

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

2 Ingmar R. Staude^{1,2}

3 1. *Institute of Biology, Leipzig University, Leipzig, Germany*

4 2. *German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany*

5 Correspondence: ingmar.staude@uni-leipzig.de

6 Running head: *Dispersal: Endangered vs. Non-native Plants*

7 **Abstract**

8 Amidst global challenges like climate change, plant dispersal corridors are essential. In
9 human-dominated landscapes, urban and rural green spaces are key dispersal avenues. Non-
10 native plants are known to benefit from these, yet the potential benefits for endangered plants
11 remain unclear. To address this question, I compared dispersal traits of endangered native
12 plants with those of non-endangered and non-native species in Germany. I also compared
13 endangered species amenable to gardening with non-native garden escapees to make my
14 analysis pertinent to understanding the potential role of gardens in aiding native plant
15 dispersal. I analyzed several traits including seed weight, terminal velocity, dispersal distance,
16 germination rate, dispersal mode, seed structures, and seedbank type. Overall, dispersal traits
17 between native and non-native plants showed minor, but in some cases statistically clear
18 differences. Endangered plants were more often wind-dispersed and had more frequently
19 seed appendages that might encourage a wider range of dispersal vectors. In contrast, non-
20 native plants leaned more towards non-assisted local dispersal with slightly heavier seeds and
21 more persistent seed banks. The other traits were largely consistent across groups. Given the
22 minor differences in dispersal traits, green corridors may provide no lesser dispersal avenue
23 for endangered native species. Gardens that have historically aided the dispersal of many
24 non-native plants, could support the dispersal of endangered native plants instead.

25 **Implications for practice**

- 26 1. Traditional plant dispersal mechanisms, like herbivore-mediated pathways linking semi-natural
27 habitats, have largely given way to human-driven dispersal connecting urban and rural areas
28 in Central Europe.
- 29 2. Given the resulting bias towards dispersing synanthropic species, an integration of endangered
30 species into urban and rural green spaces could help counteract this dispersal bias.
- 31 3. The results of this study indicate endangered plants do not have a lesser dispersal ability than
32 non-native garden escapee species.
- 33 4. This indicates their potential to benefit from modern dispersal pathways, such as gardens and
34 green corridors.

35 **Introduction**

36 There are increasing calls and efforts to establish corridors aiding the migration of organisms
37 in response to global change factors, such as climate change (European Commission, 2020;
38 Brodie et al., 2021; <https://naturaconnect.eu/>). While research on the efficacy of these
39 corridors has traditionally centered on animals (Hobbs, 1992), there is an expanding interest
40 in exploring their potential advantages for plants as well (Auffret et al., 2017; Plue et al., 2022).
41 Despite their demonstrated capacity to enhance native species diversity (Damschen et al.,
42 2019), evidence regarding the effectiveness of corridors for endangered species remains
43 scarce (Kirchner et al., 2003). Endangered species may not only decline due to extrinsic
44 factors, such as changes in land use, eutrophication, and natural successional dynamics
45 (Godefroid et al., 2014), they may possess intrinsic factors, such as inferior dispersal and
46 establishment, independently contributing to their population declines (Poschlod & Bonn,
47 1998; Young & Clarke, 2000; Ozinga et al., 2009; Holz et al., 2022). This could potentially
48 make green corridors less effective to help these species disperse. Investigating how dispersal
49 traits differ between species experiencing population increases and those that decline could
50 provide insights into the potential of corridors to facilitate endangered species dispersal.

51 One critical type of green corridor in our human-dominated landscape are private and
52 public green spaces (Tallamy, 2007; MacLagan et al., 2018; Planchuelo, Kowarik, & Von der
53 Lippe, 2020; Segar et al., 2022; Lepczyk et al., 2023). Recently, conservation gardening has
54 emerged as a participatory approach to conservation, proposing that green spaces could
55 serve as refuges for endangered native plants (Segar et al., 2022; Munschek et al., 2023).
56 Additionally, meta-community theory predicts that increasing the abundance and distribution
57 of declining plants, as can be achieved via large-scale cultivation in urban and rural green
58 spaces, enhances the likelihood of successful dispersal and sustaining populations (Leibold
59 & Chase, 2017; Thompson et al., 2020). While some evidence suggests that cultivating native
60 species may positively impact population trends and Red List status, the available data is
61 limited, particularly for endangered native plants (Segar et al., 2022; Staude, 2023). That is,
62 cultivating endangered native plants remains scarce, resulting in a paucity of data regarding
63 cultivation's effects on these species' population trends. Conversely, we better understand the
64 role of gardens in the dispersal of non-native species. Many native species have become
65 naturalized through horticulture (Reichard & White, 2001; Van Kleunen et al., 2018). Thus,
66 contrasting the dispersal ecology of species known to benefit from such corridors may be
67 particularly revealing in order to understand the dispersal potential of endangered native
68 plants.

69 In a green space setting, certain traits may be especially beneficial for plant dispersal. In these
70 contexts, dispersal by humans and wind—and their interplay—are likely to be particularly
71 important (Hodkinson & Thompson, 1997; Bullock et al., 2018; Maclagan et al., 2018;
72 Planchuelo, Kowarik, & Von der Lippe, 2020; Van Helden et al., 2020). Seeds that are smaller
73 and lighter with reduced fall velocities are likely to be wind-dispersed over greater distances
74 (Jongejans & Telenius, 2001). An inverse correlation between seed weight and fecundity
75 (Moles & Westoby, 2004) may further amplify dispersal prospects (Jakobsson & Eriksson,
76 2003). While nearly all plants might experience epizoochory (Poschlod & Bonn, 1998;
77 Couvreur et al., 2004), small seeds and those with specific seed structures like stickiness,
78 hooks or barbs may enhance attachment, promoting dispersal by humans (Ridley, 1930;
79 Wichmann et al., 2009; Auffret & Cousins, 2013). Structures such as wings or hairs can boost
80 secondary dispersal, especially with wind from passing vehicles (Lippe & Kowarik, 2008; Lippe
81 et al., 2013; Auffret, 2011; Rogers et al., 2019). Seeds with prolonged viability can persist in
82 the soil for extended periods and can be dispersed through human activities such as garden
83 throw-outs (Gioria et al., 2021; Sonkoly et al., 2022). Post-dispersal, successful germination
84 plays a vital role. Thus, traits like seed weight, aerodynamics, dispersal mode and distance,
85 seed structures, seedbank type, and germination rate are likely to greatly influence dispersal
86 success of species from green spaces within a human-dominated landscape.

87 In this study, I investigate differences in the above dispersal traits among endangered, non-
88 endangered native, and non-native species within the German flora. By contrasting non-native
89 garden escapees with endangered species amenable to conservation gardening, I aim to
90 enhance the practical implications of the findings for urban and rural green spaces. Ultimately,
91 this research seeks to illuminate the potential of corridors in aiding the dispersal of endangered
92 plant species.

93 **Methods**

94

95 **Red List status, garden escapees and conservation gardening species.** I used the 2018
96 German national Red List (RL) on vascular plants (Metzing et al., 2018) for species
97 endangerment and native status. RL categories include: 0 = Extinct or lost, 1 = Critically
98 endangered, 2 = Endangered, 3 = Vulnerable, G = Endangered - unknown extent, R = Rare,
99 V = Near threatened, * = Not endangered, nb = Not assessed. The RL details native status as
100 follows: "I" indicates indigenous, "N" indicates naturalized non-native, "U" indicates transient,
101 and "F" indicates doubtful. I distinguished between endangered native species ("I" and either
102 0, 1, 2, 3, or G), non-endangered native species ("I" and either R, V, *, or nb), and naturalized
103 non-native species ("N"). These categories correspond to three population trends: endangered

104 species are declining, non-endangered native species are stable, non-native species are
105 increasing. I only included taxa at the species level (indicated by the column "Arten"). I further
106 inferred non-native species that escaped gardens (garden escapees) from the overlap of
107 established non-native species in the RL, and species cultivated in gardens that naturalize in
108 Germany as of Rothmaler Volume 5, titled "Krautige Nutz- und Zierpflanzen" (Herbaceous
109 crop and ornamental plants; Jäger et al., 2016), which I digitized in previous work (Staude,
110 2023). Species amenable to conservation gardening are based on declining native species in
111 Germany (categories 0, 1, 2, 3, G, R and V) and their inclusion in a comprehensive gardening
112 gardening platform, natura-db.de (Munschek et al., 2023). All datasets were taxonomically
113 harmonized with rWCVP and rWCVPdata (Brown et al., 2023). In total, there were 1054
114 endangered native species, 2141 non-endangered native species, 375 naturalized non-native
115 species, 152 non-native garden escapees, and 458 conservation gardening species.

116

117 **Dispersal traits.** I used data from three trait databases: 1) Lososová et al., 2023, who
118 compiled an extensive dataset of seed-related information, including seed mass, seed
119 dispersal distance classes, and the predominant dispersal modes for most European vascular
120 plants; 2) LEDA Database (Kleyer et al., 2008), which provides data on seed terminal velocity,
121 seed structure and seedbank type for the Northwest European flora; and 3) Seed Information
122 Database (SER, INSR, RBGK, 2023) which contains germination rates derived from
123 measurements on seed collections held in Royal Botanic Garden Kew's Millennium Seed
124 Bank. I retrieved SID data via TRY (Kattge et al., 2020). All trait datasets were taxonomically
125 harmonized with rWCVP and rWCVPdata (Brown et al., 2023).

126

127 **Seed mass.** Seed mass [mg] is a key trait that can influence a plant's ability to disperse and
128 establish beyond garden boundaries. Lighter seeds are often better adapted for wind and long-
129 distance dispersal and thus colonization of new areas (Westoby et al., 1997), whereas heavier
130 seeds have a superior chance of establishing as seedlings due to a better provision of nutrients
131 (but see Moles & Westoby, 2004). Seed mass data were available for 73% of non-native
132 species, 62% of both endangered and non-endangered native species. Given that seed mass
133 can vary by ten orders of magnitude across plants (Harper, 1977), I log10-transformed seed
134 mass for subsequent analyses.

135 **Terminal velocity.** Terminal velocity [m/s] is the maximum speed a seed can reach while falling
136 due to gravity in air without accelerating further, i.e., the rate of fall when the effects of gravity
137 are balanced by air resistance. Seeds with a high terminal velocity tend to fall closer to the
138 parent plant, which means they are less likely to be dispersed by wind over long distances. If
139 species had more than one measurement, I calculated the mean terminal velocity. Terminal

140 velocity data were available for 17%, 20% and 33% of non-native, endangered native, and
141 non-endangered native species, respectively.

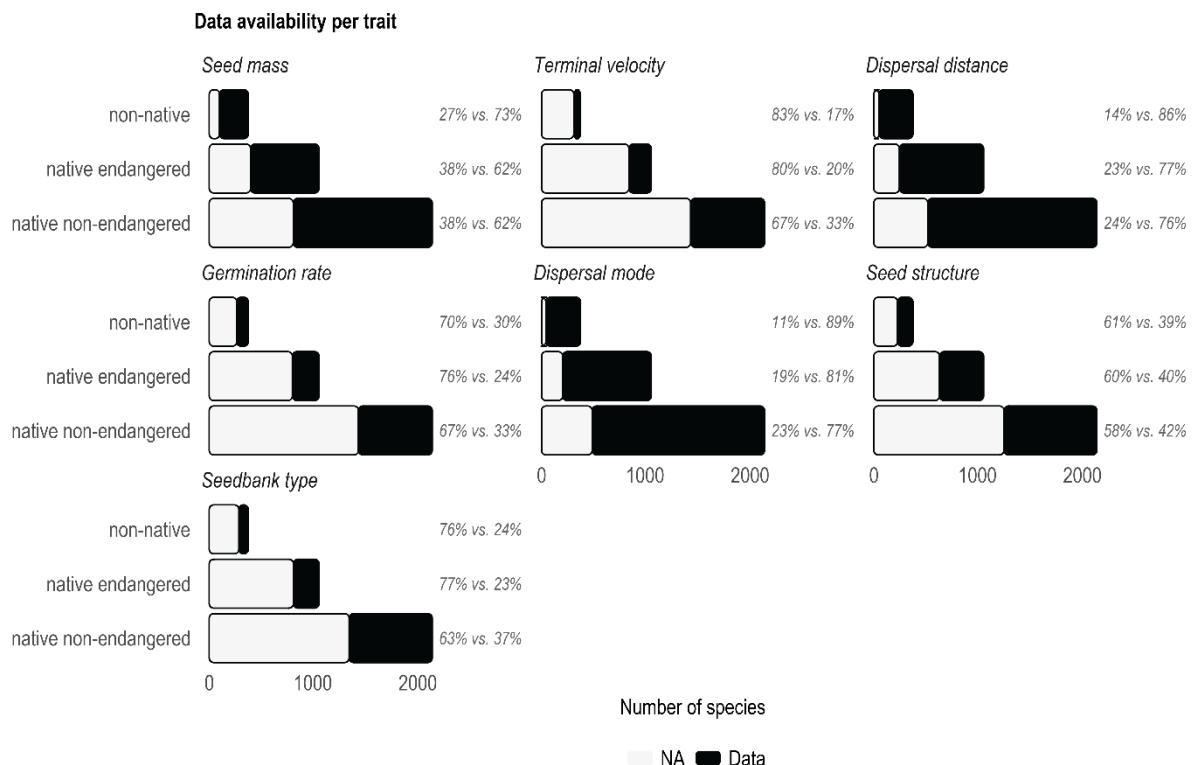
142 *Dispersal distance.* Dispersal distance is a strong indicator of dispersal ability. Lososová et
143 al., 2023, expanding on the approach of Vittoz & Engler, 2007, classified plants into six
144 dispersal distance classes based on a species' main dispersal mode, life form, plant height,
145 dispersal-related diaspore features and habitat preferences. For example, species in dispersal
146 distance class 1 have an upper distance limit of 1 m, and are small (<30cm) herbs or dwarf
147 shrubs with a local, non-specific and unassisted dispersal, whereas species in dispersal
148 distance class 6 are dispersed by animals and have an upper distance limit of 1500 m. Data
149 were available for 86%, 77% and 76% of non-native, endangered native, and non-endangered
150 native species, respectively.

151 *Germination rate.* Germination rate [%] measures the percentage of seeds from a given
152 sample that successfully develop into seedlings under specific conditions in Petri dishes. A
153 high germination rate increases the likelihood for plants to establish. These germination rates
154 however, do not reflect field emergence rates (Hitchmough, 2017). Outside the sterile lab
155 conditions under which germination rates are assessed, field emergence is almost always
156 much lower than germination rate. The specific conditions under which germination rates are
157 assessed in the Seed Information Database can vary within and between species. Conditions
158 vary in pre-sow treatment (e.g., seed scarified, soaked in smoke solution), growing medium
159 (e.g., 1% agar with varying amounts of potassium and gibberellic acid) and temperature and
160 photoperiod conditions. I calculated species mean germination rate across conditions. Data
161 were available for 20%, 24% and 33% of non-native, endangered native, and non-endangered
162 native species, respectively.

163 *Dispersal mode.* The predominant dispersal mode includes nonspecific local dispersal,
164 anemochory (dispersal by wind), hydrochory (dispersal by water) and zoolochory (dispersal by
165 animals). Zoolochory is further distinguished between epizoolochory (external dispersal on the
166 surface of animals), endozoolochory (dispersal via ingestion by animals), dyszoolochory
167 (dispersal by animals that lose seeds before ingestion), and myrmecochory (dispersal by
168 ants). Dispersal modes like anemochory, hydrochory and zoolochory are often associated with
169 long-distance dispersal (i.e., seeds can be carried by wind, water or animals to distant
170 locations), whereas more local unspecific and unassisted dispersal (e.g., by barochory) may
171 have more limited dispersal kernels. Data were available for 89%, 81% and 71% of non-native,
172 native endangered and native non-endangered species, respectively. Due to the low
173 proportion of species dispersed by dyszoolochory (0.5%), I omitted this category from
174 subsequent analyses.

175 *Seed structure.* Seed structures include six main morphological types: nutrient-rich structures,
176 balloon structures, elongated appendages, flat appendages, other specializations and no

177 appendages. Nutrient rich structures include, for example, elaiosomes, arils and pulp. Balloon
 178 structures bind air to the diaspore and include, for example, glumes (Poaceae) or uricles
 179 (Carex). Flat appendages are structures with considerably less height than width and length,
 180 for example wings as in *Acer* spec. Elongated appendages are prominent structures that make
 181 the seed look longer, for example, long pappuses as in *Centaurea* spec. or hooked structures
 182 as in *Bidens* spec. Note that in order to classify all appendages a diaspore has, any
 183 combination of the seed structure categories is possible. Data were available for 39%, 40%
 184 and 42% of non-native, native endangered and native non-endangered species, respectively.
 185 **Seedbank type.** Seedbank type is a categorical variable with three categories: transient
 186 (persists in soil less than one year), short-term persistent (persists at least one year but less
 187 than five years) and long-term persistent (persists at least five years). A longer seed longevity
 188 allows species to wait for favorable conditions to germinate and establish in new habitats. This
 189 may increase their chances of successful colonization and contributes to population
 190 persistence (Stöcklin & Fischer, 1999; Reed et al., 2002). If species had multiple seedbank
 191 types, I selected the most frequent type. Data were available for 25% of both non-native and
 192 endangered native species, and for 31% of non-endangered native species.
 193



194
 195 Fig. 1: **Data availability for examined dispersal traits.** Numerous species lacked data, yet there is no consistent
 196 pattern of less data for endangered native species.
 197

198 **Data analyses.** For the continuous dispersal traits, seed mass, terminal velocity, dispersal
199 distance, and germination rate, I employed linear models, using species type (native
200 endangered, native non-endangered, or non-native species) as the predictor variable. In
201 separate analyses, I also performed linear models for non-native garden escapees and
202 species amenable to conservation gardening. For post hoc comparisons between species
203 types, I used the emmeans package (Lenth et al., 2020). For the categorical dispersal traits,
204 dispersal mode, seed structures, and seedbank type, I employed Chi-square tests. These
205 tests helped determine whether there were statistically clear (Dushoff et al., 2019) differences
206 in the proportion of species falling into specific categories across different species types. For
207 example, I assessed whether the proportion of plants characterized by non-assisted, local
208 dispersal (a category within the dispersal mode variable) differed among non-native,
209 endangered, and non-endangered native species. All R code for data carpentry, analysis and
210 visualization are available on GitHub at <https://github.com/istaude/dispersal-endangered.git>.
211

212 Results

213 I found only minor, yet in a few cases statistically clear differences in examined dispersal traits
214 among non-native, endangered, and non-endangered native species.
215 *Seed mass.* On average, dispersules of non-native species were heavier, weighing 1.59 mg,
216 compared to 0.61 mg for endangered species and 0.94 mg for non-endangered native species
217 (Fig. 2a). Although the pairwise differences may appear small (given that seed mass varied
218 by six orders of magnitude in the data), they were statistically clear (non-native vs.
219 endangered, p-value < 0.001; non-native vs. non-endangered, p-value < 0.001; endangered
220 vs. non-endangered, p-value < 0.001).

221 *Terminal velocity.* The differences in terminal velocity were even smaller, with non-native,
222 endangered, and non-endangered native species' dispersules accelerating on average to 2.57
223 m/s, 2.19 m/s, and 2.36 m/s, respectively (Fig. 2b). None of the pairwise differences were
224 statistically clear (non-native vs. endangered, p-value = 0.074; non-native vs. non-
225 endangered, p-value = 0.371; endangered vs. non-endangered, p-value = 0.19).

226 *Dispersal distance.* Non-native species, on average, had a dispersal class of 2.81, while
227 endangered species exhibited a value of 3.01, and non-endangered species showed 3.11
228 (Fig. 2c). Statistically, there was a clear difference in dispersal class between non-endangered
229 and non-native species (p-value = 0.017), but not between endangered and non-native
230 species (p-value = 0.206) or between endangered and non-endangered species (p-value =
231 0.41).

232 *Germination rate.* Non-native species displayed an average germination rate of 91.5%, which
233 was not clearly higher than that of endangered species (90%, p-value = 0.548) or non-
234 endangered native species (90.7%, p-value = 0.801; Fig. 2d). Moreover, there was no clear

235 difference in germination rates between endangered and non-endangered native species (p-
236 value = 0.739).

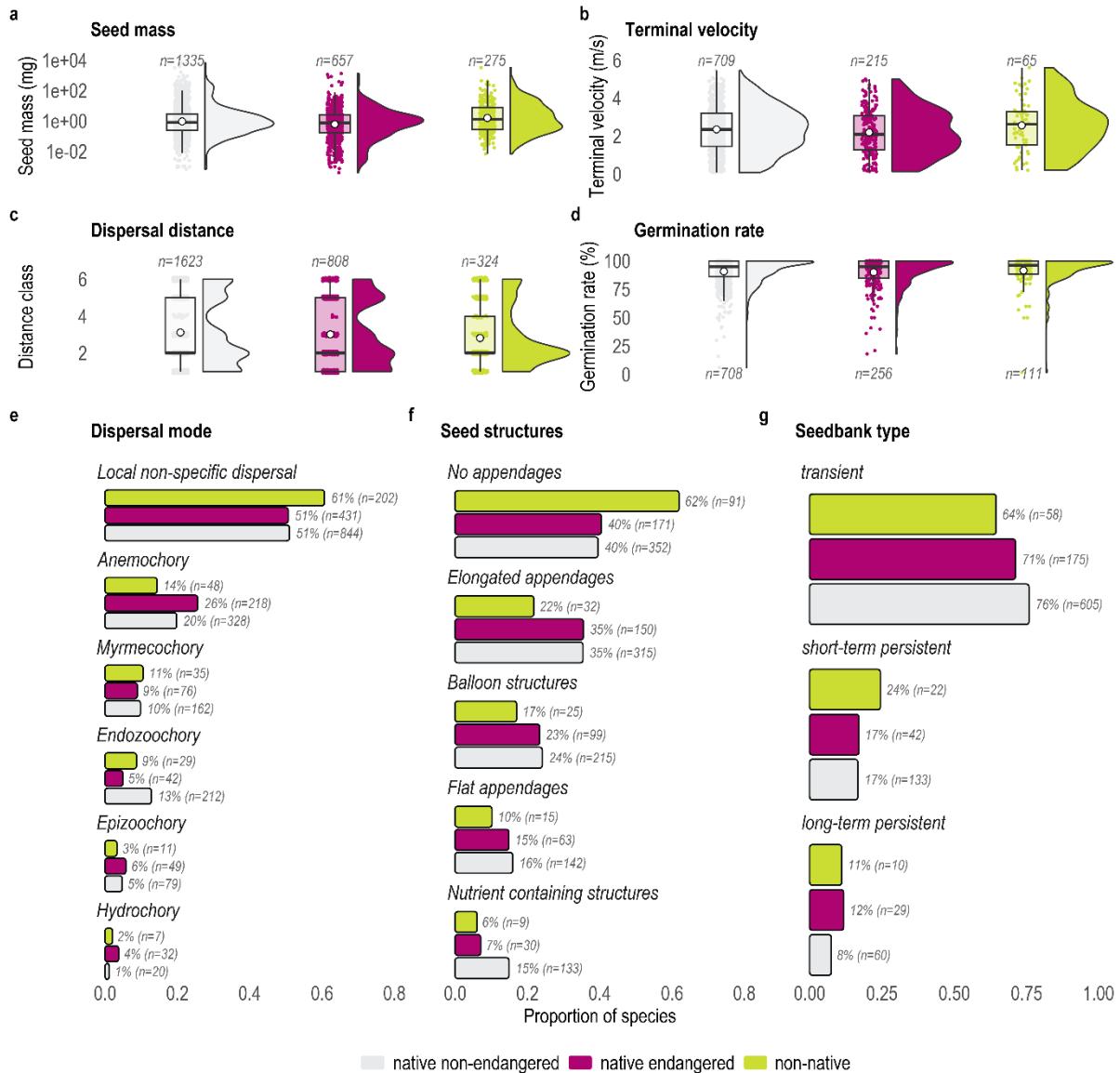
237 *Dispersal mode.* There was limited evidence to suggest that both non-endangered and non-
238 native species diverged in the same way from endangered species or that they derived
239 advantages from a particular mode of dispersal that might be considered superior (Fig. 2e).
240 For instance, non-native species statistically favored local, unassisted, and non-specific
241 dispersal to a greater extent (61%) compared to both endangered (51%; $X^2 = 9.7$, p-value =
242 0.0018) and non-endangered (51%; $X^2 = 9.2$, p-value = 0.0024) species. In contrast,
243 endangered species exhibited the highest proportion of wind-dispersed species (26%), with a
244 statistically clear difference compared to non-native (14%; $X^2 = 16.7$, p-value < 0.0001) and
245 non-endangered (20%; $X^2 = 10.6$, p-value = 0.001) species. The only dispersal mode in which
246 endangered species did not benefit to a greater extent was endozoochory (5%). Both non-
247 native (9%; $X^2 = 5.4$, p-value = 0.02) and non-endangered (13%; $X^2 = 37.6$, p-value < 0.001)
248 species were more frequently dispersed through endozoochory (for detailed pairwise
249 comparisons for each dispersal mode category, see Supplementary Table 1.)
250 *Seed structures.* Non-native species were most often with no appendage, and both non-
251 endangered and endangered species had across all types of appendages a clearly higher
252 proportion of species with a given appendage (Fig. 2f; Supplementary Table 2). There was no
253 statistically clear difference in the proportion of species with a given appendage between non-
254 endangered and endangered species (Supplementary Table 2), except for nutrient-containing
255 appendages which were proportionally more frequent in non-endangered species ($X^2 = 12.2$,
256 p-value < 0.001).

257 *Seedbank type.* For seedbank type, our analysis did not reveal any clear evidence suggesting
258 that the seed longevity of endangered species was consistently inferior to that of both non-
259 endangered and non-native species (see Fig. 2g and Supplementary Table 3). Interestingly,
260 non-endangered native species exhibited a higher prevalence of transient seedbanks
261 compared to non-native species ($X^2 = 4.0$, p-value = 0.026). However, this distinction was less
262 evident when compared to endangered native species. Notably, endangered species tended
263 to have a higher proportion of long-term persistent seeds in comparison to non-endangered
264 species ($X^2 = 3.9$, p-value = 0.049).

265

266

Dispersal ecology of endangered versus native and non-native plants



267

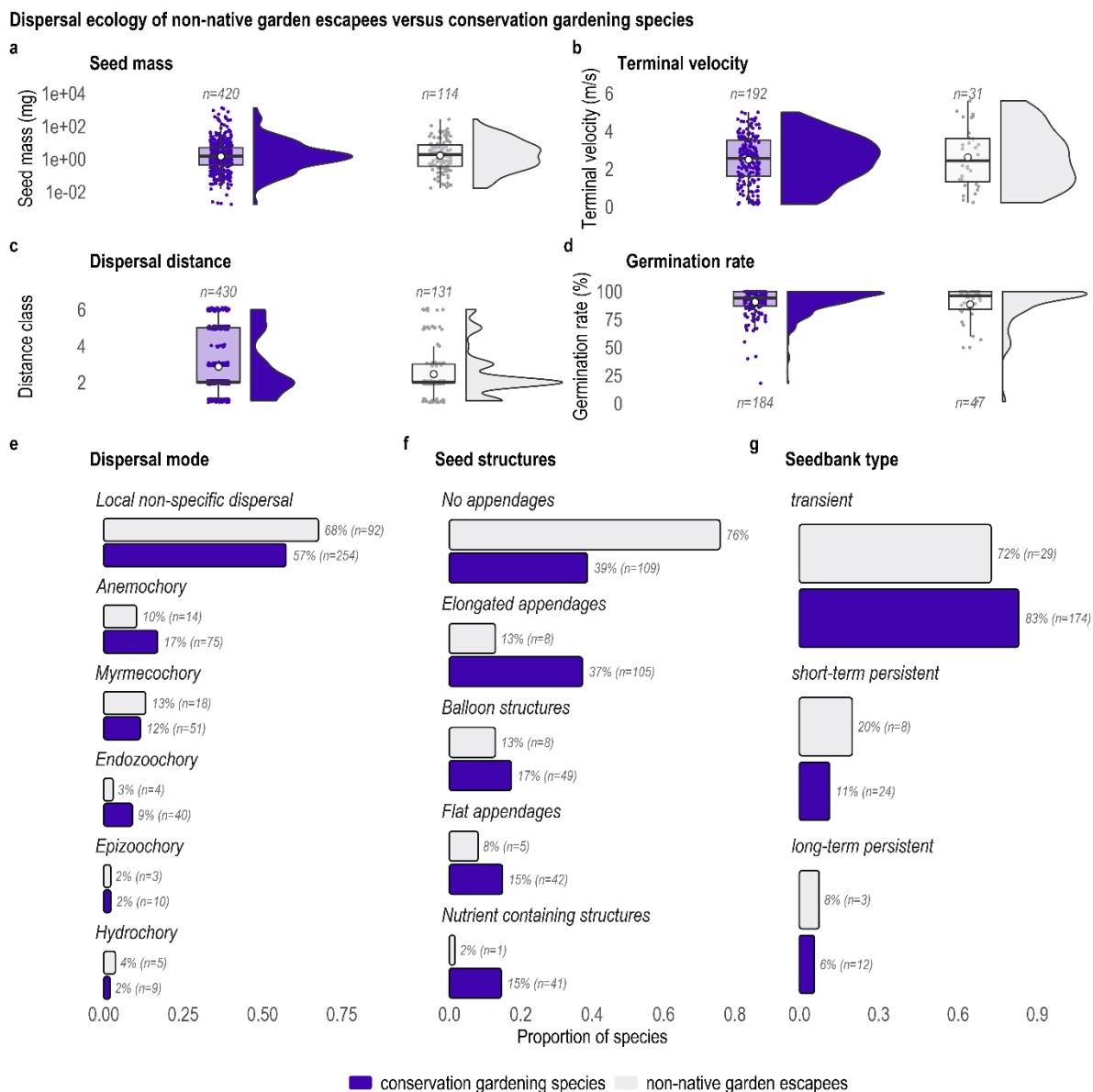
268 Fig. 2: **Comparison of dispersal traits between endangered native (red), non-endangered native (gray) and**
 269 **non-native plants (green).** a) Seed mass (log10-transformed, mg), b) terminal velocity (m/s), c) dispersal distance
 270 (ordinal), d) germination rate (%). Boxplots, jittered data, and density curves are shown; white points indicate
 271 means; 'n' signifies the number of species for which data were available. e) Dispersal mode, f) seed structures,
 272 and g) seedbank type. Bar plots illustrate species proportion in each category with adjacent percentages. E.g.,
 273 61% (or 202 species) of non-native plants exhibit local non-specific dispersal. Totals may exceed 100% for seed
 274 structures due to multiple structures per species.

275

276 The differences in examined dispersal traits between species for conservation gardening and
 277 non-native garden escapee plants were similarly minor, and largely displayed the same
 278 patterns. Conservation gardening species did not clearly differ from escapee plants in seed
 279 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
 280 = 0.612), but had a clearly higher dispersal distance (2.86 vs 2.45, p-value = 0.012).
 281 Germination rates were comparable (90.6% vs 88.5%, p-value = 0.35). Wind and

282 endozoochory were tended to be more prevalent dispersal modes for conservation gardening
 283 species ($X^2 = 3.2$, p-value = 0.076 and $X^2 = 4.8$, p-value = 0.029),, while non-native escapees
 284 predominantly relied on unassisted dispersal ($X^2 = 3.8$, p-value = 0.052). This tendency is
 285 echoed in seed structures: a majority of non-native escapees (75%) lacked appendages,
 286 whereas conservation gardening species often possessed them ($X^2 = 31.3$, p-value < 0.001).
 287 As for seedbank longevity, non-native escapees tended to more frequently exhibit short-term
 288 persistence (20% vs 11%, p), while more conservation gardening species showcased
 289 transient seedbanks, but none of these differences were statistically clear (Supplementary
 290 Table X).

291



292

293 Fig. 3: **Comparison of dispersal traits between endangered native species amenable to gardening**
 294 (**conservation gardening species; blue**), and **non-native plants grown in gardens that are known to**
 295 **naturalize (non-native garden escapees; gray)**. a) Seed mass (log10-transformed, mg), b) terminal velocity

296 (m/s), c) dispersal distance (ordinal), d) germination rate (%). Boxplots, jittered data, and density curves are shown;
297 white points mark means; 'n' signifies the number of species for which data were available. e) Dispersal mode, f)
298 seed structures, and g) seedbank type. Bar plots illustrate species proportion in each category with adjacent
299 percentages. E.g., 68% (or 92 species) of non-native garden escapees exhibit local non-specific dispersal. Totals
300 may exceed 100% for seed structures due to multiple structures per species.

301

302 Discussion

303 Given gardens' established role in dispersing non-native species (Reichard & White, 2001;
304 Van Kleunen et al., 2018), I investigated if endangered native plants could similarly benefit.
305 My analysis of multiple dispersal traits, including seed weight, terminal velocity, dispersal
306 distance, germination rate, dispersal mode, seed structures, and seedbank type, revealed only
307 subtle but in a few cases statistically clear differences. Endangered plants, both as a whole
308 and those suitable for conservation gardening, were more often wind-dispersed and featured
309 seed appendages that should enable them to harness a wider range of dispersal vectors. In
310 contrast, non-native plants and garden escapees leaned more towards non-assisted local
311 dispersal. Non-native plants further carried slightly heavier seeds and maintained a more
312 persistent seed bank, which may aid in establishment, although germination rates were similar
313 across groups. These findings indicate that, when viewed through the lens of dispersal
314 ecology, green corridors, comprising gardens and other green spaces, have the potential to
315 offer endangered native plants no lesser dispersal pathway as they currently do for non-native
316 species.

317

318 This study suggests that endangered native plants tend to produce lighter seeds with reduced
319 fall velocities, leading to marginally increased dispersal distances than non-native species
320 (Fig. 2a-c and Fig. 3a-c). The more frequent presence of appendages should further help
321 endangered plants to better capitalize on wind (via flat or elongated appendages, such as
322 wings or pappuses), water (via balloon structures) or animal-mediated (via nutrient containing
323 and elongated appendages, such as arils or hooks) primary and secondary dispersal than
324 non-native plants (Fig. 2f and Fig. 3f). The higher rate of wind-dispersed species (Fig. 2d and
325 Fig. 3d) may be particularly beneficial in urban to rural green space contexts, fostering an
326 increased likelihood of establishing in novel urban habitats (Planchuelo, Kowarik, & Von der
327 Lippe, 2020). Intriguingly, few native plants predominantly rely on animal dispersal (Fig. 2d
328 and Fig. 3d). Only 5% of all endangered plants use endozoochory, where this may in fact be
329 a notably effective mode in wildlife-friendly green spaces that are often teeming with animal
330 dispersers (Hansen et al., 2020; Lerman et al., 2021). Nonetheless, more endangered species
331 amenable to gardening may benefit from endozoochory compared to non-native escapee
332 plants (Fig. 3e). Endangered plants' more transient seed banks (Fig. 2g and Fig. 3g) could
333 imply a higher risk of reproductive failure in unpredictable, and especially early-successional

environments, as are prevalent in human dominated landscapes (Larson & Funk, 2016; Gioria et al., 2021). But this trait is also common in non-native plants (64%) and garden escapees (72%), making it unlikely that this alone would facilitate much greater dispersal success. While germination rates are comparable, it does not predict field emergence (Hitchmough, 2017), for which no data were analyzed. Nonetheless, these dispersal traits suggest that the average native plant, endangered or not, possesses a dispersal ability not too different from non-native species.

341

Might these subtle differences between increasing (non-native; Eichenberg et al., 2021) species with declining (endangered) ones indicate that dispersal is not a primary factor in these differing population trends? The answer is more complex. Over centuries, the central European landscape and its dispersal processes have undergone profound changes, reviewed for example by Poschlod & Bonn, 1998. Given that many plants can utilize epizoochory (Poschlod & Bonn, 1998; Couvreur et al., 2004), seed dispersal by animals is a key pathway that has undergone tremendous changes. Livestock management in central Europe largely shifted from transhumance or local herding to stable or paddock systems (Hornberger, 1959; Erdmann, 1983). Additionally, the number of livestock decreased, for example, sheep numbers in Germany plummeted from 25 million in 1870 to 5 million by 1907 (Lahrkamp, 1928). Since these herbivores inhabited and linked grasslands, some authors posit that this disruption in meta-communities could be responsible for the decline in grassland species (Krauss, 1977; Ruxton & Schaefer, 2012) (many of which are in fact endangered; Staude et al., 2023). Recent research suggests that many plant species may struggle to adapt to their shifting climate niches, potentially risking extinction, as a result of defaunation (Fricke et al., 2022). Hence it is important to understand how dispersal processes are changing and that the conservation of endangered species necessitates a holistic perspective on past and present dispersal mechanisms (Ruxton & Schaefer, 2012).

360

Although some of the key original dispersal processes are no longer in place, there are new ones that are simulating or replacing them (Poschlod & Bonn, 1998; Auffret, 2011; Bullock et al., 2018). 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 natural landscapes like semi-natural grasslands. Consequently, we tend to disperse species that thrive in these human-modified habitats (Kalusová et al., 2017; Segar et al., 2022). Given our tendency to enhance habitat fertility, coupled with frequent disturbances, means we favor the dispersal of fast-growing, nitrophilous species (Hodkinson & Thompson, 1997; Auffret & Cousins, 2013). This includes many ornamental plants favored in our gardens

371 (Van Kleunen et al., 2018). Together this creates a dispersal bias. To leverage the dispersal
372 avenues in an anthropocentric landscape for biodiversity conservation, we must integrate
373 endangered species into our urban and rural matrix, so that we start dispersing these species
374 as well (Segar et al., 2022). Studies show, for example, that endangered species, such as
375 orchids can thrive along roadsides, and in the neo-habitats humans create (Fekete et al., 2017;
376 Rewicz et al., 2017; Fekete et al., 2020). Our analysis indicates that, based on dispersal
377 ecological differences alone, there is no inherent reason why endangered species should not
378 benefit from this type of dispersal.

379

380 Clearly this study does not provide direct and definitive evidence that green corridors aid
381 endangered plants. Experiments are necessary to understand these dynamics, where genetic
382 studies could illuminate the extent to which green corridors, such as urban and rural green
383 spaces, facilitate gene flow among fragmented populations (Plue et al., 2022). Furthermore,
384 databases are necessary that track the field emergence of endangered species, which will
385 also be vital for conservation gardening and the design of seed mixtures. While there is
386 evidence suggesting humans spread endangered species, research often primarily
387 concentrates on non-native species (Auffret & Cousins, 2013). To harness human-mediated
388 dispersal for biodiversity conservation, we need to gain a better understanding of how humans
389 disperse endangered plants. This includes, for example, testing which and how many of these
390 species are dispersed via footwear or clothing when they are cultivated in gardens.
391 Furthermore, understanding where these plants successfully establish is vital. Identifying new
392 rural and urban habitats that are conducive, and determining ways to aid this establishment
393 process, is critical (Planchuelo, Kowarik, & von der Lippe, 2020; Planchuelo, Kowarik, & Von
394 der Lippe, 2020). Numerous questions about the effectiveness of green corridors for
395 endangered plants remain. However, this study suggests that associating endangered species
396 with our green spaces, as advocated by conservation gardening, could enhance at least one
397 critical process underlying the population persistence of declining native species: dispersal.

398 **Acknowledgements:** I am grateful to the Oak Spring Garden Foundation for both the inspiring
399 research environment and the financial support that enabled the completion of this study.

400 **References**

- 401 Auffret, A. G. (2011). Can seed dispersal by human activity play a useful role for the
402 conservation of European grasslands? *Applied Vegetation Science*, 14(3), 291–303.
- 403 Auffret, A. G., & Cousins, S. A. O. (2013). Humans as Long-Distance Dispersers of Rural
404 Plant Communities. *PLOS ONE*, 8(5), e62763.
405 <https://doi.org/10.1371/journal.pone.0062763>
- 406 Auffret, A. G., Rico, Y., Bullock, J. M., Hooftman, D. A. P., Pakeman, R. J., Soons, M. B.,
407 Suarez-Esteban, A., Traveset, A., Wagner, H. H., & Cousins, S. A. O. (2017). Plant
408 functional connectivity—Integrating landscape structure and effective dispersal.

- 464 Hitchmough, J. (2017). *Sowing beauty: Designing flowering meadows from seed*. Timber
465 Press.
466 <https://books.google.com/books?hl=en&lr=&id=pARbDgAAQBAJ&oi=fnd&pg=PP1&d>
467 q=sowing+beauty&ots=cwwJMNvci&sig=Ure8n60Wxh4oTYelpAkfkOUgufA
468 Hobbs, R. J. (1992). The role of corridors in conservation: Solution or bandwagon? *Trends in*
469 *Ecology & Evolution*, 7(11), 389–392.
470 Hodkinson, D. J., & Thompson, K. (1997). Plant dispersal: The role of man. *Journal of*
471 *Applied Ecology*, 1484–1496.
472 Holz, H., Segar, J., Valdez, J., & Staude, I. R. (2022). Assessing extinction risk across the
473 geographic ranges of plant species in Europe. *PLANTS, PEOPLE, PLANET*, 4(3),
474 303–311. <https://doi.org/10.1002/ppp3.10251>
475 Hornberger, T. (1959). *Die kulturgeographische Bedeutung der Wanderschäferei in*
476 *Süddeutschland: Süddeutsche Transhumanz*. Selbst-verlag der Bundesanstalt für
477 Landeskunde. <https://library.wur.nl/WebQuery/titel/399708>
478 Jäger, E. J., Ebel, F., Hanelt, P., & Müller, G. K. (2016). *Rothmaler—Exkursionsflora von*
479 *Deutschland: Krautige Zier- und Nutzpflanzen* (1. Aufl.). Springer Spektrum Berlin.
480 <https://doi.org/10.1007/978-3-662-50420-8>
481 Jakobsson, A., & Eriksson, O. (2003). Trade-offs between dispersal and competitive ability:
482 A comparative study of wind-dispersed Asteraceae forbs. *Evolutionary Ecology*,
483 17(3), 233–246. <https://doi.org/10.1023/A:1025526903281>
484 Jongejans, E., & Telenius, A. (2001). Field experiments on seed dispersal by wind in ten
485 umbelliferous species (Apiaceae). *Plant Ecology*, 152(1), 67–78.
486 <https://doi.org/10.1023/A:1011467604469>
487 Kalusová, V., Chytrý, M., van Kleunen, M., Mucina, L., Dawson, W., Essl, F., Kreft, H., Pergl,
488 J., Weigelt, P., Winter, M., & Pyšek, P. (2017). Naturalization of European plants on
489 other continents: The role of donor habitats. *Proceedings of the National Academy of*
490 *Sciences*, 114(52), 13756–13761. <https://doi.org/10.1073/pnas.1705487114>
491 Kattge, J., Böniisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S.,
492 Werner, G. D., Aakala, T., & Abedi, M. (2020). TRY plant trait database—enhanced
493 coverage and open access. *Global change biology*, 26(1), 119–188.
494 Kirchner, F., Ferdy, J., Andalo, C., Colas, B., & Moret, J. (2003). Role of Corridors in Plant
495 Dispersal: An Example with the Endangered *Ranunculus nodiflorus*. *Conservation*
496 *Biology*, 17(2), 401–410.
497 Kleyer, M., Bekker, R., Knevel, I., Bakker, J., Thompson, K., Sonnenschein, M., Poschlod,
498 P., Van Groenendaal, J., Klimeš, L., & Klimešová, J. (2008). The LEDA Traitbase: A
499 database of life-history traits of the Northwest European flora. *Journal of ecology*,
500 96(6), 1266–1274.
501 Krauss, G. (1977). *Über den Rückgang der Ruderalpflanzen, dargestellt an Chenopodium*
502 *bonus-henricus L. im alten Landkreis Göttingen*. [https://pascal-](https://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=PASCAL7810351626)
503 [francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=PASCAL7810351626](https://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=PASCAL7810351626)
504 Lahrkamp, W. (1928). *Die westdeutsche Wanderschäferei und ihre Standortsbedingungen*.
505 Schenk.
506 Larson, J. E., & Funk, J. L. (2016). Regeneration: An overlooked aspect of trait-based plant
507 community assembly models. *Journal of Ecology*, 104(5), 1284–1298.
508 <https://doi.org/10.1111/1365-2745.12613>
509 Leibold, M. A., & Chase, J. M. (2017). Metacommunity Ecology, Volume 59. In
510 *Metacommunity Ecology, Volume 59*. Princeton University Press.
511 <https://doi.org/10.1515/9781400889068>
512 Lenth, R. V., Buerkner, P., Herve, M., Love, J., Riebl, H., & Singmann, H. (2020). emmeans:
513 Estimated marginal means, aka least-squares means, v1. 5.1. Vienna: R Core Team.
514 Lepczyk, C. A., Aronson, M. F., & La Sorte, F. A. (2023). Cities as sanctuaries. *Frontiers in*
515 *Ecology and the Environment*, 21(5), 251–259. <https://doi.org/10.1002/fee.2637>
516 Lerman, S. B., Narango, D. L., Avolio, M. L., Bratt, A. R., Engebretson, J. M., Groffman, P.
517 M., Hall, S. J., Heffernan, J. B., Hobbie, S. E., Larson, K. L., Locke, D. H., Neill, C.,
518 Nelson, K. C., Padullés Cubino, J., & Trammell, T. L. E. (2021). Residential yard

- 519 management and landscape cover affect urban bird community diversity across the
520 continental USA. *Ecological Applications*, 31(8), e02455.
521 <https://doi.org/10.1002/eap.2455>
- 522 Lippe, M. von der, Bullock, J. M., Kowarik, I., Knopp, T., & Wichmann, M. (2013). Human-
523 Mediated Dispersal of Seeds by the Airflow of Vehicles. *PLOS ONE*, 8(1), e52733.
524 <https://doi.org/10.1371/journal.pone.0052733>
- 525 Lippe, M. von der, & Kowarik, I. (2008). Do cities export biodiversity? Traffic as dispersal
526 vector across urban–rural gradients. *Diversity and Distributions*, 14(1), 18–25.
- 527 Lososová, Z., Axmanová, I., Chytrý, M., Midolo, G., Abdulhak, S., Karger, D. N., Renaud, J.,
528 Van Es, J., Vittoz, P., & Thuiller, W. (2023). Seed dispersal distance classes and
529 dispersal modes for the European flora. *Global Ecology and Biogeography*.
- 530 Maclagan, S. J., Coates, T., & Ritchie, E. G. (2018). Don't judge habitat on its novelty:
531 Assessing the value of novel habitats for an endangered mammal in a peri-urban
532 landscape. *Biological Conservation*, 223, 11–18.
533 <https://doi.org/10.1016/j.biocon.2018.04.022>
- 534 Metzing, D., Garve, E., Matzke-Hajek, G., Adler, J., Bleeker, W., Breunig, T., Caspari, S.,
535 Dunkel, F., Fritsch, R., & Gottschlich, G. (2018). Rote Liste und Gesamtartenliste der
536 Farn-und Blütenpflanzen (Tracheophyta) Deutschlands. *Naturschutz und
537 Biologische Vielfalt*, 70(7), 13–358.
- 538 Moles, A. T., & Westoby, M. (2004). Seedling survival and seed size: A synthesis of the
539 literature: *Seedling survival and seed size*. *Journal of Ecology*, 92(3), 372–383.
540 <https://doi.org/10.1111/j.0022-0477.2004.00884.x>
- 541 Munschek, M., Witt, R., Kaltofen, K., Segar, J., Wirth, C., Weigelt, A., Engelmann, R. A., &
542 Staude, I. R. (2023). Putting conservation gardening into practice. *Scientific Reports*,
543 13(1), 12671. <https://doi.org/10.1038/s41598-023-39432-8>
- 544 Ozinga, W. A., Römermann, C., Bekker, R. M., Prinzing, A., Tamis, W. L., Schaminée, J. H.,
545 Hennekens, S. M., Thompson, K., Poschlod, P., & Kleyer, M. (2009). Dispersal
546 failure contributes to plant losses in NW Europe. *Ecology letters*, 12(1), 66–74.
- 547 Planchuelo, G., Kowarik, I., & Von der Lippe, M. (2020). Endangered plants in novel urban
548 ecosystems are filtered by strategy type and dispersal syndrome, not by spatial
549 dependence on natural remnants. *Frontiers in Ecology and Evolution*, 8, 18.
- 550 Planchuelo, G., Kowarik, I., & von der Lippe, M. (2020). Plant traits, biotopes and
551 urbanization dynamics explain the survival of endangered urban plant populations.
552 *Journal of Applied Ecology*, 57(8), 1581–1592.
- 553 Plue, J., Kimberley, A., Bullock, J. M., Hellemans, B., Hooftman, D. A., Krickl, P., Leus, L.,
554 Peeters, G., Poschlod, P., & Traveset, A. (2022). Green infrastructure can promote
555 plant functional connectivity in a grassland species around fragmented semi-natural
556 grasslands in NW-Europe. *Ecography*, 2022(10), e06290.
- 557 Poschlod, P., & Bonn, S. (1998). Changing dispersal processes in the central European
558 landscape since the last ice age: An explanation for the actual decrease of plant
559 species richness in different habitats? *Acta Botanica Neerlandica*, 47(1), 27–44.
- 560 Reed, J. M., Mills, L. S., Dunning Jr, J. B., Menges, E. S., McKelvey, K. S., Frye, R.,
561 Beissinger, S. R., Anstett, M., & Miller, P. (2002). Emerging issues in population
562 viability analysis. *Conservation biology*, 16(1), 7–19.
- 563 Reichard, S. H., & White, P. (2001). Horticulture as a pathway of invasive plant introductions
564 in the United States: Most invasive plants have been introduced for horticultural use
565 by nurseries, botanical gardens, and individuals. *BioScience*, 51(2), 103–113.
- 566 Rewicz, A., Bomanowska, A., Shevera, M. V., Kurowski, J. K., Krasoń, K., & Zielińska, K. M.
567 (2017). Cities and Disturbed Areas as Man-made Shelters for Orchid Communities.
568 *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*, 45(1), Article 1.
569 <https://doi.org/10.15835/nbha45110519>
- 570 Ridley, H. (1930). The Dispersal of Plants throughout the World. *The Dispersal of Plants
571 throughout the World*. <https://www.cabdirect.org/cabdirect/abstract/20057003410>
- 572 Rogers, H. S., Beckman, N. G., Hartig, F., Johnson, J. S., Pufal, G., Shea, K., Zurell, D.,
573 Bullock, J. M., Cantrell, R. S., & Loiselle, B. (2019). The total dispersal kernel: A

- 574 review and future directions. *AoB Plants*, 11(5), plz042.
- 575 Ruxton, G. D., & Schaefer, H. M. (2012). The conservation physiology of seed dispersal.
576 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1596),
577 1708–1718. <https://doi.org/10.1098/rstb.2012.0001>
- 578 Segar, J., Callaghan, C. T., Ladouceur, E., Meya, J. N., Pereira, H. M., Perino, A., & Staude,
579 I. R. (2022). Urban conservation gardening in the decade of restoration. *Nature
Sustainability*, 5(8), 649–656.
- 580 SER, INSR, RBGK. (2023). *Seed Information Database (SID)* (Version 2023) [dataset].
581 <https://ser-sid.org/>
- 582 Sonkoly, J., Takács, A., Molnár V., A., & Török, P. (2022). Trade of commercial potting
583 substrates: A largely overlooked means of the long-distance dispersal of plants.
584 *Science of The Total Environment*, 825, 154093.
585 <https://doi.org/10.1016/j.scitotenv.2022.154093>
- 586 Staude, I. R. (2023). *Gardens as drivers of native plant dispersal and conservation*.
- 587 Staude, I. R., Segar, J., Temperton, V. M., Andrade, B. O., De Sá Dechoum, M., Weidlich, E.
588 W. A., & Overbeck, G. E. (2023). Prioritize grassland restoration to bend the curve of
589 biodiversity loss. *Restoration Ecology*, 31(5), e13931.
590 <https://doi.org/10.1111/rec.13931>
- 591 Stöcklin, J., & Fischer, M. (1999). Plants with longer-lived seeds have lower local extinction
592 rates in grassland remnants 1950–1985. *Oecologia*, 120, 539–543.
- 593 Tallamy, D. W. (2007). Bringing nature home. *Portland Oregon: Timber Press. Search in.*
594 <https://linnconservancy.org/wp-content/uploads/2020/06/bringing-nature-home.pdf>
- 595 Thompson, P. L., Guzman, L. M., De Meester, L., Horváth, Z., Ptacník, R.,
596 Vanschoenwinkel, B., Viana, D. S., & Chase, J. M. (2020). A process-based
597 metacommunity framework linking local and regional scale community ecology.
598 *Ecology Letters*, 23(9), 1314–1329. <https://doi.org/10.1111/ele.13568>
- 599 Van Helden, B. E., Close, P. G., Stewart, B. A., Speldewinde, P. C., & Comer, S. J. (2020).
600 An underrated habitat: Residential gardens support similar mammal assemblages to
601 urban remnant vegetation. *Biological Conservation*, 250, 108760.
- 602 Van Kleunen, M., Essl, F., Pergl, J., Brundu, G., Carboni, M., Dullinger, S., Early, R.,
603 González-Moreno, P., Groom, Q. J., & Hulme, P. E. (2018). The changing role of
604 ornamental horticulture in alien plant invasions. *Biological Reviews*, 93(3), 1421–
605 1437.
- 606 Vittoz, P., & Engler, R. (2007). Seed dispersal distances: A typology based on dispersal
607 modes and plant traits. *Botanica Helvetica*, 117, 109–124.
- 608 Westoby, M., Leishman, M., & Lord, J. (1997). Comparative ecology of seed size and
609 dispersal. *Philosophical Transactions of the Royal Society of London. Series B:
610 Biological Sciences*, 351(1345), 1309–1318. <https://doi.org/10.1098/rstb.1996.0114>
- 611 Wichmann, M. C., Alexander, M. J., Soons, M. B., Galsworthy, S., Dunne, L., Gould, R.,
612 Fairfax, C., Niggemann, M., Hails, R. S., & Bullock, J. M. (2009). Human-mediated
613 dispersal of seeds over long distances. *Proceedings of the Royal Society B:
614 Biological Sciences*, 276(1656), 523–532. <https://doi.org/10.1098/rspb.2008.1131>
- 615 Young, A. G., & Clarke, G. M. (2000). *Genetics, demography and viability of fragmented
616 populations*. Cambridge University Press.
617 <https://www.cabdirect.org/cabdirect/abstract/20003009555>
- 618
- 619