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The loss of dispersal on islands hypothesis revisited: Implementing phylogeography to investigate evolution of dispersal traits in *Periploca* (Apocynaceae)

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Abstract

Aim: The loss of dispersal on islands hypothesis (LDIH) posits that wind-dispersed plants should exhibit reduced dispersal potential, particularly if island populations are old. In this study, we tested this hypothesis using a detailed phylogeographical framework across different geographical scales.

Location: Mainland and island areas of the Atlantic and Mediterranean regions, including Macaronesia (Canary Islands and Cape Verde) and Mediterranean islands in the strait of Sicily.

Methods: Forty-five populations of *Periploca laevigata*, a wind-dispersed shrub, were sampled. Plastid and nuclear microsatellite data were used to reconstruct spatio-temporal patterns of island colonization, and estimates of seed terminal velocity used as a surrogate for dispersal ability under both field and common garden conditions.

Results: Our findings did not provide evidence of loss of dispersability in any island lineage. In all of the regions considered, dispersal ability was similar on island and mainland populations, or higher on islands. Contrary to LDIH expectations, lineages inferred as the oldest (western Canaries and Cape Verde) converged towards the most dispersive seed phenotype. This pattern was supported by data obtained under common garden conditions. Within the western Canarian lineage, successful dispersal was shown to be very rare among islands and extensive within islands, but dispersability did not vary significantly from older to more recent sublineages. Considering all the study islands, we found a strong, positive correlation between dispersal ability and estimates of within-island habitat availability.

Main conclusions: This study suggests that dispersal ability can be favoured on islands, possibly because traits enhancing wind dispersal are positively selected when habitat availability is high. Our results challenge broad generalizations of the LDIH, but we discuss how overlooking species' phylogeographical history may give rise to misleading conclusions.

KEYWORDS
anemochory, dispersal ability, island colonization, Macaronesia, parallel evolution, seed dispersal

1 | INTRODUCTION

Dispersal is a key process in species biology that determines colonization, persistence and genetic connectivity of populations (Cain, Milligan, & Strand, 2000; Ronce, 2007). Dispersal success largely depends on the habitat conditions where propagules arrive, which imposes strong selective pressures on dispersal-related traits (Bonte et al., 2012). Thus, some studies support the idea that populations surrounded by a matrix of unsuitable habitats evolve towards reduced dispersal capabilities due to high mortality and/or loss of propagules arriving at unfavourable sites (i.e. cost of dispersal) (Cheptou, Carrue, & Cantarel, 2008; Bonte et al., 2012). Islands, being surrounded by large extensions of unsuitable habitat for land organisms, constitute a valuable system for testing ideas relating to seed dispersal (Nogales, Heleno, Traveset, & Vargas, 2012; Borregaard et al., 2016). For instance, early hypotheses on the evolution of reduced dispersability in wild populations were inspired by island animals, when researchers described peculiar examples of flightless species (Darwin, 1859; Zimmerman, 1948).

Plants do not appear to represent an exception, and both field observations and empirical studies to date have suggested that sessile organisms also tend to produce less dispersive seeds and fruits on insular environments than those produced by close relatives elsewhere (Carlquist, 1966a,b; Cody & Overton, 1996; Fresnillo & Ehlers, 2008; Kudoh, Takayama, & Kachi, 2013). All these studies constitute examples in support of the loss of dispersal on islands hypothesis (LDIH, hereafter), which is thought to be one of the processes associated with the "island syndrome" (see discussions in Carlquist, 1966a; Whittaker & Fernández-Palacios, 2007).

Previous studies dealing with the topic of loss of dispersal have used a wide range of species and geographical frameworks. Comparisons of seed dispersal potential between fragmented and unfragmented populations (Cheptou et al., 2008; Riba et al., 2009), and mainland versus island locations (Cody & Overton, 1996; Fresnillo & Ehlers, 2008) have provided empirical evidence that selection towards reduced dispersability can be detected at different scales. These studies conclude that factors such as population age and cost of dispersal account for loss of dispersal ability in plant species. Based on these findings, one prominent prediction of the LDIH is that young populations are expected to show high dispersal ability. According to this expectation, highly dispersive seeds should be more prone to overcome water barriers, but time would not have allowed selection for reduced dispersal to act on recently founded populations (Carlquist, 1966b; Cody & Overton, 1996). The hypothesis further predicts that, following foundation, island populations will experience reduced dispersal potential within a short evolutionary time-scale (Cody & Overton, 1996; see also Cheptou et al., 2008).

However, one limitation to formally test the effect of population age on dispersal ability of island plants is that extinction-recolonization processes within island lineages are more frequent than previously thought (Emerson, 2002; García-Verdugo et al., 2009; García-Verdugo, Forrest, Fay, & Vargas, 2010). As a consequence, complex population dynamics may lead to inaccurate assumptions on population age or erroneous inferences about colonization patterns. To overcome these potential issues, detailed information on population history should be obtained for studies testing the effect of island colonization on the evolution of plant traits (Emerson, 2002; Borregaard et al., 2016). Another limitation to drawing a broad picture of the factors and conditions that drive evolution of dispersability is that the majority of studies dealing with the LDIH have focused on small island systems, or on endemics with restricted distribution ranges (Carlquist, 1966b; Fresnillo & Ehlers, 2008; Kudoh et al., 2013). Because one key assumption of the LDIH is that populations experience substantial costs of dispersal, some studies have questioned the causal link between insularity and loss of dispersal when island species may have large areas available for colonization; that is, selection associated with dispersal costs may not be strong when propagules have higher probabilities of arriving in suitable areas (see discussions in Gravuer, von Wettberg, & Schmitt, 2003; Olivieri, 2009). In sum, the LDIH has received empirical support over the years, yet the number of study cases is too limited to conclude that it represents a widespread phenomenon on islands.

In this paper, we tested the classical LDIH using a detailed phylogeographical framework and considering multiple island systems for the widespread species *Periploca laevigata* Aiton (Apocynaceae). Populations of *P. laevigata* are found in Atlantic (Canary Islands, Cape Verde) and some Mediterranean islands, as well as in mainland areas of North Africa and the Iberian Peninsula. Sampling was conducted to test the LDIH at two geographical levels: across island systems (Canary Islands, Cape Verde and Mediterranean islands) and within the Canarian archipelago, where large population numbers allow more detailed analyses than in the other island areas. As *P. laevigata* is wind-dispersed, we would expect selection to have reduced seed dispersal ability in the island setting (Carlquist, 1966b; Morse & Schmitt, 1985), particularly in the oldest island lineages (Carlquist, 1966b; Cody & Overton, 1996; Cheptou et al., 2008). As an alternative hypothesis, however, we could expect that the evolution of dispersability in this widespread species may be driven by factors other than population age or insularity, e.g. habitat availability (Travis & Dytham, 1999; Riba et al., 2009). Genetic data were generated to reconstruct phylogeographical patterns and estimate divergence times among *Periploca* lineages, thus providing a spatio-temporal framework for hypothesis testing. With this information, we aimed at interpreting the patterns of variation in dispersal ability by addressing four questions: (1) Do island populations show evidence of loss of dispersal ability when compared to mainland populations? (2) Are phenotypic differences between island and mainland populations maintained under controlled conditions? (3) Do older island lineages show reduced dispersal ability when compared to younger ones? (4) Is habitat availability on islands related to dispersal ability?

2 | MATERIALS AND METHODS

2.1 | Study species and population sampling

Periploca laevigata is an insect-pollinated, wind-dispersed shrub (Zito, Dötterl, & Sajeva, 2015) that occupies open habitats across southern

areas of the Mediterranean region and the Macaronesian islands. It is a common element in island and mainland locations of both areas, showing a nearly continuous distribution of populations across its distribution range (see Figure S1 in Appendix S1). To address the objectives of the present study, we sampled populations across the global distribution of *P. laevigata*, but focusing on the islands and the neighbouring mainland areas where the species is more common (Figure S1 in Appendix S1). Two main areas were chosen: (1) the Mediterranean islands in the Strait of Sicily (Pantelleria, Linosa, Lampedusa, Malta, Marettimo, Levanzo and Favignana) and mainland populations of Tunisia, and (2) the Macaronesian islands (Canary Islands and Cape Verde islands) and neighbouring mainland areas of NW Africa. Two populations were additionally sampled in the Iberian Peninsula for a better representation of mainland Mediterranean populations. A total of 45 populations were considered for analyses (Table S1 in Appendix S4). In the Canarian archipelago, *P. laevigata* is a common element, particularly in areas occupied by open scrub vegetation (Browicz, 1966; García-Verdugo, 2014). For large islands, sampling included five populations scattered throughout the distribution range of the species. Following previous studies (García-Verdugo, Méndez, Vázquez-Rosas, & Balaguer, 2010; García-Verdugo, 2014), populations within islands were selected to represent contrasting environmental conditions (north and south exposure). One population from each environment was considered for seed measurements. On the easternmost islands (Lanzarote and Fuerteventura), *Periploca* populations are rare, and the main subpopulations known on each island (two in each case) were sampled. In the Cape Verde Islands, sampling was restricted to the two islands that have sufficiently large populations ($N > 30$ individuals), i.e. Santo Antão and Fogo (Gomes, Leyens, Luz, da Costa, & Gonçalves, 1999), from which three populations were included in the study.

2.2 | Experimental design: Field and common garden data

From late May to June 2014, one or two fruits from 20 to 25 individuals were sampled in selected populations and transported to the laboratory. Sample sizes were smaller ($N = 12$–15 individuals) in a few cases, depending on fruit availability during field collections and their conservation status after transportation (Table S1 in Appendix S4). Only healthy fruits bearing well-developed seed were used for analyses. To optimize sampling effort among geographical areas, only a subset of the populations considered for genetic analyses in the Canary Islands was sampled for fruits. Because populations are particularly rare on the island of Fuerteventura, and strong ungulate pressure limits availability of fruiting individuals, only one population could be sampled on this island. Pod size and some seed morphological traits typically used to characterize dispersal ability in other Apocynaceae (Morse & Schmitt, 1985; Sacchi, 1987; see below) were measured in 3–5 seeds per pod and individual. To ensure that well-developed seeds within each pod were selected and thus represent the maximum dispersal ability of each individual (Sacchi, 1987), only seeds located at medium positions were chosen for analysis. A total sample size of 2443 seeds, including samples collected from Mediterranean islands

($N_{pop} = 6$), mainland areas ($N_{pop} = 4$), Cape Verde Islands ($N_{pop} = 3$) and Canary Islands ($N_{pop} = 17$) was used for estimates of dispersal ability under field conditions. To evaluate the possibility that low sample size of mainland populations may have produced biased results in seed morphological traits for this region, we used pod size as a surrogate for dispersal ability (V_t and pod size: Spearman $r = -0.74$, $p < 0.001$), and compared our field data with those obtained from extensive sampling of herbarium specimens (Table S2 in Appendix S4).

In order to assess whether the phenotypic differences observed between island and mainland plants were mainly due to genetic differences, we set up a common garden experiment in the facilities of the "Viera y Clavijo" Botanic Garden (28°03′55″ N, 15°27′43″ W, Canary Islands). Seeds for a subset of the sampled populations were germinated. Two weeks after germination, seedlings from 24 populations were included in the experiment (see Notes S1 in Appendix S2 for further details on the experimental setting). Measurements of dispersal ability under common garden conditions focused on two *Periploca* populations representative of contrasting geographical areas: Cape Verde Islands (island region, $N = 12$ individuals) and Iberian Peninsula (mainland region, $N = 20$ individuals). One fruit was randomly collected from each individual and the same traits measured in the field material were measured in five seeds per fruit.

2.3 | Estimates of dispersal ability

Seed wind dispersal ability in anemochorus species is typically inferred by estimates of seed terminal velocity (V_t), which is the highest velocity attainable by a given seed as it free falls (Sheldon & Burrows, 1973; Sacchi, 1987; Gravuer et al., 2003; Riba et al., 2009). The rationale of this mechanistic approach is that the inverse of V_t is tightly associated with the wind dispersal ability of the seed (i.e. small V_t values represent high potential for dispersal) (Sheldon & Burrows, 1973). Following previous studies, a set of seeds representative of the morphological variation found under natural conditions in *P. laevigata* (see Figure S2 in Appendix S1) were subject to free falling trials from a fixed height, and measurements of seed drop time and related morphological traits were used to construct multivariate models that best predicted V_t (see Notes S2 in Appendix S2).

Four variables (seed mass, seed length, coma length and coma mass) accounted for 82% of the variance in observed V_t values (Figure S1 in Appendix S3). Multivariate analyses were repeated with interactions between predictor variables and their combinations (e.g. coma length/coma mass) in the model, but they did not substantially improve the reasonably good fit obtained with single variables (cf. Gravuer et al., 2003; Riba et al., 2009). This model was applied to morphological measurements of the total sample size of 2443 seeds collected under field conditions and 160 seeds from the common garden experiment to obtain an estimate of dispersal ability (V_t) for each seed.

2.4 | Generation of molecular data

Silica-dried leaves from one to five individuals per population were used for DNA extraction as indicated in García-Verdugo et al.

(2015). To represent the taxa more closely related to our focal species in the genus *Periploca*, leaves obtained from herbarium specimens provided by different institutions (E, KACST, LD, LPA, MA, P, SEV, W; see Table S3 in Appendix S4) were also used for DNA extraction following the same protocols.

Molecular analyses were performed with different combinations of markers to obtain complementary datasets and represent different geographical scales. At a broad scale (i.e. whole distribution area of *P. laevigata* and its more closely related species), plastid data were generated to infer phylogenetic relationships among *Periploca* lineages (plastid dataset 1) using four regions: *mat*K, *rbc*L, *trn*L–*trn*F and *trn*T–*trn*L. This dataset, in combination with the plastid dataset 2 (sequence data within *P. laevigata*), was used to infer divergence time estimates between *P. laevigata* lineages. To construct plastid dataset 2, nine markers obtained from Shaw, Lickey, Schilling, and Small (2007) were initially tested for polymorphism using 16 (eight Macaronesian + eight Mediterranean) samples. The tree regions that showed the highest levels of polymorphism (*trn*S$^{(GCU)}$–*trn*G$^{(UCC)}$, *psb*J–*pet*A and *ndh*F–*rpl*32) were chosen to extend amplification to the total sample (N = 195 individuals). In a second level of analysis, part of the plastid dataset 2 was used in combination with nuclear microsatellite data generated in a previous study (García-Verdugo et al., 2015) to infer phylogeographical patterns within the Canary Islands and provide some insight into the evolution of dispersability at this geographical scale (Genbank accessions KX035458-KX036042 for plastid dataset 2; see Table S3 in Appendix S4 for accession numbers of plastid dataset 1).

2.5 | Phylogenetic relationships, estimates of divergence and dispersal ability at broad scales

As a first approach, we tested the monophyly of island populations. Previous studies suggest that monophyly of monotypic lineages should not be assumed because extant island populations may be the result of multiple events of colonization (Emerson, 2002; García-Verdugo et al., 2009). To examine this possibility in *Periploca*, we first conducted a phylogenetic analysis using MRBAYES 3.2 (Ronquist et al., 2012). Sequences of the plastid dataset 1 represented 28 accessions, including one sample of all the species assigned to section *Periploca* (Venter, 1997), and a representative sampling of the global distribution of *P. laevigata*: a minimum of two samples of each island setting and one sample from seven mainland populations (Table S3 in Appendix S4). Amplification conditions followed García-Verdugo et al. (2015). Sequences from two Apocynaceae species (*Petopentia natalensis* (Schltr.) Bullock and *Phyllanthera grayi* (P. I. Forst.) Venter) obtained from GenBank (Table S3 in Appendix S4) were used as outgroups (Ionta & Judd, 2007). The GTR+G was the model selected based on the Akaike information criterion implemented in JMODELTEST 0.1.1 (Posada, 2008). We ran two parallel runs of four chains each for 200 million generations, and sampling was performed every 1000th generation. We checked the stationary phase of all parameters and convergence among chains. Twenty per cent of samples were discarded as burn-in and the remaining trees were summarized into a 50% majority rule consensus tree.

In addition, divergence time estimates within *P. laevigata* lineages were generated to provide a temporal framework for hypothesis testing. We were not interested in absolute time estimates, but rather in obtaining molecular evidence to support broad classifications of island lineages as "old" or "young". To this end, the Bayesian models implemented in BEAST 1.7 (Drummond & Rambaut, 2007) and secondary age constraints obtained from Magallón, Gómez-Acevedo, Sánchez-Reyes, & Hernández-Hernández (2015) were used following a similar approach to that adopted in previous studies (e.g. Mairal, Pokorny, Aldasoro, Alarcón, & Sanmartín, 2015a). For this approach, three datasets representing hierarchical levels of phylogenetic relationships (order Gentianales, genus *Periploca* and main lineages within *P. laevigata*) were compiled from (1) data available in GenBank (order Gentianales; Table S4 in Appendix S4), (2) plastid dataset 1 (for analyses of genus *Periploca*), and (3) plastid dataset 2 (for divergence estimates within *P. laevigata*; see Notes S3 in Appendix S2 for specific details on this approach). To analyse patterns of genetic differentiation among islands and between island and neighbouring mainland populations, the combination of polymorphisms detected in plastid dataset 2 (Table S5 in Appendix S4) was used to define haplotypes (N = 5 individuals/population). Main lineages and sublineages within *P. laevigata* were identified with the parsimony algorithm implemented in TCS 1.21 (Clement, Posada, & Crandall, 2000).

Following the results of phylogenetic and population-level genetic analyses, morphological seed traits and estimates of dispersal ability were compared among the main lineages and sublineages associated with each geographical region in a nested ANOVA with "population" as a random factor nested in "region". Seed measurements for each individual were averaged. Normality and homogeneity of variances were checked for each variable, and log-transformation was applied in some cases (e.g. pod size, coma length) to meet the ANOVA requirements.

Additionally, we tested the alternative hypothesis that habitat availability may explain differences in dispersal availability across islands (e.g. Travis & Dytham, 1999; Gravuer et al., 2003). Based on a grid of 1 × 1 km of resolution, two surrogates for habitat availability were used to characterize each island: potential habitat (as inferred from a niche modelling approach; Araújo & New, 2007), and actual occupancy of *P. laevigata* (Notes S4 in Appendix S2). Estimates of dispersal ability (V_t) were averaged across populations for each island, and correlated with the two estimates of habitat availability within islands (expressed as "log km^2").

2.6 | Regional-scale analysis: phylogeographical patterns and dispersal traits within the Canary Islands

To gain more insight into the factors affecting dispersal ability in *Periploca*, we focused on the island setting with the largest population numbers (i.e. the Canary Islands), where the effect of population age on dispersal ability was tested in two scenarios. In the first one, we assumed that colonization followed the "progression rule", i.e. starting from the areas geographically closest to the mainland (and therefore harbouring the oldest populations) to those more distant,

as typically documented in many island systems (Cowie & Holland, 2006; and references herein). Such a scenario had some *a priori* support, as preliminary results in *P. laevigata* appeared to suggest that colonization of the Canarian archipelago promoted strong lineage divergence, from eastern islands (presumably, the ancestral area) to central and western ones (García-Verdugo et al., 2015). Dispersal ability (measured as V_t) was compared among areas using an ANOVA with "population" treated as random factor and nested in "area" (N = 3: easternmost, central and westernmost islands). In the second scenario tested, we used the information obtained from phylogeographical inferences (see below) before testing for differences between ancestral and more recently colonized areas. As in the first scenario, we compared V_t values in an ANOVA with "population" treated as random factor and nested in "area", but in this case populations were assigned to the areas (i.e. island/s) inferred as old or recent following phylogeographical reconstructions.

To infer phylogeographical patterns in the Canarian archipelago, we extracted sequence information from plastid dataset 2. Each island was defined as a discrete area, but the easternmost islands were not included because they were found to constitute a separate lineage, closer to mainland populations (see Results). We applied a continuous-time Markov chain (CTMC) model with a Bayesian stochastic search variable selection (Lemey, Rambaut, Drummond, & Suchard, 2009) implemented in BEAST 1.7.5. Migration rates between islands were modelled using default gamma prior distributions. A maximum clade credibility tree was generated by using the same settings previously used in the dating analysis. A Bayes Factor test was run using the SPREAD 1.0.6 software (Bielejec, Rambaut, Suchard, & Lemey, 2011) to identify migration rates with high support (BF > 2.5). Recent studies suggest that the results from this phylogeographical approach may be sensitive to population sampling, but such biases are more likely under scenarios (i.e. high migration rates, sparse genetic data; De Maio, Wu, O'Reilly, & Wilson, 2015) that do not seem to fit the conditions of our study at the Canarian archipelago scale (see Results). However, to further test the results obtained from the Bayesian approach, we estimated levels of within-population genetic diversity (i.e. expected heterozygosity at nuclear microsatellite markers and haplotype diversity) with the expectation that the areas inferred as older should display higher levels of genetic diversity than younger areas (García-Verdugo et al., 2009; Mairal, Sanmartín, Aldasoro, Manolopoulou, Culshaw, & Alarcón, 2015b). Data from nuclear microsatellite markers (García-Verdugo et al., 2015) were analysed with SPAGEDI 1.5 (Hardy & Vekemans, 2002) in order to generate genetic parameters of interest (expected heterozygosities, F_{ST} estimates, and genetic distance matrices).

3 | RESULTS

3.1 | Genetic differentiation and divergence estimates within *P. laevigata*

Phylogenetic reconstructions clearly showed that *Periploca* populations in Macaronesia do not constitute a monophyletic lineage. All samples of the easternmost Canary Islands and Cape Verde grouped together with all of the Mediterranean samples ("Mediterranean" lineage; Figure 1), whereas samples of central and western Canary Islands constituted another well-differentiated clade ("Western Canarian" lineage; Figure 1). Sequence variation across 195 samples using three complementary plastid regions revealed a total of 25 haplotypes with a strong geographical structure (Figure 2; Table S5 in Appendix S4). Thus, parsimony networks based on plastid variation (Figure 2A) and neighbour-joining reconstructions based on nuclear microsatellite data (Figure S2 in Appendix S3) suggested further differentiation within each main lineage. The Western Canarian lineage was composed of three sublineages associated with one or two islands each: Gran Canaria (b1), El Hierro + La Palma (b2), and Tenerife + La Gomera (b3; Figure 2B). Within the Mediterranean lineage, populations on the easternmost Canary Islands displayed four private haplotypes (Figure 2B), but they showed a low degree of differentiation from mainland populations according to nuclear microsatellite markers (Figure S2 in Appendix S3). Cape Verde populations displayed two private haplotypes (Figure 2C), whereas populations on Mediterranean islands showed no clear differentiation with respect to the closest neighbouring mainland populations (Figure 2D).

Dating analyses (Figure S3 in Appendix S3, Table S6 in Appendix S4) suggested that two of these island groups (Western Canarian lineage and Cape Verde sublineage) had an older origin than populations of the two other island settings. Divergence between Western Canarian and Mediterranean lineages may have started in the Plio-Pleistocene (mean = 2.61 Ma, 95% HPD = 0.51–6.59), with further differentiation around 0.5 Ma within the Western Canarian (mean = 0.49 Ma, 95% HPD = 0.06–1.42) and Cape Verde (mean = 0.56 Ma, 95% HPD = 0.08–1.60) lineages (Figure S3 in Appendix S3, Table S6 in Appendix S4). In contrast, low divergence estimates with no statistical support suggested that the easternmost Canarian and the Mediterranean populations had a very recent origin (Figure S3 in Appendix S3).

3.2 | Broad-scale analysis of dispersal-related traits

Analyses of morphological traits and estimates of seed dispersal ability revealed that island populations, particularly those of Western Canaries and Cape Verde lineages, tended to display similar fruit and seed phenotypes. Fruits on island regions were consistently bigger than those found on mainland populations, with Western Canaries and Cape Verde lineages showing the largest pod sizes (Table 1). Pod sizes measured from herbarium samples were not significantly different from those of mainland populations considered in our study (one-way ANOVA: $F_{1,59}$ = 2.45, p = .12).

The highest estimates of dispersal ability (i.e. lowest V_t values) were found in the Western Canaries and Cape Verde populations, which were significantly different from mainland populations (Table 1). Easternmost Canaries and mainland populations showed the lowest estimates of dispersal ability (i.e. highest V_t values), whereas Mediterranean islands displayed intermediate ones, but
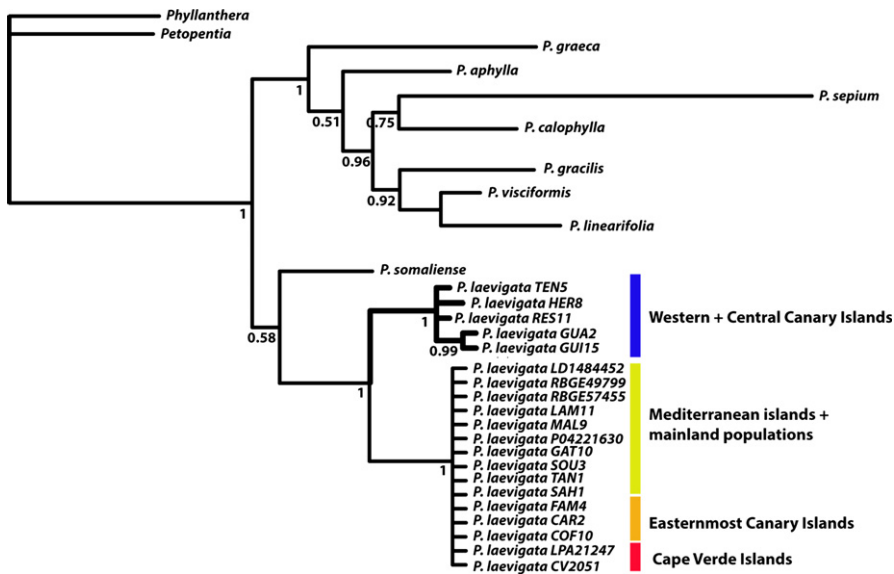
FIGURE 1 Bayesian consensus tree showing phylogenetic relationships among samples representative of the species of genus *Periploca* section *Periploca*. The two main *Periploca laevigata* clades recovered by the analysis are highlighted in the tree. Numbers in nodes indicate bootstrap (posterior probability) support
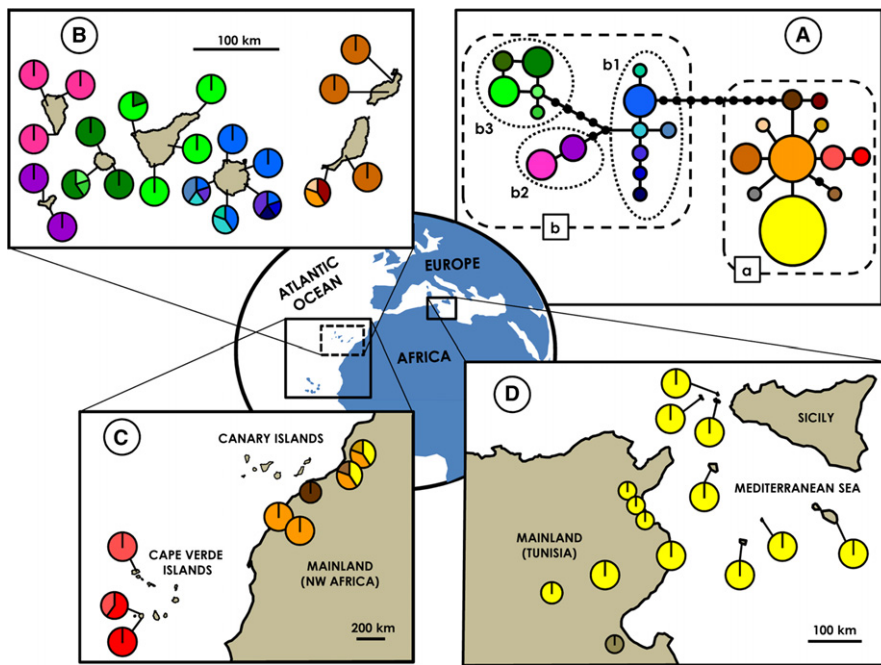

FIGURE 2 Haplotype network based on plastid polymorphism detected in 195 *Periploca laevigata* samples A and distribution of haplotypes in populations sampled in this study: Canary Islands B, NW Africa and Cape Verde Islands C and mainland Tunisia and Mediterranean islands D. The size of each pie chart is proportional to the number of individuals sampled. Black circles in A indicate missing haplotypes, and different codes identify main lineages (a, b) and sublineages (b1, b2, b3)

significantly different from those observed in mainland and Eastern Canarian populations (Table 1). Higher dispersal ability in island than in mainland populations was also supported by paired comparisons of frequency distributions (Figure 3). Thus, seeds in Western Canaries and Cape Verde lineages displayed a similar increase in dispersal ability of roughly 20% in comparison to mainland areas; such an increase was smaller (10%) in Mediterranean island populations and negligible (ca. 3%) in easternmost Canarian populations (Figure 3).

Common garden data showed that mainland individuals reared under controlled conditions experienced an increase of *ca.* 25% in seed mass and 50% in coma length with respect to fruits collected in the field. Dispersal ability, however, did not experience significant differences between field and common garden conditions in any of

the two populations, although differences in this trait between mainland and Cape Verde populations remained as large as those detected with field data and were highly significant (one-way ANOVA: $F_{1,30} = 69.9$, $p < .001$; Table 2).

Results from the niche modelling approach revealed that the potential area of habitat suitability for *Periploca* on the study islands was in all cases larger than its present occurrence, particularly on the easternmost Canarian islands (Figure S4 in Appendix S3). Correlations between surrogates of habitat availability and dispersal ability were found to be highly significant in both cases ($r^2 = .76$, $p < .001$, for occurrence data; $r^2 = .62$ $p < .001$, for niche modelling data), suggesting that islands with higher availability of potential habitats generally had populations with more dispersive seeds (smaller V_t values; Figure 4).

TABLE 1 Mean (±SE) values of morphological traits and seed dispersal ability (inverse of V_t) in *Periploca laevigata* for the geographical areas considered in this study: mainland (N = 4 populations), Mediterranean islands (N = 6), Cape Verde Islands (N = 3), easternmost Canary Islands (N = 3) and western+central Canary Islands (N = 17). Results from nested ANOVA for factor "area" (F-ratios) and significance levels are shown. Different letters among areas indicate significant differences following post hoc tests. ***$p < .001$

Area	Pod size (mm)	Seed mass (mg)	Coma length (mm)	V_t (m s^{-1})
Mainland areas	61.0 (2.1)[A]	9.3 (0.2)[A]	23.8 (0.7)[A]	0.543 (0.007)[A]
Mediterranean islands	75.7 (1.2)[B]	8.7 (0.2)[A]	31.7 (0.3)[B]	0.494 (0.005)[B]
Cape Verde islands	94.7 (2.2)[D]	12.3 (0.3)[B]	38.8 (0.6)[C]	0.443 (0.006)[C]
Eastern Canaries	82.2 (1.8)[C]	11.2 (0.2)[B]	32.7 (0.7)[B]	0.526 (0.008)[A]
West+Central Canaries	97.9 (0.9)[D]	11.6 (0.1)[B]	38.9 (0.3)[C]	0.437 (0.004)[C]
	$F_{4,25} = 15.5$***	$F_{4,25} = 11.0$***	$F_{4,25} = 23.7$***	$F_{4,25} = 19.0$***

3.3 | Regional-scale analysis: phylogeography and dispersal traits in the Canary Islands

Comparisons of V_t values across island groups under scenario A (progression rule assumed) provided strong evidence of loss of dispersal ability within the Canarian archipelago. According to ANOVA results, easternmost islands displayed lower levels of dispersal ability than central and western islands (V_t easternmost islands = 0.52 ± 0.06; V_t central islands = 0.43 ± 0.05; V_t western islands = 0.44 ± 0.05; nested ANOVA: $F_{2,14} = 27.9$, $p < .001$).

However, phylogenetic reconstructions (Figure 1), haplotype networks (Figure 2) and the pattern of differentiation inferred from microsatellite markers (Figure S3 in Appendix S3) unequivocally demonstrated that the extant distribution of *Periploca* populations in the Canary Islands is not the result of a simple pattern of colonization compatible with the progression rule. Rather, phylogeographical analyses supported the idea that the island of Gran Canaria (central islands) was the source area for subsequent dispersal to western islands (Figure 5). Although statistical support for this latter inference was moderate, genetic diversity parameters provided further evidence that Gran Canaria represented the ancestral area, as it harboured the highest levels of within-population genetic diversity at nuclear microsatellite loci ($H_E = 0.63$), haplotype diversity ($H_d = 0.52$), and number of private alleles and haplotypes (Table 3). Genetic differentiation among populations within each island (F_{ST}) was generally low, ranging from 0.03 to 0.07 (Table 3). Considering the results of phylogeographical analyses in the Western Canarian lineage, we did not find evidence that the area inferred as the oldest at this geographical scale (Gran Canaria; $V_t = 0.42 ± 0.06$) displayed less dispersal ability than more recently established populations ($V_t = 0.44 ± 0.06$; nested ANOVA: $F_{1,12} = 0.07$, $P = .93$).

4 | DISCUSSION

4.1 | No evidence of loss of dispersal ability in *Periploca* island lineages

Our results did not support the idea that island populations show reduced dispersal ability when compared to their mainland counterparts. The LDIH predicts that similar (or higher) levels of dispersability are expected between conspecific island and mainland populations when island populations are recently founded, as selection may have not acted upon dispersal-related traits yet (Cody & Overton, 1996). However, our experimental approach also allowed us to test the effect of colonization age on dispersal ability at two scales (islands-mainland, and within the Canary islands), and we did not find evidence that *Periploca* populations inferred as the oldest meet this expectation in any case. One limitation of our approach is that estimates of colonization based on molecular analyses are subject to substantial uncertainty, and thus island populations might be younger than our estimates suggest. However, we found strong evidence that Western Canarian and Cape Verde populations have experienced island conditions for a large number of generations even considering the more conservative limits obtained for our estimates (≥0.06 million years, in either case). The available data therefore suggest that loss of dispersal potential in island *Periploca* populations has not occurred yet, even though this trait has been shown to respond to selection in a few generations (Cody & Overton, 1996; see also Cheptou et al., 2008). Contrarily, evolution of seed dispersal in *Periploca* appears to have followed the opposite pattern (e.g. higher dispersal ability in Cape Verde and western Canaries versus mainland populations).

Differences in dispersal ability between mainland and old island lineages were clearly observed using data collected under field conditions, but plasticity in this trait (Riba et al., 2009; Talavera, Arista, & Ortiz, 2012) might exaggerate the magnitude of differentiation among both regions. In the present study, comparisons between field and common garden data revealed that the morphological traits more tightly related to dispersability (i.e. coma length and seed mass) are indeed significantly affected by environmental conditions. Covariance of these traits, however, resulted in similar estimates of dispersability between common garden and field conditions (Table 2). Furthermore, phenotypic correlations suggested that dispersal ability may be constrained by fruit size, particularly in mainland populations (V_t and fruit size; $r = −.74$; $p < .001$). These populations consistently displayed smaller fruit sizes, both under field and common garden conditions, than island populations. Earlier studies on *Periploca* documented that other traits, such as leaf size, follow the same pattern, which was interpreted as a
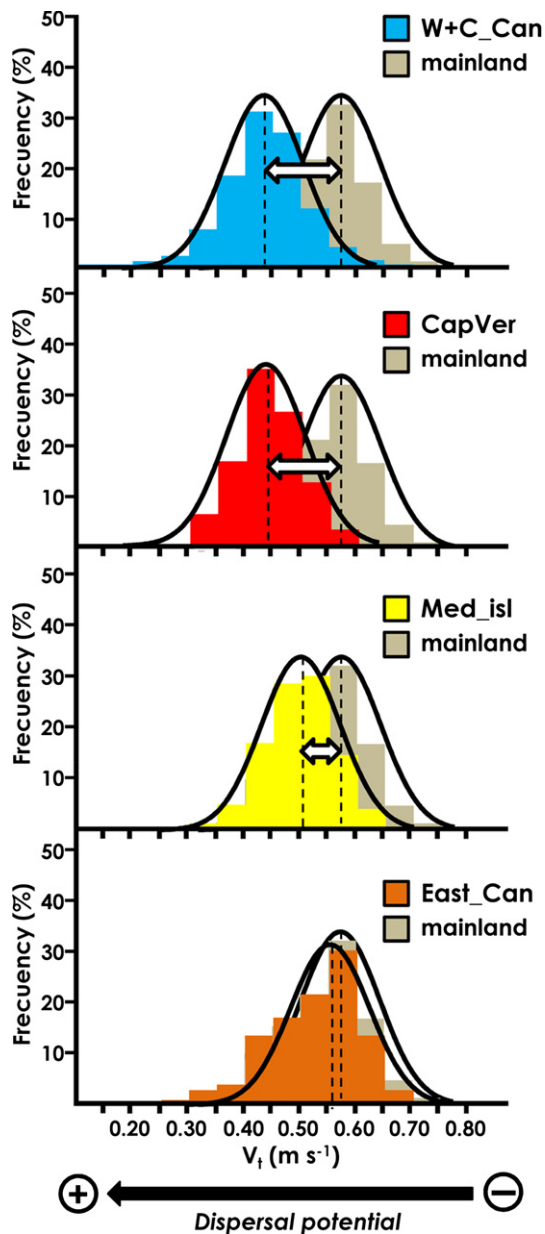
FIGURE 3 Comparison of frequency distributions of seed dispersal ability (expressed as terminal velocity, V_t) in *Periploca laevigata* between island and mainland samples considered in this study (sample sizes: mainland, N = 275; western + central (W+C) Canaries, N = 1136; Cape Verdes, N = 192; Mediterranean islands, N = 519; easternmost Canary Islands, N = 325. Each dataset was adjusted to a normal distribution, and arrows represent the magnitude of differences in mean values between mainland and island distributions

4.2 | Factors affecting dispersal ability in *Periploca* island populations

Contrary to LDIH expectations, we found that island lineages showed similar (easternmost Canaries), higher (Mediterranean islands) or substantially higher (Cape Verde and western Canaries) dispersal ability than mainland populations. Thus, another conclusion that emerges from our study is that dispersal ability may be favoured, rather than negatively selected for, on islands. This observation was reinforced by common garden data, which were indicative of a strong genetic basis for highly dispersive seeds in Cape Verde island populations. Our findings therefore suggest that colonization of the Macaronesian islands has prompted a substantial decrease in seed terminal velocity (i.e. increase in dispersal ability) with respect to mainland areas (≈20%; Figure 3; Table 2).

It is however remarkable that the levels of dispersal ability varied in a somewhat gradual pattern across island systems. At one extreme of the gradient, populations of the two oldest lineages in Macaronesia displayed very similar fruit and seed traits and estimates of dispersal ability, despite disparate genetic origins (Table 1; Figure 3). Several studies have documented that insularity promotes convergent responses across taxa, e.g. towards increased woodiness, and leaf or fruit sizes (García-Verdugo et al., 2014; Kavanagh & Burns, 2014). We hypothesize that the patterns of variation in dispersal-related traits compatible with selection for gain of dispersal on islands are explained by low dispersal costs. In *Periploca*, however, low dispersal costs cannot be associated with broad-scale patterns (i.e. frequent inter-island dispersal), as haplotype distribution across Macaronesian islands showed that island colonization in this wind-dispersed species is a very rare event (see Nogales et al., 2012; García-Verdugo, Baldwin, Fay, & Caujapé-Castells, 2014; for discussions on dispersal syndromes and colonization success). On the contrary, successful dispersal appears to be very common within islands, as we found that genetic differentiation among populations (F_{ST}) within large islands was generally low (Table 3). This result is consistent with extensive rates of dispersal within islands, particularly in large, old areas such as the islands of Gran Canaria and Tenerife, where the typical expectation among plant populations is high levels of genetic differentiation due to geographical isolation and population turnover (e.g. García-Verdugo et al., 2009; Mairal et al., 2015b).

In addition, the strong correlation found between estimates of habitat availability and dispersal ability across islands indicated that islands with higher within-island habitat availability generally have populations with more dispersive seeds. Interestingly, two large islands (Lanzarote and Fuerteventura, in the eastern Canaries) did not fit this pattern, as their populations showed levels of dispersal ability similar to those displayed by mainland populations (Table 1; Figure 4). Low dispersal ability on these islands may be the consequence of ecological (dispersal/competition trade-offs), time constraints or the co-occurrence of both factors. Increased seed size may improve competition ability (e.g. by increasing germination or survival rates), but at the cost of a poorer dispersal potential by wind due to greater propagule mass (Carlquist, 1966b; Morse & Schmitt,

response to the more stressful conditions experienced by mainland populations (i.e. high temperatures and prolonged droughts; García-Verdugo, 2014). Because leaf and fruit size tend to concomitantly decrease across environmental gradients (Herrera, 2002), low seed dispersability in mainland populations may be the by-product of allometric responses to stressful conditions (i.e. reductions in organ size).

TABLE 2 Comparison between field and common garden traits (mean values ±SE) measured in two *Periploca laevigata* populations representative of mainland (ALM, Iberian Peninsula) and island (CRU, Cape Verde) areas. Percentage of variation between field and common garden traits is shown, in addition to results (*F*-ratios) of the one-way ANOVA testing for significant differences between both data sources. **p < .01, ***p < .001, NS = non-significant

Source	Mainland (ALM)				Cape Verde (CRU)			
	Pod size (mm)	Seed mass (mg)	Coma length (mm)	V_t (m s^{-1})	Pod size (mm)	Seed mass (mg)	Coma length (mm)	V_t (m s^{-1})
Field	51.5 (2.1)	8.5 (0.3)	16.9 (0.6)	0.571 (0.010)	102.0 (3.1)	14.2 (0.4)	38.7 (0.8)	0.447 (0.010)
Common garden	58.4 (1.7)	10.6 (0.2)	25.2 (0.4)	0.593 (0.005)	102.5 (3.4)	14.7 (0.2)	43.2 (0.3)	0.469 (0.006)
%VAR	13.4	24.7	49.1	3.8	0.5	3.5	11.6	4.9
	$F_{1,33} = 6.7$**	$F_{1,33} = 69.2$***	$F_{1,33} = 76.7$***	$F_{1,33} = 2.8^{NS}$	$F_{1,34} = 0.1^{NS}$	$F_{1,34} = 0.8^{NS}$	$F_{1,34} = 11.6$**	$F_{1,34} = 2.1^{NS}$
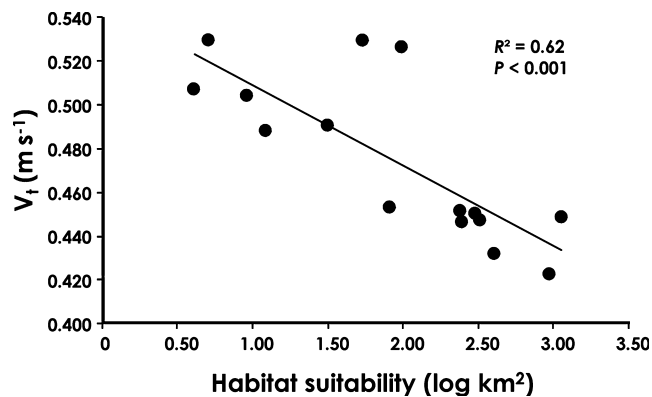
FIGURE 4 Correlation between mean dispersal ability (V_t) at the island level in *Periploca laevigata* and estimates of within-island habitat suitability (as inferred from niche modelling) across the study islands (N = 15). The two outliers correspond to the estimates for the easternmost Canary Islands

1985). Easternmost Canarian populations displayed larger seed mass than mainland populations, but the increase in dispersal mechanism (i.e. coma size) was not as large as that attained by the other Macaronesian populations, resulting in low dispersal ability (Table 1). The second possibility (limited time for increased dispersability to evolve)

is also plausible, as our genetic data suggest that colonization of the easternmost Canarian islands was recent.

Considering all these scenarios together, we can thus argue that the LDIH does not appear to represent a common phenomenon to all island taxa, but rather a condition imposed by strong dispersal costs in species with limited habitat availability and/or poor competition abilities.

4.3 | Inferring evolution of dispersal on island lineages: A note of caution

Our study illustrates that information from phylogeographical reconstructions can be essential to draw correct inferences on the evolution of dispersal ability in complex biogeographical scenarios (see also Talavera et al., 2012). Under the assumption of colonization patterns typically documented in archipelagos (Cowie & Holland, 2006) and considering taxonomic affinities between Macaronesian lineages (Venter, 1997), the scenario for *Periploca* (Figure 6a) would entail: (1) loss of seed dispersal ability in old versus more recently established populations in the Canaries and (2) phenotypic stasis of dispersal-related traits between western Canarian and Cape Verde populations.
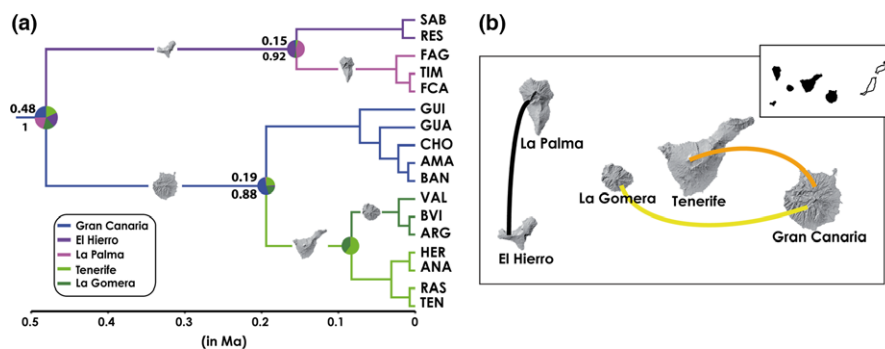

FIGURE 5 Phylogeographical reconstructions of *Periploca laevigata* populations in the Western Canarian lineage. Pie charts (a) represent marginal probabilities for potential ancestral areas (with each island represented by a different colour), whereas the colour of each branch indicates the ancestral area with the highest posterior probabilities for a given clade. Numbers in nodes show mean estimated ages of divergence (above) and Bayesian posterior probabilities (below). Migration events among islands with high Bayes Factor support are highlighted (b; colours represent the level of support: black > orange > yellow)

TABLE 3 Mean (±SE) genetic diversity indexes, number of private alleles and haplotypes (#private), and levels of within-island differentiation (F_{ST}) obtained from nuclear microsatellite (nSSR) and plastid (cpDNA) data for *Periploca laevigata* populations sampled on the islands of Gran Canaria (N = 5 populations), Tenerife (N = 4), La Gomera (N = 3), El Hierro (N = 2), and La Palma (N = 3)

Island	nSSR			cpDNA	
	H_E	#private	F_{ST}	H_d	#private
Gran Canaria	0.63 (0.04)	16	0.03	0.52 (0.21)	7
Tenerife	0.46 (0.01)	3	0.05	0.10 (0.10)	2
La Gomera	0.54 (0.01)	5	0.07	0.23 (0.23)	3
El Hierro	0.43 (0.02)	5	0.06	0.00 (0.00)	1
La Palma	0.40 (0.05)	2	0.06	0.00 (0.00)	1

Our phylogenetic and phylogeographical reconstructions, however, clearly showed that such inferences would be erroneous. First, Western Canarian and Cape Verde populations are not as genetically close as assumed thus far, most probably because parallel evolution of morphological traits between archipelagos confounded early taxonomic interpretations. Second, a simple pattern of colonization consistent with the progression rule was rejected in the Canarian archipelago due to: (1) coexistence of two well-differentiated lineages, most likely associated with multiple waves of colonization, and (2) inference of colonization routes within the western lineage not compatible with an east-to-west pattern. Thus, phylogeographical information generates a scenario (Figure 6b) which is remarkably divergent from the currently mainstream theory in that it (1) features no evidence of loss of dispersal ability associated with island colonization and (2) suggests parallel evolution of dispersal ability

between western Canaries and Cape Verde populations. Alternative scenarios of island/mainland colonization are not supported by the available data. For instance, back-colonization of mainland areas from the central Canaries (lineage B) appears to be a very unlikely explanation for the observed patterns; it would imply the occurrence of a massive extinction of *Periploca* in the continent and, more importantly, it would not be consistent with the topology of our phylogenetic reconstructions (lineage A is not embedded within lineage B, but both of them are separated into two well-supported clades). In contrast, deep phylogeographical and niche modelling analyses of mainland *Periploca* populations (García-Verdugo et al. in preparation) and population genetic studies (García-Verdugo et al., 2015) suggest that Atlantic coastal areas in NW Africa served as refugia during the Plio-Pleistocene, from which recolonization of the Eastern Canaries and dispersal to Cape Verde likely occurred in the last 0.5 Myr.

5 | CONCLUSIONS

Dispersal costs are not necessarily the same for every island species due to substantial variation in their colonization capabilities, and in the features of the islands they colonize. In general, species with high colonization abilities on large islands will have higher probabilities of arriving at suitable habitats following long-to-intermediate-distance dispersal than species with very specific habitat requirements or poor dispersal potential. This notion suggests that loss of dispersal potential on islands is context-dependent, and that evolution towards gain of dispersal ability within islands is also a plausible
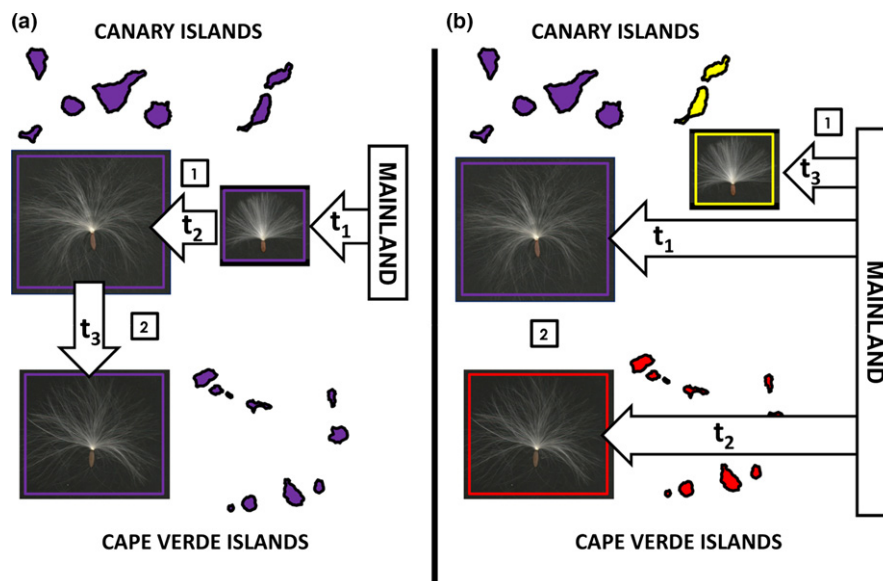

FIGURE 6 Diagram showing contrasting inferences (represented by numbers; see main text) on the evolution of dispersal traits in Macaronesian lineages of *Periploca laevigata* depending on the biogeographical scenario considered: (a) assuming monophyly of *Periploca* in the islands, with colonization starting on the easternmost Canary Islands, followed by colonization of central and western islands and Cape Verdes; and (b) implementing phylogeographical reconstructions that support three waves of island colonization: western and central Canaries, Cape Verdes, and easternmost Canaries. Arrows represent colonization events at different periods of time (t_1, t_2, t_3)

option under certain circumstances. However, lack of detailed information on the patterns of island colonization may produce misleading results when testing hypothesis of dispersal across islands. Such misinterpretations are more probable in study cases that underlie complex phylogeographical signatures (e.g. widespread lineages, islands geographically close to mainland areas and/or dramatically affected by local extinctions).

AUTHOR CONTRIBUTIONS

G. C.-V. and J. C.-C. conceived the ideas; C. G.-V., M. S., P. M. and J. C.-C. collected the samples; C. G.-V. and M. M. analysed the data; C. G.-V. wrote the paper, with input from all other coauthors.

DATA ACCESSIBILITY

DNA sequences: Genbank accessions KX035458-KX036042 (plastid dataset 2; see Table S4 in Appendix S4 for accession numbers of plastid dataset 1)

Microsatellite data: Demiurge D-NMICR-106 and Dryad https://doi.org/10.5061/dryad.9nc22.

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BIOSKETCH

All the members of the research team are interested in plant evolution, and we preferentially use widespread island species to test hypotheses relating to lineage differentiation. By combining different sources of information (molecular and phenotypic data) and approaches (field and common garden experiments), we aim at investigating the processes and mechanisms involved in early speciation.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.