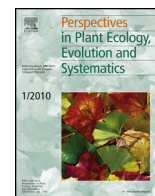


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Research article

D³: The Dispersal and Diaspore Database – Baseline data and statistics on seed dispersal

Christina Hintze^{a,b}, Felix Heydel^b, Christina Hoppe^b, Sarah Cunze^{a,b}, Andreas König^c,
Oliver Tackenberg^{b,*}

^a Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, 60325 Frankfurt am Main, Germany

^b Institute of Ecology, Evolution and Diversity, Goethe University Frankfurt, Max-von-Laue-Str. 13, 60438 Frankfurt am Main, Germany

^c Botanical Garden Frankfurt, Siesmayerstr. 72, 60323 Frankfurt am Main, Germany

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ABSTRACT

Seed dispersal is hard to measure, and there is still a lack of knowledge about dispersal-related traits of plant species. Therefore, we developed D³, the Dispersal and Diaspore Database (available at www.seed-dispersal.info), which aims at simplifying ecological and evolutionary analyses by providing and integrating various items related to seed dispersal: empirical studies, functional traits, image analyses and ranking indices (quantifying the adaptation to dispersal modes).

Currently, the database includes data for more than 5000 taxa and 33 items as well as digital images of diaspores (i.e. the dispersal units), seeds, fruits and infructescences. The included items cover common traits like diaspore mass, size, shape, terminal velocity and seed number per diaspore. Furthermore, we present newly or further developed items like ecomorphological categorizations of the diaspore and fruit as well as information from literature on prevailing dispersal modes. Finally, we introduce several items which are not covered in other databases yet: surface structure and form of the diaspore, the exposure of the diaspores in the infructescence and dispersal rankings. Dispersal rankings allow estimations of how well certain species are adapted to a specific dispersal mode in comparison to a larger species set. They are calculated as the percentile rank of an indicator of species' dispersal potential in relation to a larger species set.

Especially for the new and further developed items we outline the basic concepts in detail, describe the measurement and categorization methods and show how to interpret and integrate these data for single species as well as for larger species sets. Thereby, we calculate baseline statistics of seed dispersal of the Central European flora. We found that diaspores of 72% of the taxa show specializations related to long-distance dispersal, i.e. most often elongated appendages or nutrient-rich tissues. Diaspore masses, sizes and terminal velocities vary over several orders of magnitude and can be approximated by lognormal distributions.

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Introduction

Life history traits develop as a result of plant evolution and adaptation to different habitats and therefore reflect the effect of evolutionary and community assembly processes responding to environmental factors. Their variability and relation to environmental conditions are a matter of particular interest not only in functional but also in basic and applied plant ecology, population biology and vegetation science (Weiher et al., 1999).

Some life history traits influence seed dispersal in space and time, and therewith the distribution of species and their composition in communities (Lavorel et al., 1997; Poschlod et al., 1998; Jakobsson and Eriksson, 2000; Lososova et al., 2008; Oester et al., 2009; Latzel et al., 2011; Normand et al., 2011). Accordingly, analyses of seed dispersal may contribute to the appreciation of dispersal strategies and geographical patterns of seed dispersal as well as to our understanding of relationships, trade-offs and synergistic effects related to seed dispersal or other ecological processes (Lavorel and Garnier, 2002; Nathan, 2006; Van der Veken et al., 2007).

Different dispersal modes have evolved over time. The most important ones with a high potential for long-distance dispersal are

* Corresponding author. Tel.: +49 069 798 42136; fax: +49 069 798 42131.
E-mail address: tackenberg@bio.uni-frankfurt.de (O. Tackenberg).

dispersal by wind (anemochory), by water (hydrochory) and by animals (zoochory). The latter can be subdivided into dispersal on the coat or the hooves (epizoochory), dispersal after feeding and digestion (endozoochory) and dispersal by scatter-hoarding animals (dysochory; e.g. by rodents or birds). Meanwhile, human-mediated dispersal (hemerochory) must also be regarded as an important dispersal mode on a local scale especially in cultural landscapes (Poschlod and Bonn, 1998) as well as for intercontinental dispersal (Vittoz and Engler, 2007). Other dispersal modes like dispersal of seeds from explosive fruits (ballochory or ballistochory) or ballistic dispersal (semachory or boleochory) are capable of short-distance dispersal only. Overviews of the terminology used in many classical studies can be found in Müller-Schneider (1977), van der Pijl (1982) and in the glossary of the D³ database at www.seed-dispersal.info.

Comparative studies typically do not take seed dispersal directly into account because seed dispersal is hard to measure and quantify ('hard' trait sensu Weiher et al., 1999). Instead, dispersal is often derived from easily measurable ('soft') traits. Unfortunately, the relationship between these 'soft' traits and dispersal modes, potentials, distances or dispersal kernels (i.e. frequency distributions of dispersal distances) is often not very clear, although considerable progress has been made in this field during the last two decades. Several attempts have been made in order to assess the dispersal mode from traits or trait combinations (e.g. Hughes et al., 1994; Römermann et al., 2005c; Thomson et al., 2010). Specifically, diaspore traits like mass, size, morphology and terminal velocity, but also whole plant traits like growth form and release height are frequently used in these approaches. Thereby, the term 'diaspore' (or 'dispersule') generally refers to the dispersal unit, regardless to which part of a plant this definition applies.

Even if a plant species shows adaptations to one specific dispersal mode, these adaptations may also affect other dispersal modes via trade-offs or synergistic effects. For instance, Asteraceae with a plumed pappus and low terminal velocities are generally well adapted to wind dispersal (Tackenberg et al., 2003b), but the exposed position of the diaspores in the infructescence and their large and rough surface in combination with their low weight also enhance attachment to and retention in animals' coats (Tackenberg et al., 2006; Will et al., 2007). Accordingly, it has become widely accepted that most plant species are dispersed by more than one dispersal vector or mode (Poschlod et al., 2005). Having a variety of different dispersal modes and vectors will also increase the probability to get dispersed at all and reach favourable sites, which is – besides getting dispersed over long distances – also an important component of successful dispersal (Webb, 1998).

Therefore, a simple binary classification in species that are 'adapted' vs. 'not adapted' to a certain dispersal mode is oversimplified, and methods have been developed that quantify gradual differences in the dispersal potential, e.g. for anemochory (Tackenberg et al., 2003a) or epizoochory (Will et al., 2007; Couvreur et al., 2008). Each of these methods addresses only one dispersal mode and uses different indicators, e.g. terminal velocity for anemochory or retention on animal coats for epizoochory. In consequence, it is still difficult to compare different dispersal modes and hardly possible to quantify to which dispersal mode a species or a species set is adapted best, although this is obviously one of the basic bricks for understanding evolutionary questions related to seed dispersal. To overcome this limitation, we will introduce the concept of 'dispersal rankings', i.e. a comparison of the degree of adaptation of one species to a specific dispersal mode with those of other species within a larger species set, e.g. the regional flora or the species pools of a certain habitat.

However, the parameters required to calculate these dispersal rankings or to parameterize process based dispersal models are

still difficult to obtain despite the fact that many databases on plant functional types exist: e.g. DIASPORUS (Bonn et al., 2000), BIOLFLOR (Klotz et al., 2002), BIOPOP (Poschlod et al., 2003), LEDA (Kleyer et al., 2008), SID (Royal Botanical Gardens, 2008), CLO-PLA (Klimešová and de Bello, 2009) and TRY (Kattge et al., 2011). Even in these databases, trait data which are required to assess how well species are adapted to a certain dispersal mode are not available for larger species sets or even entirely missing.

To make such data more accessible, we established D³, the Dispersal and Diaspore Database (available at www.seed-dispersal.info). The main aim of this database is to provide information that can be used to assess and quantify seed dispersal for a wide range of ecological and evolutionary questions. D³ integrates information on seed dispersal derived from different scientific approaches including empirical studies (literature data on seed dispersal), functional approaches (continuous diaspore and plant traits, ecomorphological classifications, digital image analysis) and the newly developed dispersal ranking indices.

After giving a short overview on D³ and introducing the new traits and concepts, we present our approach on how to interpret and integrate the information from the different scientific approaches. This is presented using exemplary a single species (*Geum urbanum*) and two species sets (four common and well-studied plant families and the Central European flora). Thereby, we also provide baseline statistics for the Central European flora that might build the basis for forthcoming comparative studies.

Methods

The database: www.seed-dispersal.info

Main characteristics

D³ currently includes information on seed dispersal for more than 5000 spermatophyte taxa. The geographic focus is Central Europe, where approximately 83% of the D³-taxa occur (based on Wisskirchen and Haeupler, 1998). The remaining 17% of species mainly originate from other parts of Europe, North and Central America and Africa. In order to include these taxa, the taxonomic core of the database (based on Wisskirchen and Haeupler, 1998) was expanded from various sources (e.g. Dahlgren et al., 1985; Euro+Med, 2006; IPNI, 2008; The Plant List, 2010; Tropicos, 2011). Taxonomy of families and higher levels follows ITIS (2012).

The vast majority of the presented data are original measurements and classifications. Only a small proportion of the presented data (<3%) was taken from scattered literature. In contrast, original measurements and categorizations from other databases like BIOLFLOR (Klotz et al., 2002) or LEDA (Kleyer et al., 2008) are not included at all. The original measurements and categorizations have been made within one working group, allowing for very strict and standardized protocols as well as an effective quality control.

Based on our experience, mean values are requested by most users of trait databases. Therefore, D³ only provides the mean value for continuous traits, even if measurements from more than one population were available. More detailed information like raw data, number of measurements and data sources are available on request.

The online version of the database will be updated and expanded continuously (see section 'Outlook'). The current status of the database (January 31, 2013) concerning the Central European flora is also presented in Appendix S1 in Supporting information.

How to use the database

D³ is an open access database that can be used with a simple web browser. On the website detailed information on the content, a glossary and sample data are available without registration. After registration and login the user can view and download the data. Whereas the traits can be selected from a predefined list of all available traits, the user can select the taxa in three different ways: first, single taxa can be selected by using a look-up field; second, the user may select one or several taxa from a taxonomic tree; third, the user can upload a text file with a species list, approve whether the species names are correctly identified and then receive data for the correctly identified taxa. The results of the database query can be viewed on the website and exported to a text file. All releases of the database are recorded, and thus all queries are reconstructible.

Data in D³

We provide 33 different items which are organized in traits, dispersal rankings and information from literature (Table 1). The data matrix is currently (January 31, 2013) filled up to 69%. Additionally, we present 3185 digital images of diaspores, fruits, seeds and infructescences of 2476 taxa. Detailed information on the ecological relevance, measurements, additional data sources and further literature is given for each item in Appendix S2 and at the website (www.seed-dispersal.info). In the following, we will only give a short overview of the common traits but present more details for the new and further developed items.

Common traits like length, width and height of a diaspore (Nos. 13–15 in Table 1), diaspore shape (No. 16 in Table 1), diaspore mass (No. 19 in Table 1), terminal velocity (No. 20 in Table 1) and number of seeds per diaspore (No. 22 in Table 1) are already included in literature or other databases, e.g. LEDA (Kleyer et al., 2008), SID (Royal Botanical Gardens, 2008) or TRY (Kattge et al., 2011). The data presented in D³ are mostly original measurements or classifications which have not been published before and are thus an addition to the already available data. The measurements for these traits are mostly performed on the basis of standard procedures (cf. Knevel et al., 2005 and Appendix S2).

In some traits which are also covered by other databases we used modified concepts. Specifically, this refers to categorical traits that describe the morphology and adaptation of fruits and diaspores in respect to seed dispersal. Our categorizations of diaspore morphology and diaspore and fruit typology are based on their specific relevance for seed dispersal rather than resulting from a common evolutionary or ontogenetic perspective. For instance, we categorized the diaspores of both, cherries (*Prunus*) and strawberries (*Fragaria*), as fleshy fruits, notwithstanding that cherries are drupes with a pyrene, and the fruit flesh in strawberries develops from the receptacle which is covered by many nutlets.

Diaspore morphology (Nos. 4–12 in Table 1) is principally based on the LEDA concept (Römermann et al., 2005a), but we revised some classifications and added new categories. For example, our sub-categorization of diaspores with high nutrient contents (either in quality or quantity) is based on the probable fate of the embryo during the dispersal process rather than on morphological terms like aril, pulp or elaiosome: Species with a ‘nutrient-rich appendage’ or ‘nutrient-rich envelope’ have a reasonable chance that the embryo survives zoochory as the seed will often not be digested. In contrast, the seed of a species with a ‘nutrient-rich seed’ is typically digested, and in consequence, the embryo is on high risk to be destroyed during dispersal. Another difference from the LEDA approach is that we added the category ‘mucilaginous surface’ (see also ‘Discussion’).

The information from literature on seed dispersal modes (Nos. 26–33 in Table 1) includes references for anemochory, dysochory,

endozoochory, epizoochory, hemerochory, hydrochory and a summarized category for other dispersal modes. Raw data for these items are also available in DIASPORUS (Bonn et al., 2000) and LEDA (Kleyer et al., 2008). Here we used the raw data to calculate the proportion of citations of the respective dispersal mode in relation to the number of citations for all dispersal modes. In case that better data are not available, these proportions may be used for a rough estimate of the relevance of the respective dispersal modes as will be demonstrated below.

We also present plant traits which have not been published in other databases yet: The diaspore surface structure (No. 18 in Table 1) is an index of the smoothness of a diaspore ranging from 0 (very rough) to 1 (very smooth). The index is derived from digital image analysis as the quotient of the diameter of the diaspore and the convex hull polygon around it (see also Römermann et al., 2005c). Smoothness of the diaspore has been proved to affect the attachment of diaspores to animal coats (Will et al., 2007), and it is also affecting wind dispersal: Rough diaspores are characterized by higher drag-coefficients and lower terminal velocities (cf. Burrows, 1986).

Another ‘new’ trait is the diaspore form (No. 17 in Table 1) with four categories (‘round’, ‘elongated’, ‘flat’ and ‘elongated & flat’), which is derived from the diaspores’ dimensions (details are given in Appendix S2). In contrast to the related shape index (Thompson et al., 1993), which quantifies the deviance of diaspores from a sphere, it allows distinguishing between elongated and flat forms.

Moreover, we characterized the exposure of diaspores to the environment (No. 21 in Table 1) within three categories: ‘exposed’, ‘covered partly’ and ‘enclosed’. To our knowledge, diaspore exposure is not addressed in databases yet, although it may affect dispersal greatly in changing the probability of diaspores to come in contact with passing animals (Will et al., 2007) or to be dispersed by wind. Diaspore exposure may also be used as an indicator of how well the embryo is protected from being eaten.

In order to allow an assessment how well a plant species is adapted to a certain dispersal mode, we finally developed the concept of dispersal ranking indices (Nos. 23–25 in Table 1). They are derived from dispersal indicators, i.e. life history traits or experimental assessments that can be used to quantify the adaptation of a species to the respective dispersal mode. We use terminal velocity as an indicator for anemochory, as terminal velocity has been repeatedly proved to be closely related to wind dispersal potential (Green, 1980; Nathan et al., 2001; Tackenberg et al., 2003a). We did not use the releasing height for calculating the index, as plant height seems to be more related to processes like competition than to seed dispersal (e.g. Westoby, 1998). The epizoochory ranking index is based on the product of attachment potential (Will et al., 2007) and retention potential (Römermann et al., 2005c; Tackenberg et al., 2006). This product can be interpreted as the proportion of seeds that may be transported in the coat of an animal over a significant time period that principally allows long-distance dispersal. The epizoochory index was computed for the transport in woolly hair. Based on our knowledge, the difference between various coat types in the epizoochory ranking index is negligible for many applications. Finally, we used the proportion of seeds still floating after one week measured in a standardized lab experiment (Römermann et al., 2005b and unpublished data) as an indicator of hydrochory potential.

The ranking indices were calculated as the percentile rank of these indicators of the respective species in relation to all species for which data were available. To ensure that a high value characterizes high dispersal potentials, we used the descending order in terminal velocity because low terminal velocities characterize species that are well adapted to anemochory. In consequence,

Table 1

Current content of the database and data excerpt for *Geum urbanum*. More detailed information on the ecological relevance, measurements and methods, additional data sources and further literature is given for each trait in Appendix S2 and on the website (www.seed-dispersal.info). *N* gives the number of taxa for which data were available in the database on January 31, 2013.

No.	Item	Description and relevance	Scale, unit of measurement or categories	<i>N</i>	Data excerpt for <i>Geum urbanum</i> L.
TRAITS					
1	Diaspore type	Description of the morphological structure that acts as the diaspore, i.e. the dispersal unit.	Nominal; 10 categories: <i>seed, fruit segment, fruit, infructescence, whole plant, specialized vegetative part, no diaspore, cone, spore, other</i>	5424	Fruit segment
2	Fruit type	Description of the ecological characteristics of the fruit that are related to seed dispersal.	Nominal; 9 categories: <i>non-fleshy indehiscent fruit, fleshy fruit, pepo, fruit with upright aperture, fruit with lateral aperture, explosive release mechanism, gymnosperme type, other, not applicable</i>	5424	Non-fleshy indehiscent fruit
3	Heterodiaspory	A heterodiaspore species features more than one diaspore type.	Binary; presence (1)/absence (0)	5424	0
Morphology of the diaspore (cf. Appendix S1 in Supporting information)					
4	Nutrients	Indicator for dysochory and endozoochory.	Binary; presence (1)/absence (0)	5424	0
5	Aerenchym	Indicator for hydrochory and anemochory.	Binary; presence (1)/absence (0)	5424	0
6	Wings	Indicator for anemochory.	Binary; presence (1)/absence (0)	5424	0
7	Elongated appendages	Indicator for anemochory and epizoochory.	Binary; presence (1)/absence (0)	5424	1
8	Hooked appendages	Indicator for epizoochory.	Binary; presence (1)/absence (0)	5424	1
9	Mucilaginous surface	Indicator for epizoochory and endozoochory.	Binary; presence (1)/absence (0)	5424	0
10	No specializations		Binary; presence (1)/absence (0)	5424	0
11	Other specializations	Reserved for specialized vegetative parts.	Binary; presence (1)/absence (0)	5424	0
12	Diaspore morphology	Compact formula describing the diaspore morphology in detail.	Nominal; many categories	5424	segm 4b.4c.5
13	Diaspore length	Length of the diaspore, i.e. the longest axis, which is measured including all appendages.	Continuous [mm]	3232	7.57 mm
14	Diaspore width	Width of the diaspore, i.e. the second longest axis, which is measured perpendicular to length and includes all appendages.	Continuous [mm]	3084	2.00 mm
15	Diaspore height	Height of the diaspore, i.e. the shortest axis, which is measured perpendicular to length and width and includes all appendages.	Continuous [mm]	1404	0.70 mm
16	Diaspore shape	Deviation of a diaspore's shape from a sphere in three dimensions; spherical diaspore = 0.	Continuous; dimensionless index between 0 and 0.23	2412	0.16
17	Diaspore form	Form of the diaspore in categories.	Nominal; 4 categories: <i>spherical, flat, elongated, elongated & flat</i>	2412	Elongated
18	Diaspore surface structure	Smoothness of a diaspore's surface based on images of the diaspores, i.e. in two dimensions; very smooth surface = 1.	Continuous; dimensionless index between 0 and 1	2584	0.5
19	Diaspore mass	Weight of one diaspore including all appendages.	Continuous [mg]	1975	1.9 mg
20	Terminal velocity	Maximum speed of a falling diaspore in still air; relevant for anemochory.	Continuous [m s^{-1}]	2451	1.77 m s^{-1}
21	Diaspore exposure	Accessibility of dispersal vectors to the diaspores within the infructescence; relevant for anemochory, endo- and epizoochory.	Nominal; 4 categories: <i>exposed, covered partly, enclosed, not applicable</i>	5424	Exposed
22	Seeds per diaspore	Number of seeds per diaspore.	Ordinal; 11 classes (0 = no seeds; 1 = 1 seed; 2 = 2–10 seeds; 3 = 11–100 seeds, etc.)	5424	1
DISPERSAL RANKINGS					
23	Anemochory ranking index	This ranking allows an assessment how well a certain species is adapted to anemochory (wind dispersal) in comparison to other species and dispersal modes.	Continuous; dimensionless index between 0 and 1	2768	0.60 ^a
24	Epizoochory ranking index	This ranking allows an assessment how well a certain species is adapted to epizoochory (external animal dispersal) in comparison to other species and dispersal modes.	Continuous; dimensionless index between 0 and 1	2111	0.92 ^a

Table 1 (Continued)

No.	Item	Description and relevance	Scale, unit of measurement or categories	N	Data excerpt for <i>Geum urbanum</i> L.
25	Hydrochory ranking index	This ranking allows an assessment how well a certain species is adapted to hydrochory (water dispersal) in comparison to other species and dispersal modes.	Continuous; dimensionless index between 0 and 1	752	0.48 ^a
INFORMATION FROM LITERATURE ON DISPERSAL MODES					
26	Total number of citations		Continuous (integer number)	2841	14
27	Proportion of anemochory records		Continuous; proportion between 0 and 1	2841	0
28	Proportion of dysochory records		Continuous; proportion between 0 and 1	2841	0
29	Proportion of endozoochory records		Continuous; proportion between 0 and 1	2841	0
30	Proportion of epizoochory records		Continuous; proportion between 0 and 1	2841	0.79
31	Proportion of hemerochory records		Continuous; proportion between 0 and 1	2841	0.14
32	Proportion of hydrochory records		Continuous; proportion between 0 and 1	2841	0
33	Proportion of other records		Continuous; proportion between 0 and 1	2841	0.07
DIGITAL IMAGES					
	Images of diaspores, fruits, seeds, and infructescences		–	2476	See Fig. 2

^a The ranking indices of *Geum urbanum* are determined in comparison with a set of Central European species (cf. Appendix S1).

all dispersal rankings are directly comparable and range from 0 (poorly adapted) to 1 (well adapted). Please note that the lowest rank is used for equal values. We calculated indices for anemochory, epizoochory and hydrochory.

Data analysis

To demonstrate the concept of dispersal rankings, we compared the distribution of ranking indices for anemochory, epizoochory and hydrochory in four species-rich and well-studied families: Asteraceae, Fabaceae, Cyperaceae and Rosaceae. This analysis was restricted to the taxa listed in Ellenberg's indicator values (Ellenberg, 1992), which we used as a standard list for Central European taxa. As we yet do not have trait-based indicators that address endozoochory and hemerochory, we calculated 'provisional' ranking indices for these dispersal modes from the proportions of citations on these dispersal modes in the literature data (Nos. 29 and 31 in Table 1). For this analysis we took only species with more than four entries into account. Differences between dispersal modes (within each family) and between families (within each dispersal mode) were analyzed separately using the non-parametric Kruskal–Wallis ANOVA with the stepwise step-down option from SPSS 21 (IBM, USA).

To demonstrate our approach on how to integrate the data on seed dispersal for larger species sets, we also calculated baseline statistics for the whole Central European flora as listed in Ellenberg's indicator values (Ellenberg, 1992). For this species set ($N=2662$) we calculated frequency distribution, mean value, standard deviation (SD), median, skewness and kurtosis of each continuous trait and tested whether the observed distribution was differing from normal or lognormal distribution with Kolmogorov–Smirnov tests. For the categorical traits we calculated frequency distributions and tested for equal distribution (χ^2 test). All statistics were computed with SPSS 21 (IBM, USA).

The data for all analyses were downloaded from www.seed-dispersal.info on January 31, 2013, and are documented in Appendix S1 in Supporting information.

Results

Dispersal ranking indices

The distributions of ranking indices (calculated in comparison to the Central European flora) differ significantly from an equal distribution ($p < 0.05$ for this and all further differences mentioned

in the whole section) in the four families as well as in every tested dispersal mode (Fig. 1).

Comparing dispersal modes within families, we found in the Asteraceae (Fig. 1, first column) the highest ranking indices in epizoochory followed by anemochory. These two dispersal modes show a left-tailed distribution with many species well adapted to either anemochory or epizoochory. Hemerochory and hydrochory have intermediate ranking indices and are relatively uniformly distributed. In contrast, endozoochory is characterized by the lowest ranking indices and a right-tailed distribution with most species being poorly adapted to endozoochory.

In the Cyperaceae (Fig. 1, second column) we found the highest ranking indices in hydrochory and epizoochory, which are characterized by left-tailed distributions. The indices for endozoochory and hemerochory have the lowest values and are characterized by pronounced right-tailed distributions.

In the Fabaceae (Fig. 1, third column) we found the highest ranking indices in endozoochory and hemerochory. It seems noticeable that the indices in these dispersal modes are relatively uniformly distributed compared to the 'best' dispersal modes in the other families. The ranking indices for the other dispersal modes are lower and show somewhat right-tailed distributions.

In the Rosaceae (Fig. 1, fourth column) the highest ranking indices were found in endozoochory, which shows a left-tailed distribution. However, a distinct proportion of species is characterized by very low ranking indices for endozoochory. Anemochory, epizoochory and hydrochory have intermediate ranking indices and show more or less equal distributed ranking indices. Hemerochory has a right-tailed distribution and the lowest ranking indices.

Comparing the families regarding the particular dispersal modes, we found that in anemochory the family with the highest ranking indices were the Asteraceae (Fig. 1, first row), in endozoochory the Rosaceae (followed by the Fabaceae) (Fig. 1, second row), in epizoochory the Asteraceae again (Fig. 1, third row), in hemerochory the Fabaceae together with the Asteraceae (Fig. 1, fourth row) and finally in hydrochory the Cyperaceae (Fig. 1, fifth row).

Seed dispersal data of a single species: *Geum urbanum*

In the following we present the results of the data query for *G. urbanum*: the fruit of *G. urbanum* is composed of many not connate fruit segments (Fig. 2), which are the diaspores as they are dispersed independently. Hence, the diaspore type is a FRUIT SEGMENT (No. 1 in Table 1), which is NON-FLESHY (No. 2 in Table 1).

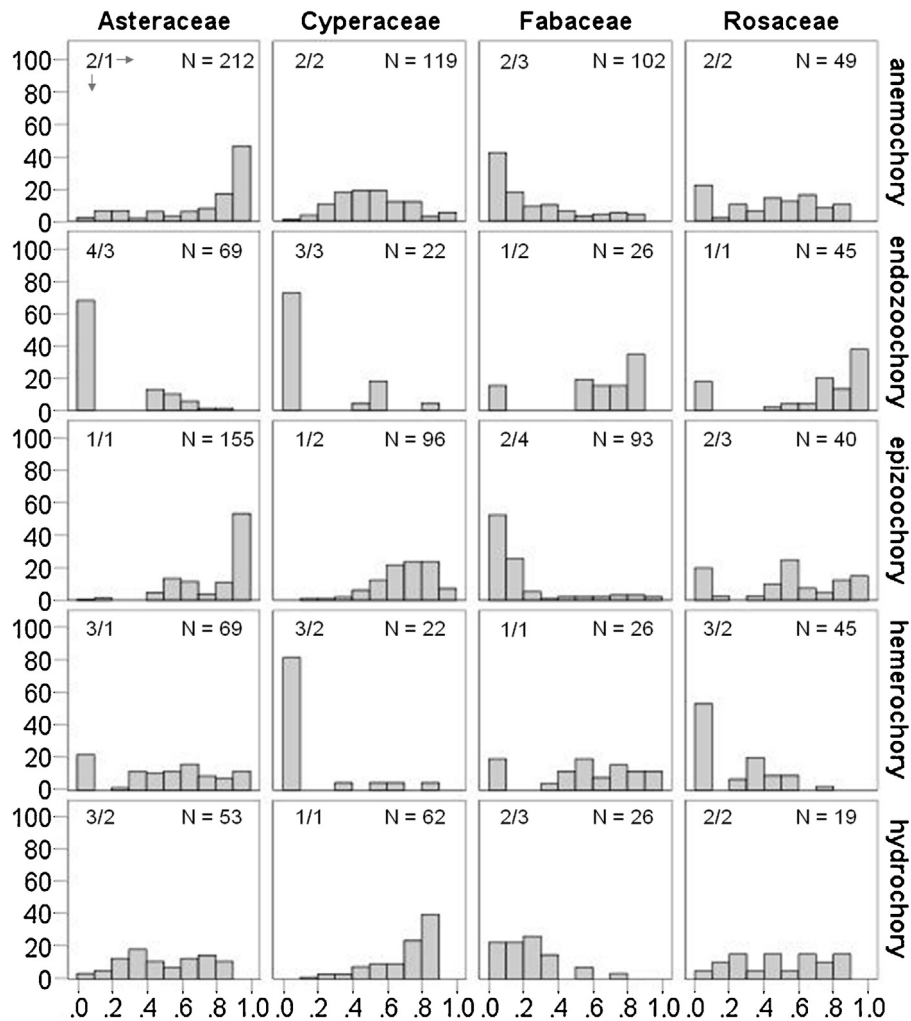


Fig. 1. Frequency distributions of ranking indices of five dispersal modes (in rows) in four different families (in columns). The X-axis shows the ranking index and the Y-axis gives the percentage of species in each bin. In the left upper corner of each graph the homogenous subgroups are given ($p < 0.05$, Kruskal–Wallis ANOVA). The first digit addresses differences between dispersal modes in each family ('1' = dispersal mode with the highest ranking indices), whereas the second digit addresses differences between families in one dispersal mode ('1' = family with the highest ranking indices). The ranking indices are calculated in comparison to the Central European flora (Ellenberg, 1992).

The ONE-SEEDED diaspores (No. 22 in Table 1) are EXPOSED to the environment (No. 21 in Table 1). They show several adaptations that may affect seed dispersal: The most apparent specialization is the elongated and hooked stylus, which is categorized as ONE LONG APPENDAGE (Appendix S2), which is HOOKED (No. 8 in Table 1). In addition, the diaspore is covered with many fine hairs, which are categorized as MANY SHORT APPENDAGES (Appendix S2). Using a compact formula, the morphology of the diaspore of *G. urbanum* can be described as SEG M|4b.4c.5| (No. 12 in Table 1, see Appendix S2 for explanation).

The diaspore has a MASS of 1.9 mg (No. 19 in Table 1) and its SIZE (including appendages) is 7.6 mm × 2.0 mm × 0.7 mm (Nos. 13–15 in Table 1). The SHAPE INDEX is 0.16 (No. 16 in Table 1) and the form is ELONGATED (No. 17 in Table 1). DIASPORE SURFACE STRUCTURE is 0.5 (No. 18 in Table 1), indicating that the diaspore surface is neither very rough structured nor absolutely smooth. The TERMINAL VELOCITY is 1.8 m s⁻¹ (No. 20 in Table 1).

The RANKING INDEX FOR EPIZOOCHORY is 0.92 (No. 24 in Table 1), indicating that only 8% of the Central European taxa in D³ are equal or better adapted to dispersal on the coat of animals.

Furthermore, the RANKING INDEX FOR ANEMOCHORY is 0.60 (No. 23 in Table 1), indicating that 40% of the Central European taxa have identical or lower terminal velocities and are equal or better adapted to wind dispersal. Finally, the RANKING INDEX FOR HYDROCHORY is 0.48 (No. 25 in Table 1), indicating that in 52% of the Central European taxa more or the same number of diaspores were floating after one week. Please note that we determined the dispersal ranking indices of *G. urbanum* here in comparison to the Central European species set, whereas the indices presented on the website are related to all species included in D³.

In literature we found 14 references (No. 26 in Table 1) which assess DISPERSAL MODES with a high potential for long-distance dispersal for *G. urbanum* (Nos. 27–33 in Table 1). From these, the most often acknowledged dispersal modes are epizoochory (79%) and hemerochory (14%).

Baseline statistics on seed dispersal for the Central European flora

All continuous traits differ significantly from normal and lognormal distributions ($p < 0.05$), but diaspore mass, length and terminal

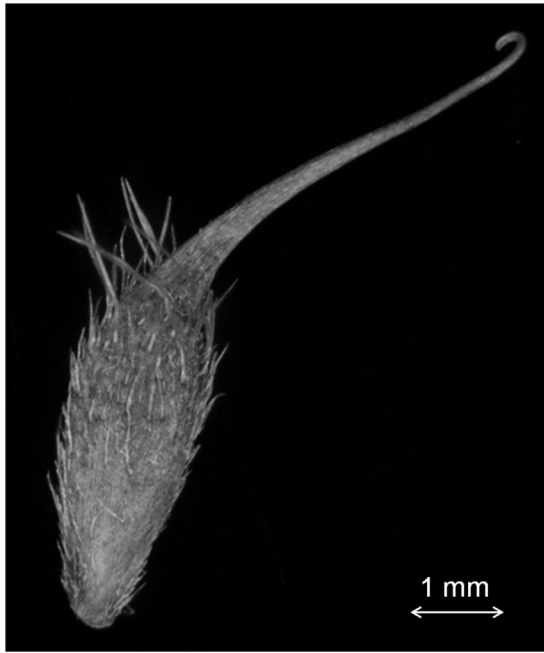


Fig. 2. Fruit segment (diaspore) of *Geum urbanum*.

velocity can roughly be approximated by lognormal distributions (Fig. 3, detailed data in Appendix S3).

All categorical traits differ significantly from an equal distribution ($p < 0.05$) (Fig. 4, detailed data in Appendix S4). 19% of the taxa produce more than one diaspore type (heterodiaspory, Fig. 4g). To simplify matters, all further analyses refer to the main diaspore type: Most often fruits (44% of the taxa), seeds (40%) and fruit segments (15%) represent the diaspores. All other diaspore types contribute less than 2%. 54% of the taxa produce non-fleshy indehiscent fruits, followed by dehiscent fruits (35%) with either lateral or upright apertures. To summarize, 72% of the species show some morphological specializations with respect to long-distance dispersal, whereas 28% have no obvious morphological specializations (see column ‘Description and relevance’ in Table 1 for the link between morphological structures and dispersal modes). The most frequent specializations are elongated appendages (38% of all taxa) and nutrient-rich tissues (27% of all taxa). Please note that these proportions refer to the number of taxa with the respective specialization, whereas Fig. 4c shows the cumulative number of all specializations which may be more than one per diaspore. On average, we found 1.18 specializations per diaspore ($SD = 1.05$).

The predominant diaspore form is spherical (80%), followed by elongated (10%). We found that more than 92% of the taxa produce one-seeded diaspores, but few fleshy-fruited taxa like *Fragaria* or *Nymphaea* have more than 100 seeds in one diaspore. The exposure of the diaspores in the infructescence is roughly equally distributed: 42% are exposed to the environment and approximately 30% are covered partly or enclosed, respectively.

In total, we found 8400 citations on dispersal modes of 1909 taxa in literature, which is on average 4.4 per taxon (Appendix S3). These data affirm 2.2 ± 1.3 (mean \pm SD) dispersal modes per taxon. The most often mentioned mode is epizoochory (52% of the taxa; Appendix S4), followed by hemerochory (41%) and anemochory (35%). Please note that these proportions refer to the number of taxa, whereas Fig. 4h shows the cumulative number of all dispersal modes that were cited in literature and which may be more than one per taxon.

Discussion

With D^3 we provide a large dataset on seed dispersal with more than 120 000 entries for more than 5000 mostly European taxa. The database considerably enlarges the amount of already existing data on common seed dispersal traits (cf. Kattge et al., 2011). Most of the common traits were measured using standardized methods and can thus be relatively easily merged with data from other resources.

As seed dispersal is a classical ‘hard’ trait (sensu Weiher et al., 1999) and can only be quantified indirectly, the need for various ‘soft’ traits regarding seed dispersal is immense. In D^3 we therefore collected and present information that comes from a variety of different scientific approaches: classical measurements of functional traits, ecomorphological categorizations, image analyses of diaspore surfaces, data derived from experimental assessments of dispersal potentials as well as empirical studies that are based on observations, experiments or other assessments of seed dispersal. The variety of presented ‘soft’ traits require guidance because it is not always obvious how the different types of information can be integrated into one synoptic assessment of seed dispersal: Is a species like *G. urbanum* (with a terminal velocity of 1.8 m s^{-1} and a haired and hooked stylus) better adapted to anemochory or to epizoochory? Are humans (14% of the literature references on seed dispersal of *G. urbanum* refer to hemerochory) more important for long-distance dispersal than water (to which *G. urbanum* is equal or better adapted than 48% of the other Central European species)? It is one of our central aims to give some advice how to answer such basic questions and how to interpret and integrate the different data types. Specifically, the dispersal ranking indices were developed to allow comparisons between dispersal modes and species. In the following, we will thus first of all discuss the ranking indices and specifics of further selected database items in order to reveal further developments and to uncover some differences to other databases. Subsequently, we will discuss our approach on how to interpret and integrate the data with the example of *G. urbanum* as well as for a larger species set, the Central European Flora.

Dispersal ranking indices

Seed dispersal is affected not only by heritable plant traits but also by the ‘dispersal infrastructure’ of the environment. For example, wind dispersal is more effective in an alpine landscape with heavy turbulences compared to lowland conditions (Tackenberg and Stöcklin, 2008). Furthermore, zoochory depends on density, behaviour and movement of animals (cf. Will and Tackenberg, 2008). Despite these important issues, many questions related to seed dispersal can also be answered when addressing only the traits that are rather controlled more directly by the species. In order to find a measure of seed dispersal that is independent from a specific environment we developed the concept of dispersal ranking indices.

The basic idea for the development of the ranking indices was to use indicators (trait measurements, experimental assessments) that allow assessing gradual differences in the dispersal potential of the plant species for specific dispersal modes. Naturally, the used indicators can be questioned, but it would be beyond the scope of this study to discuss this in detail. However, we acknowledge that there is a lot of space for improvement in this respect; this especially refers to endozoochory and hemerochory which cannot be predicted from functional traits yet.

Next, we had to find a common ‘currency’ in order to make the different indicators (terminal velocity, floating potential, attachment to and retention in animal coats) comparable. This was achieved by calculating the ranking index of the indicator of a species within a larger species set for each dispersal mode

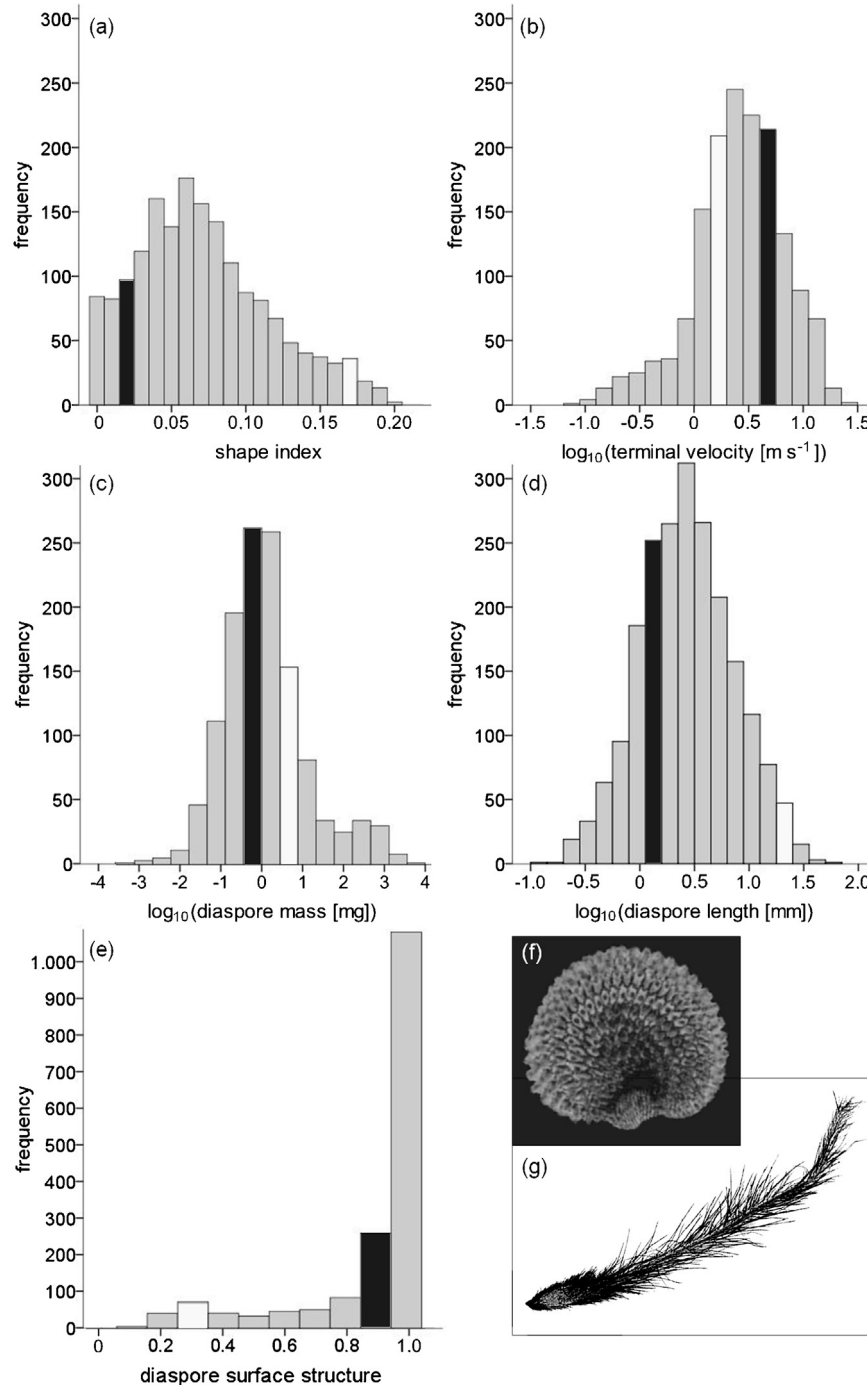


Fig. 3. Frequency distributions of selected dispersal-related traits in the Central European flora. The bars in which the diaspores of *Silene vulgaris* (f) and *Pulsatilla vulgaris* (g) are located are marked in black (*Silene*) and white (*Pulsatilla*). (a) Shape index ($N=1722$). (b) Terminal velocity ($N=1547$). (c) Diaspore mass ($N=1257$). (d) Diaspore length ($N=2113$). (e) Diaspore surface structure ($N=1712$).

separately. An important advantage of this approach is that the ranking indices directly reflect the degree of adaptation of the species. On the other hand, the approach also implies that the indices are not 'pure' species traits but depend on the species set selected for the comparison. It therefore seems critical to carefully choose an appropriate species set for the comparison.

When interpreting the ranking indices, it should also be kept in mind that the indices may also reflect phylogenetic constraints, which means that the advantages a species experiences are not the result of evolutionary selection for this dispersal mode. This

seems especially important when addressing hemerchory: It is hard to imagine that plant species have evolved towards hemerchory, except for special cases like the selection of weed seed size by agricultural corn cleaning machinery (e.g. Bonn and Poschlod, 1998 and cited literature).

Furthermore, ranking indices might also be affected by trade-offs and synergistic effects between dispersal modes: For instance, anemochory and epizoochory share a number of traits like seed mass or surface smoothness, which are negatively related to both. In consequence, species with high ranking indices for anemochory

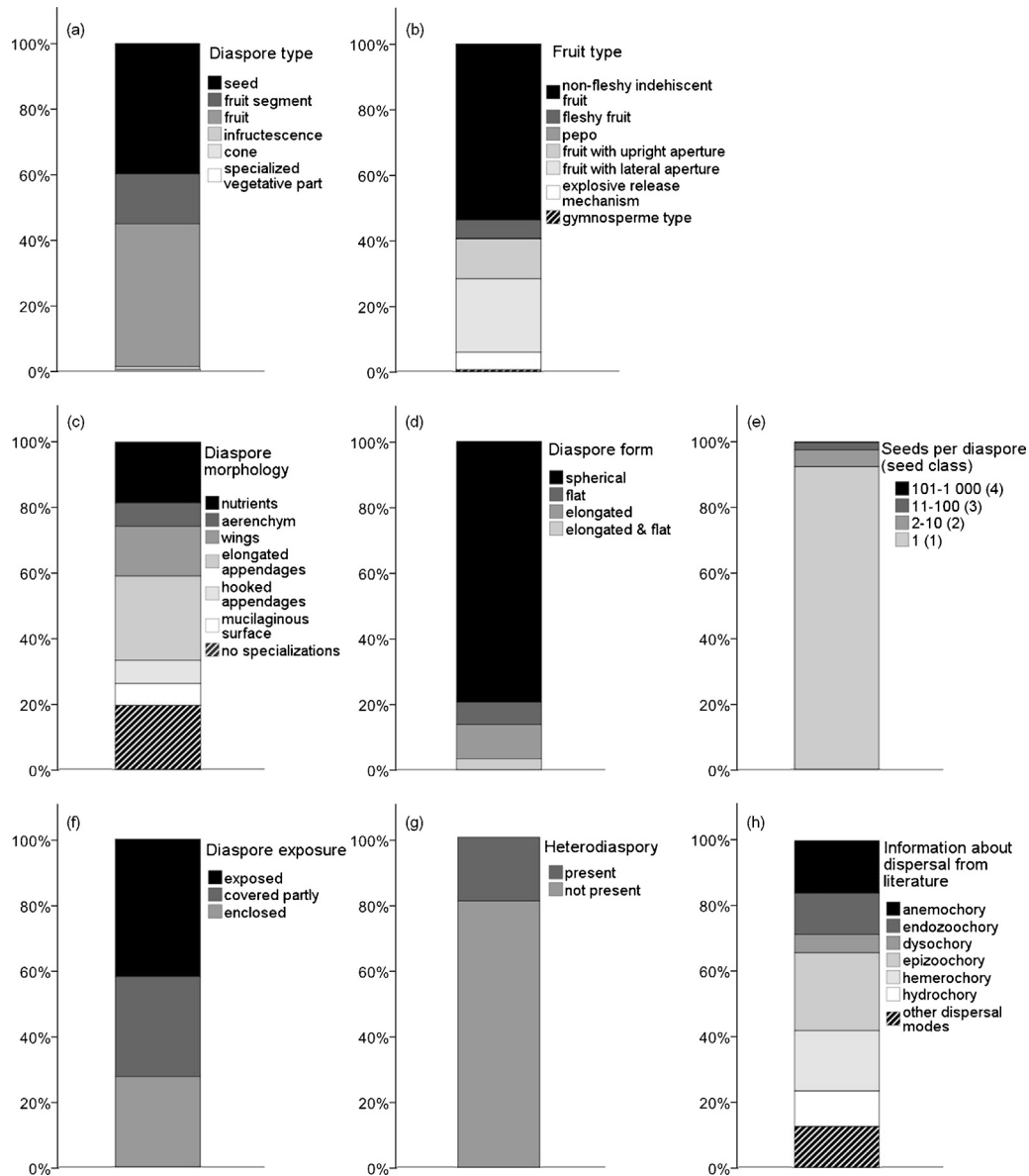


Fig. 4. Distributions of selected dispersal-related items in the Central European flora. (a) Diaspore type. (b) Fruit type. (c) Diaspore morphology (proportions calculated from cumulative sums of all morphological specializations of the taxa; one diaspore can feature several specializations). (d) Diaspore form. (e) Number of seeds per diaspore. (f) Diaspore exposure. (g) Heterodiaspory. (h) Information about dispersal from literature (proportions calculated from cumulative sums of entries regarding different dispersal modes for all taxa; one taxon can feature several dispersal modes). (a)–(f) apply to the main diaspore type of each taxon. More detailed information, also on less frequent categories, can be found in Appendix S4.

often also have high ranking indices for epizoochory and vice versa. This synergistic effect might be one of the reasons for the – at least on the first view – unexpected result that Asteraceae species show significant higher ranking indices for epizoochory than for anemochory (Fig. 1). However, this result is also confirmed by experiments where very high attachment potentials and retention times in animals' coat were found for Asteraceae (Tackenberg et al., 2006; Will et al., 2007). Furthermore, Asteraceae, although many of them are clearly adapted to anemochory, do not have the lowest terminal velocities in the Central European Flora. Most species with dust seeds like Orchidaceae or Orobanchaceae as well as species with plumed diaspores from genera like *Epilobium*, *Salix* or *Typha* have lower terminal velocities than most Asteraceae and thus show higher anemochory ranking indices. Finally, retention in animal coats is less sensitive to diaspore mass than terminal velocity (Römermann et al., 2005c and unpublished analyses). Therefore,

Asteraceae with heavier diaspores and less well-developed pappi rarely exhibit high ranking indices for anemochory but quite often have (very) high ranking indices for epizoochory. Nevertheless, despite the fact that Asteraceae seem better adapted to epizoochory than to anemochory, the Asteraceae are best adapted to anemochory when comparing the considered four families. This result clearly meets the common expectations.

When comparing families, we found that the Cyperaceae are the family with the highest ranking indices for hydrochory and within the Cyperaceae hydrochory (together with epizoochory) is the dispersal mode with the highest ranking indices. Both results are in accordance with common expectations and supported by the fact that in D³ 74% of the Central European Cyperaceae are classified as having an aerenchym (the utricle) that might enhance floating. In this family we found a (weak) relationship between hydrochory and epizoochory as both show high ranking indices and

left-tailed distributions. This can be explained by the fact that many Cyperaceae are characterized by having not only the aerenchym mentioned above but also possess elongated appendages together with a relatively low mass and an exposed exposure, all factors enhancing epizoochory. In the other families the shape of the frequency distributions of hydrochory ranking indices seems not to be related to the shapes of anemochory and epizoochory (which are similar to each other). This might indicate that hydrochory and the other dispersal modes are not subject to strong trade-offs or synergistic effects, i.e. they are affected by different functional traits. However, confirming this hypothesis would require further and more detailed analyses.

The Fabaceae (as well as the Rosaceae) are characterized by relatively low ranking indices in anemochory, epizoochory and hydrochory as, for instance, approximately 67% of the Fabaceae species show ranking indices ≤ 0.25 regarding these dispersal modes. Are the members of these families not well adapted to long-distance dispersal at all, or are they dispersed by other dispersal modes? To answer these questions, we must include other dispersal modes. However, yet we cannot predict endozoochory or hemerochory based on functional traits or experiments. Furthermore, it seems not very promising to predict dispersal by human activities (e.g. vehicles, contaminated seeds, agriculture) from plant traits, although some attempts have been made in this direction (e.g. Hodkinson and Thompson, 1997). Therefore, we introduced 'provisional' ranking indices for endozoochory and hemerochory which are based on the information from literature on dispersal modes and will be discussed in the next section.

Information from literature on dispersal modes and 'provisional' ranking indices

The literature data on dispersal modes must be interpreted with special care because the methods of data collecting differ considerably between dispersal modes and are thus hardly directly comparable. For instance, hemerochory is mainly derived from observations, whereas for anemochory observations hardly exist. In contrast, anemochory is mainly derived from diaspore morphology. Furthermore, epizoochory as well as endozoochory are mainly derived from observations, field experiments and morphology (raw data on dispersal modes and methods available from LEDA, Kleyer et al., 2008).

Nevertheless, the information from literature may give useful hints about the importance of dispersal modes. Therefore, we based our assessments on the importance of hemerochory and endozoochory on the literature data and calculated 'provisional' dispersal ranking indices from the proportion of literature that referred to these dispersal modes. To ensure that no bias between rare and frequent species distorted the analysis, we used proportions instead of the absolute number of citations and restricted the analysis to species with at least five citations. The ranking of these data ensured that the values for the different dispersal modes are comparable despite the fact that the assessment methods differed between dispersal modes. However, we would like to emphasize that these 'provisional' indices are preliminary and should be replaced by process based approaches once these are available.

Using this approach, our analysis indicates that within the Fabaceae endozoochory and hemerochory have the highest ranking indices. A high importance of endozoochory seems reasonable as Fabaceae – which are less nitrogen-limited than other families due to their root tubercles – generally have seeds with a high protein content (Harborne, 1994). Accordingly, in D^3 all Fabaceae taxa are characterized as having nutrient-rich germinules which make them attractive for animals as well

as for human nutrition (Aykroyd et al., 1982). Obviously, the members of this family also build an important component in many grassland ecosystems and are frequently used, sown and dispersed by humans in agricultural habitats. Hence, it is not surprising that hemerochory is also predominant in this family.

Ecomorphological categorizations

In D^3 we present several ecomorphological classifications related to seed dispersal, specifically diaspore and fruit type, heterodiaspory, diaspore morphology and exposure in the infructescence. One important application of the mentioned categorizations is to describe and define the diaspore per se, which builds the basis for all further measurements and categorizations. Without knowing the diaspore it may be difficult to understand dispersal at all. We hope that the commented images of seeds, diaspores, fruits and infructescences presented on the website will also support other researchers in this respect.

The detailed descriptions and categorizations of the diaspores were also the basis for detecting and quantifying how many species may produce more than one diaspore type, a phenomenon that has been addressed frequently (e.g. Hegi, 1908ff; van der Pijl, 1982). Based on an intensive literature research and own assessments, we found that 880 species (16%, $N=5424$) within the D^3 database can be classified as heterodiaspore, compared to 508 species (23%) listed in the BIOLFLOR database (Klotz et al., 2002; $N=2246$ species). However, these proportions are not directly comparable because the concepts of heterodiaspory differ slightly between these two databases.

Fruit types and diaspore morphology allow important insights into the adaptation of a species to specific seed dispersal modes, although the relationship between morphological traits and seed dispersal may often be more complicated than generally assumed (Cain et al., 2000; Tackenberg, 2003; Tackenberg et al., 2006). The categorizations used in D^3 are based on already existing approaches; specifically, we would like to acknowledge BIOLFLOR (Klotz et al., 2002) and the LEDA-concept (Knevel et al., 2005). Some differences seem also worth to be mentioned. We distinguished three types of nutrient-rich tissues (either in quality or quantity): diaspores with high nutrient contents (a) in the germinule, (b) in the fruit flesh surrounding the embryo or (c) (loosely) attached in an appendage. This is based on the idea that the fate of the embryo, dispersal modes (specifically endozoochory vs. dysochory vs. stomatochory) and the probability that the embryo is destroyed during digestion may differ between these groups (see also 'Methods' section).

Furthermore, we would like to draw attention on some newly introduced categories which may also allow assessments concerning adaptation to specific dispersal modes. For example, we introduced the fruit type 'explosive release mechanism', which occurred in 283 species (5.2%) in the D^3 database. Concerning diaspore morphology we present data on diaspores with an 'aerenchym' (453 species = 8%) and on diaspores with a 'mucilaginous surface' (439 species = 8%). Aerenchym may enhance floating capacity and thus be useful when identifying species with a high potential for hydrochory. The function of diaspores with mucilage is less clear and controversially discussed. Mucilage may act as a barrier against pathogens, enhance germination in dry environments, act against dispersal, enhance attachment to animal coats or protect diaspores during digestion (e.g. Kreitschitz, 2009; Inceer, 2011; Yang et al., 2012). The now broadened database on species with such mucilage may help uncovering its relevance.

Diaspore shape and form

The shape index, describing the deviation from a sphere, has become a popular trait in seed biology, since Thompson et al. (1993) demonstrated that it affects the vertical distribution of seeds (in fact germinules) in the soil and seed bank longevity. Seed shape is also related to mechanical resistance of seeds (Wood et al., 2012) and one of the candidates used to understand survival of seeds during digestion (cf. Bonn, 2004, and cited literature). Concerning epizoochory, it was shown that elongated diaspores retain longer on animal coats than flat diaspores (cf. Tackenberg et al., 2006). However, the shape index does not distinguish between flat and elongated forms. Therefore, we introduce some basic rules (Appendix S2) to distinguish between these forms and present the categorical data on diaspore form for more than 2400 species.

Terminal velocity

Terminal velocity is defined as the maximum speed of a falling diaspore in still air. It is reached only after an initial acceleration phase, which increases rapidly with terminal velocity (Thompson, 2005). If terminal velocity is measured during this acceleration phase, an underestimation of the 'real' terminal velocity of 6%, 33% and 100% will take place for species with a 'real' terminal velocity of 2 m s^{-1} , 5 m s^{-1} and 10 m s^{-1} , respectively (calculation following Schäfer, 2002, assuming that terminal velocity was measured between 1.5 and 1.75 m below the release point, a frequently used measurement setup). To avoid such underestimation, the terminal velocities presented in the D³ database are mathematically corrected for this initial acceleration wherever possible using a discretised simulation of free fall with drag, based on the laws of physics (Schäfer, 2002).

Having said this, it seems not surprising that the frequency distribution of terminal velocities in the D³ dataset differs considerably from other datasets, especially for the high values: While the 97.5% quantile of terminal velocity is 4.7 m s^{-1} in the TRY database ($N = 1108$, Kattge et al., 2011), it is 15.0 m s^{-1} in D³ ($N = 2451$). Here we can only speculate whether this difference can be explained by different species sets or by different measurement methods. Fortunately, a potential underestimation of the terminal velocities is only relevant for species which are not well adapted to wind dispersal and must therefore not result in serious errors in the assessment of wind dispersal potentials (Thompson, 2005). Nevertheless, we strongly recommend correcting for the initial acceleration phase, if necessary, as the correct terminal velocity seems indispensable when analysing trait frequency distributions or the physics of wind dispersal or quantifying allometric effects and trade-offs.

How to interpret and integrate data of a single species: *Geum urbanum*

The diaspores of *G. urbanum* show specializations that can easily be interpreted as adaptations to epizoochory: The diaspores are of medium weight and have a relatively rough surface. Additionally, they are hooked and exposed to the environment. Thus, they have a good chance to get attached to the coat of a passing animal (ca. 14% for animals with straight coat, according to Will et al., 2007) and stay attached in the coat over considerable time periods (Tackenberg et al., 2006). These general considerations are confirmed by the epizoochory ranking index, which is 0.92 for *G. urbanum*, indicating that only 8% of the Central European species in the database attach and retain on the coat in equal or higher proportions. As the ranking indices for anemochory and hydrochory are considerably lower, 0.60 and 0.48, respectively,

we can therefore argue that from an evolutionary perspective *G. urbanum* is best adapted to epizoochory.

The diaspore morphology of *Geum* does not show any specializations that can be interpreted as adaptations to anemochory or hydrochory, like e.g. wings or aerenchymas. Anyway, the diaspores show a terminal velocity of 1.8 m s^{-1} , which is relatively low, and therefore, they could be able to be dispersed by wind over long distances (cf. Tackenberg et al., 2003a). Also, the anemochory ranking index is 0.60, indicating that *G. urbanum* is indeed not very well adapted to wind dispersal but still equal or better adapted to be dispersed by wind than 60% of the Central European species.

Furthermore, the diaspores have the ability to float over several days (Kleyer et al., 2008). Even if the current velocity of a stream is only 1 km h^{-1} , it may disperse diaspores over several kilometres in this time. However, most *Geum* individuals will not grow in flood plains (cf. Korneck et al., 1998) and may never be dispersed by water. Thus, we conclude that hydrochory is not a typical dispersal mode for *G. urbanum* in most habitats. However, in flood plains hydrochory has the potential to disperse seeds over long distances even if the species is not very well adapted to hydrochory in comparison to other species (hydrochory ranking index = 0.48).

Generally, it should be kept in mind that dispersal always depends on the environment: If animals with large home ranges are not present in a certain habitat, anemochory may be most important even if *Geum* is not adapted very well to anemochory. To provide a more realistic ecological assessment of the importance of different dispersal modes, it is thus important to quantify the amount of dispersed diaspores, the proportion of diaspores that are dispersed by the different vectors and their dispersal distance. Dispersal kernels may be a key for answering these questions and will be addressed in one of the next versions of the database (see 'Conclusions and outlook').

Furthermore, to assess the importance of hemerochory (or other dispersal modes), we yet cannot use dispersal rankings because of lacking data and concepts, but must rely on other data: In literature we found two references (14% of all) that proved hemerochory for *G. urbanum*. It should therefore also be regarded as an important dispersal vector, especially in cultural habitats in which *G. urbanum* frequently occurs (Klotz and Kühn, 2002), because humans can disperse seeds over extraordinary long distances.

How to interpret and integrate data of a larger species set: the Central European flora

The vast majority of the Central European flora shows adaptations that affect seed dispersal (Fig. 4b and c): The diaspores of most taxa (72%) show morphological structures that can be interpreted as an adaptation for long-distance dispersal. Most often we found specializations that may enhance epizoochory (elongated appendages, hooks) and anemochory (elongated appendages), followed by endozoo- or dysochory (nutrients) and hydrochory (aerenchymas). As already pointed out, these morphological structures allow only a very rough classification, which may also be misleading: Elongated appendages may favour anemochory, epizoochory or both, depending on their quantity and fine structure. Furthermore, a mucilaginous surface in moistened diaspores occurs in 10% (!) of the taxa. Its role is unresolved, but it may enhance epizoochory, may protect the seeds from being intensively digested or can ensure that the seeds are not dispersed over long distances (ateleochory, e.g. van der Pijl, 1982). Moreover, 72% of the taxa without morphological specializations of their diaspores have adaptations in their fruits which may enhance short-distance dispersal, e.g. explosive release mechanisms or dehiscent fruits.

Conclusions and outlook

Currently, the database covers more than 5000 taxa (subspecies, species and aggregates). While basic information specifically on ecomorphological classification of fruits and diaspores is given for all included species, other traits are less well covered. We continue filling the gaps in the data matrix with a priority on the Central European flora. Additionally, we are extending the geographic focus and have already begun to systematically collect data for further European species as well as for species from African savannas. Explicitly, we welcome collaborators who are interested in applying the presented methods and concepts to species sets from other regions and are willing to broaden the database.

The design of the database easily allows extending it with more traits, which is also one of our future prospects. For example, we are currently preparing to add information on seed production per individual, which can be regarded as one of the most important functional traits related to seed dispersal. Furthermore, we aim at including dispersal kernels in the database. Dispersal kernels are a powerful tool in ecological research and can build the basis for many analyses which require quantitative assessments of seed dispersal, e.g. for predicting ‘realistic’ migration rates or calculating seed exchange in fragmented landscapes. While in the last decade a couple of process based seed dispersal models which principally allow computation of dispersal kernels have been developed (Morin et al., 2007; Will and Tackenberg, 2008; Cabral and Schurr, 2010; Nathan et al., 2011; Horn et al., 2012), the use and applicability of these models is still limited because they are difficult to parameterize or not available to the public. Therefore, we will compute dispersal kernels with selected models and make the kernels themselves available in the database. Dispersal kernels allow comparing the importance and effectiveness of dispersal modes and vectors for different plant species as well as in different environments. Thus, they are complementary to the presented dispersal rankings, which are independent from a specific environment and were mainly developed to address evolutionary issues.

Furthermore, the ranking indices might be a helpful concept quantifying the adaptation to a specific dispersal mode of a species or a species set in comparison to a larger species set. They might also support the understanding of dispersal strategies in general and reveal trade-offs and synergistic effects between dispersal modes as the exemplary application of the dispersal rankings demonstrated.

To summarize, we hope that the presented data and new concepts which are already included in D³, specifically the dispersal rankings, will – in combination with the outlined extensions – stimulate ongoing research and allow disclosing some of the many secrets still related to seed dispersal.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ppees.2013.02.001>.

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