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The LEDA Traitbase: A database of life-history traits of the Northwest European flora

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Summary

1. An international group of scientists has built, an open internet database of life-history traits of the Northwest European flora (the LEDA-Traitbase) that can be used as

a data source for fundamental research on plant biodiversity and coexistence, macro-ecological patterns and plant functional responses.

2. The species-trait matrix comprises referenced information under the control of an editorial board, for ca. 3000 species of the Northwest European flora, combining existing information and additional measurements. The database currently contains data on 26 plant traits that describe three key features of plant dynamics: persistence, regeneration and dispersal. The LEDA-Traitbase is freely available from www.leda-traitbase.org.

3. We present the structure of the database and an overview of the trait information available.

Synthesis and applications: The LEDA Traitbase is useful for large-scale analyses of functional responses of communities to environmental change, effects of community trait composition on ecosystem properties and patterns of rarity and invasiveness, as well as linkages between traits as expressions of fundamental trade-offs in plants.

Key-words: Plant functional traits, Age of first flowering, Buoyancy, Clonal traits, Canopy height, Plant life span, SLA, Dispersal, Seed weight, Seed number, Soil seed bank, Functional ecology.

Introduction

The immense variation in plant form and life history has always intrigued botanists, plant geographers and ecologists. From the middle of the 19th century, interest in disentangling relationships between plant biological traits and the environment has steadily developed, resulting in a wealth of descriptions of plant morphology as adaptations to climate and soil factors (Du Rietz 1931). This interest evolved into compilations of biological knowledge for individual plant species (e.g. Kirchner *et al.* 1908-1936; the Biological Flora of the British Isles series published in this journal; Rabotnov 1974-1990 for Russia). A further step has been taken more recently, to build up digital databases to synthesise information on plant traits. For instance, the GLOPNET database (Wright *et al.* 2004) covers chemical, structural and physiological traits of leaves for a large number of species world-wide. Seed weight data are now available for > 10^4 species (Flynn *et al.* 2006), and other databases offer bibliographic data for selected communities (e.g. APIRS for aquatic plants (http://plants.ifas.ufl.edu/)) or provide taxonomic information together with some selected traits (e.g. USDA 2006).

Within Europe, knowledge of traits for individual species is growing fast, but information remains scattered over many sources, including dozens of different journals, large monographs and floras. The sources are available in various languages and distributed across many countries, collected and stored in different ways, and are not mutually integrated. Standardisation of trait definitions and measurements is often poor among species and studies. Trait data can also be retrieved from various databases. However, currently accessible databases are often restricted to certain regions, and cover only a limited number of species or traits.

A trans-national initiative has therefore aimed at designing and filling a species-trait matrix for the NW European flora that would be freely retrievable on the Worldwide Web (Knevel *et al.* 2003). The LEDA Traitbase (www.leda-traitbase.org), which uses a

European consolidated species list, is concerned with pooling existing databases, compiling new information from published data and closing knowledge gaps through extensive new measurements across several NW European countries. It consists of a relational database linking species with traits and reference information about data source, location, habitat and trait measurement protocol on three core sets of traits: (i) persistence (vegetative) traits such as leaf, stem and clonal growth characteristics; (ii) regeneration traits such as seed production, seed longevity and (iii) dispersal traits such as seed weight, dispersal vectors, floating capacity and vertical terminal velocity of propagules.

The general objectives of the LEDA project were announced in Knevel *et al.* (2003). The present paper describes the scope and architecture of the database, the methods of collecting data and the plant life-history traits that are covered by the LEDA Traitbase. Additionally, a brief overview of applications illustrates the value of trait databases in general, and the LEDA Traitbase in particular, for research in functional ecology.

Framework of the LEDA Traitbase

TRAITS IN THE LEDA TRAITBASE

Traits covered by the LEDA Traitbase were selected according to two major criteria: (1) relevance for persistence, regeneration and dispersal as key functions for survival in patterned landscapes and (2) trait data available for the flora of Northwest-Europe, either in published sources or in unpublished databases maintained by the project partners. As LEDA was designed as a compilation of data for a large number of species, we had to exclude traits for which only a small number of records for the Northwest European flora could be expected (e.g. relative growth rate or leaf life span). Table 1 shows an overview of the traits in the LEDA Traitbase together with associated functions and selected references, whereas Table 2 describes the categories or units of measurement, and actual number of species and records for the traits (version 1, 2007). More detailed information on the trait definitions is available in the Appendix S1 in Supplementary Material.

Many trait data now available in LEDA for Northwest Europe had already attracted considerable attention in functional ecology (e.g. canopy height, seed number, seed mass, see Table 1) and are, at least in part, available elsewhere (e.g. Flynn *et al.* 2006 for seed mass, Ellenberg *et al*. 1991 for life form). For other traits, the LEDA Traitbase may be a unique source of data. For instance, seed bank longevity of many species was poorly known previously. The LEDA Project has improved this knowledge quite substantially from 21,071 records on 1189 species in the database of Thompson *et al.* (1997) to 44,353 records covering 1787 species in total in the LEDA Traitbase (Tab. 2).

The LEDA Traitbase also includes data on clonal growth and dispersal traits that are rarely available elsewhere. The morphological traits characterising clonal growth serve as indicators for vegetative multiplication, persistence and vegetative regeneration subsequent to damage (Klimeš *et al.* 1997; Klimešová & Martínková 2004). The data available in the LEDA Traitbase that are related to clonal growth encompass a categorisation of clonal growth organs, bud bank vertical distribution and seasonality (Klimešová & Klimeš 2007), lifespan of a shoot, persistence of the connections between parent and offspring shoots, lateral spread and number of offspring shoots produced per year and per parent shoot. These traits indicate speed of lateral spread, rate of clonal multiplication and duration of possibility of mutual support inside interconnected parts of a clone.

Seed dispersal influences many key aspects of the biology of plants, but is inherently hard to measure (Cain *et al.* 2000). Since every species may be dispersed through different vectors and to different distances, we have measured traits related to dispersal potential (Poschlod *et al.* 2005). Terminal velocity is a relevant predictor for wind dispersal potential. If vertical air velocity exceeds ‘terminal velocity’ then the seed can be uplifted and dispersed for larger distances (Nathan *et al.* 2002; Tackenberg *et al.* 2003). Combined with terminal velocity, seed release height is important in modelling wind dispersal. One key factor in epizoochory (dispersal by means of seeds attached to external parts of an animal) is the capacity of seeds to remain attached to fur, i.e. the attachment potential (Couvreur *et al.* 2004; Römermann *et al.* 2005). Other dispersal traits covered by the LEDA Traitbase include endozoochory (seeds dispersed after passing through the digestive tract of an animal), buoyancy (floating capacity), morphology of the dispersal unit and information about dispersal types as well as dispersal vectors of plants.

THE LEDA GEOGRAPHICAL RANGE AND TAXONOMIC CORE

The geographical range of the LEDA project (Fig. 1) roughly covers NW-Europe from the North Cape, Norway, to the Loire in France, and from the eastern borders of both Finland and Germany to the west coast of Ireland. Plant species present in Austria, Switzerland, Iceland, Poland, the Baltic States, Czech Republic, Slovakia and Hungary overlap with those in the core LEDA area by 50 to 80%, indicating the wide range of possible users of the Traitbase.

Selection of the 3000 priority vascular plant species for which we collected data was made according to the species frequencies in the core countries i.e. UK, The Netherlands and Germany, disregarding alpine species and extremely rare species.

The taxonomic core of the LEDA Traitbase consists of one synonymised plant list at the species level, complete with authorities. The list was collated from the national plant lists available for the geographical range of the LEDA project (see Appendix S1). Species names and grouping of the species in higher taxa, however, cannot be considered as a stable reference system because taxonomies are subject to research and are changed frequently. When collating existing databases and retrieving data from published literature different "taxonomic concepts" (sensu Geoffroy & Berendsohn 2003) inevitably get merged. The resulting loss in data quality can, however, be expected have little impact on the LEDA trait database for the following reasons: (1) Only a few taxonomic groups in the flora of Northwest Europe are still under profound revision, and (2) Floras were used which are interconnected by the species checklist from the SynBioSys-Europe project (Schaminée *et al.* 2007).

METHODS OF COLLECTING DATA

In LEDA, the following trait databases were collated: Ecoflora (Fitter & Peat 1994), Electronic Comparative Plant Ecology (Hodgson *et al.* 1995), Biological traits of vascular plants database (Kleyer 1995), CLOPLA (Klimešová & Klimeš 2006), the Soil seed bank database (Thompson *et al.* 1997), the Dutch Botanical Database (CBS 1997 with updates), DIASPORUS (Bonn *et al.* 2000), seed mass data from BiolFlor (Klotz *et al.* 2002), and BioPop (Poschlod *et al.* 2003; Jackel *et al.* 2006).

The remaining data were derived from literature dating back to the 19th Century. For many traits in the LEDA Traitbase we expected more data to be available in the literature than we were actually able to retrieve. A large field sampling campaign was used to obtain data identified as missing in the literature: collecting and measuring standards are described in Knevel *et al.* (2005, www.leda-traitbase.org; see also Cornelissen *et al.* 2003). Very rare species had to be excluded because sampling effort increased with rarity or because extraction of plant material from the field was prohibited by conservation authorities. Age of first flowering could not be determined during field collections and was therefore compiled solely from the literature.

The LEDA editorial board ensures that each entry in the Traitbase has a full reference to its original source, whether a published book, paper, database or recent measurement according to the LEDA standards. Also, newly measured data are referenced according to the field site, including georeference information and habitat characteristics. When habitat characteristics were missing for data from other sources, these were derived from indicator values (Ellenberg *et al.* 1991).

TECHNICAL STRUCTURE OF THE DATABASE

The LEDA Traitbase is a combination of a relational database holding the trait data and several web applications allowing for input, access and analysis of trait-related data (see Appendix S1). Users only need a web-browser to query the LEDA Traitbase. After query execution, a table containing the selected records will be displayed within the web browser, either as individual records with bibliographic reference or as aggregated values, e.g. the average of all SLA records for a species. Registered users may upload or otherwise compose a list of species names to constrain their queries, and they may instruct the system to deliver the query results to their e-mail address. For example, to obtain a GIS link, the mapping module FloraMap of the German online plant atlas (http://www.floraweb.de) is accessible from within the LEDA web query application. This allows access to further trait data, species distribution data and related information (in German for version 1). Hence, the analysis of the spatial distribution of traits (e.g. Kühn *et al.* 2006) can be facilitated easily.

APPLICATIONS OF THE LEDA TRAITBASE

Potential applications of the LEDA Traitbase cover the whole range of functional ecology and phylogenetic ecology, the fusion of ecology and evolutionary history (e.g. Grime 2006; McGill *et al.* 2006; Westoby 2006). A major field of functional ecology is the analysis of changes in community trait composition in response to environmental change to reveal functional response traits (Lavorel & Garnier 2002). Understanding how persistence, regeneration and dispersal traits respond to environmental change is essential for the prediction of species change in many ecological applications (e.g. landscape planning, restoration, mitigation of plant invasions). For instance, the LEDA Traitbase has been used to show that the predictability of local species composition from environmental conditions is constrained by dispersal traits (Ozinga *et al.* 2005). Dispersal traits were further used to assess wind dispersal potential or external animal dispersal in plants (Tackenberg *et al.* 2003). LEDA Traitbase data were also used to model relationships between plant traits, soil fertility and disturbance by land use (Kleyer 2002, Kühner & Kleyer 2008), and bud bank traits were used to explain the regeneration of biennials and perennials following disturbance of urban plant communities (Latzel *et al.* 2008).

Potential applications of the LEDA Traitbase include the analysis of changes in ecosystem functions (e.g. productivity, carbon sequestration) in response to changes in biodiversity and community composition based on the concomitant changes in “functional effect traits”. Changes in traits such as longevity, leaf dry matter content, leaf nitrogen content or woodiness can affect the productivity of plant communities (Garnier *et al.* 2007), nutrient cycling (Eviner *et al.* 2006), or soil carbon sequestration (De Deyn *et al.* 2008). Response and effect traits are linked when changes in species composition translate into modifications of ecosystem properties (Chapin *et al.* 2000). For instance, seed production may be essential for the response of plant species to strong disturbances and at the same time an essential resource for animals. On the other hand, while seeds may be important for the response to disturbance, leaf and stem traits may be more important for the effect of plant species on biomass decomposition. By coupling the LEDA Traitbase with datasets that combine species abundances with environmental information and ecosystem properties, response and effect traits and linkages between these can be identified (Suding *et al.* 2008).

LEDA data were also used for the analysis of relationships between traits and distribution patterns of rarity and endangerment of plant species (Smart *et al.* 2005, Römermann *et al.* 2008). Specifically, there has been a long quest for traits which make species invasive (e.g. Kühn *et al.* 2004, Moles *et al.* 2008, see Pyšek & Richardson 2007 for a review) or influence commonness and rarity in weeds (e.g. Lososová *et al.* 2008) or urban plant species (Thompson & McCarthy 2008).

Functional diversity, i.e. the value and range of plant functional traits in a given community (Tilman 2001), has been proposed as an important feature of communities, for instance to provide resilience in relation to regime shifts in terrestrial and aquatic communities (Folke *et al.* 2004). Functional diversity can be recorded at different biological levels, e.g. within species and between species in a community. Intraspecific diversity can be extracted from the LEDA Traitbase either by retrieving the original individual records or from aggregated information such as minimum and maximum values or standard deviations. For rare species or native species of natural landscapes without agricultural land use, the number of trait records is still small. More records will be needed throughout the geographical and environmental range of the species to assess the full extent of trait variability. Interspecific diversity can be measured with various indices (e.g. Mason *et al.* 2005) by collating LEDA data aggregated per trait and species to vegetation relevés.

Understanding how investments of carbon and mineral nutrients vary between species is central to plant ecology. Large databases on plant traits have helped to clarify the extent to which scaling relations between traits indicate potential trade-offs or allometries (e.g. Enquist & Niklas 2002, Wright *et al.* 2004). Although LEDA comprises only limited data on biomass partitioning, it can produce trait correlation structures that could assist in revealing scaling relations associated with persistence, regeneration and dispersal. In contrast to such physiologically determined trade-offs, environment-induced trade-offs are often characterised by different costs and benefits along environmental gradients. LEDA data have been used to search for trade-offs between local above-ground persistence and below-ground seed persistence (Ozinga *et al.* 2007) and between generative and vegetative reproduction in riparian vegetation (Boedeltje *et al.* 2008).

These examples show that the LEDA Traitbase can assist in clarifying the role of traits and of trait variation in the response of plants to changing environments, the assembly of communities and the functioning of ecosystems. Case studies exploring these issues will most often take place at the level of a community or a landscape. Trait measurements at these levels will profit from assessing the variation of the traits under study against variation in the flora of the region or biome. This information can now be retrieved from the LEDA Traitbase for the flora of NW Europe. The LEDA Traitbase also offers the opportunity to re-analyse large vegetation datasets in terms of functional traits. For instance, it would be interesting to combine country-wide sets of relevés aggregated to syntaxonomic classes (e.g. Schaminée *et al.* 1995-1999) with the LEDA Traitbase to extract variation in persistence and regeneration traits of plant communities. So far, this has only been done for dispersal traits (Ozinga *et al.* 2005). Such community trait profiles could be used to generate better hypotheses for detailed investigations of plant trait – environment linkages (McGill *et al.* 2006).

FURTHER PROSPECTS

At present the Traitbase supports a total of more than 8300 taxa of NW-Europe. Many taxa are subspecies to which no data are linked. However, the possibility exists to link data to these taxa, as well as to taxa that currently are not included in the LEDA priority list. The LEDA consortium welcomes new collaborators interested in delivering new data to the LEDA Traitbase. The LEDA standards (accessible through www.leda-traitbase.org) provide baseline information on how the data should be organised. To assure data quality and consistency with the LEDA data standard, the LEDA Editorial Board will review the data before incorporating them into LEDA.

The LEDA Traitbase and its applications are designed to be extended with further traits. Adapting the database scheme is relatively easy, since data for distinct traits are stored within distinct tables. The LEDA consortium welcomes any initiative that seeks to enlarge the LEDA Traitbase, either by extension of the geographical range or by extension of the traits that are covered by the database. This would include the obligation to establish appropriate data standards, support additional technical effort and to take part in the reviewing process.

Moreover, we see future prospects in the collation of LEDA to various other databases, such as plant genomics, distribution, Red Lists, plant communities, habitats and environmental factors, e.g. nutrient and disturbance data for sites with known species composition (Bekker *et al.* 2007, Schaminée *et al.* 2007). Currently, there are many initiatives across Europe and other parts of the world that intend to make available various databases. We expect that the joint analysis of data from these different sources will greatly advance our understanding of large-scale biodiversity change.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Details regarding the LEDA trait definitions and the structure of the database.

This material is available as part of the online article from:

http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2745.XXXX.XXXXX.x

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Table 1: Overview of the traits in the LEDA Traitbase, their functional significance and related publications.

The LEDA traits	Functional significance and related publications
Persistence	
Canopy height	Competitive ability (Westoby *et al.* 2002)
Leaf distribution along the stem, branching, shoot growth form	Competitive ability (Barkman 1988)
Leaf mass, leaf size, specific leaf area, leaf dry matter content	Growth rate, competitive ability, stress tolerance (Westoby *et al*. 2002)
Woodiness, stem specific density	Growth rate, investment in supporting structure (Ryser 1996)
Clonal growth organs, persistence of connection between parent and offspring shoots, number of off-spring shoots per parent shoot per year, lateral spread	Competitive ability, persistence, clonal integration, stor-age (De Kroon & Van Groenendael 1997; Klimeš & Klimešová 2000; Vesk & Westoby 2004)
Bud bank - vertical distribution and seasonality	Response to disturbance (Bellingham & Sparrow 2000, Klimešová & Klimeš 2007)
Regeneration	
Plant growth form, plant life span, age of first flowering	Response to disturbance, establishment, invasiveness (Raunkiaer 1937; Rejmánek & Richardson 1996)
Seed number, seed shedding	Response to disturbance, establishment, dispersal (Leishman 2001; Bruun & Poschlod 2006)
Seed weight, size and shape	Dispersal, establishment (Grime *et al.* 1988, Westoby *et al.* 2002)
Seed bank longevity	Storage effects, response to disturbance (Bekker *et al.* 1998)
Dispersability	
Morphology of dispersal unit, seed releasing height	Wind dispersal, ecto- and endozoochorous dispersal (Van der Pijl 1972)
Dispersal vectors	Spectra of dispersal vectors for plants (Bonn *et al.* 2000)
Terminal velocity	Wind-dispersal (Tackenberg *et al.* 2003)
Attachment capacity of the disper-sal unit, digestion survival	Ecto- and endozoochorous dispersal (Couvreur *et al.* 2004; Römermann *et al.* 2005)
Buoyancy	Dispersal in running water (Danvind & Nilsson 1997)

Table 2. Contents of the LEDA Traitbase, version 1.

Trait name in Data Standards	No. of species	No. of records	Cat. No.	Category or unit(s) of measurement
Plant growth form	2334	3154	1	Phanerophyte
			2	Chamaephyte
			3	Hemicryptophyte
			4	Cryptophyte
			4.1	Geophyte
			4.2	Helophyte
			4.2.1	Halophyte
			4.3	Hydrophyte
			5	Therophyte
			6	Liana
			7	hemi-epiphyte
			8	Epiphyte
			9	vascular semi-parasite
			10	vascular parasite
			11	mesophyte
Canopy height	2893	4934		m
Plant life span	2219	4293	1	summer annuals
			2	winter annuals
			3	strict monocarpic biennials and poly-annuals
			4	short-lived perennials (< 5 years)
			5	medium- lived perennials (5-50 years)
			6	long-lived perennials (>50 years)
			7	perennials without any further detailed information
Age of first flowering	1521	2530	1	< 1 year
			2	1 and 5 years
			3	> 5 years
Leaf mass	1665	4472		mg
Specific leaf area (SLA)	2019	5941		mm^2 mg^{-1}
Leaf size	2054	5590		mm^2
Leaf dry matter content (LDMC)	1735	3451		mg g^{-1}
Woodiness & Stem specific density	3152	5300	1	woody
			1.1	hard wood
			1.2	soft wood
			2	semi-woody
			3	herbaceous (non-woody)
				g cm^{-3}
Shoot growth form	3118	5386	1	lianas, climbers and scramblers
			2	stem erect
			3	stem ascending to prostrate
			4	stem prostrate
			5	free-floating plants
			6	emergent, attached to the substrate
			7	floating leaves, attached to the substrate
			8	submerged, attached to the substrate
Branching	2878	4055	1	yes
			2	no
			3	unknown
Leaf distribution along the stem	3491	5355	1	rosette/tufted plant
			2	semi-rosette
			3	leaves distributed regularly along the stem
			4	shoot scarcely foliated
			5	tufts and crowns, leaves concentrated as a rosette at the top of taller shoot or stem
			6	other
Bud bank: vertical layers	2442	6052	1.	no buds per shoot (not applicable)
			1.1	no buds per shoot, below soil surface, <-

				10 cm
			1.2	no buds per shoot, below soil surface, 0< x <-10 cm
			1.3	no buds per shoot at soil surface
			1.4	no buds per shoot, above soil surface, 0> x >10 cm
			1.5	no buds per shoot, above soil surface, >10 cm
			2.	1–10 buds per shoot
			2.1	1–10 buds per shoot, below soil surface, <-10 cm
			2.2	1–10 buds per shoot, below soil surface, 0< x <-10 cm
			2.3	1–10 buds per shoot at soil surface
			2.4	1–10 buds per shoot, above soil surface, 0> x >10 cm
			2.5	1–10 buds per shoot, above soil surface, >10 cm
			3.	>10 buds per shoot
			3.1	>10 buds per shoot, below soil surface, <-10 cm
			3.2	>10 buds per shoot, below soil surface, 0< x <-10 cm
			3.3	>10 buds per shoot at soil surface
			3.4	>10 buds per shoot, above soil surface, 0> x >10 cm
			3.5	>10 buds per shoot, above soil surface, >10 cm
Bud bank - seasonality	2468	6203	1	seasonal
			1.1	seasonal, above-ground
			1.2	seasonal, below-ground
			2	perennial
			2.1	perennial, above-ground
			2.2	perennial, below-ground
			3	seasonal & potential
			3.1	seasonal & potential, above-ground
			3.2	seasonal & potential, below-ground
			4	perennial & potential
			4.1	perennial & potential, above-ground
			4.2	perennial & potential, below-ground
Clonal growth organs	1958	5540	17	17 categories hierarchical classified according to their placement (above, at or below soil surface) and again subdivided to their origin (stem, root or leaf origin) (see Data Standards)
Life span of a shoot	1737	4233	1	monocyclic (1 year)
			2	dicyclic or polycyclic (> 1year)
Persistence of connection between parent and offspring shoots	1834	4683	1	<1 year
			2	1-2 years
			3	>2 years
Number of offspring shoots per parent shoot per year	1740	4263	1	<1 shoot/parent shoot/year
			2	1 shoot/parent shoot/year
			3	2-10 shoots/parent shoot/year
			4	>10 shoots/parent shoot/year
Lateral spread	555	1089	1	<0.01 m yr^{-1}
			2	0.01-0.25 m yr^{-1}
			3	0.25 m yr^{-1}
			4	dispersable diaspores
Seed number	1767	6165		number of seeds per ramet
Seed crop frequency	196	201	1	more than once a year
			2	once a year
			3	once in 2 years
			4	once in > 2 years
			5	not applicable

			6	unknown
Seed shedding	1640	3331		month of the year (1-12)
Seed weight	2025	7239		mg
Seed size	2401	6578		length, width and height (mm)
Seed shape	2401	6578		calculated from seed length, width and height (unitless, see Data Standards)
Soil seed bank type	1479	44353		transient - short-term persistent - long-term persistent
Seed bank longevity index	1479	44353		short-lived (0) – long-lived (1)
Soil seed bank density	1479	44353		per m^2
Diaspore type categories	2082	4162	1	vegetative dispersule
			2	generative dispersule
			2.1	one-seeded
			2.2	multi-seeded
			3	germinule
			4	unknown
Morphology of dispersal unit	2082	4162	1	nutrient containing structures
			2	elaiosome
			3	aril
			4	pulp
			5	balloon structures
			5.1	open balloons
			5.2	closed balloons
			8	flat appendages
			8.1	small flat appendages
			8.2	large flat appendages
			9	elongated appendages
			9.1	one short elongated appendage
			9.2	two or more short elongated appendages
			9.3	one long elogated appendage
			9.4	two or more long elongated appendages
			9.1 - 4	additional info: hooked structures
			10	no appendages
			10.1	seed with coarse surface, no appendages
			10.2	seed with smooth surface, no appendages
			11	other specialisations
			12	unknown
Seed release height	2586	3921		m
Terminal velocity seeds	1328	2592		$m\ s^{-1}$
Buoyancy	989	8081		number or % of floating seeds
Epizoochory	192	559		number or % of attached seeds
Endozoochory	149	179		number or % seeds that survived ingestion
Dispersal data obtained from literature	2956	13920		14 dispersal type categories (see Data Standards), 32 dispersal vector categories (see Data Standards)
Habitat characteristics	1401	1401		Categories referring to soil moisture, acidity, substrate, type, nutrient status. Water column acidity, alkalinity, and sediment redox potential for aquatic plants

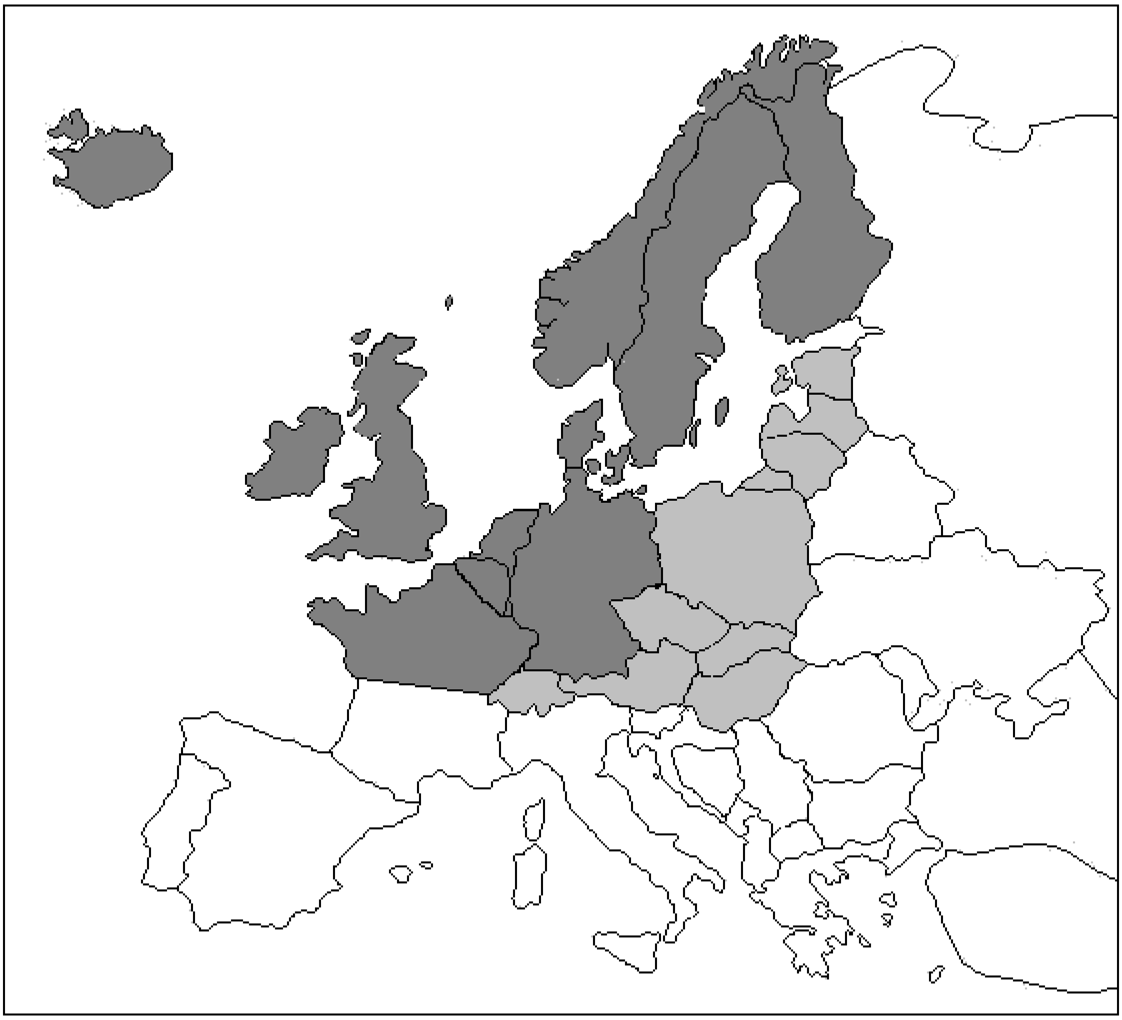

Figure 1. Geographical range covered by the database. Dark grey: core regions; light grey: overlap > 50 % with the national floras.

Appendix S1: Details regarding the LEDA trait definitions and the structure of the database.

TRAITS DEFINITIONS

PERSISTENCE TRAITS

Growth form of the mature plant: A combination of the life-form classification of Raunkiaer (1937) completed with other specialised forms which are based upon their type of nutrient acquisition or living conditions (e.g. halophyte).

Canopy height: The distance between the highest photosynthetic tissue and the base of the plant (Weiher *et al.* 1999).

Plant life span: The mean number of years of persistence of a plant. It refers to genets when individual plants can be distinguished and to ramets in clonal plants where genets could not be identified. This remains problematic when genet longevity and total reproductive output per genet is of interest. Most long-lived species were only assigned to the category perennial, as no further detailed information about life span was available.

Age of first flowering: The earliest age at which a plant can flower in the field. For true monocarpic species age of first flowering is identical with plant life span. For all other species age of first flowering was categorised separately.

Leaf size and *specific leaf area (SLA)*: The one-sided area of a fresh leaf divided by its dry mass, hence dry leaf mass is one component of the SLA measurements.

Leaf dry matter content (LDMC): The dry weight per unit volume.

Woodiness: Three broad categories (soft or hard wood, semi-woody and non-woody or herbaceous).

Stem specific density (or wood density): The dry mass of a stem segment divided by its fresh volume (Weiher *et al.* 1999).

Shoot growth form, *branching* and *distribution of leaves along the stem*: Categories (see Table 2).

Clonal traits:

As plants are highly plastic in their vegetative growth, clonal traits are given mostly in nominal categories rather than numerical measurements. Only adult plants are considered, ontogenetic changes of clonal growth and bud banks in earlier developmental stages are not included.

Bud bank: (1) The number of buds in vertical layers from the root to the top of a plant. (2) The longevity of the bud bank: Seasonal (on plant organs with a life span shorter than two years), perennial (on plant organs with a life span of two or more years) and potential (reflecting the ability of a plant to sprout adventitiously from roots or leaves).

Clonal growth organs (CGO): Classification according to their position (above, at or below soil surface) and again subdivided to their origin (stem, root or leaf origin) within a hierarchical structure of 17 categories. Then, the role of CGOs has been specified for plant growth: either regenerative, additive, necessary or unknown.

Lifespan of a shoot: Duration of a small life-cycle, i.e. from sprouting of a bud, through the growth, flowering and fruiting of the shoot, until its death. Also known as shoot cyclicity.

Persistence of connection parent-offspring: Duration (or persistence) of the connection between parent and offspring shoots.

Lateral spread/year: Distance covered by lateral spread in one year, given in metres. This trait should not be confused with the distance between offspring ramets or the distance between parent and offspring ramets.

Number of offspring shoots/parent shoot/year: A measure of intensity of clonal multiplication given as the number of offspring shoots produced per year and per parent shoot.

REGENERATION TRAITS

Seed number: The total seed (or spore) production per ramet/shoot/individual species.

Seed crop frequency: The frequency of generative reproduction cycles over time, in other words how often species produce seeds in a certain time period (Silvertown & Lovett Doust 1993).

Seed shedding: The month in which shedding takes place.

Seed weight: The air dried weight of seeds (germinating unit) or dispersules (dispersing unit).

Seed shape (V_s): Length, width and height of a seed separately divided by length. Calculation of the variance of the three values with the formula: $V_s = \Sigma (x_i - \text{mean}(x))^2/n$ with $n = 3$ and x_1 = length/length, x_2 = height/length and x_3 = width/length. V_s is dimensionless, and spans from a minimum value 0 in perfectly spherical seeds to a maximum value of 0.2 in needle- and disc-shaped seeds.

Types of soil seed banks: 'Transient', 'species with seeds that persist in the soil for less than one year, often much less'; 'short-term persistent, species with seeds that persist in the soil for between one year and five years'; and 'long-term persistent, species with seeds that persist in the soil for at least five years' (Bakker 1989; Thompson 1992; Poschlod & Jackel 1993). One of the unique features of LEDA is that the database can generate, on request, the most updated figure for the Seed Longevity Index (c.f. Bekker *et al.* 1998) by calculating this over all available records per species.

DISPERSAL TRAITS

Morphological dispersal syndromes: Classification according to the shape and length of the appendages (e.g. a wing). Other categories are fruit pulps, nutritious nuts, or airfilled balloon structures. If seeds do not display appendages, seed surface is categorised to be either smooth or coarse (Van der Pijl 1972; Hughes *et al.* 1994).

Terminal velocity: The rate of fall of a dispersule in still air, using the machine described in Askew *et al.* (1996).

Seed releasing height: The distance between the soil and the highest part of the plant from where seeds are released.

Buoyancy (floating capacity): Floating capacities of diaspores measured after different time periods. We measured buoyancy only for species growing in habitats that are associated with water dispersal, such as open water, river banks, wet meadows, and mires.

Epizoochory: The number of seeds released from fur for a certain time period using a shaking machine (see Tackenberg *et al.* 2006). Additionally, potential attachments predicted from seed weight and seed morphology by a regression function are included (see Römermann *et al.* 2005).

Endozoochory: Survival capacity determined by a lab-method simulating the digestion system of a ruminant (see Bonn 2004). Additionally, published data on survival of digestion from feeding experiments as well as data on endozoochory derived from dung analyses were included.

Seed dispersal vector: Seeds are dispersed by various vectors. General information about dispersal types as well as more specific information about the dispersal vector of plant species was compiled in the database DIASPORUS (Bonn *et al.* 2000). In the LEDA Traitbase, DIASPORUS has been extended with more data on dispersal type and vector including improved referencing. It is now possible to calculate dispersal spectra instead of assigning one exclusive dispersal type to a single plant species.

THE LEDA TAXONOMIC CORE

The taxonomic core of the LEDA Traitbase consists of one synonymised plant list at the species level, completed with authorities. The list was collated from the national lists of the British Isles (Stace 1997), the Netherlands (Van der Meijden 1990), Germany (Wisskirchen & Haeupler 1998), Norway (based on Lid & Lid 1994) and species lists composed by local experts of Belgium, the Czech Republic (an updated version for Central Europe based upon Ehrendorfer 1973), the Nordic list for Scandinavia (Thomas Karlsson, http://linnaeus.nrm.se/flora/chk/chk3.htm), Poland, France (Kerguélen 1999), Latvia (Gavrilova & Šulcs 1999), and Lithuania.

TECHNICAL STRUCTURE OF THE DATABASE

The LEDA Traitbase is a combination of a relational database holding the trait data and several web applications allowing for input, access and analysis of trait related data. The database features structured data storage and provides transaction-based multi-user access to the data. The database structure is described by a relational database scheme following the entity relationship model. It is used to declare tables (entity types) for data storage and the relationships of records within these tables (entities) to each other.
The functionality of the LEDA Traitbase is delivered through web based applications.

DATA RETRIEVAL

In order to retrieve data, one can either use the species fact sheet or the LEDA web query tool. The species fact sheet accepts a species name as input and returns a single aggregated value for each trait of the selected species. As an example for a GIS link, the German plant atlas FloraMap (http://www.floraweb.de) is accessible from within the LEDA web query application. This allows access to further trait data, species distribution data and related information (in German).

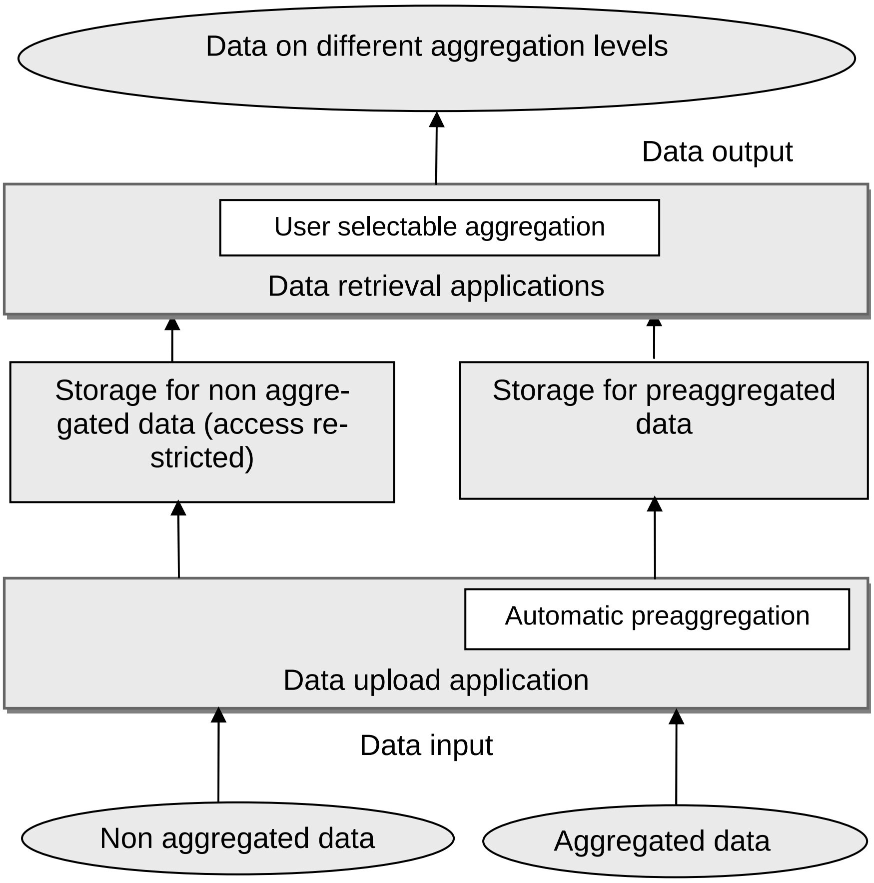

Fig. S1. Aggregation levels in data flow through the LEDA Traitbase.

Within the LEDA web query tool, aggregated results are computed at run-time (Fig. S1). Depending upon the trait considered, several types of aggregated values are available. Examples are: relative frequency of categories, absolute frequency of categories, modal categories, index functions, maximum, minimum, average, standard deviation and median. Aggregation may either be carried out on the original values stored in the database or from derived values (Stadler *et al.* 2004). For instance, if the average canopy height of a species is to be calculated both from records containing a maximum observed value and a minimum observed value and from records containing a single observed value, a single value is calculated on a per-record basis from minimum and maximum values for the former records. The resulting calculated single values are then aggregated together with the single values present in the database.

DATA ANALYSIS

For data analysis purposes, a web based tool for data mining called DIONE has been designed (Stadler *et al.* 2005) which is available on request. It supports the construction of decision trees, decision rules and association rules as well as the centre-based calculation of clusters (see e.g. Han & Kamber 2001). LEDA data to be analysed can directly be transferred from the Traitbase to the data miner. It is also possible to upload external data to DIONE.

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