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1 **Sailing the waves of dispersal: unrevealing the role of sea currents as key dispersal mechanism**
2 **for Mediterranean coastal and inland plant species**

3
4 **Abstract**

5 (1) Thalassochory, the dispersal of propagules through marine currents, is a key long-distance
6 dispersal (LDD) mechanism with implications for global biogeography and particularly for
7 island colonization. The propagules of coastal plant species are generally assumed to be better
8 adapted for sea dispersal than those of inland ones, but this hypothesis remains largely
9 untested.

10 (2) We conducted experiments on four genera (*Juniperus*, *Daucus*, *Ferula*, and *Pancreatium*) and
11 compared the traits among nine species with different habitats and distributions.

12 (3) Our results showed that *Juniperus* spp. and *Pancreatium maritimum* have a strong
13 thalassochorous potential within the Mediterranean Basin. Interestingly, we did not find a
14 clear association on the thalassochorous potential of coastal vs. inland species within the
15 tested *Daucus* and *Ferula* genera, while such association was clear between *P. maritimum* and
16 the endemic inland *P. illyricum*.

17 (4) These findings suggest that thalassochory may be a more common dispersal mechanism than
18 previously assumed. The apparently weak link between dispersal syndrome with species
19 ecology broadens the possibility of dispersal by the sea also for inland plants, although
20 considered to be poorly salt-tolerant. Moreover, our results reveal significant differences in
21 sea dispersal between endemic and widespread species, suggesting an important role of
22 thalassochory in shaping the distribution patterns of the Mediterranean flora. The presented
23 method is largely replicable and could be used for further studies with a larger set of species
24 to better delineate trends of sea dispersal syndrome along species with different ecology or
25 dispersal traits.

26
27 **Keywords**

28 diaspore buoyancy, island colonization, long-distance dispersal, seed viability, *Juniperus*, *Daucus*,
29 *Ferula*, *Pancreatium*, Sardinia.

30 **Introduction**

31 Understanding the mechanisms behind the establishment of plant communities is a significant topic
32 of research in plant ecology. In plants, adults are usually sessile, and dispersal is the primary means
33 of habitat selection that typically occurs as vector-mediated transport of propagules (i.e., fruits, seeds,
34 or vegetative units) (Bazzaz 1991; Clobert *et al.* 2012). Although species composition at regional
35 scale is primarily determined by environmental conditions, at global scale plant assemblages are
36 largely determined by dispersal processes (Ozinga *et al.* 2005). Dispersal is the movement of
37 individuals from their place of origin to another location where they might establish and reproduce
38 (Bullock *et al.* 2002; Nathan *et al.* 2008). The morphological structure of a propagule is often
39 indicative of its most likely dispersal vector (Clobert *et al.* 2012), however propagules can often be
40 dispersed by non-standard vectors (i.e., other than those predicted by their traits) (Heleno & Vargas
41 2015). For instance, not all winged propagules will be dispersed by wind (Tackenberg *et al.* 2003), or
42 not all fleshy fruits will be dispersed by vertebrates (Hampe 2004). In most plant species, propagules
43 are dispersed over relatively short distances from the source, rarely exceeding a few dozen meters
44 (Jordano *et al.* 2007). Among all dispersal vectors, only those that can promote long-distance dispersal
45 (LDD) events, namely: wind (anemochorous), sea currents (thalassochorous), and animals, either
46 internally (endozoochorous) or externally (epizoochorous), can explain the colonization of islands
47 (Nathan 2006; Heleno & Vargas 2015; Fuster-Calvo *et al.* 2021). LDD also play a critical role in
48 determining population spread, metacommunity dynamics, and regional plant persistence of fugitive
49 plant species (Hubbell 2001; Arjonna *et al.* 2018).

50 Thalassochory (from the Greek *thalassa* meaning ‘the sea’ and *khōrein* ‘to spread’) is a key LDD
51 mechanism for the colonization of coastal territories by plants, especially islands (Arjonna *et al.*
52 2018). Long-distance dispersal across the sea surface is considered a rare event but one whose reality
53 is abundantly documented for oceanic islands (e.g., Carlquist 1974; Vargas *et al.* 2015). For example,
54 Higgins *et al.* (2003) demonstrated that most of plant *taxa* arrived by sea currents at the islands
55 (Tvärminne archipelago, Finland), although only one quarter of those *taxa* were morphologically
56 adapted for water dispersal. Another example with similar results was in the volcanic island Surtsey
57 (35 km from Iceland), where all plant species colonizing in the first decade after its emergence, 78%
58 were recorded as arriving by ocean currents, although only 25% had apparent morphological
59 adaptations for dispersal by water (Nogales *et al.* 2012). Darwin (1859), Godman (1870), Guppy
60 (1906) and successive researchers support for the importance of oceanic drift for island colonization;
61 only recently, thalassochory has been used to explain phylogenetic or phylogeographical patterns in
62 the Mediterranean Basin (Kadereit *et al.* 2005). For instance, it has been used to explain hybridization

63 and gene flow events that determine the complex phylogeographic patterns of *Beta* and *Patellifolia*
64 genera in Western Mediterranean and Macaronesia (Romeiras *et al.* 2016) and of *Convolvulus*
65 *soldanella* L. throughout Mediterranean and Atlantic coasts (Arafeh & Kadereit 2006). Other striking
66 examples illustrating the importance of marine currents in acting both as a means of dispersal and as
67 a barrier to the distribution and evolution of Mediterranean coastal flora were reported to explain the
68 phylogeography of *Cakile maritima* Scop., *Eryngium maritimum* L., *Halimione portulacoides* (L.)
69 Aellen., *Crithmum maritimum* L. (Kadereit *et al.* 2005) or, more recently, for *Pancratium maritimum*
70 L. (De Castro *et al.* 2020). Although dispersed over a shorter distance, thalassochory was suggested
71 for the colonisation of the endemic *Anchusa crispa* Viv. and *Ferula arrigonii* Bocchieri from Corsica
72 to Sardinia (Mansion *et al.* 2009; Dettori *et al.* 2014). Nonetheless, thalassochory has rarely been well
73 established experimentally, perhaps because of the difficulty of establishing it, compared to other
74 dispersal mechanisms that are more easily attributable to different plant traits, such as endozochory
75 (e.g., pulp), epizoochory (e.g., hooks, glue) or anemochory (e.g., hairs, wings). Consequently, the few
76 papers that tried to estimate thalassochorous potential for large floras (e.g., Heleno & Vargas 2015)
77 have usually relied on indirect evidence based on habitat (e.g., often assuming that coastal plants are
78 thalassochorous, even when no data is available). Indeed, as anemochory in sparsely vegetated
79 grasslands, epizoochory in open communities, and bird endozochory in forests and shrub
80 communities, it makes sense to assume that thalassochorous traits might be more common in
81 communities growing close to the sea (Heleno & Vargas 2015). Coastal plants, and especially those
82 living in islands, provide ideal opportunities for studying sea dispersal and the effectiveness of
83 thalassochorous traits as all plants need to overcome the biogeographic barrier imposed by the sea,
84 which might be facilitated by specific propagule adaptations (Kadereit *et al.* 2005; Gandour *et al.*
85 2008; Westberg & Kadereit 2009), such as propagules' buoyancy and salt tolerance, to account for
86 colonization success (Arjonna *et al.* 2018; De Castro *et al.* 2020; Cortés-Fernández *et al.* 2022).
87 Nonetheless, many coastal species, as most of those belonging to the genus *Limonium* and to the
88 *Silene mollissima* aggregate, are hardly considered to be thalassochorous according to their narrow
89 distribution, despite their ability to survive and germinate under high salt concentrations (Murru *et*
90 *al.* 2015; Koutroumpa *et al.* 2021). Furthermore, the inability of inland species to be dispersed by the
91 sea have been often hypothesized but never systematically tested.

92 In order to evaluate the differential capacity of coastal and inland plants to be dispersed by sea
93 currents, we experimentally measured (i) propagule buoyancy, (ii) viability after the saltwater
94 immersion, and (iii) the estimated sea dispersal potential (SDP) of four native Mediterranean genera:
95 *Juniperus*, *Daucus*, *Ferula* and *Pancratium*. We compared such information among *taxa* from

96 Sardinia with different habitat and distribution to test the following hypotheses: (i) coastal species
97 have a greater sea dispersal potential than inland relatives, (ii) widely distributed plants have a higher
98 sea dispersal potential than plants with narrower distribution, (iii) thalassochorous traits can be
99 suggested by the type of dispersal units and/or are highly conserved along the plan phylogenetic tree.
100
101

102 **Materials and methods**

103

104 *Study species*

105 To test these hypotheses, we evaluated the sea dispersal potential of nine species from four genera.
106 These species were chosen based on the presence of different diaspore traits (i.e., species with clear
107 hydrochorous dispersal units, such as large and light seeds, or less clearly hydrochorous ones, such
108 as fleshy and dry diaspores; Figure 1), habitat range (i.e. including species with strictly coastal or
109 inland distributions and others with broad habitat requirements), and distribution ranges, from
110 endemics to wide distribution ranges (Table 1). All diaspores were collected from the mother plants
111 during the releasing time from at least 25 individuals randomly selected from the entire population.
112 Diaspores were selected by removing visually damaged ones and stored until the start of the
113 experiments at room temperature (ca. 20°C and 40% RH). The nine focal species belong to four
114 genera: *Juniperus*, *Daucus*, *Ferula*, and *Pancratium*.

115 Within the genus *Juniperus* (Cupressaceae), all species have fleshy cones which are functionally
116 equivalent to the fruits of angiosperms (Herrera 1992) and highly attractive to vertebrate dispersers
117 (endozoochory) (e.g., García 2001; Nogales *et al.* 1999; Farris *et al.* 2017). The selected *Juniperus*
118 were: (i) *J. macrocarpa* Sm. which has its optimum on coastal dunes, palaeodunes and stream beds
119 of the entire Mediterranean Basin, also reaching the coasts of the Black Sea (Farjon 2005); (ii) *J.*
120 *turbinata* Guss., with a distributional range limited to the western Mediterranean Basin (Mazur *et al.*
121 2016), mainly found on the coast both in dunes and rocky habitats becoming rarer inland (Arrigoni
122 2006); and (iii) *J. oxycedrus* L., widely distributed throughout the Mediterranean region (Cano-Ortiz
123 *et al.* 2021) across a wide range of altitudes becoming rarer at the cost (Rupprecht *et al.* 2011).

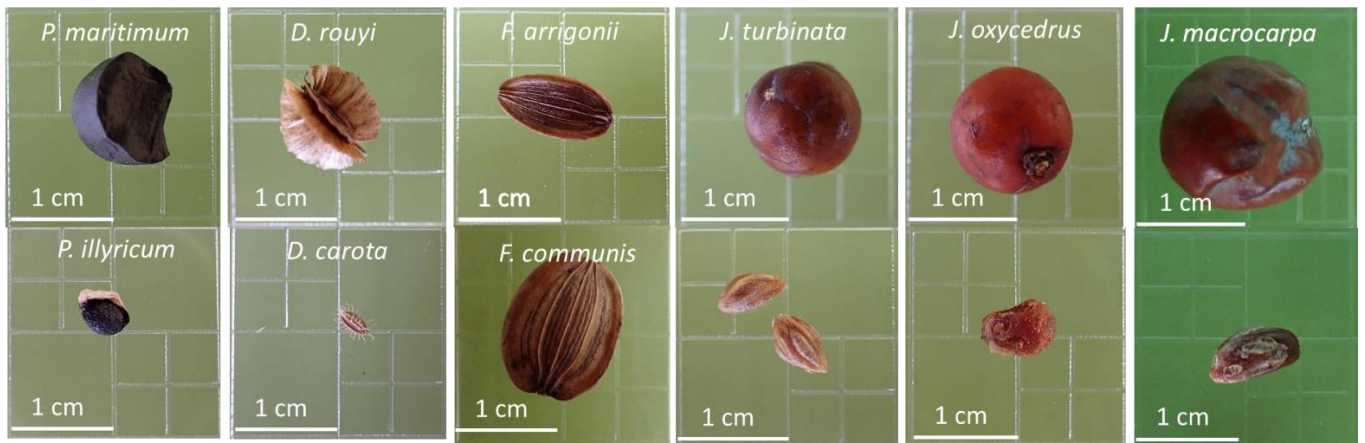
124 Within the genus *Daucus* (Apiaceae) we selected two species: *D. carota* L. subsp. *carota* and *D. rouyi*
125 Spalik & Reduron). The genus is widely distributed worldwide, but with a concentration of diversity
126 in the Mediterranean biogeographic region (Spooner 2019). The former, has hooked indehiscent fruits
127 - diachenes - well adapted to the external adhesion to the fur and feather of animal dispersers
128 (epizoochory) and is globally distributed in inland environments (Banasiak *et al.* 2016). The later, *D.*

129 *rouyi* occurs mostly in littoral psammophilous habitats poor in carbonate of the southwest
130 Mediterranean costs and islands (Corsica, Sardinia), and has winged seeds well adapted to wind
131 dispersal (anemochory) (Santo *et al.* 2014; Fois *et al.* 2022).

132 The genus *Ferula* (Apiaceae) has a wide distribution across Eurasia and Northern Africa. Within this
133 genus we selected *F. communis* L. subsp. *communis*, a circum-Mediterranean species most common
134 inland, and *F. arrigonii* is a coastal species endemic to Sardinia and Corsica (Dettori *et al.*, 2016;
135 Orsenigo *et al.* 2016). The dispersal units of both species are flat and winged diachenes, so likely
136 adapted to wind-dispersal (Figure 1).

137 Finally, within the genus *Pancratium* (Amaryllidaceae), present in Asia, Africa and Europe (De
138 Castro *et al.* 2012), we selected *P. illyricum* L. and *P. maritimum*. *Pancratium illyricum* grows on
139 shady or sunny rocky places from sea level to the mountains in Corsica, Sardinia and Tuscan
140 archipelago (Carta *et al.* 2018; Fois *et al.* 2022). Although mentioned as thalassochorous by Vargas
141 *et al.* (2023), the presence of elaiosomes on their seeds can also suggest a dispersion by ants
142 (myrmecochory). *Pancratium maritimum* is widely distributed along the coastal sands of the
143 Mediterranean Basin (Sanaa *et al.* 2015; 2016; De Castro *et al.* 2016), and its seeds may stay afloat
144 in the sea and be dispersed by the waves (Grassi *et al.* 2005). Among the selected species is the only
145 clearly adapted to thalassochory (Werker & Fahn 1975; De Castro *et al.* 2020).

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149 **Figure 1.** Dispersal units' images of the studied species. See details for each *taxon* in Table 1.

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151

152 **Table 1.** Information of selected species. Dispersal units were collected in Sardinia (municipalities
153 reported) in 2022. Taxonomy follows the World Checklist of Vascular Plants 2023
154 (<https://powo.science.kew.org/>). Acronyms reported for endemics are for: Sardinia (SA), Corsica
155 (CO), Tunisia (TN), Algeria (AG).

| Species/subsp. | Family | Distribution | Dispersal syndrome | Habitat | Dispersal units | Collection site | Collection date |
|--|----------------|--------------------|--------------------|-----------------|-----------------|-----------------|-----------------|
| <i>Daucus carota</i> L. subsp. <i>carota</i> | Apiaceae | Subcosmop. | Epizoochorous | Coastal /inland | Diachene | Capoterra | 16/06/2022 |
| <i>Daucus rouyi</i> Spalik & Reduron | Apiaceae | Endem. SA-CO-AG-TN | Anemochorous | Coastal | Diachene | Arbatax | 17/09/2022 |
| <i>Ferula communis</i> L. subsp. <i>communis</i> | Apiaceae | Circum-Medit. | Anemochorous | Coastal /inland | Diachene | La Maddalena | 13/06/2022 |
| <i>Ferula arrigonii</i> Bocchieri | Apiaceae | Endem. SA-CO | Anemochorous | Coastal | Diachene | Buggerru | 15/07/2022 |
| <i>Juniperus macrocarpa</i> Sm. | Cupressaceae | Euri-Medit. | Endozoochorous | Coastal | Fleshy cone | Arbus | 27/02/2022 |
| <i>Juniperus oxycedrus</i> L. | Cupressaceae | Euri-Medit. | Endozoochorous | Coastal /inland | Fleshy cone | Burcei | 12/11/2022 |
| <i>Juniperus turbinata</i> Guss. | Cupressaceae | W-Medit. | Endozoochorous | Coastal /inland | Fleshy cone | Cuglieri | 21/02/2022 |
| <i>Pancreatium maritimum</i> L. | Amaryllidaceae | Circum-Medit. | Thalassochorous | Coastal | Seed | Sarroch | 14/02/2022 |
| <i>Pancreatium illyricum</i> L. | Amaryllidaceae | Endem. SA-CO-AT | Myrmecochorous | Coastal /inland | Seed | Villasalto | 28/08/2022 |

156

157

158 ***Buoyancy experiments***

159 Since buoyancy is very important for seed dispersion by marine currents (Guja *et al.* 2010), we tested
160 diaspores buoyancy in saltwater by placing 150-200 freshly fruits of each species (depending on
161 dispersal units' availability) in 30 × 20 × 10 cm plastic containers with sea water (taken from the
162 Mediterranean Sea) and recording the number of floating units every week, until no seeds remained
163 floating (the maximum duration was eleven weeks). Sunken seeds were carefully removed with
164 tweezers. Water was replaced weekly to maintain oxygenation and avoiding eutrophication (Esteves
165 *et al.* 2015). Each week of the experiment, the number of floating diaspores was recorded and their
166 germination and viability tested (see below).

167

168 ***Seed viability and Sea Dispersal Potential index (SDPi)***

169 In order to assess seed viability after immersion in saltwater, we performed germination tests for two
170 months after which we cut ungerminated seeds to look for healthy (i.e., dormant) embryos. Each
171 week, ten floating units were selected to conduct germination tests. Before the tests, if necessary,
172 seeds were released from their fruits and washed with deionized water. Germination tests were carried
173 out in Petri dishes with a surface of 1% agar water and placed in a germination chamber at 25/10 °C
174 under 12/12 h day/night photoperiods for all species tested. The germination was recorded twice a
175 week for two months, after which ungerminated were cut to determine the presence of a vital embryo

176 (Bacchetta *et al.* 2008; ISTA 2021). Seeds were considered viable if they germinated, or if a vital
177 embryo was found after two months. Germination potential of seeds not exposed to sea water, was
178 also determined by directly incubating collected seeds following the same protocols. Finally, we
179 calculated the Sea Dispersal Potential index (SDPi, Fuster-Calvo *et al.* 2021) by combining the
180 percentage of floating diaspores (% floating) and viable embryos (% viability) for each flotation time
181 (t). The index corresponds to the percentage of floating and viable seeds at a given flotation time and
182 ranges from 0% to 100%.

183 We calculated the correlation matrix to examine the relationships between the buoyancy, seed
184 viability, SDPi in our dataset. For the correlation analysis, we used the 'cor' function to compute the
185 Pearson's correlation coefficients. The potential differences in buoyancy, seed viability, and SPDi
186 based on their distribution, habitats, dispersal syndromes, and units were tested by ANOVA followed
187 by post-hoc Tukey's HSD test. These tests allowed to identify specific group differences and to
188 determine which groups significantly differed from each other. Percentage values for buoyancy
189 capacity and seed viability were arcsine-transformed before the one-way ANOVA to meet the test
190 assumptions. A significance level of 0.05 was used for all statistical analyses. All statistical
191 calculations and analyses were performed using R (R Core Team 2020).

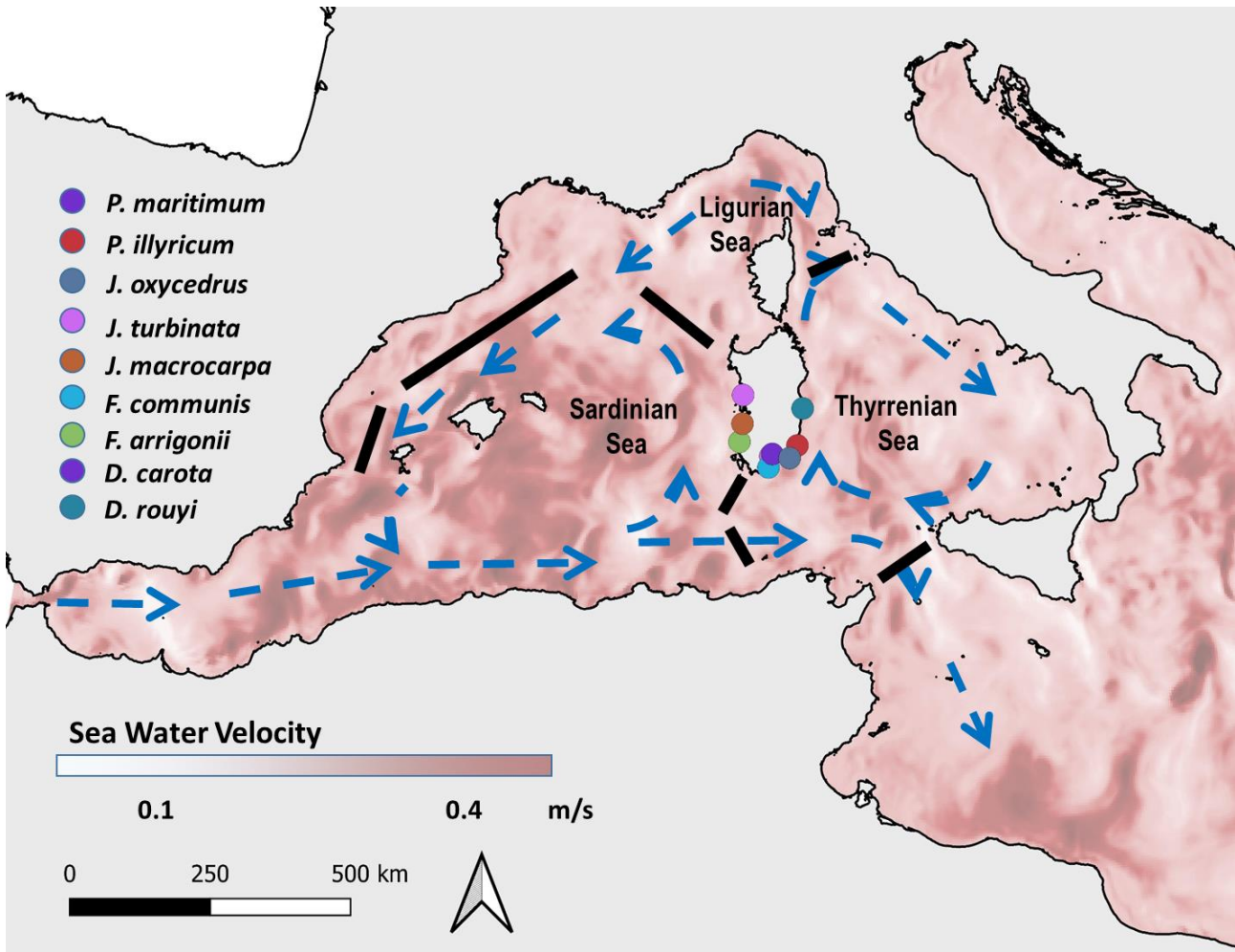
192

193 ***Sea currents and estimation of long-distance dispersal capacity***

194 To estimate the maximum distance that the dispersal units can reach through the marine currents, we
195 used the average velocity of 0.1 m/s (= ca. 60 km/week) following the hydrodynamic model, supplied
196 by the Nucleous for European Modelling of the Ocean (NEMO) and the variational data assimilation
197 scheme (OceanVAR) for temperature and salinity vertical profiles data (Escudier *et al.* 2020) (see
198 Figure 2). To date, as in the recent past, the surface main water circulation of the Mediterranean
199 follows mainly cyclonic (anti-clockwise) patterns shown on Fig. 2 (El-Geziry & Bryden 2010). These
200 marine currents determine the main regional biogeographic regions for marine organisms (Perret *et*
201 *al.* 2023), and also several genetic barriers for thalassochorous plants. For example, for *P. maritimum*,
202 De Castro *et al.* (2020) detected four main barriers that determine genetic breaks between
203 thalassochorous species from the Iberian Peninsula, due to the barrier along Balearic Islands, and a
204 split between western and eastern Mediterranean, due to the barriers at the Sardinian, Corsican and
205 Sicilian straits that split the western Mediterranean into the Ligurian, Sardinian and Tyrrhenian seas.
206 We included all this information to the viable buoyancy period and subsequent SDPi to estimate how
207 far and where each species can be dispersed by sea currents and colonise other territories. The
208 estimation was made from each collection site or, for inland collections, from the nearest coast of the

209 drainage basin, assuming that inland species can also reach the coast through other means such as
210 rivers, wind, or simple gravity.

211



212

213 **Figure 2.** Hydrodynamic models for the Mediterranean Sea extracted from Sea Water velocity of
214 Escudier et al. (2020) and main sea currents from De Castro et al. (2020). Black lines delimit main
215 genetic barriers detected by De Castro et al. (2020). Dots indicate the collection sites of the nine
216 selected species.

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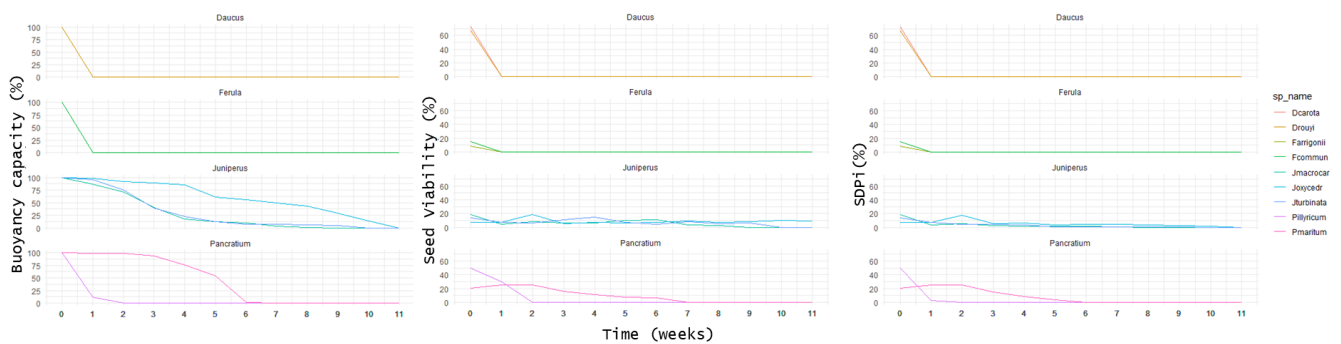
219 Results

220

221 *Buoyancy experiments, seed viability and SDPi*

222 Among the three investigated responses, seed buoyancy, viability, and seed dispersal potential (SDPi),
223 only seed buoyancy was significantly affected by all the considered factors, with the exception of
224 Habitat (Table 2, Supporting Information - Table S1). However, our analysis revealed a significant
225 relationship between buoyancy capacity and seed viability ($r = 0.65$, Supporting Information - Figure

226 S1) and, consequently, with SDPi ($r = 0.67$, Supporting Information - Figure S1). Specifically, SDPi
 227 decreased along with buoyancy in most of cases (*Ferula* and *Daucus* genera and *P. illyricum*), while
 228 SDPi remained approximately constant in the rest of cases (Fig. 3). All species floated initially, but
 229 the diaspores of the non-thalassochorous *Daucus* and *Ferula* genera sank during the first week of the
 230 experiment with no significant differences between species within genera ($p > 0.05$, Figure 3 and 4c,
 231 e). Within the genus *Juniperus*, the coastal *J. macrocarpa* showed less buoyancy capacity (41% at the
 232 third week, Figure 3) than its congeneric *J. oxycedrus* showing marginally statistical differences
 233 between them (Figure 4e). The buoyancy of *J. turbinata* fleshy cones decreased drastically after the
 234 third week (40% Figure 3), although a small percentage remained floating until the ninth week (4%).
 235 Two species (*P. maritimum* and *J. oxycedrus*) floated more than five weeks with more than the 50%
 236 of the dispersal units (54 and 61% respectively), and only fleshy cones of *J. oxycedrus* were still
 237 floating after 10 weeks (14%). In the case of *P. illyricum*, all dispersal units were sunken at the second
 238 week, showing a statistically significant difference (Figure 3 and 4e) with the congeneric coastal *P.*
 239 *maritimum*.
 240



241
 242 **Figure 3.** Evaluation of the buoyancy capacity, seed viability and Sea Dispersal Potential index
 243 (SDPi) in seawater over time in weeks of the nine selected species.
 244
 245

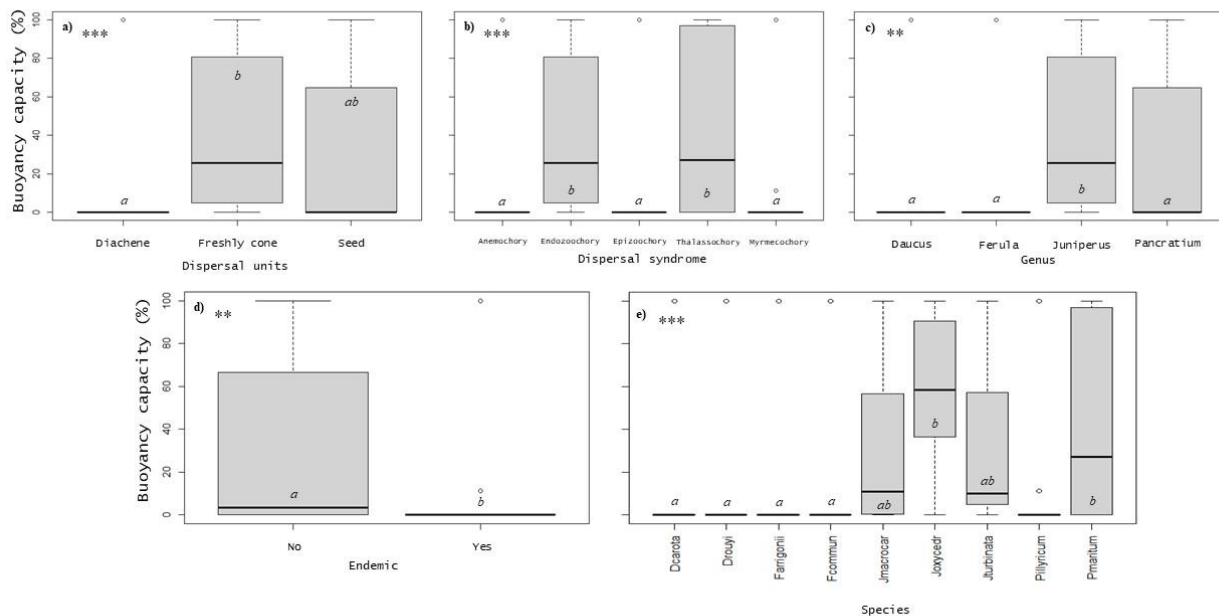
246 Examining separately the factors highlighted by the ANOVA, dispersal units and dispersal syndrome
 247 are the main factors influencing the buoyancy capacity (Table 2). Among the different types of
 248 dispersal units (Figure 4a), fleshy cones demonstrated the highest buoyancy capacity, followed by
 249 seeds. In contrast, diachenes exhibited very limited buoyancy. The endozoochory and the
 250 thalassochory syndromes showed significant higher buoyancy capacity than other dispersal
 251 syndromes (Figure 4b). Despite the genus *Pancratium* showed no significant differences with *Ferula*
 252 or *Daucus* (Figure 4c), *P. maritimum* had significantly higher buoyancy capacity at the species level
 253 than species of *Ferula* and *Daucus* genera, as well as compared to the congeneric *P. illyricum* (Figure
 254 4e).

255 **Table 2.** ANOVA results on finding differences of buoyancy capacity between species, genus, Habitat
 256 (inland or coastal), distribution (endemic or widespread) dispersal syndrome, and type of dispersal
 257 units.
 258

| ANOVA_Buoyancy | Df | Sum sq | Mean Sq | F value | Pr(>F) |
|--------------------|----|--------|---------|---------|-------------------|
| Species | 8 | 35111 | 4389 | 3.815 | 0.0006 *** |
| Genus | 3 | 20712 | 6904 | 5.597 | 0.0013 ** |
| Distribution | 1 | 10872 | 10872 | 8.343 | 0.0047 ** |
| Habitat | 1 | 30 | 30.2 | 0.022 | 0.8840 |
| Dispersal syndrome | 4 | 27798 | 6950 | 5906 | 0.0002 *** |
| Dispersal units | 2 | 20712 | 10356 | 8.476 | 0.0004 *** |

259

260



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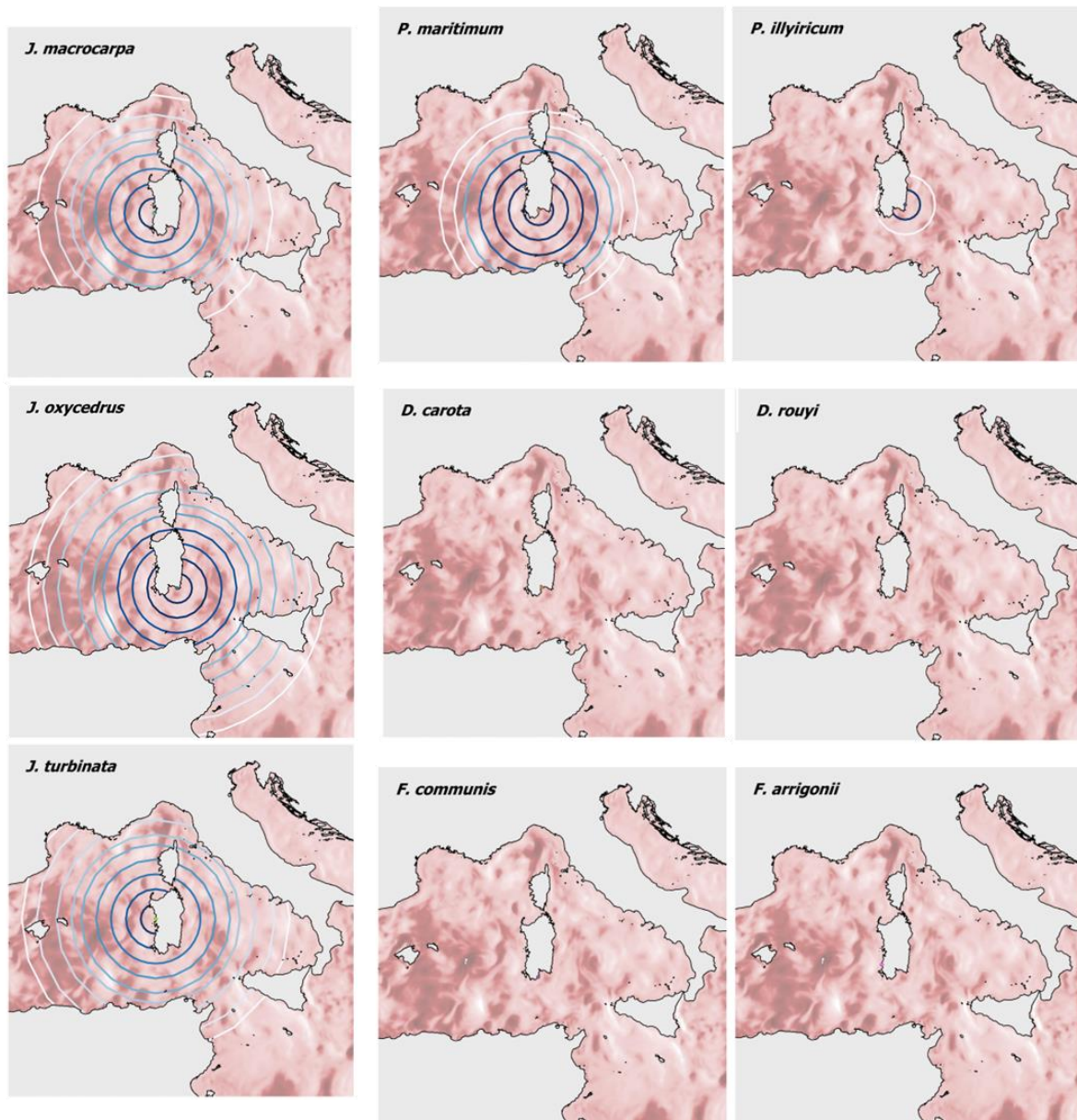
262 **Figure 4.** Box plot depicting the distribution of the buoyancy capacity values across different type of
 263 dispersal units (a), dispersal syndrome (b) genus (c), distribution (d) categories and by single species
 264 (e). ANOVA tests were performed, and significant differences were observed. Post-hoc Tukey's HSD
 265 test were conducted to compare differences between the groups. The *p*-values are indicated by
 266 asterisks: * <0.05 , ** <0.01 , *** <0.001 .
 267

268

269 ***Sea currents and estimation of long-distance dispersal (LDD) capacity***

270 The significant relationship between buoyancy capacity with seed viability and SDPi indicated its
 271 association with LDD potential. Based on an average velocity of 0.1 m/s, we estimated a dispersal of
 272 ca. 60 km per week (Figure 5). The maximum LDD was found for the *Juniperus* genus, from near

273 540 km for the coastal *J. macrocarpa*, ca. 600 km in the case of *J. turbinata*, up to 660 km for *J.*
274 *oxycedrus* (Figure 5). In contrast, the *Daucus* and the *Ferula* genera displayed a shorter buoyancy
275 duration, less than one week, suggesting a dispersal range of less than 60 km (Figure 5). The two *P.*
276 *maritimum* and *P. illyricum* species remain floating from 6 to 2 weeks, respectively (Figure 5). The
277 maximum dispersal distance of *P. maritimum* was estimated in 360 km, indicating its potential LDD.
278 In contrast, *P. illyricum* displayed lower buoyancy capacity and viability, with a dispersal range
279 limited to around 120 km (Figure 5).
280



281
282 **Figure 5.** Estimation of long-distance dispersal capacity for the nine species from their donor sites
283 until reaching all dispersal units sunken. The estimation assumed an averaged current velocity of 0.1
284 m/s (ca. 60 km per week) and did not consider the underimposed Sea Water velocity of Escudier et
285 al. (2020).

286 Discussion

287 In general, most studies of hydrochory have focussed on genetic impacts, or the relationship between
288 diaspore floating time and morphology, with a primary focus on freshwater wetland environments
289 (Lopez 2001; Van den Broek *et al.* 2005; Leyer & Pross 2009) or salt lakes (Coops & Van der Velde
290 1995; Rand 2000), with more limited investigation of the impact of sea hydrochory (thalassochory).
291 Recently, there is a renewed interest on the role of different LDD mechanisms for the colonization of
292 oceanic islands, and particularly thalassochory (e.g., Esteves *et al.* 2015; Fuster-Calvo *et al.* 2021).
293 However, to our knowledge, this is the first attempt to experimentally test the sea dispersal potential
294 of the flora of the Mediterranean Basin.

295 Our data revealed that the factors that most significantly influenced thalassochory were the buoyancy
296 capacity, since some diaspores, such as those of *Juniperus*, might remain viable independently of
297 their buoyancy decrease with time. Propagules buoyancy was strongly correlated with the
298 phylogenetic (i.e., similar behaviour among species of the same genus), distribution (i.e., widely or
299 not), the type of dispersal units, and the main dispersal syndrome. These findings emphasize the
300 importance of considering multiple factors when assessing the potential for thalassochory and, more
301 in general, LDD and highlight the complex interplay between dispersal traits, species distribution
302 patterns, phylogenesis and dispersal syndromes. We found little evidence that diaspores of coastal
303 species are more often physiologically adapted to seawater dispersal than inland relatives, despite
304 having been previously hypothesized (Heleno & Vargas 2015). Indeed, this was confirmed in this
305 study only for some coastal and salt-tolerant species, widely distributed in the Mediterranean, like *P.*
306 *maritimum* and *J. oxycedrus*, while other coastal species with limited distribution, as *D. rouyi* and *F.*
307 *arrigonii* did not show a high tolerance to sea water exposure and extremely low buoyancy capacity,
308 suggesting a low possibility to be dispersed by sea. The inland congeneric of the above-mentioned
309 species coincided in buoyancy capacity and potential to be dispersed by sea. These species have main
310 dispersal syndromes related to epizoochory (*D. carota* subsp. *carota*) and anemochory (genus *Ferula*
311 and *D. rouyi*). In these cases, the possibility of long-distance dispersal by the marine currents seems
312 highly unlikely for the entire genera and thus conserved along the phylogenetic tree. In particular,
313 *Ferula arrigonii* was hypothesized to have colonized Sardinia from Corsica by sea (Dettori *et al.*
314 2014). Even if for relatively short distances, our results led to assume that this species might have
315 instead used some terrestrial dispersal mean, such as anemochory, during the last connections of the
316 Pleistocene eustatic changes, as hypothesized for other endemic taxa, such as *Borago pygmaea* (DC.)
317 Chater & Greuter or *Carex microcarpa* Bertol. (Fois *et al.* 2022).

318 Diaspores morphologies are instead often indicative of the most likely dispersal mechanism. For
319 instance, the morphological traits of *Daucus* and *Ferula* spp. showed the typical light and dry
320 (di)achenes, which are more adapted to tolerate dryness and to be dispersed by wind throughout in
321 open land. Here we confirm the sea dispersal potential of *Juniperus* fleshy cones, as these can float
322 and survive in seawater and therefore capable of germination once lower salt concentrations are
323 encountered when washed ashore (Esteves *et al.* 2015). Although the main dispersal method in this
324 genus is endozoochory, successful thalassochorous dispersal and establishment can occur
325 occasionally. All junipers showed similar results, although surprisingly the inland species, *J.*
326 *oxycedrus*, was the one with higher capacity of buoyancy (11 weeks), compared to the coastal
327 congeneric *J. macrocarpa* (nine weeks). Especially in case of extreme meteorological events, marine
328 currents can transport plant propagules of various nonspecialized dispersal morphologies over tens
329 and even hundreds of kilometres, as in the case of the three species of *Juniperus* presented here and
330 given new opportunities of habitat colonization. According to our results, Juan *et al.* (2012) postulated
331 by genetic analysis that *J. macrocarpa* could have potentially colonized the Azores via fruits washed
332 away from the shores of Europe and drifting on ocean currents. In the Mediterranean Basin,
333 considering sea currents and velocity profiles, it is possible to assume that they could reach the coasts
334 of the Balearic Islands or Algeria, if dropped from western Sardinia, or a large part of the Tyrrhenian
335 coast of the Italian peninsula, if from eastern Sardinia.

336 Among the species included in this study, only *P. maritimum* shows clear traits for thalassochory
337 which is possibly the only syndrome that can explain its phylogeographic pattern reported by De
338 Castro *et al.* (2016; 2020). The Mediterranean species of this genus probably have a common ancestor
339 which was established on dry slopes or cliffs (De Castro *et al.* 2012). From the same ancestor, *P.*
340 *maritimum* s.l. and *P. sickenbergeri* Asch. & Schweinf. developed adaptations that allowed the
341 colonization of beaches and apparently found a niche on sand not yet exploited by other *Panocratium*
342 *taxa*. In particular, *P. maritimum* is the only species, which has a wide distribution that was explained
343 by its floating ability that enabled it to disperse their propagules by sea (Werker & Fahn 1975; De
344 Castro *et al.* 2012). In contrast, the rest of the narrowly distributed *taxa*, like the endemic *P. illyricum*,
345 retained an ecology and diaspores traits similar to those of the ancestor and thus a hypothesized low
346 thalassochorous dispersal ability (De Castro *et al.* 2012). This was confirmed by our study, as *P.*
347 *maritimum* showed a buoyancy capacity for six weeks, with an accumulated viability of more than
348 80% in at the end of the experiment, while *P. illyricum* showed a buoyancy capacity for only two
349 weeks and an accumulated viability of around 70%. Nevertheless, this could allow *P. illyricum* to
350 overcome short marine distances, such as those between Sardinia and Corsica or between the latter

351 and the Tuscan archipelago. The same results of the two *Panocratium* species would be expected after
352 comparing inland and coastal species of the genera *Daucus* and *Ferula*. However, as previously
353 explained, the type of dispersal units seemed to play a more significant role in determining
354 thalassochorous dispersal ability compared to the ecological assumptions derived from living near
355 the sea. The high buoyancy capacity of fleshy cones suggested their great tolerance and adaptability
356 to dispersion by marine currents. Conversely, species with achenes as dispersal units may generally
357 be less prone to dispersal by marine currents compared to other types. Indeed, species with dried
358 fruits are likely showing anemochorous and epizoochorous traits and did not seem to have any
359 relevant capacity to endure sea dispersal, as observed for *Daucus* and *Ferula* genera.

360 All the above suggest that non-standard dispersal events are more important for island and coastal
361 colonization than previously believed, and their relevance for biogeography is not merely anecdotal
362 (Nathan *et al.* 2008; Nogales *et al.* 2012). When studying diaspores, it is important to exercise caution
363 and examine the specific characteristics of each single species. Factors such as low specific gravity,
364 trapped air, corky tissues, and high surface area to volume ratios may inadvertently enhance
365 hydrochorous dispersal capability in many cases (Middleton 2000). However, it is important to
366 confirm such assumptions with empirical tests, such as on seed buoyancy and viability. Our results
367 suggest that dispersal by sea currents in the Mediterranean Basin can have significantly influenced
368 the distribution of several plants. Some species are likely evolved specific thalassochory syndromes,
369 probably in parallel with their adaptation to coastal environments, as in the case of *Panocratium*.
370 However, thalassochory can also be important even for species that are often dispersed by other
371 mechanisms, such as the fleshy cones of *Juniperus* that are likely more frequently dispersed by
372 vertebrates but can also be dispersed by sea currents. Taken all together, our results reveal significant
373 differences in sea dispersal between endemic and widespread species, suggesting an important role
374 of thalassochory in shaping the distribution patterns of the Mediterranean flora. The apparently weak
375 link between diaspore traits and habitat (i.e., coastal or inland) and actual dispersal vectors makes it
376 very difficult to predict the most important mechanisms at work during the colonization of islands
377 and Mediterranean coasts by plants (Heleno & Vargas 2015). The simple and low-cost method here
378 presented can shed further light in this field, if largely replicated.

379

380

381 **Conclusion**

382 In this research, we investigated the dispersal capacities of nine Mediterranean plant species in
383 relation to their habitat preference, distribution, and specific dispersal traits. The fact that it is in our

384 knowledge the first experiment to test for thalassochory in the Mediterranean confirms the difficulties
385 in establishing it. Here, we presented an approach that could be widely replicated for many other
386 species from the inland and coastal Mediterranean. Our findings suggest that the propagules of coastal
387 plant species not seem to have a consistently greater buoyancy capacity and seed viability after
388 saltwater immersion than inland species. However, we observed differences between widely
389 distributed and endemic plants, suggesting that their current distribution is likely correlated with their
390 LDD ability. The estimated LDD distances provided insights into the potential dispersal capabilities
391 of different species. Species such as *J. macrocarpa* and *J. oxycedrus* exhibited longer buoyancy
392 durations, indicating a greater potential for long-distance dispersal. These results contribute to our
393 understanding of plant dispersal dynamics and have implications for the colonization and distribution
394 patterns of plant species. Overall, this study is a drop on the ocean that for the first time offers useful
395 suggestions and a practical approach for the study of LDD in the Mediterranean Basin. Many other
396 *taxa* could be tested, and our simple, low-cost approach allows for extensive replication of many *taxa*
397 such as those mentioned to be hypothesized as thalassochorous on the basis of their population genetic
398 structure or their simple distribution, for example, in the case of Sardinia, *Genista etnensis* (Raf.)
399 DC., the distribution of which is difficult to explain being native to eastern Corsica, Sardinia, and
400 Sicily (De Castro *et al.* 2022). Future work, in particular marine currents models, ecological niche
401 modelling, phylogeographic and evolutionary research, and seed ecophysiological investigations,
402 would be needed to support such experimental tests.

403

404

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408

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