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Research article

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

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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

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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.

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