

See discussions, stats, and author profiles for this publication at:
<https://www.researchgate.net/publication/323477245>

Plant dispersal strategies: a new classification based on multiple dispersal modes of individual species

Article in *Preslia* · March 2018

DOL: 10.23855/preslia.2018.001

CITATIONS

0

READS

302

4 authors, including:



Petr Pyšek

The Czech Academy of Sciences

484 PUBLICATIONS 29,840

CITATIONS

SEE PROFILE



Jan Pergl

Institute of Botany, The Czech ...

179 PUBLICATIONS 7,196

CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



The role of rivers in maintaining biodiversity of African savannas [View project](#)



Detection and monitoring of invasive plant species using remote sensing [View project](#)

All content following this page was uploaded by [Petr Pyšek](#) on 01 March 2018.

The user has requested enhancement of the downloaded file.

Plant dispersal strategies: a new classification based on the multiple dispersal modes of individual species

Strategie šíření rostlin: nová klasifikace založená na existenci více způsobů šíření u téhož druhu

Jiří Sádlo¹, Milan Chytrý², Jan Pergl¹ & Petr Pyšek^{1,3}

¹*The Czech Academy of Sciences, Institute of Botany, Department of Invasion Ecology, CZ-252 43 Průhonice, Czech Republic, e-mail: jiri.sadlo@ibot.cas.cz, jan.pergl@ibot.cas.cz, pysek@ibot.cas.cz;* ²*Department of Botany and Zoology, Masaryk University, Kotlářská 2, CZ-611 37 Brno, Czech Republic, e-mail: chytry@sci.muni.cz;* ³*Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-128 44 Praha 2, Czech Republic*

Sádlo J., Chytrý M., Pergl J. & Pyšek P. (2018): Plant dispersal strategies: a new classification based on the multiple dispersal modes of individual species. – *Preslia* 90: 1–22

The diaspores of vascular plants are transported by vectors from which the dispersal modes are inferred, such as anemochory as a spread by wind. Traditionally, each species was assigned a single dispersal mode, based on the morphology of its diaspore; for example the presence of pappus indicated anemochory. In this paper we present a different approach to plant dispersal, based on the fact that plant species are spread by multiple vectors that differ in terms of how frequently they are employed and how efficiently they work. The combinations of dispersal modes are repeated in species with similar ecology and diaspore morphology. For example, for species in wetland and riparian habitats (e.g. those of the genera *Phragmites*, *Typha* and *Salix*) that have very small seeds with hairy flying apparatus, dispersal by both wind and water is important, but the seed can also attach to animal fur or human clothes and a portion of seed fall close to the parental plant. Even such less common dispersal modes contribute to species' spread and cannot be disregarded. To characterize such combinations of dispersal modes occurring repeatedly with different frequencies, we propose here the concept of 'dispersal strategies'. We tested this approach by using the flora of the Czech Republic, excluding rare alien species and the majority of hybrids. The data on the type and morphology of above-ground diaspores and on dispersal modes of plant species were obtained from the literature and databases, and completed by expert knowledge based on personal observations. Where the data was lacking, the taxa were assigned a dispersal strategy based on that of their relatives with similar seed. We describe nine dispersal strategies that are defined by the combinations of dispersal modes and their relative importance, and named after representative genera: *Allium*, *Bidens*, *Cornus*, *Epilobium*, *Lycopodium*, *Phragmites*, *Sparganium*, *Wolffia* and *Zea*. We related these strategies to the origin status, invasion status and habitat affinities of their representatives. The majority of the taxa in the Czech flora (92.8%) are dispersed exclusively by generative diaspores, in 4.5% generative and vegetative diaspores are combined, 0.7% rely exclusively on vegetative diaspores and the remaining 2.0% (*Zea* strategy) do not produce viable above-ground diaspores and spread exclusively by below-ground organs (which were not considered as vegetative diaspores in our system) or with human assistance. Native species are statistically significantly more represented in the *Epilobium*, *Lycopodium*, *Sparganium* and *Wolffia* strategies, while alien species are over-represented in the *Allium*, *Bidens* and *Zea* strategies. The *Allium* strategy is the commonest in the Czech flora, despite being the least specialized, hence seemingly poorly equipped for successful dispersal. This indicates that morphological adaptations for dispersal by natural vectors might be less important for plants than previously thought.

K e y w o r d s: anemochory, Czech Republic, database, dispersal mode, dispersal vector, hydrochory, temperate flora, vascular plants, zoochory

Introduction

Vascular plants have evolved a broad range of modes of dispersal, relying on different dispersal vectors such as wind, water or animals (Eriksson & Kiviniemi 2001). Studies of plant dispersal have a long tradition in botany and plant ecology (Sernander 1927, Ridley 1930, van der Pijl 1982), because knowledge of dispersal strategies is important both for understanding the processes of plant evolution and for explaining current distribution of plants across landscapes, as well as predicting future changes.

Almost a century ago, Sernander (1927) introduced the term ‘diaspore’ for the plant particles that are dispersed, regardless of their morphological origin. Diaspores can be both generative, such as spores, seed or fruit, and vegetative such as fragments of stems, stolons, rhizomes or bulbils (van der Pijl 1982). In the literature, the diaspore is called by a number of synonymous terms: propagule, disseminule, dispersule (Pérez-Harguindeguy et al. 2013, Garnier et al. 2017), germule, migrule or chore (van der Pijl 1982).

The descriptions of plant dispersal are usually simplified by assigning plant species to dispersal modes (also called ‘dispersal syndromes’; Pérez-Harguindeguy et al. 2013), which refer to the transport of diaspores by different vectors. Dispersal modes include categories such as anemochory (dispersal by wind), hydrochory (by water), epizoochory (= exozoochory; by attachment to an animal’s body), endozoochory (by animals via ingestion) or anthropochory (by humans) (Poschlod et al. 2013, Thorsen et al. 2009). Assignments of north-western and central-European plant species to such dispersal modes reported in the literature were collected in the LEDA database (Kleyer et al. 2008). Such assignments have traditionally been inferred from presumed relationships between certain diaspore- or plant traits and dispersal modes (e.g. Hughes et al. 1994, Thomson et al. 2010), for example presence of plumed pappus in some *Asteraceae* species has been considered to be an indication of anemochory, presence of hooks on fruits or infructescences (e.g. in *Arctium* or *Geum*) an indication of epizoochory, or presence of elaiosome on seeds (e.g. in *Luzula* or *Viola*) a sign of myrmecochory, i.e. dispersal by ants.

Some recent studies rigorously tested these assumptions, by measuring traits such as diaspore weight (Thomson et al. 2011), terminal velocity (Tackenberg et al. 2003), buoyancy (Boedeltje et al. 2003), ability to attach and remain attached to animal fur (Römermann et al. 2005, Moravcová et al. 2010) and germination after endozoochoric transport (Cosyns et al. 2005). Considerable progress has been made in collecting data on these and other traits that are potentially related to dispersal modes, and in assembling them in databases such as Diasporus (Bonn et al. 2000), BiolFlor (Klotz et al. 2002), BioPop (Poschlod et al. 2003), LEDA (Kleyer et al. 2008) and D³ (Hintze et al. 2013). Still, the relationships between these easily measurable (“soft”) traits and actual dispersal modes remain largely elusive for many plant species.

Another issue is that there is no simple one-to-one relationship between these traits and dispersal modes. A single plant species can use several dispersal modes, depending on a specific ecological context and availability of dispersal vectors (Poschlod et al. 2013). Some morphological features can serve as adaptations for different dispersal modes, for example colourful and fleshy fruit indicate dispersal by animals but as the pulp is often light and buoyant, fruit can also be dispersed by water (e.g. Parolin et al. 2013). Moreover, the dispersal effectivity of some diaspore traits may interact with other plant traits, for example, plant height can be a more important factor than seed mass in determining the diaspore dispersal distance (Thomson et al. 2011).

Instead of the traditional binary (yes/no) assignments of species to dispersal-mode categories, attempts have been made to quantify the potential of each species to disperse by individual dispersal modes, e.g. anemochory (Tackenberg et al. 2003) or epizoochory (Will et al. 2007, Couvreur et al. 2008). To compare the degrees of adaptation of individual species to different dispersal modes, Hintze et al. (2013) introduced dispersal-ranking indices based on trait measurements and experimental assessments of diaspore adaptations to individual dispersal modes. These indices, transformed to a uniform scale for all dispersal modes and contained in the D³ database, facilitate a more realistic assessment of plant dispersal patterns than the traditional binary assessments.

In spite of the recent progress in accumulation of dispersal data and experimental work on plant dispersal for north-western and central-European flora, actual dispersal modes are still unknown for a large number of species. Nevertheless, some kind of classification of plant species according to their dispersal modes is needed for ecological analyses of species' spread, persistence or decline in the landscape. Such classification should be based not only on measured or observed diaspore traits that may be important for dispersal, but also on the landscape context in which individual species occur and spread, especially considering whether dispersal vectors compatible with individual dispersal traits are present in the landscape and how frequent or strong they are. It is also important that this classification considers the fact that most species are dispersed by several vectors and cannot be simply assigned to one or two dispersal modes. Due to the lack of data for a large number of species, however, compilation of such a classification for the whole floras must, to a large degree, rely on expert judgement.

Here we propose a new approach to the assessment of dispersal patterns across whole regional floras, by introducing the concept of dispersal strategies. We define the dispersal strategies of plant species as distinct repeatedly occurring combinations of dispersal modes, of which some are usually prevailing in a particular species while others are less common but still contribute to its dispersal. We tested this approach on the flora of the Czech Republic, for which we assessed dispersal traits based on the data available in various literature sources and databases, including the new Pladias database of the Czech flora and vegetation (www.pladias.cz; see also Kaplan et al. 2015, 2016, 2017), and potential dispersal vectors. Based on this assessment we define nine dispersal strategies relevant for the Czech (i.e. temperate European) flora. Besides presenting the new approach and classification of dispersal strategies, we also introduce a database of the vascular flora of this country classified according to these dispersal strategies. We relate particular dispersal strategies to species' origin, invasion status and habitat affinities, and discuss our experience of this assessment.

Methods

Selection of taxa

A slightly revised version of the Checklist of vascular plants of the Czech Republic (Danihelka et al. 2012), which reflects the taxonomic development since its publication, and is used in the Pladias Database of the Czech Flora and Vegetation (www.pladias.cz) served as the basic list of species assessed in this study. From this list, we considered the taxonomic level of species as well as intraspecific taxa such as subspecies, variety and

Group, the latter used for plants that originated in cultivation following the International Code of Nomenclature for Cultivated Plants (Brickell et al. 2009). Agamospecies were included with the exception of the genus *Taraxacum*, from which we used sections, *Rubus hirtus* agg. and *Ranunculus auricomus* agg., in which we applied sensu lato groups as in Danihelka et al. (2012). Other supraspecific taxa occurring in the above Checklist (marked as agg. and s.l.) were not considered. We further excluded all taxa labelled in Danihelka et al. (2012) as cultivated and never recorded as escaped because we regard the dispersal of such species as completely human-assisted. Very rare casual neophytes and the majority of interspecific hybrids were also not considered. Rare casual neophytes usually form short-living populations and disappear (e.g. past finds of Australian species introduced with imported wool; Dvořák & Kühn 1966, Pyšek 2005), therefore it often cannot be retrospectively assessed whether they formed any viable diaspores. The status of alien species was taken from Pyšek et al. (2012b).

After this selection, the following taxa of the Czech vascular flora were assessed in the database: (i) all native and archaeophytic taxa, including extinct and missing ones (2547 taxa); (ii) all naturalized and frequently occurring neophytes (577 taxa); and (iii) hybrids that pertain in the wild independent of populations of their parental species (e.g. *Aconitum × cammarum*, a sterile garden escape, or *Crataegus × macrocarpa*, a hybridogeneous species with distinct habitat preferences and distribution range; in total 39 taxa). In total the database included 3163 taxa.

Definitions of terms associated with dispersal

For the purpose of this paper and the database we use the following terms:

- ‘diaspore’ (synonyms: dispersule, propagule) is a generative or vegetative part of the plant body that is dispersed from the parental plant and can produce a new individual
- ‘dispersal mode’ is a distinct single type of dispersal used by a plant species (e.g. anemochory when spread by wind, hydrochory by water etc.); this term corresponds to dispersal syndrome as used by Pérez-Harguindeguy et al. (2013)
- ‘dispersal strategy’ is a term newly introduced here, defined as a set of several dispersal modes that are used by a single plant species to disperse its diaspores

Dispersal, diaspores and dispersal modes

We considered both generative and vegetative diaspores (Table 1). Vegetative diaspores are different from sedentary clonal modules and represent viable and movable parts of plants that originate above ground or in water and disconnect from the parent plant before sprouting. We did not consider as vegetative diaspores (i) clonal organs connected with the maternal plant until the new plant becomes independent (e.g. stolons in *Fragaria*) and (ii) various types of below-ground organs or shoot bases embedded in soil (e.g. tubers of *Helianthus tuberosus* or grass tillers). In some species, below-ground parts are regularly dispersed by water (e.g. *Reynoutria japonica*; Pyšek & Prach 1993), burrowing rodents (e.g. *Corydalis solida*; Borghi & Giannoni 1997) or scree slides (e.g. *Rumex scutatus*; Jenny-Lips 1930). However, this dispersal strategy can be hardly delimited and separated from accidental transport events such as floods. In general, below-ground organs are linked with sessile rather than a mobile phase of plant life.

Table 1. – Classification of diaspore types.

1. Generative diaspores

- 1.1. Spores:** They occur in pteridophytes. Also sporocarps releasing spores are included (*Pilularia* and *Salvinia* only).
- 1.2. Seeds:** They occur in gymnosperms (e.g. *Pinus*) and angiosperms (e.g. *Papaver*).
- 1.3. Fruits.** This category includes dry or fleshy fruits (e.g. *Acer*) and analogous dispersal units (e.g. aggregate or multiple fruits in *Fragaria* or *Morus*, respectively, gymnosperm cones, epimatium-bearing seed in *Taxus*, spikelets or their various fragments in *Poaceae*). Dehiscence or release of seed from ripe or decaying fruit is expressed by the combination seed+fruit, while indehiscent fruit is considered only as fruit.
- 1.4. Tumbleweeds.** Mature plant parts including stem branches and large inflorescence (e.g. *Falcaria vulgaris* and *Rapistrum perenne*).

2. Vegetative diaspores

- 2.1. Turions** (e.g. *Myriophyllum* and *Utricularia*) and similar overwintering structures (detachable buds in *Elodea* and *Groenlandia*). Shortened shoots of some pondweeds (e.g. *Potamogeton alpinus*) produced by underground rhizome are also included here, because they regularly detach and drift away in spring.
- 2.2. Bulbils and tubers** of stem origin (e.g. *Allium oleraceum* and *Dentaria bulbifera*) or root origin (*Ficaria* only).
- 2.3. Plantlets born by pseudovivipary** (e.g. *Poa alpina*).
- 2.4. Plantlets born from buds on leaves** (*Cardamine pratensis*).
- 2.5. Plantlets born on free ends of stolons**, detachable before establishing (e.g. *Hydrocharis* and *Jovibarba*).
- 2.6. Unspecialized fragments** of shoot (e.g. *Sedum album* and many aquatic plants), shoot tips (e.g. *Ceratophyllum demersum*) or detachable offsprings born from axillary buds (e.g. *Agrostis canina*, *Arabidopsis halleri* and *Rorippa amphibia*).
- 2.7. Budding plants** (*Lemnaceae* only).
- 2.8. Gemmae** produced by gametophytes (*Trichomanes speciosum* only).

The classification of generative diaspores follows current morphological terminology (e.g. spore, seed, fruit; modified from Hintze et al. 2013). The terms for vegetative diaspores correspond to those used in the CLO-PLA database (Klimešová et al. 2017). The information on the types of diaspores was taken from the Flora of the Czech Republic (Hejný & Slavík 1988–1992, Slavík 1995–2000, Slavík & Štěpánková 2004, Štěpánková 2010) and the CLO-PLA database (Klimešová et al. 2017).

Dispersal modes were classified based on a simplified system of dispersal vectors and assigned to species by using information from LEDA (Kleyer et al. 2008), CLO-PLA (Klimešová et al. 2017) and other databases, literature referring to morphology and dispersal of individual species (e.g. Deyl 1956, Lhotská & Chrtková 1978, Bojnanský & Fargašová 2007), expert assessment based on the field experience of the first author, and inferred from data on species with similar diaspores, especially in cases of phylogenetically related species occurring in similar habitats.

Finely defined autochoric strategies for short-distance dispersal, such as blastochory, herpochory, barochory and ballochory were subsumed to autochory. Ombrochory (dispersal by rain drops), myrmecochory (by ants) and (rather hypothetical) malacochory (by molluscs) were also included within autochory because they are effective mainly in short-distance dispersal (Culver & Beattie 1978, Andersen 1988). Moreover, myrmecochory has usually been reported mainly for species with an elaiosome (Peters et al. 2003),

whereas the role of occasional transport by ants of many species lacking this structure remains unclear (Kovář et al. 2001). Chamaeochory (relevant for tumbleweeds) was also subsumed to autochory, based on the limited dispersal efficiency of tumbleweeds in central-European conditions. Meteorochory (transport of very light seeds in air) was subsumed to anemochory. Stomatochory (transport in an animal's mouth) and dysochory (transport of accidentally ingested diaspores) were subsumed to endozoochory. If necessary, habitat context was taken into account, e.g. hydrochory was considered in species colonizing rivers or springs, or species restricted to mossy and grassy swamps were assumed to be dispersed mainly by autochory due to the lack of water movement. Dispersal by humans (although possibly the strongest vector in modern landscapes) was not considered because of the difficulties with its quantification and assignment to individual species and separating deliberate vs accidental dispersal pathways (Hulme 2008).

Dispersal strategies

Each species was characterized by their types of diaspores, dispersal modes and vectors, listing all modes that are reported or very probably occur. Species with similar combinations of dispersal modes were grouped. Essential (most frequent or most efficient) dispersal modes were distinguished from occasional and less important ones. This approach resulted in distinguishing nine polychoric dispersal strategies, with rare combinations of vectors merged with functionally similar groups to make the system simple, avoiding inclusion of strategies represented by few species.

Statistical analysis

To test whether there are differences in the numbers of native vs alien (origin status), and casual vs naturalized and invasive species (invasion status) among dispersal strategies, species counts in different combinations of categories were analysed by row \times column contingency tables using generalized linear models (GLMs) with log-link function and Poisson distribution of errors (e.g. Crawley 2007). For the models that indicated significant effects of species categories, adjusted standardized residuals of G-tests were compared with critical values of the normal distribution to ascertain for which groups of species the counts are lower or higher than expected by chance (Řehák & Řeháková 1986). The calculations were done in R 3.0.2 (R Core Team 2017).

Results

Classification of dispersal strategies

Each dispersal strategy described below combines essential dispersal modes (in upper case letters) and occasional dispersal modes (lower case letters; Table 2), the latter are recorded only for some species or some environments. For each dispersal strategy, the essential modes are listed first, followed by occasional modes, with modes ranked alphabetically within these two groups. Each strategy is named by the genus name of its typical representative. The assignment of individual taxa to particular strategies is shown in Electronic Appendix 1.

Table 2. – Cross-tabulation of dispersal strategies and dispersal modes. The bars and points indicate essential and occasional dispersal modes, respectively, within each dispersal strategy.

Dispersal mode	I. Allium	II. Bidens	III. Cornus	IV. Epilobium	V. Lycopodium	VI. Phragmites	VII. Sparganium	IX. Wolffia	IX. Zea
Autochory	■	■	■	■	●	●	■	–	–
Epizoochory	●	■	–	●	●	●	●	●	–
Endozoochory	●	●	■	●	●	●	●	●	–
Anemochory	●	–	–	■	■	■	–	–	–
Hydrochory	–	–	–	–	●	■	■	■	–

I. Allium type: AUTOCHORY, anemochory, endozoochory, epizoochory. This broadly defined type of dispersal includes 56% (1783 of 3163) of the assessed taxa (Fig. 1). Taxa with this strategy are herbaceous plants preferring mesic and dry habitats, with some exceptions such as *Rhododendron tomentosum*. About half of the included taxa are dispersal generalists lacking a clear morphological indication of anemochory or zoochory. Large diaspores such as bulbils in the inflorescences of some *Allium* species, or smooth nutlets in most *Lamiaceae* fall off the maternal plant and remain in its surroundings, whereas smaller diaspores (e.g. seed of *Calluna* and *Sagina*) are occasionally spread over greater distances, e.g. by water, wind, ants or grazing mammals. Some species show minor adaptations indicating other dispersal modes, which however work less efficiently, e.g. short and sparse flying and attaching apparatus in *Centaurea*. The majority of awned grasses were also assigned to this strategy. While awned lemmae can contribute to the transport of caryopses by animal or wind, their main function is physiological (e.g. transpiration; Grundbacher 1963) and autochoric burial of the caryopsis into the soil (Peart 1981). Species with short-distance dispersal modes that we included under

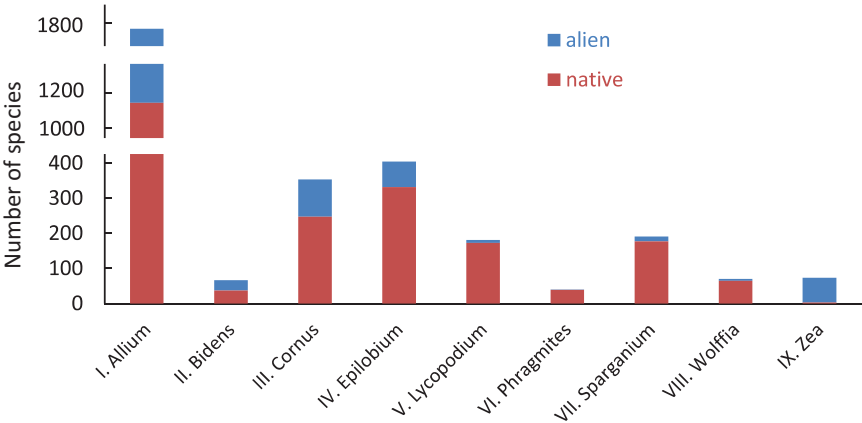


Fig. 1. – Representation of the native and alien taxa in the Czech flora across dispersal strategies.

autochory, such as myrmecochory or balistochory, are also classified in this strategy. This strategy further includes species with large or hard fruit or seed with nutrient storage that are occasionally dispersed by endozoochory; in some cases the efficiency of this kind of dispersal is obvious (e.g. oat spread by horses, or pea by pigeons), but evidence is lacking for assessing its real efficiency in the wild (e.g. the fate of caryopses after passage through the intestinal tract of horses), which makes these zoochoric species difficult to separate from species with prevailing autochory. Tumbleweed species, if they bear seed indicating classification within this group (e.g. smooth samaras in *Falcaria vulgaris*), were also included despite their apparent anemochoric features. Unlike in the vast steppe plains of continental Eurasia, this dispersal mode has a limited efficiency in central Europe. In continental plain steppes the tumbleweeds dry out and then are released by wind, whereas in the central-European climate the stems of the same species mostly remain flexible and do not detach from their root, hence the seed is released on the spot. Overall, the *Allium* dispersal strategy applies to many representatives of large families such as *Poaceae*, *Lamiaceae* and *Caryophyllaceae*.

II. *Bidens* type: AUTOCHORY, EPIZOOCHORY, endozoochory. This dispersal strategy is characterized by two essential dispersal modes, of which autochory is the more important, despite the presence of morphological structures indicating epizoochory. For example in *Arctium* some of achenes are dispersed by means of the prickly capitulum but many fall to the ground before the separation of the capitulum from the stem. Similarly, caryopses of *Stipa pennata* are occasionally anemochoric but their flight is short; moreover, their hairy awns often interlace and the seeds fall down together instead of flying. Endozoochory in this dispersal strategy is often represented by large nutritious diaspores, e.g. in *Echinops*. Many taxa in this group are annuals or short-lived perennials confined to mesic or dry ruderal habitats. Some wetland species are also included here, such as *Bidens* sp. and *Geum rivale*, in which hydrochory is also relevant.

III. *Cornus* type: AUTOCHORY, ENDOZOOCHORY. Herbaceous plants, shrubs and small trees with fleshy fruit, often of the *Rosaceae* family, typically have this strategy. Furthermore, tall trees bearing big, dry and heavy nutrient-rich seeds are also included, e.g. *Aesculus* and *Quercus*. Fruit and seed are spread by endozoochory either by birds if they remain attached to the plant or by rodents and weasels if they fall to the ground. After transportation, seeds are often eaten again and dispersed by rodents, or spread by other dispersal modes. Herbaceous plants with soft but toxic or unpalatable fruit (e.g. *Arum*, *Atropa*, *Bryonia* and *Convallaria*) are also classified within this strategy, although it is unclear whether the seed is swallowed by birds or only spread around.

IV. *Epilobium* type: ANEMOCHORY, AUTOCHORY, endozoochory, epizoochory. This species group is typical of mesic and dry habitats. Anemochory is obvious (of the 463 taxa in this category 72% are *Asteraceae*), while the role of autochory is less clear and its importance probably underestimated. The importance of epizoochory varies; for example, birch seed is frequently found attached to animal fur but this is not the case for the heavy seed of maple and ash (Heinken & Raudnitschka 2002). The participation of endozoochory also varies. Small-seeded herbaceous plants are spread mainly by occasional ingestion by ungulates (dysochory), large-seeded trees by granivorous birds such

as *Loxia curvirostra* specialized for feeding on conifer seeds or polyphagous *Pyrrhula pyrrhula* and *Carduelis spinus*.

V. Lycopodium type: ANEMOCHORY, autochory, endozoochory, epizoochory, hydrochory. This dispersal strategy relies on light, very small spores and seeds that are dispersed by a wide range of vectors. Dispersal by vegetative diaspores is rare (only in *Huperzia*, *Hymenophyllum*, *Selaginella* and *Trichomanes*). Compared to other groups, the role of autochory is small. The roles of endozoochory and epizoochory are still poorly known and possibly underestimated (Mountain & Moe 2014, Troia 2016). This strategy is only recorded for species of vascular cryptogams, species of the families *Orchidaceae* and *Pyrolaceae*, and of the genera *Orobanche* and *Phelipanche*. Spore-producing wetland representatives such as *Equisetum fluviatile* and *Thelypteris palustris* could be alternatively subsumed to the dispersal strategies that rely more heavily on hydrochoric dispersal modes, but we included them here owing to their spores being functionally distinctive structures. The efficiency of dispersal by spores in some ferns is doubtful but clear evidence is missing; for example, in the clonal species *Matteucia struthiopteris*, whole plants are spread by floods and it is unclear whether new populations are initiated by spores.

VI. Phragmites type: ANEMOCHORY, HYDROCHORY, autochory, endozoochory, epizoochory. Wetland species with light diaspores (both seed and fruit) equipped with a hairy flying apparatus. With the only exception of *Salix euxina*, species with this dispersal strategy lack vegetative diaspores. This dispersal strategy is recorded for a small group of species, especially from the families *Cyperaceae*, *Poaceae* and *Salicaceae*. Woody plants, stout clonal graminoids and herbaceous plants are typical growth forms associated with this dispersal strategy.

VII. Sparganium type: AUTOCHORY, HYDROCHORY, endozoochory, epizoochory. This dispersal strategy is a wetland analogue of the Wolffia type, assigned to aquatic plants. It applies to mostly monocotyledonous species producing achenes with good buoyancy and with vegetative diaspores having an important role. Production of vegetative buds on leaves is a special syndrome associated mainly with this strategy; these autochoric structures occur in the genera *Cardamine* and *Drosera*, and two orchids *Hammarbya paludosa* (Dickie 1873) and *Liparis loeselii* (Irmisch 1850).

VIII. Wolffia type: HYDROCHORY, endozoochory, epizoochory. This dispersal strategy is typical of aquatic macrophytes spread by fruit, seed or spores. However, vegetative reproduction dominates in most cases, while sexual reproduction is often reduced (Barrat-Segretain 1996) and even lost in some populations (e.g. *Stratiotes aloides*; Eckert 2001). The main or even exclusive means of dispersal in most species is through stem fragmentation, formation of stolons or, in *Lemnaceae*, budding colonies. *Wolffia*, in which the vegetative diaspore is a whole plant, and seed production is extremely rare (Hicks 1932), is the ultimate stage in the development of this strategy. In some species the fragments are shoots, in others only shoot tips. The rooting success depends on the type of fragment (Barrat-Segretain et al. 1999, Riis et al. 2009). Furthermore, nearly half of the species with this dispersal strategy also form movable turions as a specific diaspore type. In addition to the spread of hydrochoric generative parts, entire seedlings are also

reported as dispersal units in some species (e.g. *Hottonia palustris*; Brock et al. 1989). All types of diaspores, seed, fruit and fragments are usually buoyant. In some species ichthyochory (dispersal by fish) is possible (*Nuphar lutea*; Fér & Hroudová 2008).

IX. Zea type (very rare or no formation of movable aboveground diaspores). Species with this dispersal strategy rarely reproduce generatively and do not form vegetative above-ground diaspores. Low fertility is caused genetically (e.g. triploids such as *Acorus calamus*, some hybrids such as *Mentha ×piperita*) or breeding pattern (e.g. dioecious species occurring in female clones only such as the introduced *Salix acutifolia*). Despite the seemingly unambiguous difference between plant sterility vs fertility, the delimitation of this strategy is not sharp. Some hybrids with this strategy are regarded as substerile, such as *Helianthus ×laetiflorus* and *Symphyotrichum* spp. (Clevenger & Heiser 1963, Hoffmann 1996), but clear information about the germinability of their seed is missing. Poor production, survival or establishment of seed is mostly caused by special requirements for habitat, climate or, rarely, pollinators such as in the *Ficus carica* populations introduced into central Europe. In *Zea mays*, kernels are kept on the corncobs that decay, and germination is enabled only by their release by humans. Of the aliens, this group includes only deliberately introduced species such as weedy but originally ornamental *Oxalis debilis* or medical plants such as *Acorus calamus* and *Artemisia verlotiorum*. Instead of above-ground diaspores, the dispersal in these species is achieved exclusively by below-ground organs or even whole plants. They are dispersed by humans either deliberately (clonal reproduction of ornamental aliens such as the never fruiting *Hemerocallis fulva*), or unintentionally (e.g. transport with soil or waste material such as in the tropical *Mirabilis jalapa*) and also by floods or wild boar (e.g. tubers of the late flowering *Helianthus tuberosus*).

Association between dispersal strategies and diaspores

In total, the vast majority of taxa in the Czech flora disperse exclusively via generative diaspores (92.8%), whereas 4.5% combine generative and vegetative diaspores, a few (0.7%) spread only by vegetative diaspores and the remaining 2% (taxa with the Zea strategy) form no viable above-ground diaspores and propagate by below-ground organs or with human assistance.

The particular dispersal strategies differ in the relative representation of species with generative and vegetative diaspores. There are two dispersal strategies in which above-ground vegetative diaspores have an important role: *Wolffia* (46.6%), and *Sparganium* (22.9%). In the remaining strategies the representation of vegetative diaspores is negligible or absent (Table 3).

In terms of diaspore type, whole fruit (48.8%) and seed (41.2%) are by far the most frequent, with fragments (3.1%) and spores (1.9%) the only other types of diaspore exceeding 1% (Table 3).

Taxonomic pattern

The distribution of dispersal strategies within families is shown in Table 4. The most represented strategy, *Allium*, is commonest in 16 of 20 families with the highest numbers of species in the Czech flora, but all other strategies except *Bidens*, *Wolffia* and *Zea* are important (present in at least 30% of total number of taxa) in at least one family.

Table 3. – Representation of diaspore types (see Table 1 for classification and description) in particular dispersal strategies. The numbers of taxa with the respective diaspore type in particular dispersal strategies are shown.

Diaspore type	I. Allium	II. Bidens	III. Cornus	IV. Epilobium	V. Lycopodium	VI. Phragmites	VII. Sparganium	VIII. Wolffia	IX. Zea	Total
1.1 Spores	71	.	.	4	.	75
1.2 Seed	968	1	340	60	109	19	73	23	.	1593
1.3 Fruit	924	67	346	355	.	21	119	52	.	1884
1.4 Tumbleweeds	20	1	.	1	22
2.1 Turions	35	.	35
2.2 Bulbils & tubers	16	.	.	.	1	.	1	.	.	18
2.3 Plantlets (pseudovivipary)	2	1	.	.	3
2.4 Plantlets (leaf buds)	2	6	.	.	8
2.5 Plantlets (stolons)	8	2	.	10
2.6 Fragments	18	.	.	.	2	1	49	52	.	122
2.7 Budding plants	7	.	7
2.8 Gemmae	1	1
Infertile taxa	9	.	.	.	1	.	1	5	73	89
1. Generative total	1771	67	353	404	180	40	188	65	0	3158
2. Vegetative total	38	0	0	2	0	1	57	61	11	170

Differences in dispersal of native and alien species

There were significant differences in relative representation of native and alien species within particular dispersal strategies (interaction of origin status \times dispersal strategy tested by F-statistics because of overdispersion: $F = 46.04$; $df = 0, 8$; $P < 0.001$). Native species are over-represented in the Epilobium, Lycopodium, Sparganium and Wolffia strategies, whereas aliens are over-represented in Allium, Bidens and Zea (Table 5).

The differences in representation of casual and naturalized species within the subset of all aliens were less pronounced although still significant (interaction of invasion status \times dispersal strategy: $F = 2.26$; $df = 0, 8$; $P < 0.05$), with this result mainly determined by over-representation of casual taxa within the Zea strategy (Table 5).

The differences in frequencies of species with particular types of diaspore based on the species origin (native vs alien) interaction with diaspore type ($F = 17.36$; $df = 0, 8$; $P < 0.001$) and invasion status ($F = 1.77$; $df = 0, 8$; $P < 0.05$) were also significant. There was no difference in the two most important diaspore types, fruit and seed, but native species more often disperse as spores and vegetative fragments, while aliens such as tumbleweed are more represented in the group of infertile taxa (Table 6).

Distribution of dispersal strategies in habitats

The occurrence of taxa with particular dispersal strategies in habitats of the Czech Republic is not random (GLM model with Poisson distribution of errors, tested using F-statistics because of overdispersion: $F = 19.70$; $df = 0, 96$; $P < 0.001$). The Allium dispersal strategy prevails in several types of grassland and anthropogenic vegetation.

Table 4. – Distribution of dispersal strategies within the 20 most species-rich families in the Czech flora. Strategies present in more than 30% of taxa of a particular family are highlighted.

Family	I. Allium	II. Bidens	III. Cornus	IV. Epilobium	V. Lycopodium	VI. Phragmites	VII. Sparganium	VIII. Wolffia	IX. Zea
<i>Asteraceae</i>	83 (20.2%)	16 (3.9%)	(0%)	296 (72.2%)	(0%)	3 (0.7%)	1 (0.2%)	(0%)	11 (2.7%)
<i>Rosaceae</i>	75 (24.2%)	4 (1.3%)	226 (72.9%)	1 (0.3%)	(0%)	(0%)	(0%)	(0%)	4 (1.3%)
<i>Poaceae</i>	179 (77.5%)	21 (9.1%)	(0%)	9 (3.9%)	(0%)	5 (2.2%)	14 (6.1%)	(0%)	3 (1.3%)
<i>Brassicaceae</i>	140 (92.7%)	(0%)	(0%)	(0%)	(0%)	(0%)	10 (6.6%)	(0%)	1 (0.7%)
<i>Fabaceae</i>	144 (96.6%)	1 (0.7%)	(0%)	(0%)	(0%)	(0%)	(0%)	(0%)	4 (2.7%)
<i>Cyperaceae</i>	69 (54.3%)	(0%)	(0%)	(0%)	(0%)	6 (4.7%)	52 (40.9%)	(0%)	(0%)
<i>Caryophyllaceae</i>	108 (93.1%)	(0%)	1 (0.9%)	2 (1.7%)	(0%)	(0%)	3 (2.6%)	(0%)	2 (1.7%)
<i>Lamiaceae</i>	89 (87.3%)	(0%)	(0%)	(0%)	(0%)	(0%)	5 (4.9%)	(0%)	8 (7.8%)
<i>Apiaceae</i>	74 (79.6%)	13 (14%)	(0%)	(0%)	(0%)	(0%)	5 (5.4%)	(0%)	1 (1.1%)
<i>Ranunculaceae</i>	69 (76.7%)	(0%)	1 (1.1%)	9 (10%)	(0%)	(0%)	2 (2.2%)	8 (8.9%)	1 (1.1%)
<i>Orchidaceae</i>	(0%)	(0%)	(0%)	(0%)	74 (97.4%)	(0%)	2 (2.6%)	(0%)	(0%)
<i>Plantaginaceae</i>	57 (79.2%)	(0%)	(0%)	(0%)	(0%)	(0%)	14 (19.4%)	1 (1.4%)	(0%)
<i>Amaranthaceae</i>	61 (93.8%)	(0%)	2 (3.1%)	1 (1.5%)	(0%)	(0%)	1 (1.5%)	(0%)	(0%)
<i>Orobanchaceae</i>	38 (59.4%)	(0%)	(0%)	(0%)	24 (37.5%)	(0%)	2 (3.1%)	(0%)	(0%)
<i>Polygonaceae</i>	29 (59.2%)	(0%)	(0%)	(0%)	(0%)	(0%)	18 (36.7%)	(0%)	2 (4.1%)
<i>Boraginaceae</i>	37 (78.7%)	5 (10.6%)	(0%)	(0%)	(0%)	(0%)	5 (10.6%)	(0%)	(0%)
<i>Asparagaceae</i>	28 (77.8%)	(0%)	7 (19.4%)	(0%)	(0%)	(0%)	(0%)	(0%)	1 (2.8%)
<i>Rubiaceae</i>	32 (88.9%)	4 (11.1%)	(0%)	(0%)	(0%)	(0%)	(0%)	(0%)	(0%)
<i>Juncaceae</i>	18 (54.5%)	(0%)	(0%)	(0%)	(0%)	(0%)	15 (45.5%)	(0%)	(0%)
<i>Salicaceae</i>	(0%)	(0%)	(0%)	14 (43.8%)	(0%)	15 (46.9%)	(0%)	(0%)	3 (9.4%)

Table 5. – The numbers of native and alien species in particular dispersal strategies. Significant differences in origin (between native and alien taxa), and invasion status (between casual and naturalized, the latter including invasive, within aliens) are indicated: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. The direction of the significant effects is indicated by arrows.

Dispersal strategy	Origin		Invasion status	
	Native	Alien	Naturalized	Casual
I. Allium	1172 ↓**	611 ↑***	320	292
II. Bidens	37	30 ↑*	15	15
III. Cornus	247	106	42	64
IV. Epilobium	332 ↑**	73 ↓***	43	30
V. Lycopodium	173 ↑***	8 ↓***	3	5
VI. Phragmites	39	1 ↓***	1	0
VII. Sparganium	177 ↑***	14 ↓***	9	5
VIII. Wolffia	65 ↑*	5 ↓***	3	2
IX. Zea	3 ↓***	70 ↑***	22 ↓*	47 ↑*

Table 6. – The numbers of native and alien species according to the frequency of diaspores associated with their dispersal (see Table 1 for diaspore classification). Significant differences in origin (between native and alien taxa) and invasion status (between casual and naturalized, the latter including invasive, within aliens) are indicated: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. The direction of the significant effects is indicated by arrows.

Diaspore type	Origin status		Invasion status	
	Native	Alien	Casual	Naturalized
1.1 Spores	73 ↑*	2 ↓***	0	2
1.2 Seed	1111	484	243	241
1.3 Fruit	1366	520	250	271
1.4 Tumbleweeds	10	12 ↑*	5	7
2.1 Turions	32	3 ↓**	1	2
2.2 Bulbils & tubers	14	4	0 ↓*	4
2.3 Plantlets (pseudovivipary)	3	0	0	0
2.4 Plantlets (leaf buds)	8	0 ↓*	0	0
2.5 Plantlets (stolons)	8	2	0	2
2.6 Fragments	108 ↑*	14 ↓***	5	9
2.7 Budding plants	5	2	1	1
2.8 Gemmae	1	0	0	0
Infertile taxa	14 ↓***	75 ↑***	48	26 ↓*

The latter is also characterized by a relatively high representation of the *Bidens* and *Zea* strategies. The *Cornus* strategy is over-represented in heathlands and scrub and forests, *Epilobium* in alpine and subalpine habitats, and in acidophilous grasslands. The *Lycopodium* strategy occurs more often than expected by chance on cliffs, scree, walls and in forests, *Phragmites* in springs and mires, and in heathland and scrub, *Sparganium* and *Wolffia* in aquatic and wetland habitats, and *Sparganium* also in springs and mires (Table 7).

The spectra of dispersal strategies in the main habitat types of the Czech Republic, showing their relative representation, are shown in Fig. 2.

Table 7. – Distribution of dispersal strategies across habitats (see Sádlo et al. 2007 for details of habitat classification). Significant differences are indicated: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. The direction of the significant effects is indicated by arrows. Cells with over-represented dispersal strategies are highlighted. Based on 2187 taxa in the new database of dispersal strategies that were assigned to habitats by Sádlo et al. (2007).

	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.
	Allium	Bidens	Cornus	Epilobium	Lycopodium	Phragmites	Sparganium	Wolffia	Zea
No. of spp.	1305	49	145	303	112	36	154	50	17
1 Cliffs, screes & walls	121	3	9	35	24 ↑***	0 ↓*	1 ↓***	0 ↓**	1
2 Alpine & subalpine	80 ↓*	0 ↓*	11	66 ↑***	7	2	1 ↓***	0 ↓**	0
3 Aquatic	8 ↓***	2	0 ↓***	1 ↓***	0 ↓**	0	35 ↑***	49 ↑***	0
4 Wetland	8 ↓***	2	0 ↓***	1 ↓***	0 ↓**	0	35 ↑***	49 ↑***	0
5 Springs & mires	142 ↓*	2 ↓*	8 ↓*	30	13	16 ↑***	61 ↑***	2 ↓*	0
6 Meadows & pastures	394 ↑**	8	3 ↓***	76	17	5	35	0 ↓***	5
7 Acidophilous grasslands	142	0 ↓**	5 ↓**	63 ↑***	9	0	3 ↓***	0 ↓**	0
8 Dry grasslands	428 ↑**	15	27 ↓*	89	31	0 ↓***	0 ↓***	0 ↓***	0
9 Sandy grasslands & outcrops	173 ↑***	5	0 ↓***	14 ↓**	0 ↓***	0 ↓*	0 ↓***	0 ↓**	1
10 Saline grasslands	64	0	0 ↓***	13	1 ↓*	1	11 ↑*	0 ↓*	0
11 Heathlands & scrub	260 ↓***	12	100 ↑***	105 ↑**	13 ↓*	18 ↑***	25	0 ↓***	3
12 Forests	434 ↓*	12	102 ↑***	100	66 ↑***	15	41	2 ↓***	3
13 Anthropogenic vegetation	541 ↑***	27 ↑**	22 ↓***	79 ↓**	12 ↓***	2 ↓**	10 ↓***	0 ↓***	9 ↑*

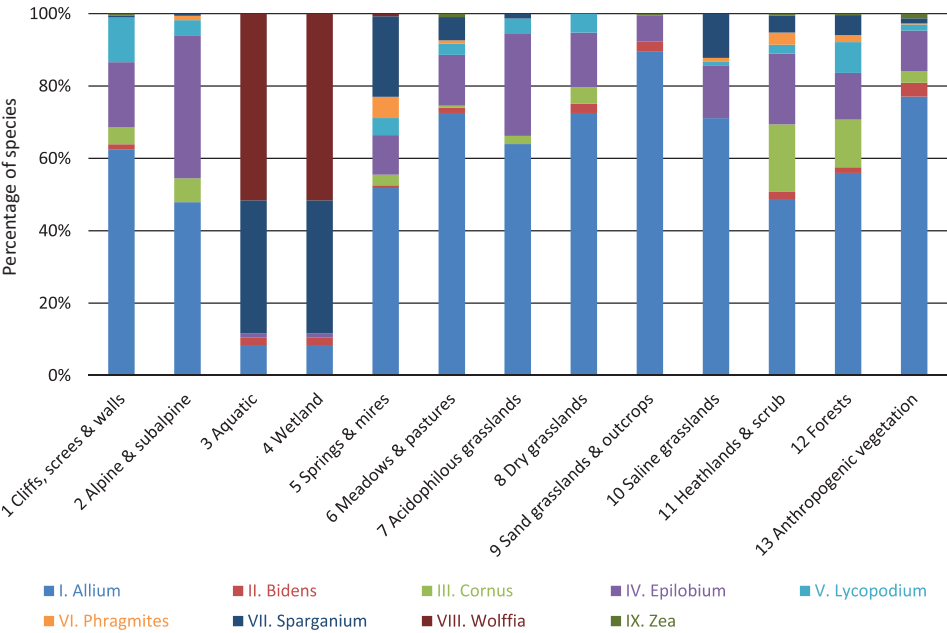


Fig. 2. – Spectra of dispersal strategies in the main habitat types in the Czech Republic. Relative representation of dispersal strategies in each habitat is shown. See Table 6 for species numbers and statistical differences.

Discussion

Does a complex approach to the classification of plant dispersal overcome the problem of data deficiency?

The new classification of plant dispersal proposed in this paper is based on the notion that the majority of plant species are dispersed by multiple vectors and cannot therefore be simply assigned to one or two dispersal modes. This makes our database different from others summarizing data on plant dispersal such as Diasporus (Bonn et al. 2000), BiolFlor (Klotz et al. 2002), BioPop (Poschlod et al. 2003), LEDA (Kleyer et al. 2008) and D³ (Hintze et al. 2013). The traditional approach to plant dispersal highlights the specialized morphological adaptations of diaspores that facilitate their spread, especially over long distances. The traditional approach to plant dispersal emphasizes spread by specialized morphological adaptations of diaspores, and focuses on long distance. This macroecological view is useful in studying long-term biogeographic or evolutionary processes, but differs from the perspective of small spatial and temporal scales, which is also valid and needed. The local survival of most populations depends on the occasional presence of generalized vectors acting without appropriate morphological adaptations, whereas long-distance spread is too rare to be considered at such a scale. Therefore, our concept of dispersal strategies targets this small spatial and temporal scale, which is suitable when considering local processes such as plant invasion, relict survival or succession.

The main problem with the classification of such a complex phenomenon as plant dispersal is the lack of hard data. Technically, relevant parameters can be measured for a single or a few species, in one or several regions (as shown by Strykstra et al. 1998a, b for *Arnica montana*), but it becomes logistically much more difficult, or even impossible to collate such data for an entire regional or national flora. Rather than exact measurements, we base our classification on extensive field observations and estimates of which processes are most efficient in the real environment. Aiming at the greatest achievable degree of generalization, we estimated the frequency and efficiency of particular dispersal modes in individual species, as observed in the field and assessed by expert judgment. This was considered a more important criterion than morphology of dispersal structures that can sometimes be misleading.

The distribution of different modes of dispersal across the entire flora reveals that species lacking an opportunity for specialized dispersal are rather numerous and abundant. This can be taken as an indication that the role of some specific structures (such as elaiosomes or pappus) is overestimated and that of generalized dispersal modes such as autochory underestimated. For example, in many species we assume that autochory is a key mechanism, even though the least efficient as far as dispersal distance is concerned. Contrary to the common belief, dandelion (*Taraxacum* spp.) is not a narrowly specialized anemochorous plant; in fact it is dispersed by a broad range of occasional vectors, such as autochory (typically in autumnal heads that never open), hydrochory (Boedeltje et al. 2003), endozoochory (ingested seed in stock excrements; Cosyns 2005), epizoochory (Tackenberg et al. 2006, Will et al. 2007) and myrmecochory (Pearson et al. 2014). Furthermore, wind is a less effective vector than convective updrafts, which spread seed over extremely long distances (Tackenberg et al. 2003). Finally, various human activities on a local to intercontinental scale are responsible for extensions in the distribution of dandelions and its invasive status outside Europe; in total 44 taxa in this genus are reported as naturalized in areas beyond their native range (Pyšek et al. 2017).

The general validity of our classification is necessarily limited. Partly, the compilation of such a classification for the whole floras must, to a large degree, rely on expert judgement due to the lack of data for a large number of species. Even more importantly, dispersal traits differ between geographic regions and in our case they refer only to a part of central Europe. For some individual taxa the relative importance of different modes of dispersal is likely to vary depending on their position in the distribution range. This may be the case especially for rare species at the margins of their distribution, or for alien species introduced into new geographic ranges. Some of these species may even belong to different dispersal strategies in their native and alien range. Nevertheless, we suggest that as a general principle the classification concept and dispersal strategy types introduced here are applicable regardless of geographic area.

Dispersal strategies, habitat types and alien plants

The knowledge of plant dispersal strategies is of key importance for the conservation of the diversity of native plants in landscapes with increasingly fragmented habitats and decreasing availability of dispersal vectors such as frugivores (McConkey et al. 2012) and for the management of invasive alien plants. In the brief explorative analyses in this paper, we present some basic patterns that are relevant to these issues but deserve more detailed examination in future studies.

The spectra of dispersal strategies recorded in the main habitats of the Czech Republic (Sádlo et al. 2007) suggest that there are four main groups of habitats with characteristic dispersal patterns: aquatic and wetland habitats, grasslands, woody vegetation and anthropogenic vegetation. The wetland flora is generally associated with hydrochory (e.g. due to representation of *Alismatales*), woodland species with endozoochory (e.g. *Fagales*), grasslands are dominated by autochoric and anemochoric species (e.g. *Poaceae* and *Asteraceae*) and in anthropogenic flora dispersal modes are less specific but autochory is common.

Aquatic and wetland habitats are characterized by over-representation of dispersal strategies involving hydrochory (*Phragmites*, *Sparganium* and *Wolffia*). In the *Wolffia* strategy and partly in *Sparganium*, generative dispersal and formation of specialized vegetative diaspores such as turions is much less important than dispersal by simple stem fragments lacking substantial adaptations, which indicates that hydrochory is an unspecialized mode. Fast clonal dispersal, combined with a low viability of diaspores once out of water, results in the emergence of superabundant local populations that are, however, restricted to a single or several close basins. This is the case for rare native species such as *Najas minor* and *Trapa natans*, new successful invaders such as *Lemna turionifera*, ephemeral occurrences of tropical species such as *Pistia stratiotes* and locally (re)introduced species such as *Nymphoides peltata*. However, invasions in streams can proceed rapidly, such as in *Elodea canadensis* or *Sagittaria latifolia* (Pyšek et al. 2012b).

In most types of grassland vegetation the over-represented strategies are *Allium* and *Epilobium*, which occur in many autochoric and anemochoric herbaceous plants, such as representatives of the families *Poaceae* or *Asteraceae*.

Woody vegetation is characterized by the *Cornus*, *Epilobium* and *Lycopodium* strategies, the latter being typical of understorey herbaceous plants. Shrubs and trees often bear large and heavy seed equipped with structures facilitating transport by animals (such as in *Prunus* and *Quercus*, belonging to the *Cornus* type) or wind (e.g. *Carpinus* and *Acer*, belonging to the *Epilobium* type). The dispersal strategy of woody species producing numerous light seeds, such as *Salix*, is determined by the habitat in which they grow; the *Epilobium* strategy prevails in mesic habitats and *Phragmites* in wet habitats. It is often stated that zoochory or anemochory facilitate the woody species colonization of new areas even in modern fragmented landscapes (Willson 1993, Butaye et al. 2002), but this is also valid especially for light-seeded species, including aliens. The dispersal of other species is mostly restricted to very short distances and therefore colonization is very slow, which is important for conservation.

The group of herbaceous plants with the *Allium* strategy and associated with non-ruderal habitats includes a high number of rare species and few aliens, which could be considered as an outcome of unspecialized autochory. But in fact, in the non-ruderal *Epilobium*-type or *Lycopodium*-type herbaceous plants the pattern is the same, with rare species being abundant and aliens exceptional, despite their specialized dispersal; in this case the pattern seems to result from evolutionary constraints, such as endomycorrhiza in orchids or apomictic speciation in some *Asteraceae*.

In anthropogenic vegetation, the *Allium*, *Bidens* and *Zea* strategies are markedly over-represented, indicating that humans play an important role in the dispersal of these taxa. The role of humans in dispersal is undisputed and anthropochory is the main dispersal mode for many species, even if their history of coexistence with humans has been too

short on the evolutionary time scale to evolve specialized adaptations to anthropochory. Nevertheless, this is only seemingly paradoxical; despite the disparity of these strategies, they simply follow their evolutionary preadaptations (Baker 1974, Diamond 1997) and besides many of their traits result from the currently running rapid adaptive evolution (Viguiera et al. 2013).

Allium strategy is based on autochory as a little specialized mode, which is rather accessoric here since the species are more frequently spread by much stronger human dispersal pathways. Autochory is, however, expedient at least in some species such as segetal weeds that need no specialized dispersal due to permanent circulation of their seed bank among fields. The *Bidens* strategy, as the second most over-represented, is based on a special set of features allowing adaptation to epizoochory. The species with this strategy simply follow their preadaptation in the new context, and epizoochory is clearly more effective in cultural landscapes than in more natural habitats due to the easy transport and establishment of seed at disturbed sites.

Anthropogenic vegetation also supports species with the *Zea* strategy, which is dependent on human assistance. These clonal species, in which viable above-ground diaspores are absent, are mostly aliens that were intentionally introduced and dispersed by humans. Only three taxa among those assigned to this strategy are native (hybridogenous taxa of *Mentha*), but they were also cultivated. The spread of species with the *Zea* strategy by below-ground organs reduces their ability to naturalize and their populations after introduction to a new area mostly tend to remain casual (sensu Richardson et al. 2000). Therefore they do not require much attention in the screening systems of potentially invasive plants (e.g. Pheloung et al. 1999, Daehler & Carino 2000, Gordon et al. 2010, Hulme 2012, Pergl et al. 2016b). For example, some ornamental plants such as *Hemerocallis* only persist and do not spread after their escape (Pyšek et al. 2012b, Pergl et al. 2016a). However, even some successful invaders belong to this group, especially those spreading in riparian habitats such as *Armoracia rusticana*, *Helianthus tuberosus* and *Symphyotrichum x salignum*, in which floods uncover and spread rhizomes or tubers (Pyšek et al. 2012a). In contrast, great attention should be paid especially to taxa of the *Bidens* type, which includes the highest proportion of aliens to native taxa within the Czech flora.

See www.preslia.cz for Electronic Appendix 1.

Acknowledgements

This study was funded by the Czech Science Foundation (project no. 14-36079G, Centre of Excellence Pladias). JS, JP and PP were also funded by long-term research development project RVO 67985939 (The Czech Academy of Sciences).

Souhrn

Diaspory cévnatých rostlin jsou přenášeny vektory, podle nichž se rozlišují způsoby šíření, např. přenos větrem vymezuje anemochorii. Tradičně se ke každému druhu přiřazoval jediný způsob šíření, který se odvozoval hlavně od morfologie diaspor; např. druhy s létacím aparátem byly automaticky považovány za anemochorní. Tento článek nabízí odlišný přístup ke klasifikaci rostlin podle způsobu šíření. Vycházíme z toho, že velká část rostlinných druhů se ve skutečnosti šíří pomocí více vektorů, které se ovšem vzájemně liší svou frekvencí výskytu a účinností. Jejich kombinace se opakuje u druhů s podobnou ekologií a morfologií diaspor. Například pro druhy pobřežních stanovišť z rodů *Phragmites*, *Salix* a *Typha*, které mají drobná ochmýřená semena, je

významný transport jak větrem, tak vodou, semena se však také zachytávají na zvířecí srsti nebo na oděvu a část jich prostě jen spadne poblíž mateřské rostliny. I tyto méně časté způsoby přenosu přispívají k šíření druhu, a proto je nelze pominout. Takové opakovaně se vyskytující kombinace různých častých způsobů šíření zde označujeme jako strategie šíření. Pomocí dostupných literárních pramenů, databází a vlastních pozorování jsme stanovili typy diaspor a možné způsoby šíření jednotlivých taxonů flóry České republiky po vyloučení vzácně zplaňujících nepůvodních taxonů a většiny hybridů. Kde chyběla data nebo osobní zkušenost, usuzovali jsme podle příbuzných druhů s podobnou morfologií. Celkem jsme rozlišili devět strategií šíření definovaných kombinacemi dominantních a příležitostných způsobů šíření. Tyto strategie jsme pojmenovali rodovým jménem jednoho typického zástupce: *Allium*, *Bidens*, *Cornus*, *Epilobium*, *Lycopodium*, *Phragmites*, *Sparganium*, *Wolffia* a *Zea*. Jednotlivé strategie charakterizujeme původností, invazním statutem a stanovištní vazbou taxonů, které do nich byly zařazeny. Převážná většina taxonů české flóry (92,8 %) se rozšiřuje jen pomocí generativních diaspor. Kombinací generativních a vegetativních diaspor využívají 4,5 % taxonů; některé taxony (0,7 %) se šíří jen vegetativními diasporami a zbývajících 2,0 % (strategie *Zea*) nemají žádné životaschopné nadzemní diaspory a rozmnožují se buď vegetativně podzemním šířením, anebo díky lidské asistenci. Původní druhy české flóry jsou statisticky významně hojnější u strategií *Epilobium*, *Lycopodium*, *Sparganium* a *Wolffia*, kdežto podíl nepůvodních druhů je významný u strategií *Allium*, *Bidens* a *Zea*. Strategie *Allium* je navíc i celkově nejhojnější v rámci naší flóry, ačkoli je nejméně specializovaná a zdánlivě nejhůře vybavená pro úspěšné šíření. To naznačuje, že morfologické adaptace pro dálkové šíření přírodními vektory jsou pro rostliny méně významné, než se často soudí. Klasifikace strategií šíření taxonů české flóry publikovaná jako elektronická příloha tohoto článku je včleněna do vznikající Databáze české flóry a vegetace (Pladias).

References

- Andersen A. N. (1988): Dispersal distance as a benefit of myrmecochory. – *Oecologia* 75: 507–511.
- Baker H. G. (1974): The evolution of weeds. – *Ann. Rev. Ecol. Syst.* 5: 1–24.
- Barrat-Segretain H. M. (1996): Strategies of reproduction, dispersion, and competition in river plants: a review. – *Vegetatio* 123: 13–37.
- Barrat-Segretain M. H., Henry C. P. & Bornette G. (1999): Regeneration and colonization of aquatic plant fragments in relation to the disturbance frequency of their habitats. – *Arch. Hydrobiol.* 145: 111–127.
- Boedeltje G., Bakker J. P., Bekker R. M., van Groenendael J. M. & Soesbergen M. (2003): Plant dispersal in a lowland stream in relation to occurrence and three specific life-history traits of the species in the species pool. – *J. Ecol.* 91: 855–866.
- Bojnanský V. & Fargašová A. (2007): Atlas of seeds and fruits of Central and East-European flora: the Carpathian Mountains region. – Springer, Dordrecht.
- Bonn S., Poschlod P. & Tackenberg O. (2000): Diasporus – a database for diaspore dispersal – concept and applications in case studies for risk assessment. – *Z. Ökol. Natursch.* 9: 85–97.
- Borghi C. E. & Giannoni S. M. (1997): Dispersal of geophytes by mole-voles in the Spanish Pyrenees. – *J. Mammal.* 78: 550–555.
- Brickell C. D., Alexander C., David J. C., Hetterscheid W. L. A., Leslie A. C., Malécot V., Jin X.-B. & Cubey J. J. (eds) (2009): International Code of Nomenclature for Cultivated Plants. Ed. 8. – International Society for Horticultural Science, Leuven.
- Brock T. C., Mielto H. & Oostermeijer G. (1989): On the life cycle and germination of *Hottonia palustris* L. in a wetland forest. – *Aquat. Bot.* 35: 153–166.
- Butaye J., Jacquemyn H., Honnay O. & Hermy M. (2002): The species pool concept applied to forests in a fragmented landscape: dispersal limitation versus habitat limitation. – *J. Veg. Sci.* 13: 27–34.
- Clevenger S. & Heiser C. B. (1963): *Helianthus laetiflorus* and *Helianthus rigidus*: hybrids or species? – *Rhodora* 65: 121–133.
- Cosyns E., Claerbout S., Lamoot I. & Hoffmann M. (2005): Endozoochorous seed dispersal by cattle and horse in a spatially heterogeneous landscape. – *Plant Ecol.* 178: 149–162.
- Couvreur M., Verheyen K., Vellend M., Lamoot I., Cosyns E., Hoffmann M. & Hermy M. (2008): Epizoochory by large herbivores: merging data with models. – *Bas. Appl. Ecol.* 9: 204–212.
- Crawley M. J. (2007): The R book. – John Wiley & Sons, Chichester.
- Culver D. C. & Beattie A. J. (1978): Myrmecochory in *Viola*: dynamics of seed-ant interactions in some West Virginia species. – *J. Ecol.* 66: 53–72.
- Daehler C. C. & Carino D. A. (2000): Predicting invasive plants: prospects for general screening system based on current regional models. – *Biol. Invas.* 2: 93–102.

- Danihelka J., Chrtěk J. Jr. & Kaplan Z. (2012): Checklist of vascular plants of the Czech Republic. – *Preslia* 84: 647–811.
- Deyl M. (1956): Plevelé polí a zahrad [Weeds of the fields and gardens]. – Československá akademie věd, Praha.
- Diamond J. (1997): Guns, germs, and steel: the fates of human societies. – W. W. Norton & Company, New York.
- Dickie G. (1873): Note on the buds developed on leaves of *Malaxis*. – *Bot. J. Linn. Soc.* 14: 1–3.
- Dvořák J. & Kühn F. (1966): Zavlečené rostliny na pozemcích přádelny vlny Mosilana n. p. v Brně [Introduced species in the area of the wool-processing factory Mosilana in Brno]. – *Preslia* 38: 327–332.
- Eckert C. G. (2001): The loss of sex in clonal plants. – *Evol. Ecol.* 154: 501–520.
- Eriksson O. & Kiviniemi K. (2001): Evolution of plant dispersal. – In: Vuorisalo T. O. & Mutikainen P. K. (eds), *Life history evolution in plants*, p. 215–237, Kluwer, Dordrecht.
- Fér T. & Hroudová Z. (2008): Detecting dispersal of *Nuphar lutea* in river corridors using microsatellite markers. – *Freshw. Biol.* 53: 1409–1422.
- Garnier E., Stahl U., Laporte M.-A., Kattge J., Mougenot I., Kühn I., Laporte B., Amiaud B., Ahrestani F. S., Bönisch G., Bunker D. E., Cornelissen J. H. C., Díaz S., Enquist B. J., Gachet S., Jaureguiberry P., Kleyer M., Lavorel S., Maicher L., Pérez-Harguindeguy N., Poorter H., Schildhauer M., Shipley B., Violle C., Weiher E., Wirth C., Wright I. J. & Klotz S. (2017): Towards a thesaurus of plant characteristics: an ecological contribution. – *J. Ecol.* 105: 298–309.
- Gordon D. R., Mitterdorfer B., Pheloung P., Ansari S., Buddenhagen C., Chimera C., Daehler C. C., Dawson W., Denslow J. S., LaRosa A., Nishida T., Onderdonk D. A., Panetta F. D., Pyšek P., Randall R. P., Richardson D. M., Tshidada N. T., Virtue J. G. & Williams P. A. (2010): Guidance for addressing the Australian Weed Risk Assessment questions. – *Plant Protect. Quart.* 25: 56–74.
- Grundbacher F. J. (1963): The physiological function of the cereal awn. – *Bot. Rev.* 29: 366–381.
- Heinken T. & Raudnitschka D. (2002): Do wild ungulates contribute to the dispersal of vascular plants in central European forests by epizoochory? A case study in NE Germany. – *Forstwiss. Centralbl.* 121: 179–194.
- Hejný S. & Slavík B. (eds) (1988–1992): Květena České republiky [Flora of the Czech Republic]. Vols 1 (1988), 2 (1990), 3 (1992). – Academia, Praha
- Hicks L. E. (1932): Flower production in the *Lemnaceae*. – *Ohio J. Sci.* 32: 115–132.
- Hintze C., Heydel F., Hoppe C., Cunze S., König A. & Tackenberg O. (2013): D³: The Dispersal and Diaspore Database – baseline data and statistics on seed dispersal. – *Persp. Plant Ecol. Evol. Syst.* 15: 180–192.
- Hoffmann M. H. (1996): Die in Zentraleuropa verwilderten und kultivierten nordamerikanischen Asten. – *Feddes Repert.* 107: 163–188.
- Hughes L., Dunlop M., French K., Leishman M., Rice B. L., Rodgers P. & Westoby M. (1994): Predicting dispersal spectra: a minimal set of hypotheses based on plant attributes. – *J. Ecol.* 82: 933–950.
- Hulme P. E. (2012): Weed risk assessment: a way forward or a waste of time? – *J. Appl. Ecol.* 49: 10–19.
- Hulme P. E., Bacher S., Kenis M., Klotz S., Kühn I., Minchin D., Nentwig W., Olenin S., Panov V., Pergl J., Pyšek P., Roques A., Sol D., Solarz W. & Vila M. (2008): Grasping at the routes of biological invasions: a framework for integrating pathways into policy. – *J. Appl. Ecol.* 45: 403–414.
- Irmisch T. (1850): Zur Morphologie der monokotylichen Knollen- und Zwiebelgewächse. – G. Reimer Verlag, Berlin.
- Jenny-Lips H. (1930): Vegetationsbedingungen und Pflanzengesellschaften auf Felsschutt. – *Beih. Bot. Centralbl.*, Abt. II, 46: 119–296.
- Kaplan Z., Danihelka J., Koutecký P., Šumberová K., Ekrť L., Grulich V., Řepka R., Hroudová Z., Štěpánková J., Dvořák V., Dančák M., Dřevojan P. & Wild J. (2017): Distributions of vascular plants in the Czech Republic. Part 4. – *Preslia* 89: 115–201.
- Kaplan Z., Danihelka J., Lepší M., Lepší P., Ekrť L., Chrtěk J. Jr., Kocián J., Prančl J., Kobrlová L., Hroneš M. & Šulc V. (2016): Distributions of vascular plants in the Czech Republic. Part 3. – *Preslia* 88: 459–544.
- Kaplan Z., Danihelka J., Štěpánková J., Bureš P., Zázvorka J., Hroudová Z., Ducháček M., Grulich V., Řepka R., Dančák M., Prančl J., Šumberová K., Wild J. & Trávníček B. (2015): Distributions of vascular plants in the Czech Republic. Part 1. – *Preslia* 87: 417–500.
- Kleyer M., Bekker R. M., Knevel I. C., Bakker J. P., Thompson K., Sonnenschein M. P., Poschlod P., van Groenendael J. M., Klimeš L., Klimešová J., Klotz S., Rusch G. M., Hermy M., Adriaens D., Boedeltje G., Bossuyt B., Dannemann A., Endels P., Götzenberger L., Hodgson J. G., Jackel A.-K., Kühn I., Kunzmann D., Ozinga W. A., Römermann C., Stadler M., Schlegelmilch J., Steendam H. J., Tackenberg O., Wilmann B., Cornelissen J. H. C., Eriksson O., Garnier E. & Peco B. (2008): The LEDA Traitbase: a database of life-history traits of the Northwest European flora. – *J. Ecol.* 96: 1266–1274.

- Klímešová J., Danihelka J., Chrtěk J., de Bello F. & Herben T. (2017): CLO-PLA: a database of clonal and bud bank traits of Central European flora. – *Ecology* 98: 1179.
- Klotz S., Kühn I. & Durka W. (2002): BIOLFLOR: eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. – *Schriften. Vegetationsk.* 38: 1–334.
- Kovář P., Kovářová M., Dostál P. & Herben T. (2001): Vegetation of ant-hills in a mountain grassland: effects of mound history and of dominant ant species. – *Plant Ecol.* 156: 215–227.
- Lhotská M. & Chrtková A. (1978): Karpologie a diasporologie československých zástupců čeledi *Fabaceae* [Carpology and diasporology of the Czechoslovak representatives of *Fabaceae*]. – Academia, Praha.
- McConkey K. R., Prasad S., Corlett R. T., Campos-Arceiz A., Brodie J. F., Rogers H. & Santamaria L. (2012): Seed dispersal in changing landscapes. – *Biol. Conserv.* 146: 1–13.
- Moe D. (2014): Endo- and epizoochory: an underestimated factor in cultural landscape management and vegetation historical studies, especially in upper mountain/alpine areas. – In: Efe R. & Ozturk M. (eds), *Environment and ecology in the Mediterranean region II*, p. 169–184, Cambridge Scholars Publ., Newcastle upon Tyne.
- Moravcová L., Pyšek P., Jarošík V., Havlíčková V. & Zákravský P. (2010): Reproductive characteristics of neophytes in the Czech Republic: traits of invasive and non-invasive species. – *Preslia* 82: 365–390.
- Parolin P., Wittmann F. & Ferreira L. V. (2013): Fruit and seed dispersal in Amazonian floodplain trees: a review. – *Ecotropica* 19: 15–32.
- Pearson D. E., Icasatti N. S., Hierro J. L. & Bird B. J. (2014): Are local filters blind to provenance? Ant seed predation suppresses exotic plants more than natives. – *PLoS One* 9: e103824.
- Peart M. H. (1981): Further experiments on the biological significance of the morphology of seed-dispersal units in grasses. – *J. Ecol.* 69: 425–436.
- Pérez-Harguindeguy N., Díaz S., Garnier E., Lavorel S., Poorter H., Jaureguiberry P., Bret-Harte M. S., Cornwell W. K., Craine J. M., Gurvich D. E., Urcelay C., Veneklaas E. J., Reich P. B., Poorter L., Wright I. J., Ray P., Enrico L., Pausas J. G., de Vos A. C., Buchmann N., Funes G., Quétier F., Hodgson J. G., Thompson K., Morgan H. D., ter Steege H., van der Heijden M. G. A., Sack L., Blonder B., Poschlod P., Vaieretti M. V., Conti G., Staver A. C., Aquino S. & Cornelissen J. H. C. (2013): New handbook for standardised measurement of plant functional traits worldwide. – *Austr. J. Bot.* 61: 167–234.
- Pergl J., Sádlo J., Petřík P., Danihelka J., Chrtěk J. Jr., Hejda M., Moravcová L., Perglová I., Štajerová K. & Pyšek P. (2016a): Dark side of the fence: ornamental plants as a source for spontaneous flora of the Czech Republic. – *Preslia* 88: 163–184.
- Pergl J., Sádlo J., Petrušek A., Laštůvka Z., Musil J., Perglová I., Šanda R., Šefrová H., Šíma J., Vohralík V. & Pyšek P. (2016b): Black, Grey and Watch Lists of alien species in the Czech Republic based on environmental impacts and management strategy. – *NeoBiota* 28: 1–37.
- Peters M., Oberath R. & Bohning-Gaese K. (2003): Seed dispersal by ants: are seed preferences influenced by foraging strategies or historical constraints? – *Flora* 198: 413–420.
- Pheloung P. C., Williams P. A. & Halloy S. R. (1999): A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. – *J. Environ. Manage.* 57: 239–251.
- Poschlod P., Abedi M., Bartelheimer M., Drobnik J., Rosbakh S. & Saatkamp A. (2013): Seed ecology and assembly rules in plant communities. – In: van der Maarel E. & Franklin J. (eds), *Vegetation ecology*, Ed. 2, p. 164–202, Wiley, Chichester.
- Poschlod P., Kleyer M., Jackel A.-K., Dannemann A. & Tackenberg O. (2003): BIOPop: a database of plant traits and internet application for nature conservation. – *Folia Geobot.* 38: 263–271.
- Pyšek P. (2005): Survival rates in the Czech Republic of introduced plants known as wool aliens. – *Biol. Invas.* 7: 567–576.
- Pyšek P., Chytrý M., Pergl J., Sádlo J. & Wild J. (2012a): Plant invasions in the Czech Republic: current state, introduction dynamics, invasive species and invaded habitats. – *Preslia* 84: 575–630.
- Pyšek P., Danihelka J., Sádlo J., Chrtěk J. Jr., Chytrý M., Jarošík V., Kaplan Z., Krahulec F., Moravcová L., Pergl J., Štajerová K. & Tichý L. (2012b): Catalogue of alien plants of the Czech Republic (2nd edition): checklist update, taxonomic diversity and invasion patterns. – *Preslia* 84: 155–255.
- Pyšek P., Pergl J., Essl F., Lenzner B., Dawson W., Kreft H., Weigelt P., Winter M., Kartesz J., Nishino M., Antonova L. A., Barcelona J. F., Cabezas F. J., Cárdenas D., Cárdenas-Toro J., Castaño N., Chacón E., Chatelain C., Dullinger S., Ebel A. L., Figueiredo E., Fuentes N., Genovesi P., Groom Q. J., Henderson L., Inderjit, Kupriyanov A., Masciadri S., Maurel N., Meerman J., Morozova O., Moser D., Nickrent D., Nowak P. M., Pagad S., Patzelt A., Pelser P. B., Seebens H., Shu W., Thomas J., Velayos M., Weber E., Wieringa J. J., Baptiste M. P. & van Kleunen M. (2017): Naturalized alien flora of the world: species

- diversity, taxonomic and phylogenetic patterns, geographic distribution and global hotspots of plant invasion. – *Preslia* 89: 203–274.
- Pyšek P. & Prach K. (1993): Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. – *J. Biogeogr.* 20: 413–420.
- R Core Team (2017): R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna.
- Richardson D. M., Pyšek P., Rejmánek M., Barbour M. G., Panetta F. D. & West C. J. (2000): Naturalization and invasion of alien plants: concepts and definitions. – *Diversity Distrib.* 6: 93–107.
- Ridley H. N. (1930): The dispersal of plants throughout the world. – Reeve, Ashford.
- Řehák J. & Řeháková B. (1986): Analýza kategorizovaných dat v sociologii [Analysis of categorized data in sociology]. – Academia, Praha.
- Riis T., Madsen T. V. & Sennels R. S. (2009): Regeneration, colonisation and growth rates of allofragments in four common stream plants. – *Aquat. Bot.* 90: 209–212.
- Römermann C., Tackenberg O. & Poschlod P. (2005): How to predict attachment potential of seeds to sheep and cattle coat from simple morphological seed traits. – *Oikos* 110: 219–230.
- Sádlo J., Chytrý M. & Pyšek P. (2007): Regional species pools of vascular plants in habitats of the Czech Republic. – *Preslia* 79: 303–321.
- Sernander R. (1927): Zur Morphologie und Biologie der Diasporen. – Uppsala.
- Slavík B. (ed.) (1995–2000): Květena České republiky [Flora of the Czech Republic]. Vol. 4 (1995), Vol. 5 (1997), Vol. 6 (2000). – Academia, Praha.
- Slavík B. & Štěpánková J. (eds) (2004): Květena České republiky [Flora of the Czech Republic]. Vol. 7. – Academia, Praha.
- Štěpánková J. (ed.) (2010): Květena České republiky [Flora of the Czech Republic]. Vol. 8. – Academia, Praha.
- Strykstra R. J., Bekker R. M. & Bakker J. P. (1998a): Assessment of dispersule availability: its practical use in restoration management. – *Acta Bot. Neerl.* 47: 57–70.
- Strykstra R. J., Pegtel D. M. & Bergsma A. (1998b): Dispersal distance and achene quality of the rare anemochorous species *Arnica montana* L.: implications for conservation. – *Acta Bot. Neerl.* 47: 45–56.
- Tackenberg O., Poschlod P. & Bonn S. (2003): Assessment of wind dispersal potential in plant species. – *Ecol. Monogr.* 73: 191–205.
- Tackenberg O., Römermann C., Thompson K. & Poschlod P. (2006): What does seed morphology tell us about external animal dispersal? Results from an experimental approach measuring retention times. – *Bas. Appl. Ecol.* 7: 45–58.
- Thomson F. J., Moles A. T., Auld T. D. & Kingsford R. T. (2011): Seed dispersal distance is more strongly correlated with plant height than with seed mass. – *J. Ecol.* 99: 1299–1307.
- Thomson F. J., Moles A. T., Auld T. D., Ramp D., Ren S. Q. & Kingsford R. T. (2010): Chasing the unknown: predicting seed dispersal mechanisms from plant traits. – *J. Ecol.* 98: 1310–1318.
- Thorsen M. J., Dickinson K. J. M. et Seddon P. J. (2009): Seed dispersal systems in the New Zealand flora. – *Persp. Pl. Ecol. Evol. Syst.* 11: 285–309.
- Troia A. (2016): Dispersal and colonization in heterosporous lycophytes: palynological and biogeographical notes on the genus *Isoetes* in the Mediterranean region. – *Webbia* 71: 277–281.
- van der Pijl L. (1982): Principles of dispersal in higher plants. – Springer, New York.
- Vigueira C. C., Olsen K. M. & Caicedo A. L. (2013): The red queen in the corn: agricultural weeds as models of rapid adaptive evolution. – *Heredity* 110: 303.
- Will H., Maussner S. & Tackenberg O. (2007): Experimental studies of diaspore attachment to animal coats: predicting epizoochorous dispersal potential. – *Oecologia* 153: 331–339.
- Willson M. F. (1993): Dispersal mode, seed shadows, and colonization patterns. – In: Fleming T. H. & Estrada A. (eds), *Frugivory and seed dispersal: ecological and evolutionary aspects*, p. 261–280, Springer, Dordrecht.

Received 18 October 2017

Revision received 30 January 2018

Accepted 2 February 2018