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RESEARCH ARTICLE



The dispersal potential of endangered plants versus non-native garden escapees

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Abstract

- 1. Amidst climate change, enhancing plant dispersal pathways is crucial for adapting ecosystems and preserving biodiversity. In our human-dominated landscapes, urban and rural green spaces, especially gardens, are promising conduits for plant dispersal. Non-native plants are known to benefit from these spaces, yet the potential benefits for at-risk native plants remain unclear.
- 2. Here, I synthesized data on dispersal traits, comparing endangered native plants with non-endangered and non-native species in Germany. To make my analysis pertinent to understanding the potential role of gardens in aiding the dispersal of at-risk native plants, I further contrasted the dispersal ecology of garden-friendly endangered plants with non-native plants known to escape gardens. I analysed several traits including seed weight, terminal velocity, dispersal distance, germination rate, dispersal mode, seed structures and seedbank type.
- 3. Overall, dispersal traits between native and non-native plants showed minor, but in some cases statistically significant differences. Endangered plants were more often wind-dispersed and more frequently had seed appendages conducive to a wider range of dispersal vectors. Conversely, non-native plants leaned more towards non-assisted local dispersal, heavier seeds and more persistent seed banks. Other traits were largely consistent across groups.
- 4. This research shows that endangered native plants possess a dispersal ecology similar to non-native species, which frequently spread from green spaces like gardens. Thus, integrating endangered flora into our green spaces could help to promote an essential aspect of species survival: dispersal.

KEYWORDS

anthropogenic dispersal, conservation gardening, garden ecology, green corridors, green infrastructure, seed dispersal

1 | INTRODUCTION

There are increasing calls and efforts to establish corridors aiding the migration of organisms in response to global change factors, such as

climate change (Brodie et al., 2021; European Commission, 2020). While research on the efficacy of these corridors has historically centred on animals, there is an increasing interest in exploring their potential advantages for plants as well (Auffret et al., 2017; Plue

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et al., 2022). Despite their demonstrated capacity to enhance native species diversity (Damschen et al., 2019), evidence regarding the effectiveness of corridors for endangered plants remains scarce (Kirchner et al., 2003). Endangered plants may not only decline due to extrinsic factors, such as changes in land use, but they may also possess intrinsic factors, such as subpar dispersal and establishment, independently contributing to their population declines (Ozinga et al., 2009; Poschlod & Bonn, 1998; Young & Clarke, 2000). This could potentially make green corridors less effective to help these species disperse. A comparative analysis of dispersal traits between species known to benefit from corridors and endangered species could shed light on the potential of corridors in aiding endangered plant dispersal.

One critical type of green corridor in our human-dominated landscape is urban and rural green spaces (Lepczyk et al., 2023; Segar et al., 2022; Tallamy, 2007). Framed within the broader context of socio-ecological restoration, conservation gardening has recently emerged. This approach suggests green spaces could act as sanctuaries for endangered native plants (Munschek et al., 2023; Segar et al., 2022). Drawing from meta-community theory, it further posits that increasing the abundance and distribution of declining plants, as can be achieved via large-scale cultivation in gardens, enhances the likelihood of successful dispersal and sustaining wild populations (Leibold & Chase, 2017). While some evidence suggests that widespread cultivation of native species may positively impact population trends, the available data are limited, particularly for endangered plants (Segar et al., 2022; Staude, 2024a). In contrast, gardens' role in dispersing non-native species is well-documented, with up to 75% of the world's naturalized flora being garden plants (Reichard & White, 2001: Van Kleunen et al., 2018). Studving the dispersal ecology of these non-native plants, as species known to disperse and benefit from green spaces, could offer insights into the dispersal opportunities for endangered plants. If their dispersal traits are similar, our urban and rural green spaces could similarly benefit endangered species.

In urban and rural landscapes, dispersal by humans and windand their interplay-are likely to be particularly important (Bullock et al., 2018; Hodkinson & Thompson, 1997; Planchuelo et al., 2020). Currently, 55% of the global population lives in urban areas, with forecasts predicting an increase to 92% by 2100 (Jiang & O'Neill, 2017). With the human footprint stretching well beyond settlement areas, this offers ample opportunities for anthropogenic dispersal (Venter et al., 2016). Our network of roads and other mobility infrastructure creates substantial opportunities for anemochory, that is, the transport of seeds by wind, as vehicle movement produces wind currents (von der Lippe et al., 2013). Likewise, human movements open the potential for epizoochory, that is, the transport of seeds via attachment (Wichmann et al., 2009). Our green spaces also attract a wealth of animal diversity (Davies et al., 2009; Hansen et al., 2020; Theodorou et al., 2020), providing resources that have become scarce in our modern agricultural landscape (e.g. ponds; Möckel, 2015). Thus, not only zoochory by humans but also zoochory by animals, especially endozoochory, that is, the transport of seeds by the ingestion of animals, is

probably an important means of dispersal away from urban and rural green spaces (e.g. Tóth et al., 2023).

Certain traits may significantly enhance plant dispersal from urban and rural areas. Smaller, lighter seeds with slower descent are more likely to be carried farther by wind (Jongejans & Telenius, 2001). The tendency of plants with smaller seeds to produce more of them may further amplify their chances of dispersal (Moles & Westoby, 2004). Seed structures like wings or hairs can improve wind dispersal, for example, from vehicle-induced airflow (Auffret, 2011; von der Lippe et al., 2013; von der Lippe & Kowarik, 2008). Seed stickiness, hooks or barbs may enhance attachment and facilitate dispersal by humans (Auffret & Cousins, 2013; Ridley, 1930; Wichmann et al., 2009). Also, floating devices like balloon structures can make seeds more accessible to waterbirds in garden ponds, aiding in endozoochory (Tóth et al., 2023). Nutrient-rich structures may increase seed ingestion, also promoting endozoochory. Seeds that remain viable for a long time can survive in the soil and be spread by human activities, like discarding garden waste (Gioria et al., 2021). Lastly, after dispersal, successful seed germination is crucial for establishment. Thus, traits like seed weight, terminal velocity, dispersal distance, dispersal mode, seed structures, seedbank type and germination rate are likely to influence the dispersal success of species from green spaces.

In this study, I synthesized data on the above dispersal traits and integrated this with information from the German Red List on vascular plants (Metzing et al., 2018) to conduct a comparative analysis of the dispersal ecology among endangered, non-endangered native and non-native species in Germany. Additionally, by leveraging a comprehensive resource on German cultivated plants, 'Rothmaler's Herbaceous Crop and Ornamental Plants' (Jäger et al., 2016), I identified non-native garden escapees and, through recent databases on conservation gardening. By contrasting the dispersal ecology of non-native garden escapees with endangered species amenable to gardening, I aim to enhance the practical implications of the findings for urban and rural green spaces. This research explores how our green spaces, especially gardens, may support the dispersal of endangered plant species.

2 | METHODS

2.1 | Red List status, garden escapees and conservation gardening species

I used the 2018 German National Red List (RL) on vascular plants (Metzing et al., 2018) for species endangerment and native status. RL categories include: 0=Extinct or lost, 1=Critically endangered, 2=Endangered, 3=Vulnerable, G=Endangered-unknown extent, R=Rare, V=Near threatened, *=Not endangered, nb=Not assessed. The RL details native status as follows: 'I' indicates indigenous, 'N' indicates naturalized non-native and 'U' indicates transient. I distinguished between endangered native species ('I' and either 0, 1, 2, 3 or G), non-endangered native species ('I' and either R, V or *) and naturalized non-native species ('N'). These categories correspond to three population trends: endangered species are declining, nonendangered native species are mostly stable and non-native species are increasing. I only included taxa at the species level (indicated by the column 'Arten'). I further inferred non-native species that escaped gardens (garden escapees) from the overlap of established non-native species in the RL and species cultivated in gardens that naturalize in Germany as of Rothmaler Volume 5, titled 'Krautige Nutz- und Zierpflanzen' (Herbaceous crop and ornamental plants; Jäger et al., 2016), which I digitized in previous work (Staude, 2024a). Species amenable to conservation gardening are based on declining native species in Germany (categories 0, 1, 2, 3, G, R and V) and their inclusion in a comprehensive garden plant platform, natura-db. de (Munschek et al., 2023). All datasets were taxonomically harmonized with rWCVP and rWCVPdata (Brown et al., 2023). In total, there were 1054 endangered native species, 2141 non-endangered native species, 375 naturalized non-native species, 152 non-native garden escapees and 458 conservation gardening species.

2.2 **Dispersal traits**

I used data from three trait databases: (1) Lososová et al., 2023, who compiled an extensive dataset of seed-related information, including

Data availability per trait

seed mass, seed dispersal distance classes and the predominant dispersal modes for most European vascular plants; (2) LEDA Database (Kleyer et al., 2008), which provides data on seed terminal velocity, seed structure and seedbank type for the Northwest European flora; and (3) Seed Information Database (SER, INSR, RBGK, 2023) which contains germination rates derived from measurements on seed collections held in Royal Botanic Garden Kew's Millennium Seed Bank. All trait datasets were taxonomically harmonized with rWCVP and rWCVPdata (Brown et al., 2023). For detailed information on all traits and the ecological rationale for inclusion see Supplement S1. While several species had no trait data available, there was no data availability bias towards a particular group of species (Figure 1).

Data analyses 2.3

For the continuous dispersal traits (seed mass, terminal velocity, dispersal distance and germination rate), I employed linear models, using species type (native endangered, native non-endangered or non-native species) as the predictor. In separate analyses, I also performed linear models for non-native garden escapees and conservation gardening species. For post hoc comparisons between species types, I used the emmeans package (Lenth et al., 2020). I tested whether the results were robust when accounting for



FIGURE 1 Data availability for examined dispersal traits. Displayed are the number of species with data (black) versus no data (white) for non-native, native endangered and native non-endangered species. Percentages indicate data availability for each group.



phylogeny by fitting linear mixed-effects models with plant family included as a random intercept using the Ime4 package (Bates et al., 2014). For the categorical dispersal traits (dispersal mode, seed structures and seedbank type), I used Chi-square tests to identify statistically significant differences between species types. All data and R code for data carpentry, analysis and visualization are available on GitHub at https://github.com/istaude/ dispersal-endangered.git.

RESULTS 3

I found only minor, yet in a few cases statistically significant differences in examined dispersal traits among non-native, endangered and non-endangered native species.

3.1 Seed mass

On average, seeds of non-native species were heavier, weighing 1.59 mg, compared to 0.61 mg for endangered species and 0.94 mg for non-endangered native species (F_{2.2664}=18.6, R²=0.016, p-value <0.001; Figure 2a). Although the pairwise differences are small (given that seed mass varied by six orders of magnitude in the data), they were statistically significant (non-native vs. endangered, p-value <0.001; non-native vs. non-endangered, p-value <0.001; endangered vs. nonendangered, p-value <0.001). When accounting for phylogeny, none of the pairwise differences was statistically significant (Figure S1a).

3.2 **Terminal velocity**

The differences in terminal velocity were even smaller, with nonnative, endangered and non-endangered native species' seeds accelerating on average to 2.57, 2.19, and 2.36 m/s, respectively $(F_{2,986}=2.8, R^2=0.006, p$ -value=0.06; Figure 2b). None of the pairwise differences was statistically significant (non-native vs. endangered, p-value=0.074; non-native vs. non-endangered, pvalue=0.371; endangered vs. non-endangered, p-value=0.19). Results were robust in accounting for phylogeny (Figure S1b).

3.3 **Dispersal distance**

Non-native species, on average, had a dispersal class of 2.81, while endangered species exhibited a value of 3.01, and non-endangered species showed 3.11 ($F_{2,2752}$ =4, R^2 =0.003, p-value=0.019; Figure 2c). Statistically, there was a significant difference in dispersal class between non-endangered and non-native species (pvalue = 0.017), but not between endangered and non-native species (p-value=0.206) or between endangered and non-endangered species (p-value=0.41). When accounting for phylogeny, endangered native species exhibited a statistically significant higher mean

dispersal class than non-native species, while the other contrasts remained unchanged (Figure S1c).

3.4 Germination rate

Non-native species displayed an average germination rate of 91.5%, which was similar to endangered (90%) and non-endangered (90.7%) native species ($F_{2,1072} = 0.6$, $R^2 = 0.001$, *p*-value = 0.556; Figure 2d). Neither the difference between non-native and endangered species (p-value=0.548), non-native and non-endangered species (p-value=0.801), nor between endangered and non-endangered native species (p-value=0.739) was statistically significant. Results were robust to accounting for phylogeny (Figure S1d).

3.5 **Dispersal mode**

There was limited evidence to suggest that both non-endangered and non-native species diverged in the same way from endangered species or that they derived advantages from a particular mode of dispersal that might be considered superior (Figure 2e). For instance, non-native species statistically favoured local, unassisted and nonspecific dispersal to a greater extent (61%) compared to both endangered (51%; $\chi^2 = 9.7$, p-value = 0.0018) and non-endangered (51%; χ^2 =9.2, *p*-value=0.0024) species. In contrast, endangered species exhibited the highest proportion of wind-dispersed species (26%), with a statistically significant difference compared to nonnative (14%; $\chi^2 = 16.7$, *p*-value <0.0001) and non-endangered (20%; $\gamma^2 = 10.6$, p-value = 0.001) species. The only dispersal mode in which endangered species did not benefit to a greater extent was endozoochory (5%). Both non-native (9%; $\chi^2 = 5.4$, p-value = 0.02) and nonendangered native (13%; χ^2 =37.6, *p*-value <0.001) species were more frequently dispersed through endozoochory (for detailed pairwise comparisons for each dispersal mode category, see Table S1).

Seed structures 3.6

Non-native species were most often with no appendage, and both non-endangered and endangered species had across all types of appendages a significantly higher proportion of species with a given appendage (Figure 2f; Table S2). There was no statistically significant difference in the proportion of species with a given appendage between non-endangered and endangered species (Table S2), except for nutrient-containing appendages which were proportionally more frequent in non-endangered species ($\chi^2 = 12.2$, *p*-value <0.001).

Seedbank type 3.7

For seedbank type, my analysis revealed no clear evidence that the longevity of seeds of endangered species is lower than that of both



native non-endangered mative endangered non-native

FIGURE 2 Comparison of dispersal traits between endangered native (red), non-endangered native (grey) and non-native plants (green). (a) Seed mass (log10-transformed, mg), (b) terminal velocity (m/s), (c) dispersal distance (ordinal), (d) germination rate (%). Boxplots, jittered data and density curves are shown; white points indicate means; 'n' signifies the number of species for which data were available. (e) Dispersal mode, (f) seed structures and (g) seedbank type. Bar plots illustrate species proportion in each category with adjacent percentages. For example, 61% (or 202 species) of non-native plants exhibit local non-specific dispersal. Totals may exceed 100% for seed structures due to multiple structures per species.

non-endangered and non-native species (see Figure 2g; Table S3). Non-endangered native species exhibited a higher prevalence of transient seedbanks compared to non-native species ($\chi^2 = 4.0$, pvalue=0.026). Yet, endangered natives tended to have a higher proportion of long-term persistent seeds in comparison to nonendangered natives ($\chi^2 = 3.9$, p-value = 0.049).

The differences in examined dispersal traits between species for conservation gardening and non-native garden escapee plants were similarly minor (Figure 3). Conservation gardening species did not significantly differ from escapee plants in seed mass (1.47 mg vs. 1.65 mg, *p*-value = 0.6), or terminal velocity (2.49 m/s vs. 2.62 m/s, p-value=0.612), but had a significantly higher dispersal distance (2.86 vs. 2.45, p-value=0.012). Germination rates were comparable (90.6% vs. 88.5%, p-value = 0.35). Results were again robust to accounting for phylogeny, with one exception: terminal velocities of conservation gardening species were significantly lower than those





plants (green). (a) Seed mass (log10-transformed, mg), (b) terminal velocity (m/s), (c) dispersal distance (ordinal), (d) germination rate (%). Boxplots, jittered data and density curves are shown; white points mark means; 'n' signifies the number of species for which data were available. (e) Dispersal mode, (f) seed structures and (g) seedbank type. Bar plots illustrate species proportion in each category with adjacent percentages. Totals may exceed 100% for seed structures due to multiple structures per species.

17% (n=49)

15% (n=42)

Nutrient containing structures

Flat appendages

8% (n=5)

2% (n=1)

of non-native garden escapees (Figure S2). For the categorical traits, wind dispersal was again found to be more prevalent in conservation gardening species ($\chi^2 = 3.2, p$ -value = 0.076), while non-native escapees predominantly relied on unassisted dispersal methods ($\chi^2 = 3.8$, *p*-value=0.052). In contrast to the patterns observed between all endangered and non-native species, endozoochory emerged as a

Endozoochory

9% (n=40) Epizoochory

3% (n=4)

2% (n=3)

2% (n=10)

Hydrochory

4% (n=5)

significantly more prevalent dispersal mode for conservation gardening species (χ^2 =4.8, p-value=0.029). A majority of non-native escapees (75%) lacked appendages, whereas conservation gardening species often possessed them (χ^2 =31.3, *p*-value <0.001). As for seedbank longevity, non-native escapees tended to more frequently display short-term persistence (20% vs. 11%), while more

11% (n=24)

long-term persistent

8% (n=3)

6% (n=12)

0.3

0.6

0.9

0.0

STAUDE

83% (n=174)

conservation gardening species had transient seedbanks, but none of these differences was statistically significant. See Tables S4–S6 for all pairwise comparisons.

4 | DISCUSSION

Given the well-documented role of gardens in dispersing non-native plant species (Reichard & White, 2001; Van Kleunen et al., 2018), I conducted a comparative analysis of dispersal ecologies to explore the potential for analogous benefits for endangered native plants. Endangered plants tended to produce slightly lighter seeds that fall more slowly, enhancing their dispersal distances. They were more often wind-dispersed and with seed appendages conducive to a broader spectrum of dispersal vectors. Conversely, non-native species showed more non-assisted local dispersal, had heavier seeds and tended to have more short-term persistent seed banks. However, the distinctions in these and other relevant dispersal traits were quantitatively modest, as were the differences between endangered species amenable to gardening and non-native plants known to escape gardens. Together this indicates that the dispersal ecology of endangered native plants is comparable to that of nonnative species, which frequently spread from green spaces like gardens. Hence, integrating endangered plants within our green spaces could prove to be an effective strategy to bolster their dispersal and, in turn, aid their survival.

The higher rate of wind-dispersed species among endangered native plants may be particularly beneficial in urban to rural contexts due to human mobility infrastructure and wind from passing vehicles, fostering an increased likelihood of dispersing to novel urban or natural remnant habitats (Planchuelo et al., 2020; von der Lippe & Kowarik, 2008). Endozoochory likely serves as another important dispersal avenue in urban green spaces (Tóth et al., 2023), which can foster a high diversity of animals, such as birds (Davies et al., 2009). Conservation gardening plants showed a modestly higher tendency for endozoochory than non-native garden escapees. Yet, the broader comparison across all endangered natives versus nonnatives, reveals more frequent use by non-native plants. This inconsistency, plus endozoochory's limited overall prevalence, suggests that any difference in dispersal ability between non-native and endangered natives may not be markedly attributed to endozoochory. While endangered plants had frequently transient seed banks, suggesting a potential vulnerability in unpredictable, early-successional habitats (Gioria et al., 2021; Larson & Funk, 2016), this trait was not unique to them; many non-native plants (64%) and garden escapees (72%) shared it. Though germination rates were comparable across groups, they do not always correlate with field emergence (Hitchmough, 2017), a trait that would offer deeper insights into the likelihood of establishment post-dispersal if data were available. Overall, the dispersal traits of endangered native plants appeared on par with, and not less effective than, those of non-native species.

Do these subtle differences between increasing non-native species (c.f. Eichenberg et al., 2021) and endangered ones indicate that cological Solutions

dispersal is not key to their population trends? Central European landscapes and their associated dispersal mechanisms have dramatically changed over the centuries (Poschlod & Bonn, 1998). Of particular note is the role of both endo- and epizoochory, where numerous plants benefit from animal-mediated seed dispersal (Couvreur et al., 2004; Poschlod & Bonn, 1998), a process that has seen profound changes. Historical shifts in livestock management, transitioning from transhumance (i.e. the seasonal movement of people with their livestock between fixed summer and winter pastures) to more contained systems, and dramatic reductions in livestock populations, such as the decline of sheep numbers in Germany from 25 million in 1870 to 5 million in 1907 (Lahrkamp, 1928) suggest major changes in dispersal pathways. These livestock once linked grasslands, and their decreasing numbers have been associated with declines in grassland species (Krauss, 1977; Ruxton & Schaefer, 2012), many now endangered (Staude et al., 2023). Recent research further suggests that many plant species may struggle to track climate change, potentially risking extinction, as a result of seed dispersal interactions lost through defaunation (Fricke et al., 2022). Thus, it is key to understand how dispersal processes are evolving and how species dispersal traits align with these changes for conserving endangered species and restoring habitat.

Although some of the key original dispersal processes are no longer in place, there are new ones that are simulating or replacing them (Auffret, 2011; Bullock et al., 2018; Poschlod & Bonn, 1998). Modern landscapes are dominated by human-centric infrastructures-roads, railways and gardens-that shape plant dispersal patterns (Poschlod & Bonn, 1998; Wichmann et al., 2009). These man-made pathways primarily connect human habitats, sidelining diverse habitats like semi-natural grasslands. Consequently, we tend to disperse species that thrive alongside humans, particularly those that grow quickly in nutrient-rich environments (Auffret & Cousins, 2013; Kalusová et al., 2017; Segar et al., 2022). This has led to a dispersal bias in our landscapes. To harness these new dispersal avenues for conservation, we need to integrate endangered species into our urban and rural matrix so that we start dispersing these species as well (Segar et al., 2022). Studies show, for example, that endangered species, such as orchids can thrive along roadsides and in the neo-habitats humans create (Fekete et al., 2020; Rewicz et al., 2017). Similarly, numerous animals use human-made habitats, such as gardens and ponds, and can effectively disperse native plants from urban areas to natural ecosystems (Tóth et al., 2023). My analysis indicates that, based on dispersal ecological differences alone, there is no inherent reason why endangered native plants, especially those suited to gardening, should not benefit from these types of dispersal.

Clearly, this study does not provide conclusive evidence that green corridors aid endangered plants. Experiments, involving genetic studies, are necessary to reveal the frequency and contextdependency by which declining native plants disperse from urban and rural green spaces, and the extent to which these spaces enhance gene flow among fragmented wild populations of declining natives (Plue et al., 2022). There is also a need for empirical research into the unintentional dispersal of endangered plants by humans,



such as through clothing, shoes, garden waste or traffic, when we start cultivating these species within our private gardens and public green spaces. Additionally, creating databases to record the field emergence rates of endangered species is essential for guiding conservation gardening and designing seed mixes. The absence of these data is a notable gap in this study. Despite indications that humans help disperse endangered species (Auffret & Cousins, 2013), research tends to focus on non-native species. To harness humanmediated dispersal in conservation efforts effectively, it is vital to gain a deeper insight into how we can support the dispersal of native plants.

5 | CONCLUSIONS

Given the enormous potential for human-mediated plant dispersal in our modern landscapes, and the tendency for this type of dispersal to favour species that thrive in human habitats, this research raised the question of whether we could use this potential to benefit our endangered native flora by growing them in our habitats, such as gardens. My findings show that endangered native plants have a dispersal ecology that is broadly comparable to that of nonnative plants, which are known to often spread from managed green spaces. The key takeaway from this study for practitioners is that integrating endangered species into our green spaces could help to promote an essential aspect of species survival: dispersal.

AUTHOR CONTRIBUTIONS

IRS conceived the study, analysed the data and wrote the manuscript.

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CONFLICT OF INTEREST STATEMENT

The author declares no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All Data and R code to reproduce the analyses and figures of this work are archived and available on Zenodo at https://doi.org/10.5281/zenodo.10825321 (Staude, 2024b). The data used in this analysis have been previously published. The 2018 German Red List can be downloaded from https://www.rote-liste-zentrum.de/de/Download-Pflan zen-1871.html. Information on the amenability of native plant species to gardening is available from Munschek et al., 2023, and can be accessed at https://conservation-gardening.shinyapps.io/app-de/. Data on the cultivated flora of Germany and non-native garden escapees are provided by Staude, 2024a. Dispersal traits were compiled from several sources: Lososová et al., 2023 (covering seed mass, seed dispersal distance class and predominant dispersal mode), Kleyer et al., 2008 (providing data from the LEDA database on seed terminal velocity, seed structure and seedbank), and the Seed Information Database (SER, INSR, RBGK, 2023) for germination rates.

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DATA SOURCES

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article. **Data S1:** Trait description and ecological rationale for inclusion.

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