RESEARCH ARTICLE

# Sea dispersal potential and colonization of the Galápagos littoral flora

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## Abstract

**Aim:** Seed dispersal by oceanic currents (thalassochory) is considered one of the main long-distance dispersal (LDD) mechanisms for the colonization of oceanic islands by plants. Diaspores of littoral species are often hypothesized to be physiologically adapted to seawater dispersal, favouring interisland colonization. In this study, we experimentally tested the sea dispersal potential of a large proportion of Galápagos littoral flora and explored its correlation with plant distribution across the archipelago. We propose a simple Sea Dispersal Potential index (SDPi) to quantify the thalassochorous potential of any species.

**Location:** Galápagos archipelago.

**Taxon:** Littoral angiosperms.

**Methods:** We combined information on seed floatability (flotation time) and viability experiments (tetrazolium test) into an SDPi for 19 native littoral plants and tested whether increasing dispersal potential is associated with broader interisland distributions. We then tested if the presence of morphological structures related to thalassochory is associated with the functional SDPi.

**Results:** A relatively low, albeit highly variable, SDPi across Galápagos littoral plant species was found. No correlation was found between SDPi and species distributions. Morphological traits hypothesized to favour sea dispersal are not related to thalassorous potentials to reach closest islands, but they are positively associated with SDPi to reach the farthest islands.

**Main conclusions:** SDPi is shown to be a useful tool to compare the thalassochorous potentials of entire floras in a given geographical context. The low performance of most of the species questions the general assumption that most littoral plants are highly adapted to long-distance sea dispersal. Our results support the view that island colonization is a multifactorial process and that the use of dispersal syndromes is insufficient to make biogeographical predictions in macroecology studies. Further research should integrate functional indices (e.g., SDPi) with complementary tools (genetics, remote diaspore tracking) to determine the actual drivers of species dispersal and establishment.

**KEYWORDS**
island colonization, long-distance dispersal, seed flotation, seed viability, seed-dispersal index, thalassochory

# 1 | INTRODUCTION

Oceanic islands, such as the Galápagos, arise initially as pieces of land in the middle of the ocean, devoid of terrestrial life and historically disconnected from continental landmasses (Gillespie & Clage, 2009). Colonization of this new land has to rely on long-distance dispersal (hereafter LDD) of propagules. In most ecological studies, the assignment of plants to particular dispersal modes has been based on the analysis of morphological traits of the diaspores, that is, visual attributes of the reproductive propagules that are dispersed. Among all seed dispersal syndromes, only four can explain the colonization of oceanic islands (LDD syndromes), namely, syndromes associated with dispersal by wind (anemochorous), sea (thalassochorous) and either internal (endozoochorous) or external (epizoochorous) dispersal by animals (Carlquist, 1967; Heleno & Vargas, 2015; Porter, 1976). However, it is inherently speculative to infer the dispersal mechanism that was actually responsible for the arrival of a particular species onto a given island (Clark et al., 2001; Higgins et al., 2003). For instance, birds can potentially disperse seeds and fruits with any type of syndrome (Costea at al., 2019; Lovas-Kiss et al., 2019). Alternatively, testing the effectiveness of morphological specializations potentially associated with species distributions across islands provides an important probabilistic information to infer the success of particular syndromes in insular colonization (Arjona et al., 2018; Heleno & Vargas, 2015; Vargas et al., 2012).

In this study, we focus on sea dispersal by plants or thalassochory (from the Greek *thalassa* meaning 'the sea' and *khōrein* 'to spread'), based on data from a large proportion of littoral plant species, that is, those growing in the narrow littoral strip, defined as the zone under direct influence of salt, typically a few metres from the sea (Wiggins & Porter, 1971). For centuries, scientists have interpreted colonization of oceanic islands by littoral plants as a result of specializations for floatability and survival in saltwater (Bramwell, 1985; Carlquist, 1965; Porter, 1976). Support for the importance of oceanic drift for island colonization initiated with Darwin (1859) and was followed by Godman (1870), Carlquist (1966) and others. For instance, concerning the colonization of Hawaii, Guppy (1906) states that 'The littoral plants of such an island are found all over the coasts of the tropical Pacific, and for the explanation of this fact we look mainly to the agency of the ocean-currents'. Also, Ridley (1930) when considering the colonization of recently formed islands concludes that 'we get a coast flora fringing the land which consists of plants adapted to life under saline conditions, the littoral flora, which is derived from other similar coasts by sea-dispersal'.

The first condition for plants to be successfully dispersed by sea currents is that their diaspores float for sufficient time to reach a receiving island. Secondly, the embryo inside the seed has to survive under saline conditions to successfully establish new populations in the new territory. These two assumptions led several authors to test thalassochorous potential by conducting flotation experiments and viability tests after exposure to saltwater (Esteves et al., 2015; Guja et al., 2010; Stafford-Bell et al., 2015; Wu et al., 2018). Plant species with both attributes are expected to have a higher probability of being dispersed by sea currents and thus of colonizing new territories, likely resulting in a broader distribution across oceanic islands.

This two-step approach was an active field of research by early naturalists, even becoming an 'obsession' for Charles Darwin towards the end of his career (Darwin, 1856; Grant & Estes, 2009). Recent studies suggest that ocean currents play an important role in the transcontinental dispersal of diaspores (De Queiroz, 2005; Fajardo et al., 2019; Nathan et al., 2008). Similarly, population genetics analyses on some littoral plants suggest a major role of thalassochory in their distribution (Gandour et al., 2008; Kadereit et al., 2005; Takayama et al., 2006; Wee et al., 2014). However, detailed studies on the biology of species dispersal potential by ocean currents are extraordinarily scarce and only focus on one or few species (Guja et al., 2010; Nakanishi, 1988; Stafford-Bell et al., 2015; Yang et al., 2012).

Due to the capacity of littoral plants to withstand high salt concentrations (Flowers & Colmer, 2015; Rozema & Schat, 2013), we hypothesize that their diaspores have a high potential for sea dispersal and that such thalassochorous potential is positively associated with species distributions across the Galápagos. To test this hypothesis, our study addresses the following objectives: (a) to experimentally evaluate the thalassochorous potential of Galápagos littoral species based on seed floatability and post-dispersal seed viability; (b) to propose a metric of thalassochorous potential (Sea Dispersal Potential index or SDPi) that combines the potential for overcoming those two key filters; (c) to evaluate if species with higher SDPi have wider distribution ranges as a result of their greater colonization probabilities; and (d) to explore if species with morphological traits associated with thalassochory have a higher SDPi.

# 2 | MATERIALS AND METHODS

## 2.1 | Study site and sampling

The Galápagos archipelago consists of 13 volcanic islands larger than 10 km$^2$ that are located c. 1000 km west of continental Ecuador (0.5°S, 90.5°W). Here, we considered 12 large islands because Santa Cruz and Baltra were recently connected, forming a single island about 10,000 years ago (Poulakakis et al., 2012). The Galápagos flora comprises around 550 native species of angiosperms, 32% of which are endemic (Lawesson et al., 1987; Wiggins & Porter, 1971).

Diaspore sampling and experimentation were carried out in May and June 2018. We performed 21 transects consisting of 200 m stretches along both sandy and rocky littoral zones of Santa Cruz, Isabela, and San Cristóbal (Figure 1). Along these transects, we sampled diaspores (seeds, fruits and infructescences) of native species that occur under the direct influence of seawater due to flooding or sea spray (Wiggins & Porter, 1971). For each species, a total of 200
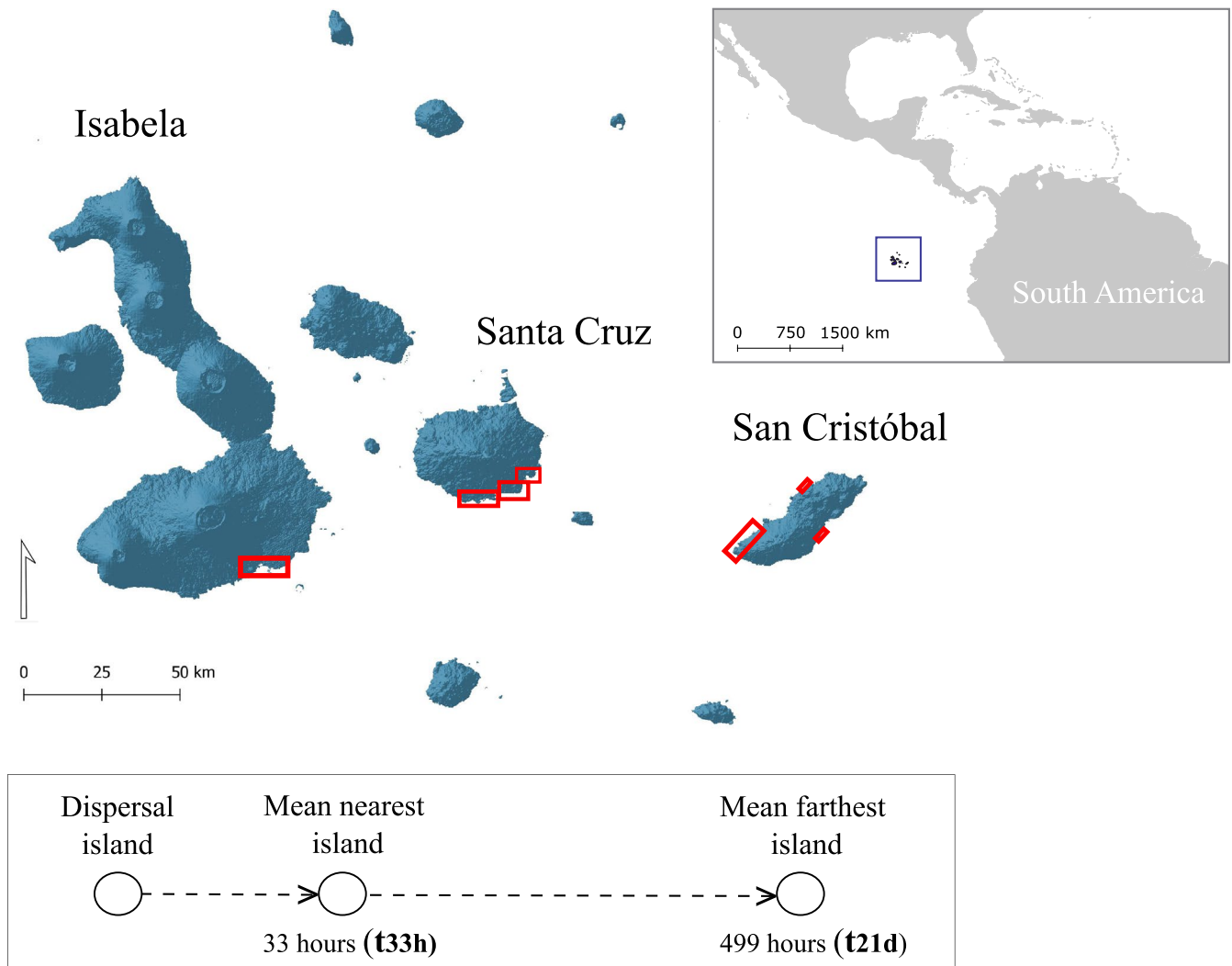
**FIGURE 1** Map of the Galápagos archipelago (Darwin and Wolf not shown). Only the names of islands where diaspores were sampled are indicated. Red polygons mark the littoral areas where transects were performed. At the bottom, a schema represents the dispersal spatio-temporal scenario considered for the study

diaspores were typically collected from several individuals (ideally more than three) at different locations. As a result, c. 5000 well-formed seeds, fruits and infructescences of 22 species were assembled. Well-formed diaspores that had recently fallen to the ground were preferred as they may be sufficiently mature to undergo sea dispersal. When diaspores were not found on the ground, we collected them directly from the plant, selecting those showing an advanced maturation process, almost ready for diaspore excision and dispersal.

## 2.2 | Plant dispersal conditions

Colonization of new territories is a two-stage process, contingent on successful dispersal and establishment (MacArthur and Wilson, 2001). Dispersal is conditioned by the dispersal vector and the physical context, chiefly interisland distance and island size. In addition, the establishment of new organisms depends upon the local conditions at the seed deposition site, such as habitat suitability, presence

of mutualists and lack of antagonism (Gillespie & Clague, 2009). In this study, the experimentation is based only on the first step (dispersal process).

The sea dispersal potential of the Galápagos littoral flora for interisland colonization was calculated, based on floatability and viability experiments.

## 2.3 | Diaspore floatability

Two-hundred diaspores of each species were placed in plastic recipients containing seawater from the coast of Santa Cruz. Only diaspores showing good condition in terms of shape, size and weight were used for the experiments. Water containers were shaken between 50 and 100 rpm (Mophorn Orbital Shakers) daily for 2–4 h to simulate the physical movements of the sea surface (Esteves et al., 2015). Water in containers was replaced every 3–4 days to allow oxygenation and avoid eutrophication.

Since we were interested in studying interisland colonization across the Galápagos archipelago, we considered two measurement times: (a) the minimum time needed to colonize the nearest island (corresponding to the potential to colonize at least one island), and (b) the minimum time required to colonize the farthest island (corresponding to the potential to colonize all islands of the archipelago). To calculate both times, mean sea surface current velocity in the archipelago (2.94 km/h) was obtained from data provided by the Ecuadorian navy's 'Servicio Hidrográfico y Oceanográfico Insular de la Armada (SHOIAR)'. Secondly, the distances between the closest shores of all possible pairs of the twelve islands considered were extracted from GoogleEarth, from where the mean distance to the closest (11.2 km) and farthest islands (169.6 km) were calculated. Accordingly, the estimated minimum flotation times needed to colonize the nearest ($t_{33 h}$) and the farthest ($t_{21d}$) islands of the archipelago were 33 and 499 h (21 days) (see Appendix S1; Tables S9 and S10). Empty diaspores (either sunk or floating) were discarded from the initial number of diaspores.

## 2.4 | Seed viability

At the beginning of the experiment ($t_0$) and at both measuring times ($t_{33 h}$ and $t_{21d}$), c. 20 floating diaspores of each species were evaluated for embryo viability using the 'tetrazolium chloride test' (TZ test; Porter et al., 1947). As the tetrazolium solution penetrates the living tissue of the embryo, hydrogen ions released during the respiration process reduce the 2,3,5-triphenyl tetrazolium chloride to form an insoluble reddish compound (Figure 2). Procedure and staining interpretation followed the AOSA/SCST Tetrazolium Testing Handbook (Miller, 2010). In viviparous mangroves, germination and initial growth occurs while the seed is still enclosed in the fruit, which remains attached to the tree. Seed tissues become dark brown if the seedling dies, and then not collected. In contrast, the presence of green photosynthetic tissues in the seeds of *Rhizophora mangle* (red mangrove), *Avicennia germinans* (black mangrove), and *Laguncularia racemosa* (white mangrove) were considered evidence of diaspore viability. All these experiments were performed at the laboratories of the Galápagos National Park.

We could not perform the viability tests in the Galápagos Islands for *Batis maritima*, *Cyperus laevigatus* or *Portulaca howelli*. Therefore, experiments for these three species were conducted at the Royal Botanic Garden of Madrid (Spain) following the same protocol but with seeds from different sources, as the exportation of live seeds from Ecuador is forbidden by law. Seeds of *B. maritima* and *C. laevigatus* were obtained from the U.S. National Germplasm System and Rancho Santa Ana Botanic Garden (USA), respectively. Since *P. howelli* seeds were not available by seed request from any institution, we decided to do the experiments with its close relative *P. oleracea*, (Ocampo & Columbus, 2012) collected on the coast of Alicante (Spain). Nevertheless, *P. oleracea*

also occurs across the archipelago under littoral conditions, although there is no clear evidence on its native status in Galápagos (Guézou et al., 2010).

## 2.5 | Sea Dispersal Potential index

We herein propose a simple index to express the sea dispersal potential of species for a given dispersal scenario. This was obtained by combining the percentage of floating diaspores (% Floating) and viable embryos (% Viability) for any specific flotation time ($t$).

$$SDPi_t = \frac{\% \, Floating_t \cdot \% \, Viability_t}{100}$$

This metric combines the two main functional requirements for thalassochory so that it is proportional to the probability that at least one viable diaspore will float for the minimum time required to reach a new territory. Therefore, we assume equal weight for floatability and viability variables. The index value corresponds to the percentage of floating and viable seeds at a given flotation time and ranges from 0% to 100%. Accordingly, the SDPi of interisland colonization in the Galápagos was implemented for each littoral species, considering the minimum mean floating time needed to colonize the closest ($t_{33 h}$) or the farthest ($t_{21d}$) island of the archipelago.

The index can be used to compare the sea dispersal potential for different sets of diaspores. We exemplify this versatility by comparing the SDPi of *Scaevola plumieri* seeds directly collected from plants on dunes (Tortuga bay, Santa Cruz), with seeds retrieved from bird pellets found at the same site (i.e., potential for secondary dispersal by birds + sea). This process has been poorly studied and is gaining recognition as an important means of seed dispersal (Chambers & MacMahon, 1994; Vander Wall & Longland, 2004).

## 2.6 | Morphological syndromes and SDPi

We analysed whether the plants' morphologically recognizable thalassochorous syndromes (Vargas et al., 2014) and other diaspore characteristics (fleshiness and eccentricity; see Appendix S1; Table S2) are associated with their functional capabilities for sea dispersal. Mann-Whitney *U* tests were used to compare the SDPi of thalassochorous versus nonthalassochorous plant species and fleshy *vs* dry diaspores. We used this nonparametric test given that SDPi values are not normally distributed. In addition, we fitted a linear model to evaluate if SDPi is associated with diaspore length or diaspore eccentricity (Length/Width; Cervantes et al., 2016). We applied Tukey's ladder of powers transformation in the 'rcompanion' package on variables SDPi $t_{21d}$, Length, and Shape ($\lambda$ = 0.33, −0.125, and −2.95, respectively) to address model assumptions of residual heteroscedasticity and

**FIGURE 2** Tetrazolium chloride test (TZ test) results on embryos of *Hibiscus tiliaceus* ((a) viable), *Ipomoea pes-caprae* ((b) viable), *Scaevola plumieri* ((c) nonviable and viable), *Sesuvium portulacastrum* ((d) nonviable), *Alternanthera filifolia* ((e) nonviable), and *Maytenus octogona* ((f) viable). Capital letters indicate the location of the cotyledons (C) and radicle (R). The presence of insoluble reddish compound as a result of the TZ reaction indicates living tissues. Seeds were considered viable or nonviable, depending on surface area and intensity of stained embryo tissues (see AOSA/SCST Tetrazolium Testing Handbook)
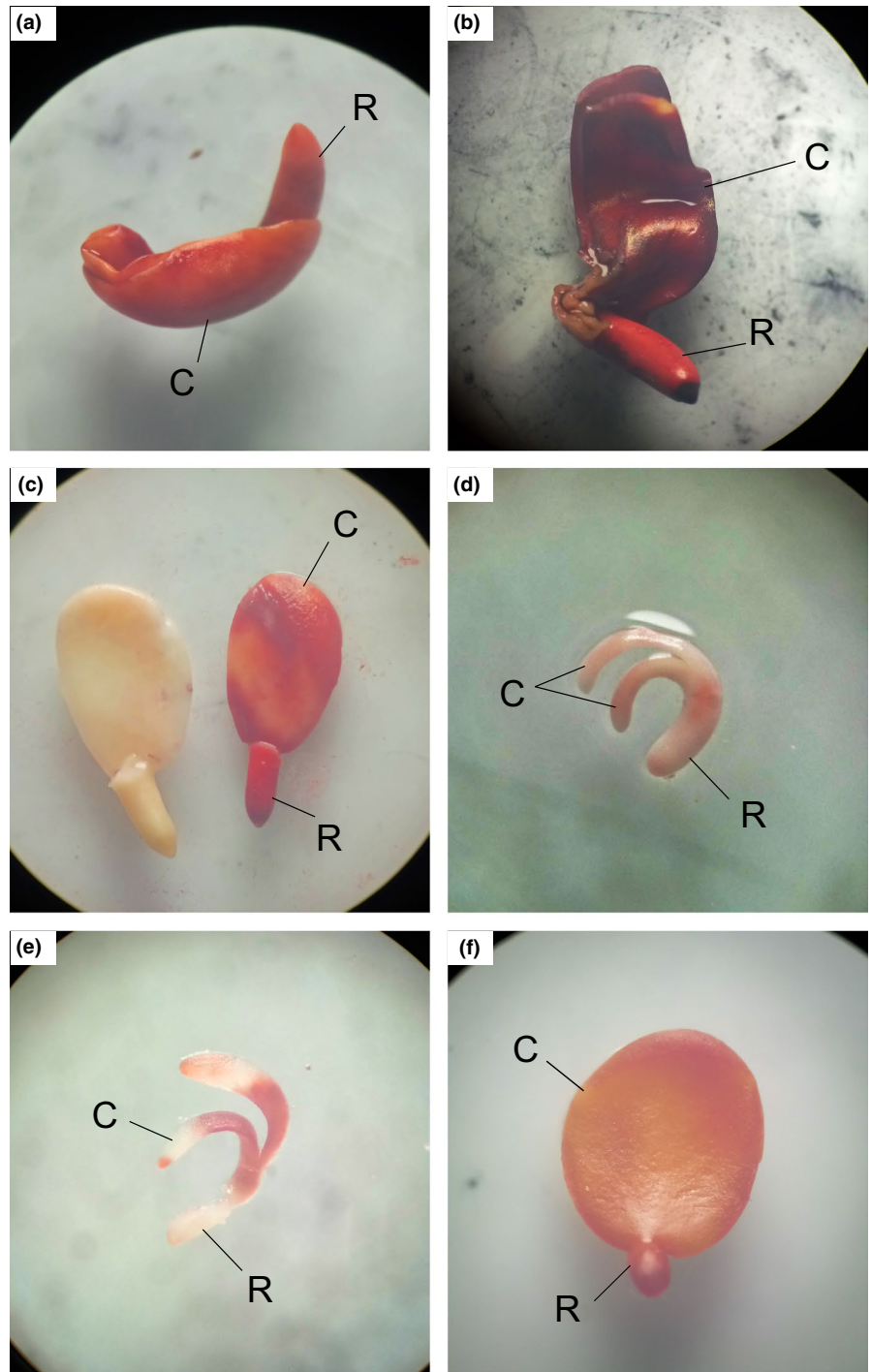
normality (Mangiafico, 2020). This method finds the power value (i.e., lambda) that maximizes the Shapiro–Wilk $W$ statistic for a given dataset.

## 2.7 | SDPi and colonization across islands

The relationship between SDPi and plant distribution across the Galápagos (a proxy for colonization ability) was calculated using generalized linear models (GzLM). Species distribution data were obtained from Vargas et al., (2014). For the fitted model, the response variable was the number of islands where each species is present (Poisson distribution errors), and the predictor was the SDPi for each species. We then built a second model considering only species distributions across the six Galápagos palaeo-islands that were never connected to other islands (see Ali & Aitchison, 2014). For this second model, we used a power transformation for the variable SDPi $t_{21d}$ ($\lambda = 0.33$) to meet the model assumptions.

# 3 | RESULTS

## 3.1 | Diaspore sampling of littoral species

Twenty-three littoral plants were found along the 21 transects performed (total length 4200 m) on the coast of Santa Cruz (2300 m), Isabela (1000 m) and San Cristóbal (900 m). Only one species found along the transects (*Grabowskia boerhaaviaefolia*) was not sampled since none of the individuals had fruits. We collected approximately 200 diaspores from each species, except for *Nolana galapagensis* (*n* = 150 diaspores), *Batis maritima* (*n* = 100) and *Cyperus laevigatus* (*n* = 52) due to low numbers of well-formed seeds.

The number of sampled species constituted 77% of the littoral plant species and 80% of the littoral plant genera, according to the list of littoral plant species provided by Wiggins and Porter (1971) (see Appendix S1; Table S1).

## 3.2 | Sea dispersal tests

Sixteen (73%) of the 22 locally sampled species were tested in the Galápagos National Park laboratories. The other six species (*B. maritima*, *Conocarpus erectus*, *Cryptocarpus pyriformis*, *Cyperus ligularis*, *P. howellii*, *Sporobolus virginicus*) showed either an extremely high proportion of aborted (i.e., empty) seeds and/or staining problems that prevented gathering reliable data for the TZ test. We eventually tested a total of 19 species, including diaspores of *C. laevigatus* and *B. maritima*, requested from seedbanks and *P. oleracea* sampled in Spain (Table 1; Figure 3).

### 3.2.1 | Diaspore floatability

Only two species (11%), *Lycium minimum* and *N. galapagensis*, were not able to float for the minimum time (33 h) needed to colonize the nearest island (Table 1). The mean percentage of diaspores of the 17 species floating at $t_{33\,h}$ was 67% (*SD* = 35; Min. = 0; Max. = 100). After 21 days—the time needed to potentially colonize all the islands of the archipelago ($t_{21d}$)—six species (32%) had no remaining diaspores floating. For the 13 species (68%) that were still floating at this time, the mean percentage of diaspores floating was 32% (*SD* = 39; Min. = 0; Max. = 100). Four species (21%) (*Alternanthera filifolia*, *Laguncularia racemosa*, *Maytenus octogona*, and *Scutia spicata*) were able to remain floating for 33 h ($t_{33\,h}$) but were no longer floating at $t_{21d}$. *Rhizophora mangle* was the only species for which all diaspores (100%) floated until the end of the experiment (21 days; Table 2).

### 3.2.2 | Seed viability

Estimated mean seed viability decreased from 82% at the time of collection to 73% after 33 h of exposure to saltwater, and 65% after 21 days. Embryo staining at the start of the experiment ($t_0$) indicated that viability was greater than 60% for all species (Mean = 82%;

*SD* = 19; Min. = 61%; Max. = 100%), except for *P. oleracea* (25%) (Table 1). The number of embryos tested (ideally, *n* = 20) varied among species, depending on the number of diaspores floating at each time: the mean number per species at $t_{33\,h}$ and $t_{21d}$ was 17 (Min. = 9; Max. = 21) and 13 (Min. = 6; Max. = 21), respectively. The seeds floating at $t_{33\,h}$ (*n* = 17 spp.) and $t_{21d}$ (*n* = 13 spp.) showed a mean viability of 73% (*SD* = 29; Min. = 18%; Max. = 100%) and 64% (*SD* = 27; Min. = 17%; Max. = 100%), respectively.

*Scaevola plumieri* fruits found in nearby bird pellets showed a higher SDPi than fruits collected from the plants for both short and long distances (SDPi $t_{33\,h}$ = 88% vs. 69%, and SDPi $t_{21d}$ = 29% vs. 23%) (Appendix S1; Table S15).

## 3.3 | Morphological traits and SDPi

The SPDi of thalassochorus and nonthalassochorous plants did not differ significantly at $t_{33\,h}$ (N = 14 and 5, Median = 72 and 32, respectively; *U* = 16.5, *p* = 0.095). At $t_{21d}$, thalassochorous species showed significantly higher SDPi than nonthalassochorous species (Median = 13 and 0, respectively; *U* = 11, *p* = 0.027). Fleshiness and eccentricity were not significantly associated with the observed SDPi, neither at $t_{33\,h}$ (*N*(Fleshy) = 8, *N*(Dry) = 11, Median = 70 and 36; *U* = 43, *p* = 0.967; and *Z*(16) = −0.8, *p* = 0.393, respectively) nor at $t_{21d}$ (Median(Fleshy) = 8, Median(Dry) = 8, *U* = 46, *p* = 0.899; and *Z*(16) = 0.5, *p* = 0.631, respectively). Diaspore length was positively associated with species SDPi $t_{33\,h}$ ($R^2$ = 0.53, *Z*(16) = 3.7, *p* = 0.002) (Appendix S1; Figures S1–S3; Tables S3–S6).

## 3.4 | SDPi and colonization pattern

All but two species showed a lower SDPi at $t_{21d}$ than that at $t_{33\,h}$. Exceptions were *R. mangle*, which maintained the same index value (SDPi = 100%), and *C. laevigatus*, whose SDPi at $t_{21d}$ was slightly greater than at $t_{33\,h}$ (38 and 30, respectively). The mean SDPi values for the 19 species tested were 53 at $t_{33\,h}$ and 21 at $t_{21d}$. Two (*L. minimum* and *N. galapagensis*) and six (*A. filifolia*, *Laguncularia racemosa*, *L. minimum*, *Maytenus octogona*, *N. galapagensis*, *S. spicata*) species revealed an SDPi of 0% at $t_{33\,h}$ and $t_{21d}$, respectively (Table 2).

Species distributions across the archipelago (number of islands where present) was not significantly associated with their SDPi (*Z*(18) = 0.6, $p_{t33\,h}$ = 0.567; *Z*(16) = −1.2, $p_{t21d}$ = 0.227). The same is true when considering historical land connections between current islands. In other words, island geodynamic history did not help explain species distribution ranges (*Z*(18) = 1.1, $p_{t33\,h}$ = 0.280; *Z*(16) = −1.9, $p_{t21d}$ = 0.061) (Appendix S1; Table S16).

# 4 | DISCUSSION

Our experiments revealed lower sea dispersal potential than expected for littoral plant species, which questions the general

**TABLE 1** Origin of the species (endemic or native: nonendemic natives), diaspore type, number of tested diaspores per species (N), percentages of floating (% Floating) and viable seeds (% Viability) as control values before experimentation ($t_0$)

| Species | Family | Origin | Fruit type | Diaspore tested | N seeds tested | $t_0$%Floating | $t_0$%Viability | Time floating (h)* |
|---|---|---|---|---|---|---|---|---|
| Alternanthera filifolia+ | Amaranthaceae | Endemic | Utricle | Infructescence | 200 | 100 | 65 | 72 |
| Avicennia germinans– | Verbenaceae | Native | Capsule | Fruit | 200 | 100 | 100 | 499 |
| Batis maritima*+ | Batidaceae | Native | Drupe-like | Seed | 100 | 100 | 90 | 499 |
| Cyperus laevigatus*+ | Cyperaceae | Native | Achene | Seed | 52 | 100 | 85 | 499 |
| Heliotropium curassavicum+ | Boraginaceae | Native | Nutlet | Seed | 181 | 100 | 75 | 499 |
| Hibiscus tiliaceus+ | Malvaceae | Native | Capsule | Seed | 191 | 100 | 95 | 499 |
| Hippomane mancinella– | Euphorbiaceae | Native | Drupe-like | Fruit | 200 | 100 | 90 | 499 |
| Ipomoea pes-caprae+ | Convolvulaceae | Native | Capsule | Seed | 200 | 100 | 85 | 499 |
| Laguncularia racemosa– | Combretaceae | Native | Drupe-like | Fruit | 200 | 99 | 100 | 432 |
| Lycium minimum+ | Solanaceae | Endemic | Berry | Fruit | 200 | 0 | - | 3 |
| Maytenus octogona+– | Celastraceae | Native | Capsule | Fruit | 200 | 77 | 90 | 360 |
| Nolana galapagensis+ | Solanaceae | Endemic | mericarp | Fruit | 150 | 42 | - | 0.04 |
| Portulaca oleracea ~+ | Portulacaceae | ? | Capsule | Seed | 448 | 93 | 25 | 499 |
| Prosopis juliflora– | Mimosaceae | Native | Pod | Fruit | 200 | 100 | 95 | 499 |
| Rhizophora mangle– | Rhizophoraceae | Native | Berry | Fruit | 100 | 100 | 100 | 499 |
| Scaevola plumieri– | Goodeniaceae | Native | Drupe | Fruit | 200 | 92 | 90 | 499 |
| Scutia spicata+ | Rhamnaceae | Native | Nutlet | Fruit | 390 | 95 | 89 | 432 |
| Sesuvium portulacastrum+ | Aizoaceae | Native | Capsule | Seed | 200 | 1 | 61 | 499 |
| Trianthema portulacastrum+ | Aizoaceae | Native | Capsule | Seed | 200 | 48 | 62 | 499 |

*Note*: Asterisks indicate those species whose seeds were requested from seed banks. *Portulaca oleracea* seeds (~) were sampled from the coast of Alicante (Spain) and subjected to experimentation, assuming similar responses to its close relative *Portulaca howellii*. Number of hours that diaspores remained floating is shown. Signs '+' and '–' indicate whether diaspores where sampled directly from the plant or from the floor, respectively.
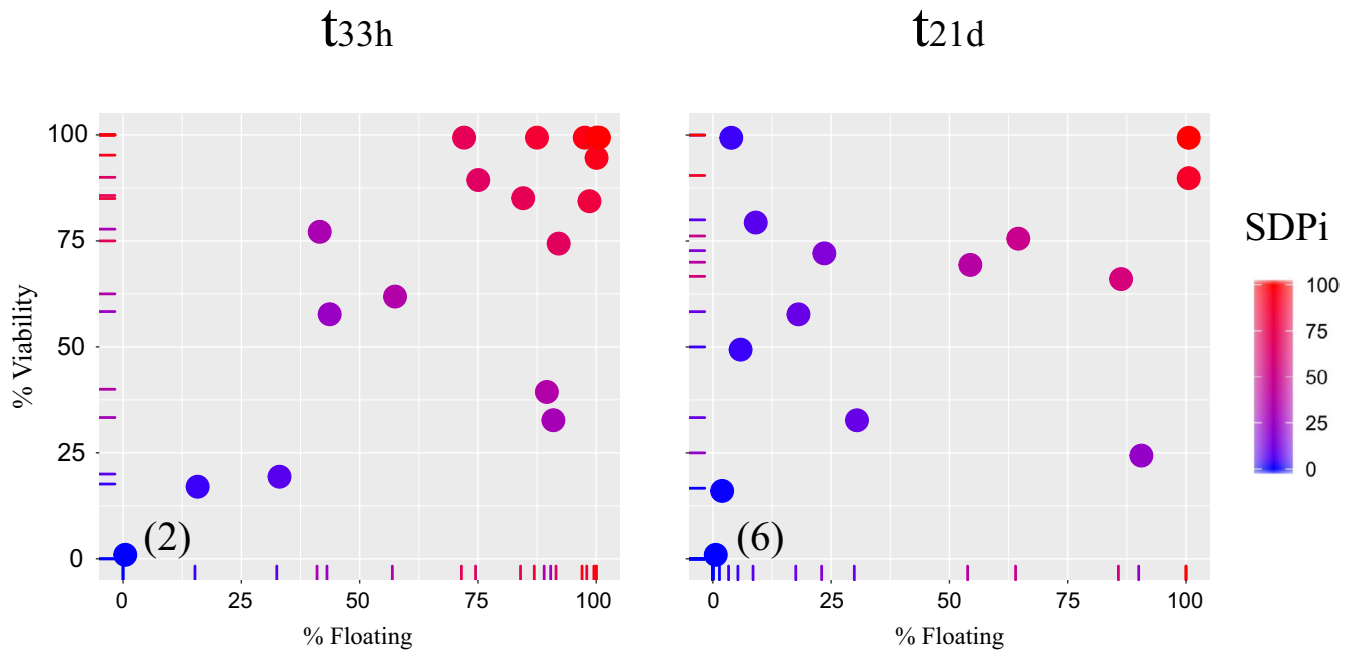
**FIGURE 3** Scatterplot representing each species SDP index (blue-red scale) as the combination of the percentage of diaspores floating and embryo viability at measuring times $t_{33h}$ and $t_{21d}$. Numbers in brackets indicate the number of points (species) with the same % Floating and % Viability

assumption that many of them are well adapted to sea salt conditions, including sea currents favouring long-distance dispersal of salt-tolerant seeds (Carlquist, 1966; Davy & Figueroa, 1993; Guppy, 1906; Ridley, 1930). In addition, greater thalassochorous potential was not associated with broader species distributions across the archipelago, which suggests that thalassochorous traits alone cannot explain island colonization of native plants across the Galápagos (Vargas et al., 2014). Taken all together, our results reveal highly variable sea dispersal potential among littoral species and question the assumed pivotal role of sea dispersal adaptations in interisland colonization (e.g., Guppy, 1906; Porter, 1983; Ridley, 1930).

## 4.1 | Thalassochorous specializations of the littoral flora

Galápagos littoral plants are often assumed to be highly adapted to extreme habitat conditions under constant sea spray (Porter, 1983). Although 17 of the 19 littoral species we tested (90%) showed some capacity to float and remain viable in saltwater for short periods of time, only 10 species showed an SDPi >50% at $t_{33h}$ and the majority of species (16 spp.) had SDPi <50% at $t_{21d}$ (Table 2).

There is, however, a substantial variation in sea dispersal potential across species, which suggests different levels of adaptation to thalassochory. Only *Hippomane mancinella* and *R. mangle* exhibited very high floatability and viability over long dispersal periods. These results partially support previous expectations for mangrove species, which are thought to include some of the angiosperm species best adapted to sea dispersal (Allen & Krauss, 2006; Clarke et al.,

2001). However, two more mangroves (*Avicennia germinans* and *Laguncularia racemosa*) showed high floatability and embryo survival over short periods of time (33 h), with both dropping considerably at longer intervals (21 days). Together with the negligible thalassochorous potential shown by some species at the beginning of the experiment (*Lycium minimum*, *Nolana galapagensis*, *P. oleracea* and *Trianthema portulacastrum*), these results indicate that the sea dispersal potential of the Galápagos littoral plants as a whole is not as high as historically considered (Carlquist, 1967; Guppy, 1906; Porter, 1983; Ridley, 1930). Geographical conditions should make dispersal even more difficult over longer distances in continent-archipelago colonization, such as that of the Galápagos from South America (1000 km) (but see Fajardo et al., 2019). Thus, our results suggest that large bodies of seawater are an important dispersal filter, even for some of the most typically abundant littoral plants that occur in the salt spray zone of the Galápagos.

## 4.2 | Applications of the SDPi

A novel metric to test sea dispersal potential for any plant is herein proposed by formulating a simple index based on floatability and seed viability. Mean SDPi values of 53% at $t_{33h}$ and 21% at $t_{21d}$ were obtained for the 19 species tested. This index gathers information on the two main drivers of thalassochorous dispersal: (a) proportion of diaspores floating, and (b) proportion of viable embryos after exposure to seawater. Both rates depend on time to dispersal given by the geographical context under study. Comparing these results with a priori categorization of the species' LDD syndromes

**TABLE 2** Littoral species included in the experiments ranked according to their distribution across the archipelago (number of islands where present) (Vargas et al., 2014).

| Species | N islands | N paleo-islands | $t_{33h}$ % Floating | % Viability | SDPi $t_{33h}$ (%) | $t_{21d}$ % Floating | % Viability | SDPi $t_{21d}$ (%) | LDD syndromes (Vargas et al., 2014) |
|---|---|---|---|---|---|---|---|---|---|
| *Alternanthera filifolia* | 10 | 6 | 41 | 77.8 | 32 | 0 | - | 0 | UNS |
| *Heliotropium curassavicum* | 10 | 4 | 56.9 | 62.5 | 36 | 17.5 | 58.3 | 10 | UNS |
| *Rhizophora mangle* | 10 | 5 | 100 | 100 | 100 | 100 | 100 | 100 | THA |
| *Sesuvium portulacastrum* | 10 | 5 | 89 | 40 | 36 | 29.9 | 33.3 | 10 | THA |
| *Trianthema portulacastrum* | 10 | 5 | 32.5 | 20 | 7 | 5.3 | 50 | 3 | THA |
| *Avicennia germinans* | 9 | 6 | 97 | 100 | 97 | 3.3 | 100 | 3 | THA |
| *Maytenus octogona* | 9 | 6 | 74.5 | 90 | 67 | 0 | - | 0 | END |
| *Prosopis juliflora* | 9 | 5 | 99.5 | 95.2 | 95 | 8.5 | 80 | 7 | THA |
| *Laguncularia racemosa* | 8 | 5 | 71.5 | 100 | 72 | 0 | - | 0 | THA |
| *Lycium minimum* | 8 | 5 | 0 | - | 0 | 0 | - | 0 | END |
| *Portulaca oleracea* | 8 | 4 | 15.2 | 17.6 | 3 | 1.4 | 16.7 | 0.2 | THA, UNS |
| *Scutia spicata* | 8 | 5 | 43.1 | 58.3 | 25 | 0 | - | 0 | END |
| *Ipomoea pes-caprae* | 7 | 3 | 98 | 85 | 83 | 85.7 | 66.7 | 57 | THA |
| *Batis maritima* | 6 | 3 | 84 | 85.7 | 72 | 23 | 72.7 | 17 | THA |
| *Hippomane mancinella* | 5 | 3 | 100 | 100 | 100 | 100 | 90.5 | 90 | END, THA |
| *Hibiscus tiliaceus* | 4 | 2 | 86.9 | 100 | 87 | 63.9 | 76.2 | 49 | THA |
| *Nolana galapagensis* | 4 | 2 | 0 | - | 0 | 0 | - | 0 | THA |
| *Scaevola plumieri* | 4 | 2 | 91.5 | 75 | 69 | 90.0 | 25 | 22.5 | END, THA |
| *Cyperus laevigatus* | 2 | 2 | 90.4 | 33.3 | 30 | 53.9 | 70 | 38 | THA, UNS |
| Mean | | | 66.9 | 72.9 | 53 | 30.7 | 64.6 | 21 | |

*Note*: Sea Dispersal Potential index (SDPi) at $t_{33h}$ and $t_{21d}$ (after 33 h and 21 days of immersion in saltwater), corresponding to the minimum time needed to reach the nearest and the farthest island, respectively (SDPi = % Floating$_t$ * % Viability$_t$/100). The percentages of floating diaspores and viability of embryos at each measuring time are shown. Categorization of the LDD syndromes as in Vargas et al. (2014).

Abbreviations: END, endozoochory; THA, thalassochory; UNS, unspecialized.

based exclusively on morphological traits, we observed that species categorized as thalassochorous showed a significantly higher SDPi compared to nonthalassochorous plants only at $t_{21d}$. This result suggests that the presence of specialized tissues favouring thalassochory may confer an important advantage for the colonization of distant islands, but their effects are negligible when considering the colonization of nearby islands. For some species, the low SPDi calculated here contrasts with the assumed functional thalassochorous potential inferred exclusively from morphological traits. For instance, an indisputably littoral species considered thalassochorous by numerous authors is *Nolana galapagensis* (Wiggins & Porter, 1971), which showed an SDPi of zero at both $t_{33h}$ and $t_{21d}$. Its endemic status is, however, compatible with the loss of dispersal potential in the course of speciation; further SDPi analysis of its sister species (*N. adansonii*), also distributed along coastal areas of America (Peru, Chile), may shed light on loss of dispersability in *Nolana* (Dillon et al., 2007). In contrast, *Maytenus octogona* was not previously considered thalassochorous but showed a high SDPi over short floating times ($t_{33h}$ = 67%) (endozoochorous in Vargas et al., 2014; but see diplochory in Valcárcel & Vargas, 2014). Therefore, experimentation continues to be essential to elucidate the biology of dispersal potential for each species (Table 2). Interestingly, diaspore length explained 70% of the variability in SDPi at $t_{33h}$ (with longer diaspores having a greater thalassochorous potential), suggesting that it may be a relatively good predictor of sea dispersal potential at this scale, as suggested by Darwin (1859).

The methodology for calculating the index permits overcoming the delicate balance between the proportion of plants that can be tested and the time required for experimentation. Our approach facilitates comparisons across plant species, higher taxa and regional floras, for a given set of dispersal ranges. In this case, $t_{33h}$ and $t_{21d}$ were relevant to test our specific hypothesis for littoral species in the Galápagos geographical context. To illustrate this idea, we estimated mean dispersal times required for colonization of the nearest and farthest islands in three oceanic archipelagos, namely the Canaries: 21 h/9 days; the Azores: 23 h/18 days; and Hawaii: 29 h/21 days (see Appendix S1; Tables S11–S14). Therefore, implementation of the SDPi at different time scales is required for comparing floras of each archipelago. To assess a general pattern for diaspore floatability and viability of any littoral species, experimentation over longer periods is needed (i.e., functional curves) (see floatability assessments from the LEDA database, Kleyer et al., 2008). This assessment of sea dispersal potential characterizes any species irrespective of any spatio-temporal framework as proposed by our study, and thus allows comparison among littoral plants worldwide.

Finally, the SPD index can also be useful to compare the thalassochorous potential of conspecific seeds from different populations, or those that have undergone different natural treatments, such as secondary dispersal (see diplochory discussed in Vander Wall & Longland, 2004 and Vargas et al., 2015). For instance, we obtained higher SDPi for *Scaevola plumieri* seeds retrieved from bird

pellets, compared to those collected directly from the plant (SDPi $t_{33h}$ = 88% vs. 69%; SDPi $t_{21d}$ = 29% vs. 23%). This preliminary result suggests that birds can also play an important role in dispersing plants through secondary dispersal processes as seeds ejected over the sea during flight can potentially be disseminated to other islands via oceanic currents. However, further studies are needed to confirm the extent of this finding.

## 4.3 | Is sea dispersal potential correlated with current species distributions?

Darwin's transoceanic hypothesis considered ocean currents the vector responsible for disjunct distributions of insular organisms (Darwin, 1856). This hypothesis has been further supported using molecular and phylogenetic data for some widely distributed plants (Guo et al., 2018; Kudoh et al., 2006; Wee et al., 2014; Wu et al., 2018). However, our results show that broader distributions of littoral species are not significantly associated with a higher SDPi, which implies a low contribution of adaptations for sea drift in interisland colonization. This pattern was already suggested by floatability experiments conducted in the Galápagos for some species (Grant et al., 1975). These researchers found a low probability of interisland dispersal by sea for a set of 22 plant species (including two littoral species). However, our study shows that most littoral species (17 out of 19 species tested, 90%) can disperse by sea over relatively short distances ($t_{33h}$) and thus reach the closest islands. Such capacity could allow littoral species to establish on most islands of the archipelago by consecutively colonizing nearby islands in a 'stepping-stone' pattern, even if they cannot directly disperse over long stretches of sea. However, a greater level of detail on sea current and wind dynamics is needed, including estimates of the drifting speed of different diaspore types.

A recent study by Arjona et al., (2020) combining next-generation sequencing (ddRADseq), reciprocal causal modelling, and spatial eigenvector analysis, suggested extensive and frequent dispersal of the littoral plant *Cryptocarpus pyriformis* across Galápagos by sea currents. We could not include this species in our experiments because most collected fruits were empty. However, this species occupies long stretches of the coastal zone of many islands and each individual produces hundreds of thousands of fruits. Such a massive fruit set naturally increases the chances that at least some viable seeds might reach nearby islands after sea dispersal, thus maintaining genetic flux across the archipelago. Future studies will be necessary to test the floatability and viability of *C. pyriformis* and investigate whether its widespread distribution across the islands could be explained by short-distance dispersal between islands.

The lack of association between the sea dispersal potential and species distributions suggests that other dispersal factors and establishment requirements may have been crucial for the colonization of littoral plants. There is indeed evidence that ecological filtering has a preponderant role in shaping the distribution of oceanic island floras (Carvajal-Endara et al., 2017). Further research

should consider different factors affecting germination and establishment of a new population once its diaspores arrive in a new territory (Chambers & MacMahon, 1994; Nathan, 2006). Zoochory by birds, especially shorebirds, could also play a major role in long and short distance dispersal of Galápagos littoral plants (Carlquist, 1967; Lovas-Kiss et al., 2019; Proctor, 1968), independently of diaspore dispersal syndromes (Nogales et al., 2012). The importance of birds in seed dispersal is illustrated by frugivory (fruit consumed and no information on seed fate) and viability of dispersed seeds by Galápagos birds (8 of the 19 littoral plants tested, 42%; Appendix S1; Tables S7 and S8). Furthermore, several species have diaspores that may also favour dispersal by more than one mechanism (diplochory): such as thalassochorous/endozoochorous traits (e.g., *Atriplex peruviana*, *M. octogona*, *Scaevola plumieri*), and thalassochorous/anemochorous traits (e.g., *Conocarpus erectus*, *Physalis* spp.; see Vargas et al., 2015). One more factor affecting the current distribution of species is the time since its arrival in the archipelago (Patiño et al., 2017), which can be estimated using phylogenetic studies. Additional factors, such as stochastic processes, also contribute to distributions across archipelagos (Lomolino, 2000; Nogales et al., 2012; Vargas et al., 2012).

In summary, we interpret interisland colonization of littoral plants as a multifactorial process driven by various dispersal agents (e.g., sea currents, wind and birds), establishment conditions (ecological conditions) and stochastic events. Continued assessment of functional dispersal potentials of other floras and archipelagos applying new tools (e.g., genetics, remote sensing) and quantification of key establishment conditions (vs. stochastic factors) are required, to gain a better insight into the complex processes of plant colonization.

## 5 | CONCLUDING REMARKS

In this study, we propose a simple standardized metric (SDPi) based on diaspores' floatability and viability, which quantifies the species' thalassochorous potential for a given biogeographical context. Our experimental data suggest that littoral species in the Galápagos have lower potential for interisland dispersal by sea currents than generally considered for littoral plants. Nearby islands are likely required as stepping stones during the colonization of the archipelago. Our novel approach also provides additional species information to complement hypothetical adaptations revealed by diaspore morphotypes (syndrome categories). Surprisingly, seed floatability and viability do not seem determinant drivers of species distributions across the Galápagos. These findings point to cautious use of dispersal syndromes to make biogeographical predictions and interpretations in future ecology studies. In contrast, we stress the importance of functional experimentation, exploring other long-distance dispersal mechanisms (e.g. zoochory by shorebirds irrespective of diaspore syndromes), establishment constraints (including biotic and abiotic interactions), and stochastic processes as drivers of species distributions in oceanic archipelagos.

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### BIOSKETCH

All the authors are fascinated by island biology, with broad interests spanning from the ecology, evolution, biogeography and conservation of island biota, and a particular interest in the processes guiding the colonization of remote islands.

### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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