Similarly, Herrera (1984) noted that the bird assemblage of southern Spain shows a higher proportion of small-sized species. He suggested that the dense vegetation structure, the mild climate and the abundance of energy-rich fruits are favourable to these small-sized species. Regarding the major diaspores distributors, Debussche and Isenmann (1992) reported from their study site in Montpellier (France), dominated by *Quercus ilex* and *Viburnum tinus*, more or less the same species we recorded in the riparian vegetation of the Podunajská nížina Lowland. In the suburb of Montpellier, small-sized passerines *S. atricapilla* and *E. rubecula* were by far the major dispersers. Thrushes *T. merula* and *T. philomelos* were the two most frequent medium-sized dispersers. The small-sized (<30 g) *P. major*, *C. caeruleus*, *F. coelebs*, *C. carduelis* and *C. chloris* were the major fruit-consumers. In the oak-turkey oak forest fragment Lindava in the Podunajská nížina Lowland, the most frequent diaspore distributors were *C. coccothraustes*, *G. glandarius*, *P. major*, *P. colchicus*, *S. europaea*, *P. pica*, *T. merula*, *D. major*, *F. coelebs*, *C. palumbus*, *C. caeruleus*, *T. philomelos* and *T. pilaris* (Gulyášová and Ružičková, 2013).

Jordano et al. (2007) found that although small-sized birds (<110 g) were by far the major seed dispersers of fleshy fruits seeds which were moved up to 250 m, larger frugivores (110–500 g) were the major dispersers of seeds that were moved between 250–990 m. Medium-sized birds (*T. viscivorus* and *Corvus corone*) contributed to short-distance dispersal (to 100 m), but they dispersed most seeds beyond 100 m. In contrast, small birds rarely dispersed seeds more than 100 m. By applying the conclusions of Jordano et al. (2007) in the study area, large and medium-size bird species (Table 3) belong to important distributors, which are able to spread plants' diaspores to longer distances. Vittoz and Engler (2007) elaborated typology of dispersal distances for seven dispersal types. Dispersal distance for endozoochory (seeds eaten by birds and large vertebrate) 400–1,500 m was estimated as the upper limit of the distances within which 50% and 99% of the seeds of a plant population are dispersed.

Snow and Snow (1988) presented in detail 43 plant species connected to 19 bird species in Southern England; 17 plant species were common and were found in our study area as well. Fleshy-fruited plants in the northern temperate zone commonly produce mature fruit crops in late summer and autumn when avian frugivores are usually abundant, however, a little further south, more fruit maturation occurs in winter when flocks of wintering migrant birds are foraging. According to Turček (1961b) in the dissemination of fleshy fruits of lianas *H. helix* and *V. album*, participated *T. merula*, *T. philomelos*, *T. viscivorus*, *S. vulgaris* and *S. atricapilla*. The mentioned species were observed by Snow and Snow (1988) in the period from December to May when fruits of *H. helix* were consumed. From granivorous species, the wood pigeon (*C. palumbus*) was observed to have eaten ripe and unripened fruits. According to Snow and Snow (1998), feeding on *V. opulus* fruits was observed in winter (December, January), in which *T. philomelos* was involved and *Pyrrhula pyrrhula*, from granivorous birds, made up a significant percentage.

The feeding strategy of birds depends on the seasons (Hume, 2002). In the period of breeding, they focus on insects which are often preferred by explicitly granivorous or omnivorous bird species. In the non-breeding season, they adapt to the available nutrition options. In the non-breeding season, tits feed also on the seeds of trees and plants as well as berries, fruits etc. (Glutz von Blotzheim and Bauer, 1993). In autumn and winter, woodpeckers feed on the seeds of coniferous and deciduous trees and nuthatches feed on insects and plants seeds (Glutz von Blotzheim and Bauer, 1994). Granivorous species (*Carduelis chloris*, *Passer montanus*, *Carduelis carduelis*) prefer different seeds throughout the year, even when feeding their offspring, and later feed on grain softened in crops (Snow and Snow, 1988).

Seed dispersal events take place within complex natural landscapes. As those landscapes are fragmented over time, the ability of seeds to move long distances may be reduced (Cain et al. 2000). Riparian zones might act as a refuge for bird populations in times of disturbance and as a stock of genetic biodiversity that can potentially be redistributed throughout fragmented landscapes by means of ornithochory (Bell et al., 2009). According to Garcia et al. (2010), temperate frugivorous birds should be classified as effective suppliers of the seed-dispersal ecosystem service on

the landscape scale. The authors encourage conservationists and land managers to explicitly consider such a classification if they aim to develop integrative plans focused on specific species or target habitats and on the ecological interactions driving ecosystem fluxes.

Conclusions

The obtained results confirmed the specified hypotheses. Ornithochory plays important role in the formation of riparian vegetation of the study area. The 34 assessed bird species are the significant distributors of trees' and shrubs' diaspores within riparian vegetation, as well as among the streams, adjacent forest fragments and non-forest woody vegetation. On the other hand, woody plants of riparian vegetation in the study area provide seeds, dry and fleshy fruits which are available as food for birds throughout the year. In April and May, the maturity of dry fruits and seeds prevail, in summer, fleshy fruits dominate and in autumn, dry and fleshy fruits are available. More than half of the evaluated bird species (34) are small-sized birds (68%), weighing up to 100 grams. The average number of woody species, transferred by one bird species in the given size category, shows a significant share of small-sized birds in the weight category 50–100 g and large-sized birds (500–1,000 g). From the viewpoint of biodiversity protection and management evident differences among the four indication groups in seed dispersal appear to be significant. Among diaspores of alluvial forests woody species (indication group IG1), seeds and dry fruits were dominant which resulted in the highest presence of anemochory (78%). The share of endozoochory (including ornithochory) is about 50%. In the stream banks, we also recorded species of adjacent forest communities (IG2), for which dry fruits are typical. For forest species in IG2, a high share of endozoochory (87.5%) is characteristic in combination with anemochory. In terms of diaspore dispersion of autochthonous woody species (IG3), endozoochory dominates in combination with different diaspore dispersal patterns, including epizoochory and anemochory. In comparison with the other indication groups, endozoochory is the most widely used (93.8%) in IG3. In the distribution of non-native tree species (IG4), hemerochory prevails as was expected. Fleshy fruits slightly prevail over dry fruits; consequently, endozoochory is more frequent in the group as anemochory. All methods of plants' diaspore dispersal are important for maintaining diversity in deforested agricultural landscape. The results were obtained through joint interdisciplinary research; our synthetic study is a contribution to this issue and methodical approach to tackling the topic. Tree and shrub stands along the studied streams are ecologically significant linear elements in the agricultural and urbanised landscape of the Podunajská nížina Lowland. During the constant changes of the surrounding landscape, such spaces become refuges for many plants and bird species that not only find shelter and food there, but are also stopping points for migratory birds. The results confirm the importance of the studied streams for nature conservation as hydric biocorridors, which serve as essential habitats for birds.

Acknowledgements

This research was funded with KEGA grant No. 070UK-4/2015. The authors thank to Canadian lecturer Michael Sabo for his help with the English improvement.

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Received March 16, 2016
Accepted June 1, 2016