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DATA ARTICLE

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Seed dispersal distance classes and dispersal modes for the European flora

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Abstract

Motivation: Although dispersal ability is one of the key features determining the spatial dynamics of plant populations and the structure of plant communities, it is also one of the traits for which we still lack data for most species. We compiled a comprehensive dataset of seed dispersal distance classes and predominant dispersal modes for most European vascular plants. Our seed dispersal dataset can be used in functional biogeography, dynamic vegetation modelling and ecological studies at local to continental scales.

Main Types of Variables Contained: Species were classified into seven ordered classes with similar dispersal distances estimated based on the predominant dispersal mode, the morphology of dispersal units (diaspores or propagules), life form, plant height, seed mass, habitat and known dispersal by humans. We evaluated our results by comparing them with dispersal distances calculated using the 'dispeRsal' function in R.

Spatial Location: Europe.

Time Period: Present.

Major Taxa and Level of Measurement: The seed dispersal dataset contains information on dispersal distance classes and the predominant dispersal mode for 10,327 most frequent and locally dominant European vascular plant species.

Software Format: Data are available in .csv format.

KEYWORDS

anemochory, dispersal distance, dispersal mode, Europe, plant trait, vascular plant, zoochory

1 | INTRODUCTION

The dispersal ability of seeds and other generative dispersal units (also called diaspores or propagules) is one of the crucial plant traits that determine the spread of plant species to new habitats and regions. It not only affects plant colonization ability but also determines plant coexistence through processes of colonization (Levin et al., 2003; Nathan et al., 2008). Dispersal becomes even more important under environmental changes as species are forced to either adapt to new conditions or shift their geographical range. Therefore, plant dispersal ability must be considered in ecological studies and models of species response to changing environmental conditions (Thuiller et al., 2008, 2013). Incorporating dispersal ability into such models is a fundamental step in estimating the potential distribution of species (Jiménez & Soberón, 2022).

Recently, several databases of plant traits have become available that contain information on seed morphology and dispersal strategies, for example, TRY (Kattge et al., 2020), LEDA (Kleyer et al., 2008), D^3 (Hintze et al., 2013), BROT 2.0 (Tavşanoğlu & Pausas, 2018), Flora of Italy (Pignatti et al., 2018), Pladias (Chytrý et al., 2021; Sádlo et al., 2018), SID (Royal Botanic Gardens Kew, 2021) and Tela Botanica (www.tela-botanica.org). These databases use different approaches to characterize plant dispersal ability, although most of them provide only information on seed mass and seed shape. Most databases additionally include categories of dispersal modes (also called dispersal syndromes or dispersal types, e.g. anemochory, hydrochory, zoochory) or dispersal vectors (e.g. wind, water, animals), usually for regionally restricted sets of species. Such characteristics are usually estimated from seed or diaspore morphology and size. However, the morphological adaptations and sizes of seeds and other diaspores do not fully describe the dispersal potential of a given species, which limits the use of such data in ecological studies (e.g. Beckman et al., 2018; Bullock et al., 2017; Nogales et al., 2007; Tamme et al., 2014; Thompson et al., 2010, 2011).

Few studies have measured, estimated or mathematically modelled dispersal distances, which seem to be a more reliable indicator of dispersal ability. These were reviewed by Vittoz and Engler (2007) and Thompson et al. (2011). Unfortunately, such data are only available for a limited number of European plant species. Recently, Tamme et al. (2014) developed a statistical method to estimate dispersal distances based on several plant traits (dispersal mode, growth form, seed mass, seed release height and terminal velocity) using data on 576 plant species. Although estimating dispersal distances from plant traits is a promising approach, there are other important factors affecting dispersal distances, namely human-assisted dispersal (anthropochory) and species habitat preferences (Vittoz & Engler, 2007). Plant dispersal patterns have been significantly influenced by humans, who intentionally or unintentionally transport species at long distances, often outside their natural distribution range. Most databases only consider dispersal mode estimated from species morphological characteristics, such as dispersal by wind, water or animals (e.g. Royal Botanic Gardens Kew Seed Information Database, 2021; SID). Indeed, natural dispersal strategy is crucial for colonizing new areas at the landscape scale. However, rare events of human-assisted dispersal should also be considered. Information on the dispersal by humans is directly available in some databases (e.g. LEDA, Kleyer et al., 2008), or it can be inferred for species with native ranges on other continents (e.g. GloNAF; van Kleunen et al., 2019). Another group of species that are commonly dispersed by humans are weeds of arable fields or other man-made habitats (compare the characteristic species combinations in the EUNIS Habitat Classification; Chytrý et al., 2020). Dispersal distance is also influenced by the interaction between the environment and plant traits (Vittoz & Engler, 2007). For example, while some diaspores can be dispersed over long distances in an open landscape, the same diaspores can be dispersed less effectively when the parent plants grow under a closed canopy. Global databases containing information on other relevant traits, such as plant height (TRY; Kattge et al., 2020), and data on habitat preferences of individual plants (Chytrý et al., 2020; Mucina et al., 2016) make it possible to combine this information to estimate the actual plant dispersal distances.

Vittoz and Engler (2007) proposed to estimate plant dispersal distances using a clearly defined and methodologically simple approach. They assigned plant species to seven dispersal distance classes based on the morphology of dispersal units (diaspores), other species traits and habitat preferences. The original dataset of Vittoz and Engler (2007) contained 1262 species of Swiss flora. Boulangeat et al. (2012) extended this dataset to 1786 plant species occurring in Switzerland and the French Alps. However, as both studies focussed on the Alps and nearby areas, they included only a small part of the European vascular flora.

Here, we present a new dataset of seed dispersal distance classes and predominant dispersal types for 10,327 widely distributed European vascular plants. We use the approach of Vittoz and Engler (2007) with a slight modification of some classes. To evaluate our approach, we compared our seed dispersal distance classes with dispersal distances estimated using the trait-based method proposed by Tamme et al. (2014).

2 | METHODS

2.1 | Species selection

We prepared a list of frequent European vascular plant species based on species occurrence frequency in vegetation plots in the European Vegetation Archive (EVA, Chytrý et al., 2016), a centralized database of European vegetation plots. We standardized species taxonomy and nomenclature according to Euro+Med (http://europlusmed.org). Subspecies, varieties and forms were merged at the species level. Species in taxonomically difficult groups were merged into aggregates following the EUNIS-ESy expert system for the EUNIS Habitat Classification (Chytrý et al., 2020). Hereafter, we use the term 'species' to refer to both species and aggregates.

As we aimed to include all frequent species and species that could attain high cover in plant communities, we selected those species that occurred in >1% of plots, had a cover of >25% in >0.1% of plots or had the highest cover of all vascular plant species in >0.1% of plots. This selection included 5569 frequent or locally dominant vascular plant species of the European flora. Hereafter, we refer to them as priority species.

2.2 | Trait data

We compiled several species traits necessary for assigning species to different dispersal distance classes (dispersal mode, dispersal vector, diaspore type, seed or diaspore mass (further in the text

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referred to as seed mass), plant height and life form) from the following sources: Flora of GDR (Frank & Klotz, 1990), LEDA database (Kleyer et al., 2008), D^3 database (Hintze et al., 2013), Ladouceur et al. (2017), BROT 2.0 database (Tavşanoğlu & Pausas, 2018), Flora of Italy (Pignatti et al., 2018), Pladias database (Chytrý et al., 2021), SID database (Royal Botanic Gardens Kew, 2021) and Tela Botanica database (www.tela-botanica.org). In addition, we used data from Vittoz and Engler (2007) and Boulangeat et al. (2012), which also contained assignments to dispersal distance categories.

For seed mass and plant height, we checked the frequency distribution across all species and excluded outlying, improbable values. We then calculated the median value of each trait for each species across all databases.

2.3 | Occurrence in habitats

We compiled available information on the broadly defined habitats where each species typically occurs (Chytrý et al., 2020, 2021; Heinken et al., 2022; Mucina et al., 2016; Pignatti et al., 2018). On this basis, we estimated species affinity for forest or open habitats.

Another important aspect was whether or not the species is native to Europe, which indicates human-assisted long-distance dispersal. For the assignment of the alien or native status, we used several additional sources, particularly the list of European alien species in the FloraVeg.EU database (https://floraveg.eu).

2.4 | Indicators of human-assisted dispersal

We have considered several groups of alien species: (1) Species that were introduced to Europe unintentionally or as a curiosity rather than for economic profit and that are now freely spreading and have well-established populations in different habitats. (2) Crops and weeds, that is, plants introduced with agriculture and restricted to anthropogenic habitats such as arable land and human settlements. They are dispersed mainly due to human activities, especially by speirochory (unintentional dispersal with seeds of cultivated plants) or ethelochory (intentional introduction by seeds or seedlings into new areas). To determine the most important weeds that are unintentionally dispersed by humans, we used lists of weeds for EUNIS arable habitats (Chytrý et al., 2020). (3) Planted trees and shrubs. To distinguish frequently cultivated species from naturally occurring species, we used the list of non-native trees planted in Europe (Chytrý et al., 2020; Wagner et al., 2017). We did not include cultivated species that do not spread spontaneously.

Some native species are also strongly supported by humans and are repeatedly planted or sown in the landscape, especially in the case of seed mixtures used for establishing new grasslands or increasing grassland productivity. We have considered these species to be both naturally dispersed and human-dispersed.

2.5 | Delimitation of dispersal distance classes

We adopted the delimitation of dispersal distance classes from Vittoz and Engler (2007). They compiled all available measurements of seed dispersal distances of Central European species and classified them into (1) mean, mode and median values, (2) maximum values (99th percentiles of distribution kernels) and (3) values for long-distance dispersal events, that is, extreme distances reached by only a very small fraction of seeds. They did not consider the last category in the delimitation of dispersal classes. They assigned each dispersal distance to a dispersal mode. Dispersal distance classes were then defined by grouping dispersal modes with similar dispersal distances and similar diaspore adaptations and traits. Finally, Vittoz and Engler (2007) estimated, for each class, the upper limits of the distances within which 50% and 99% of seeds would disperse. We adopted a similar delimitation of dispersal distance classes (Table 1).

2.6 | Assignment to dispersal distance classes

We summarized the plant characteristics obtained from various sources in a table (Supplement S1) that includes plant height, life form, predominant dispersal mode, seed mass and typical habitat. We also included data on plant geographical origin and the use by humans to distinguish a group of plants intentionally dispersed by humans (Table 1). Plants were classified into seven dispersal distance classes based on the above-mentioned characteristics, as illustrated in a decision tree (Figure 1). Examples of typical species are shown in Figure 2.

In contrast to the original approach of Vittoz and Engler (2007), we have slightly modified the definitions of the dispersal distance classes. Their original definition of the dispersal classes combined two different types of information: classes 1–6 were based on species characteristics and natural dispersal vectors, whereas class 7 included human-dispersed species, although the natural dispersal strategy of these species was different and often less efficient than long-distance dispersal by humans. For example, *Robinia pseudoacacia* is a tree with dry fruits suitable for wind dispersal, which corresponds to dispersal distance class 4 in the scheme of Vittoz and Engler (2007). However, this species was introduced to Europe by humans and is frequently planted, which would lead to a classification in class 7. Nowadays, long-distance dispersal of this species by humans rarely happens, but once introduced to a new area, it can spread locally due to wind dispersal (Vítková et al., 2017).

For animal dispersal, we did not distinguish between dispersal by small and large animals as proposed by Vittoz and Engler (2007) because such information is missing for most plant species. However, we did distinguish between dispersal by ants and vertebrates. We also modified the delimitation of species with dusty seeds. Vittoz and Engler (2007) referred to these species as cystometeorochorous and included all ferns and species of the families *Orchidaceae*, *Orobanchaceae* and *Pyrolaceae*. However, in the most recent delimitation of plant families (APG version 2017; Stevens, 2021), the former

TABLE 1 Characteristics of dispersal distance classes.

Dispersal distance class	Dispersal distances (m) for 50 and 99% seeds	Dispersal mode	Dispersal vector	Growth form	Plant height	Habitat	Dispersal-related diaspore features
1	0.1–1	Local nonspecific	Unassisted	Herbs, dwarf shrubs	<30 cm	Any	No special features
2	1–5	Local nonspecific	Unassisted	Herbs, dwarf shrubs, shrubs	>30 cm	Any	No special features
3	2–15	Anemochory	Wind	Herbs, dwarf shrubs	Any	Forests	Wing, hem, pappus, dusty seed
		Myrmecochory	Ants	Herbs, dwarf shrubs, trees	Any	Any	Elaiosome
4	40–150	Anemochory	Wind	Trees, shrubs	>30 cm	Any	Wing, hem
		Anemochory	Wind	Herbs	Any	Open	Tumbleweed
5	10–500	Anemochory	Wind	Herbs, dwarf shrubs	Any	Open	Pappus, dusty seed
6	400–1500	Dyszoochory	Animals	Any	Any	Any	Any
		Endozoochory	Animals	Any	Any	Any	Any
		Epizoochory	Animals	Any	Any	Any	Any
7	500–5000	Anthropochory	Humans	Any	Any	Any	Any

Note: Species are classified into seven dispersal distance classes based on predominant dispersal mode, life form, plant height, dispersal-related diaspore features and habitat preferences. Each class comprises species with similar dispersal distances estimated as upper limits of distances within which 50% and 99% of seeds are dispersed (modified from Vittoz & Engler, 2007).

Pyrolaceae are included in *Ericaceae*. In addition to species of the *Pyroloideae* subfamily, dusty seeds are also characteristic of European species of *Monotropoideae* and *Cassiopoideae*. By contrast, not all species of the *Orobanchaceae* family are anemochorous. For example, the seeds of the genus *Melampyrum* are dispersed by ants. Therefore, we combined the recent delimitation of families with information on seed mass to define anemochorous species with dusty seeds.

After standardizing nomenclature, the dataset contained 13,333 species. These species had at least partial information necessary for their assignment to the dispersal distance classes. We assigned the priority species with incomplete or no data to dispersal distance classes based on our expert judgement combined with the information available for other species in the same genus. For example, dispersal mode information was available for several species of the genus *Abies* but not for *Abies borisii-regis* and *A. sibirica*. We decided to classify these species in the same dispersal distance class as the other *Abies* species. However, we did this only for the genera with uniform dispersal traits, similar height and similar habitat preferences. We did not do this for the genera with diverse diaspores (e.g. *Anemone*, *Medicago* and *Ranunculus*) or for anemochorous species without information on habitat preferences or height. Finally, we were able to classify 10,327 species and aggregates of European vascular plants.

2.7 | Analyses

To evaluate our classification of species into dispersal classes, we related dispersal classes to estimated maximum dispersal distances obtained using the dispeRsal function proposed by Tamme et al. (2014). We used four model formulas with various combinations of plant traits as explanatory variables to calculate dispersal distances. Model 1 included dispersal mode (syndrome; DS) and growth form (GF); model 2 included dispersal mode, growth form and plant height (release height; RH); model 3 included dispersal mode, growth form and seed mass (SM); and model 4 included all four traits. In addition to these four models, Tamme et al. (2014) also considered a model that included terminal velocity. However, such information was not available for the vast majority of species, so we could not include it in the tests.

We ran all models with the 'dispeRsal' function (Tamme et al., 2014), which estimates dispersal distances using simple linear regressions and mixed-effect models that account for taxonomic dependencies by using species taxonomy (either as family or order) as a random variable. We determined species families using the 'TPL' function of the R package *Taxonstand* (Cayuela et al., 2017). Finally, to estimate the dispersal distance for each species, we averaged dispersal distances for each model and structure type (i.e. simple regression, species' family or order as a random component).

To test the relationship between mean estimated dispersal distances and our dispersal distance classes, we fitted linear models with dispersal distances as dependent variables and dispersal distance classes as categorical predictors and visually inspected the distribution of dispersal distances within each class. Such analyses were conducted for comparisons within dispersal distance classes 1–6, considering natural dispersal modes only and within all seven classes.

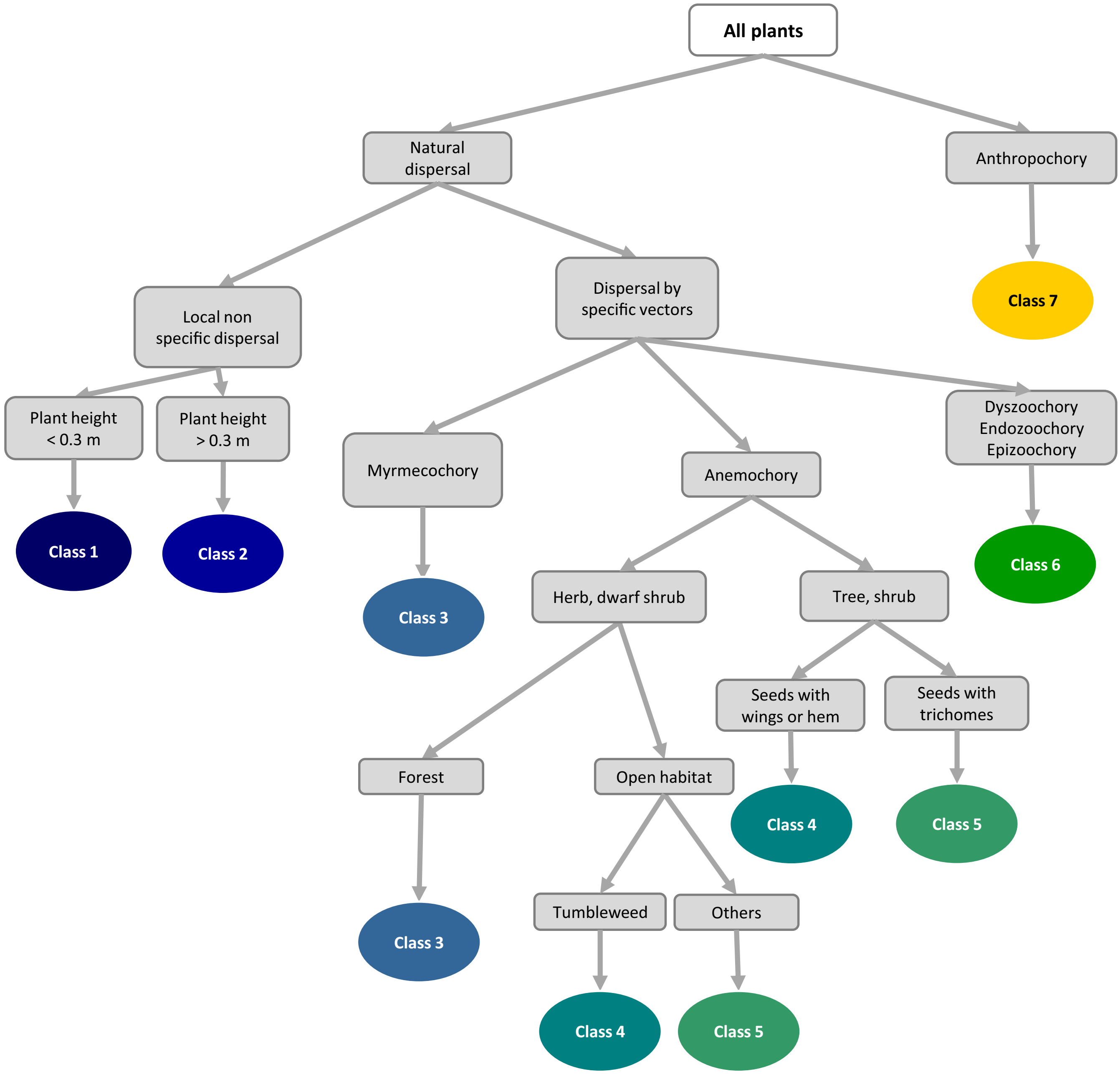

FIGURE 1 Decision tree used to classify European vascular plant species to the dispersal distance classes. Hydrochorous species are not classified.

All analyses were performed using R version 4.1.0 (R Core Team, 2021).

3 | RESULTS

Our dataset (Supplement S1) contains information on the dispersal distance class and the predominant dispersal mode for 10,327 species. The dispersal distance classes are ordered from class 1, which contains species with the shortest dispersal distances, to class 7, which contains species with the longest dispersal distances (Figure 3). Class 1 contains 2430 species shorter than 0.3 m. Their seeds do not have any specific dispersal features. Species are mostly self-dispersed, although seed dispersal can be initiated by wind, for example, by shaking the fruit, which causes the diaspore to fall. Class 2 is the most species-rich (2748 species), including species with nonspecific local dispersal strategy taller than 0.3 m. Class 3 includes 1278 species, combining ant-dispersed (myrmecochorous) species with wind-dispersed (anemochorous) forest herbs and dwarf shrubs. Class 4 is the least species-rich (99 species), including less efficient wind-dispersed woody plants and tumbleweeds. Class 5 includes 1340 wind-dispersed herbs and shrubs of open habitats and wind-dispersed trees with more efficient dispersal units (with trichomes). Class 6 includes 1144 species with different modes of animal dispersal. They can be dyszoochorous (i.e. foraged by

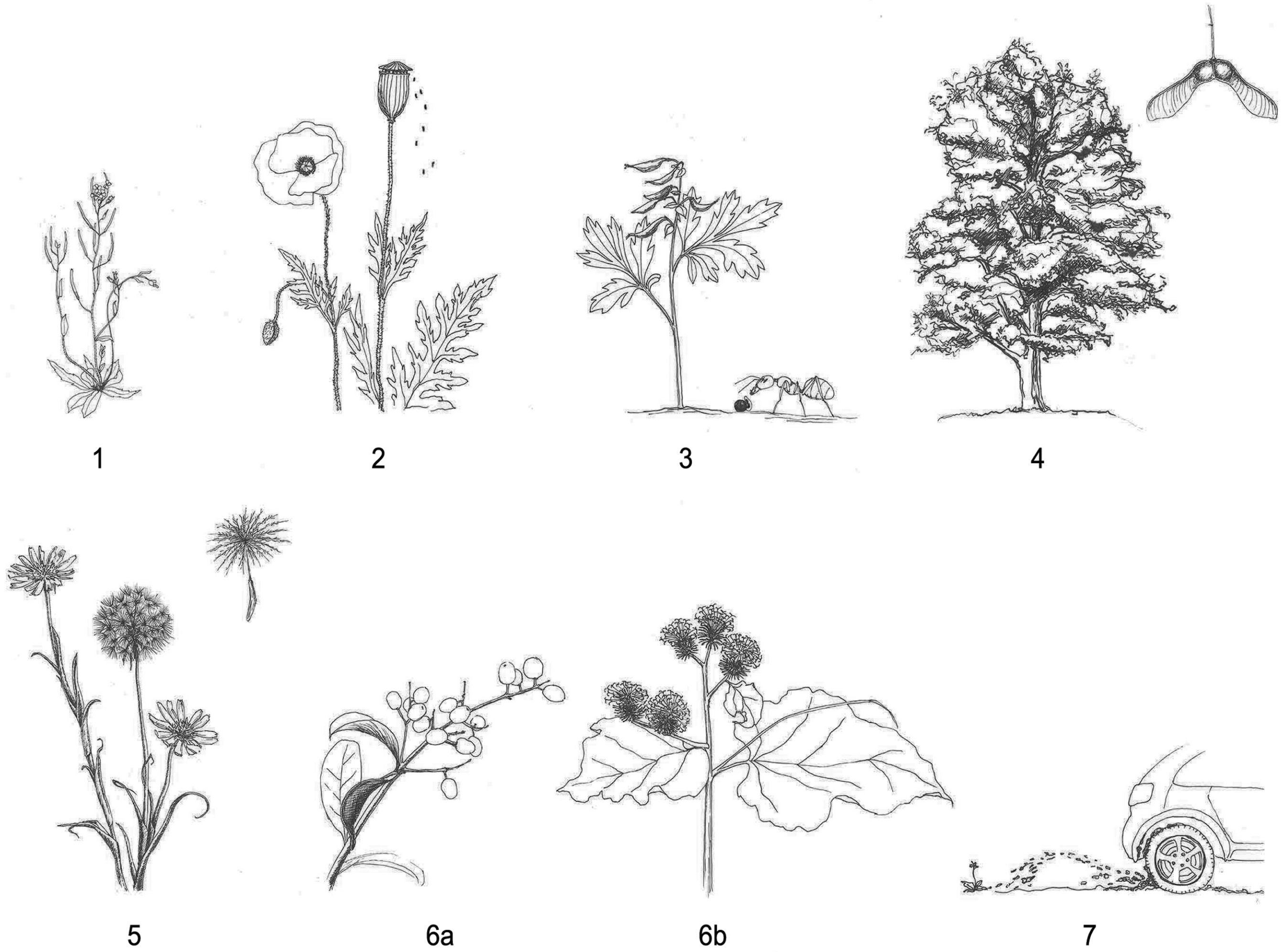

FIGURE 2 Examples of species assigned to dispersal distance classes 1 to 7. (1) *Arabidopsis thaliana*, an example of a small plant with no specific dispersal features, (2) *Papaver rhoeas*, an example of a taller plant, where dispersal is initiated by wind, but seeds are not wind-dispersed), (3) *Corydalis cava*, a myrmecochorous plant (= dispersal by ants), (4) *Acer platanoides*, an anemochorous tree (= dispersal by wind), (5) *Tragopogon orientalis*, anemochorous herb of open habitats, (6a) *Ligustrum vulgare*, endozoochorous plant (= dispersal in animal gastrointestinal tract), (6b) *Arctium lappa*, epizoochorous plant (= dispersal on animal fur), (7) anthropochorous plant. Drawn by Ivana Mileová.

animals, which sometimes hide them as stock), endozoochorous (i.e. dispersal in animal gastrointestinal tract) or epizoochorous (i.e. dispersal on animal fur). Finally, class 7 contains 1288 human-dispersed (anthropochorous) species. The species of the last class are also classified into one of the previous six classes based on their natural dispersal mode (see Supplement S1).

Our dispersal classes were positively related to dispersal distances estimated using the 'dispeRsal' function. When included as categorical predictors in a linear model, dispersal classes explained a significant portion of the variation in dispersal distances (R^2=0.75 for six naturally dispersed classes and R^2=0.70 for all seven classes; Figure 4).

4 | DISCUSSION

We estimated dispersal distances for 10,327 European plant species using dispersal distance classes following the method proposed by Vittoz and Engler (2007). This semi-quantitative trait provides better information for ecological studies than categorical proxies of dispersal distance, such as dispersal modes and dispersal vectors.

Our dataset is based on the definition of the predominant dispersal modes, which are also given for all 10,327 species. We recognize that plants usually combine multiple dispersal vectors and that the efficiency of these vectors varies in space and time (Beckman et al., 2020; Bullock et al., 2017; Sádlo et al., 2018; Thompson et al., 2010). We have attempted to overcome this uncertainty by dividing species adapted to human dispersal into two groups reflecting less effective but more frequent natural dispersal and more effective but rare human-assisted dispersal. Consequently, researchers can decide whether to use only the first six dispersal classes (corresponding to natural dispersal) or all seven dispersal classes (also including rare events of human-assisted dispersal). Six classes are appropriate for landscape-scale studies, while seven classes may be more suitable for studies at the continental scale and over longer time periods.

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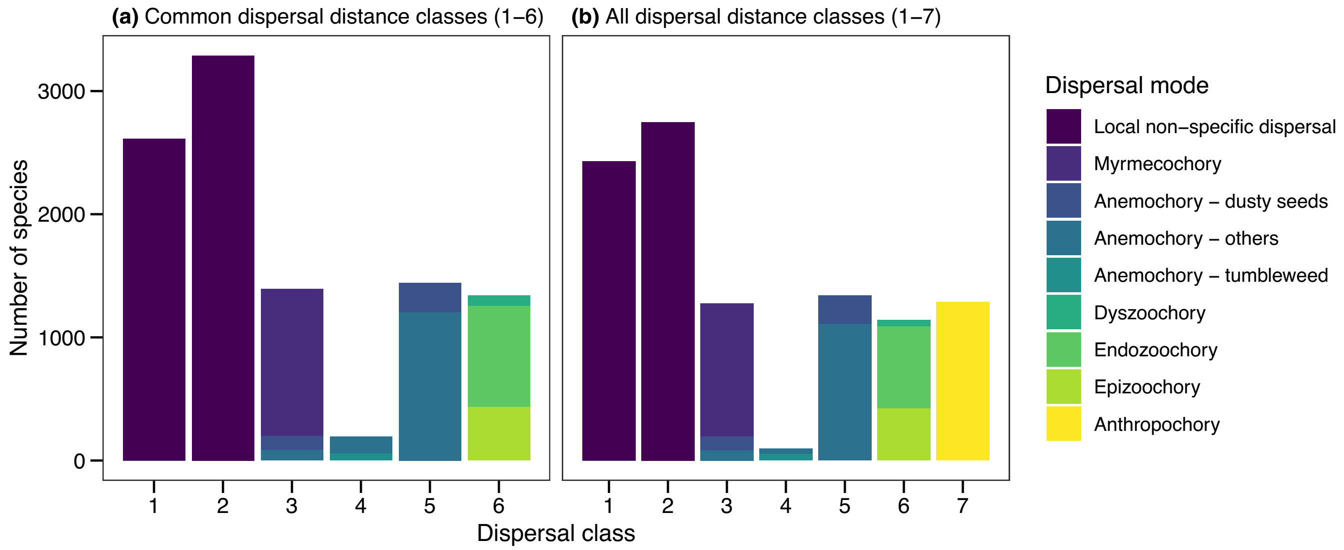

FIGURE 3 Numbers of species included in dispersal distance classes classified into (a) six classes, excluding anthropochorous dispersal and (b) seven classes, also including dispersal distance class 7 with anthropochorous dispersal.

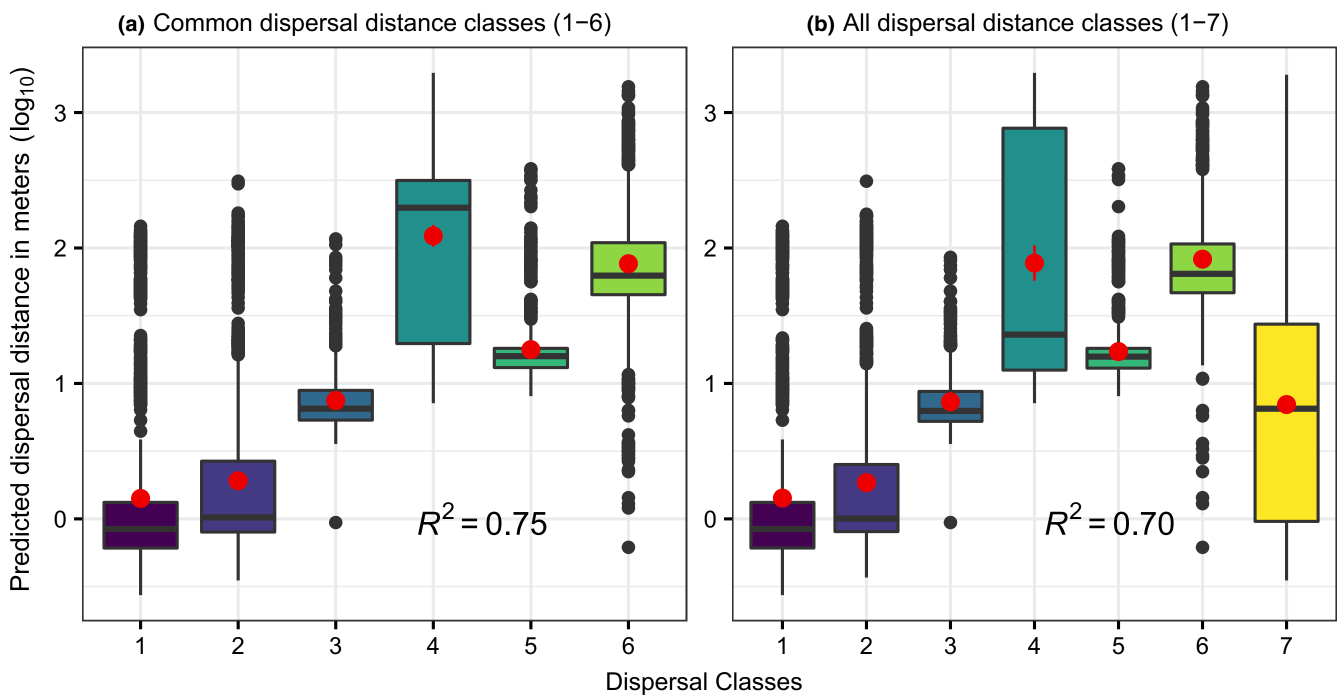

FIGURE 4 Distribution of estimated maximum dispersal distances (following the trait-based approach of Tamme et al. 2014) across dispersal classes. (a) The left plot contains only six common dispersal distance classes, and (b) the right plot contains all seven classes, including anthropochorous dispersal distance class 7. The red dots correspond to the mean maximum dispersal distance within each dispersal class. The R^2 value was obtained from linear regression models with dispersal distance as the dependent variable and dispersal classes as categorical predictors.

Completeness of data on traits and other characteristics of plant species varies by region, species commonness and habitat preferences. While data coverage is relatively high for Central and Western Europe, less information is generally available for plants from the Balkan Peninsula and Eastern Europe and for rare species. However, the dataset can be extended with new data using our decision tree.

We have shown that our classification is consistent with predictions of seed dispersal distances using the 'dispeRsal' function (Tamme et al., 2014). Relatively low dispersal distances estimated using this function for classes 5 and 7 (see Figure 4) are due to considering more factors in our approach. Tamme et al. (2014) did not consider the habitat preferences of anemochorous species, leading to an underestimate of dispersal distances for class 5. They also did not account for human dispersal, which is partly based on human preferences for some species rather than on the biological traits of species, resulting in an underestimate of dispersal distances for class 7.

The seed dispersal dataset is important for several types of macroecological studies. Dispersal distance has significant implications for the distribution and coexistence of plant species (Beckman et al., 2020; Levin et al., 2003). For example, Poschlod et al. (1998) have shown the importance of dispersal ability for the diversity of calcareous grasslands, Pärtel and Zobel (2007) have demonstrated its effect on the diversity–productivity relationship, and Ozinga et al. (2009) have detected its effect on plant diversity losses in northwestern Europe. Our dataset can be used to test similar hypotheses on the continental scale. In addition, the data could be used to describe dispersal patterns in specific vegetation types (Bullock et al., 2017; Morgan & Venn, 2017). Knowledge of species dispersal potential is important for island biogeography (Cody & Overton, 1996; Ottaviani et al., 2020; Riba et al., 2009) and conservation management (Driscoll et al., 2014). Classification by dispersal classes or dispersal modes can be considered in vegetation modelling (see e. g. Boulangeat et al., 2014; Bullock et al., 2012; Engler et al., 2009), predicting species responses under different scenarios of novel environmental conditions (Beckman et al., 2020) or estimating the potential spread of invasive species (Chapman et al., 2017). Our dataset contains all the necessary information to assign species to dispersal distance classes, including relevant traits, predominant dispersal modes, species biogeographical origin (native vs. alien) and habitat preferences. Besides using the dispersal distance classes, it is also possible to work with partial data. For example, in landscape-scale studies focused on a single habitat type, one might want to consider only dispersal traits without habitat preferences.

The seed dispersal dataset for the European flora is a resource for addressing a variety of ecological and evolutionary questions. We hope this dataset and approach will stimulate research in ecology and vegetation modelling related to plant dispersal potential on a broad continental scale. It can be used to create more realistic models of plant species range shifts and vegetation changes in response to global environmental changes.

AUTHOR CONTRIBUTIONS

W.T. and M.C. conceived the idea. Z.L. classified the species. I.A. prepared the trait data and carried out nomenclature unification. G.M. conducted the statistical analyses. J.R., S.A., J.V.E. and P.V. provided background databases. Z.L. wrote the manuscript. All authors discussed and critically commented on the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The seed dispersal dataset of European plants is provided in the supplementary material to this article. It is also available at the FloraVeg.EU website (https://floraveg.eu/download/), where future updates will be published.

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BIOSKETCH

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SUPPORTING INFORMATION

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