

Baker's law and the island syndromes in bryophytes

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Summary

1. The evolution of island syndromes has long served as a model to understand the mechanisms accounting for phenotypic differentiation. Combining literature data with actual observations, we determine whether typical syndromes such as the loss of dispersal power and the bias towards self-compatibility (Baker's law) apply to vagile organisms, using bryophytes as a model.

2. The life-history traits (LHTs) observed in oceanic island floras were statistically different from those observed on continents, evidencing the evolution of island syndromes. In contrast, LHTs of continental and continental island floras were similar, pointing to differences in migration intensity between continents, continental islands and oceanic islands.

3. The proportion of bisexual species was significantly higher on oceanic islands than on continents. A significant proportion of species that are unisexual or bisexual on continents shifted towards exclusive bisexuality on oceanic islands, suggesting that Baker's law applies to bryophytes. The underlying mechanisms, however, probably differ from *in situ* selection for selfing.

4. The proportion of species producing specialized asexual diaspores, which are assumed to play a role in short-distance dispersal (SDD), was higher on oceanic islands than on continents. The proportion of species producing spores, which are involved in long-distance dispersal (LDD), exhibited the reverse trend, suggesting a shift in the prevalent reproductive strategy to favour SDD on oceanic islands. Approximately 50% of the species, however, maintained the ability to produce sporophytes on oceanic islands, and the relative frequency of fertile shoots within collections of four model species was even higher on islands than on continents.

5. *Synthesis.* Bryophytes exhibit typical island syndromes, indicating that migration rates between oceanic islands and continents are not sufficient to prevent the effects of genetic drift and contradicting the view that the sea does not impede migration in the group. Significant shifts in life-history traits (LHTs) towards increased production of specialized asexual diaspores and decreased sporophyte production on oceanic islands indeed point to a global loss of long-distance dispersal (LDD) ability. The maintenance of traits characteristic for LDD in a large number of species has, however, substantial consequences for our understanding of island plant evolution, and in particular, for our vision of islands as evolutionary dead ends.

Key-words: Baker's law, dispersal, island syndrome, life-history trait, liverwort, mating system, moss, oceanic island

Introduction

Reproduction and dispersal are intrinsically linked in plants, as the primary mode of dispersal (spores or seeds) is the

product of sexual reproduction. The association between mating system and dispersal has, however, led to various and often conflicting predictions (see Cheptou 2012 for review). In fact, successful colonizers should exhibit life-history traits (LHTs) promoting dispersal and establishment on the one hand, and diversification on the other (Crawford, Anderson & Bernardello 2011), which may not necessarily be compatible.

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Because sexual reproduction is possible from a single self-compatible individual, Baker's law predicts that, in flowering plants, 'occurrence in localities most likely to have been reached by more or less long-distance dispersal (LDD)' is correlated with the development of self-compatibility (Baker 1955, 1967). This prediction has been supported by an important body of evidence (see Crawford, Anderson & Bernardello 2011 for review). Similar observations were made during the colonization process of invasive species outside of their native range (Ward, Johnson & Zalucki 2012; but see Colautti, White & Barrett 2012), in agreement with Baker's (1955) observation that 'the vast majority of weeds are self-compatible or possess strong powers of vegetative reproduction'.

Some of the most striking cases of radiations were, however, shown to have originated from self-incompatible ancestors (see Crawford, Anderson & Bernardello 2011 for review). Furthermore, the proportion of dioecious species peaks in islands such as Hawaii (14.5%), which is the highest level of dioecy in angiosperms world-wide (Sakai *et al.* 1995). Modelling the joint evolution of seed dispersal and self-fertilization when local pollen limitation varies stochastically over time, Cheptou & Massol (2009) predicted that successful colonizers should either be outcrossing dispersers or non-dispersing selfers. While the advantages of selfing for island colonization are apparent, selection of outcrossing mechanisms after establishment and 'escape from homozygosity' are, in fact, often seen as an essential pre-requisite for subsequent radiation (Barrett 1996). Metapopulation viability is dependent on the selfing rate because of the demographic effect of inbreeding depression, so that the likelihood of establishing a new population is identical for two nearby outcrossing colonizers and for a single selfer (Dornier, Munoz & Cheptou 2008).

In contradiction with the idea that selfers predominate on oceanic islands because of enhanced chances for sexual reproduction, and hence, dispersal, island biogeography theory further predicts that insular organisms typically lose their dispersal power (Carlquist 1965; Whittaker & Fernández-Palacios 2007). Although experimental support for this prediction is equivocal (contrast, e.g. Cody & Overton 1996 and Fresnillo & Ehlers 2008; Talavera, Arista & Ortiz 2012), oceanic islands are therefore traditionally perceived to be evolutionary dead ends (Bellemain & Ricklefs 2008). These predictions are similar to theoretical metapopulation studies suggesting that dispersal ability significantly decreases along a successional gradient owing to genetic differences between young and old populations (Olivieri, Michalakakis & Gouyon 1995). Models that take plasticity in dispersal trait variation into account, however, predict that selection should generally favour strategies allowing plants to increase their dispersal rate with population age (Ronce *et al.* 2005).

Bryophytes potentially offer an insightful model to address the application of such typical island syndromes such as Baker's law and the loss of dispersal power. Bryophytes disperse by spores and asexual diaspores, which are assumed to play a complementary role, the former contributing to random LDD and the latter to frequent short-distance dispersal (SDD;

Löbel, Snäll & Rydin 2009). If the loss of dispersal power hypothesis holds true in the group, island bryophytes would be expected to shift reproductive strategies towards increased levels of asexual reproduction. Previous investigations failed to demonstrate a significant loss of dispersal ability on islands (Hutsemékers *et al.* 2011). Paradoxically, however, the number of individuals of clonal origin was higher in island populations as compared to continental ones (Hutsemékers *et al.* 2011), suggesting a shift in the prevalent reproductive strategy to favour SDD.

Bryophytes further display a wide range of mating systems with an unparalleled evolutionary lability, with at least 133 transitions between sexual systems in mosses (McDaniel, Atwood & Burleigh 2013). The application of Baker's law in the group is, however, challenged by the fact that selection for selfing is reduced when multiple founder events occur (Busch 2011), a condition that has been reported in several instances (Hutsemékers *et al.* 2011; Laenen *et al.* 2011; but see Karlin *et al.* 2011). Yet, two specific features of bryophyte biology suggest that Baker's law might still be relevant in the group.

On the one hand, although sperm cells might tolerate desiccation for extended periods (Shortlidge, Rosenstiel & Eppley 2012), sexual reproduction depends on sperms swimming to eggs via a continuous film of water. As a consequence, fertilization ranges, which are of one to a few tens of decimetres (Bisang, Ehrlén & Hedenäs 2004; Rydgren, Cronberg & Økland 2006), are extremely short as compared to angiosperm's pollen ranges. On islands, this renders the issue of having both sexes occurring within the close vicinity of each other following LDD much more acute than in flowering plants. In addition, sporophyte production in unisexual bryophytes might be compromised by a suite of specific LHTs and population features. First, bryophyte population sex ratios are frequently strongly biased (Bisang & Hedenäs 2005; Stark, McLetchie & Eppley 2010; Pereira Alvarenga, Pôrto & Zartman 2013). Secondly, a growing body of evidence suggests that conspecific male and female sex expressing individuals may exhibit contrasting ecological niches, potentially enhancing the spatial segregation of the sexes (Groen *et al.* 2010; Benassi *et al.* 2011; Pereira Alvarenga, Pôrto & Zartman 2013). Thirdly, low fecundity levels in unisexual species can be a consequence of the genetic interactions of particular male and female gametophytes (McLetchie 1996). The production of sporophytes hence relies on a restrictive conjunction of factors including the occurrence of expressed mixed-sex colonies, a short distance between male and female individuals, and favourable environmental factors (Pepin, Hugonnot & Celle 2013). Altogether, these factors account for the comparatively low production of sporophytes in many unisexual bryophyte species (Longton 1997). Production of asexual diaspores is hence of utmost importance for unisexual species. A strong association between dioecy and the ability to produce specialized asexual propagules has therefore long been identified (Longton & Schuster 1983; During 2007; but see Crawford, Jesson & Garnock-Jones 2009).

On the other hand, bisexual bryophytes may exhibit lower sporophytic inbreeding depression than unisexual ones (Taylor, Eppley & Jesson 2007). While unisexual gametophytes either outcross or undergo intergametophytic selfing (i.e. mating among haploid siblings from the same sporophyte), bisexual species are potentially capable of intragametophytic selfing (i.e. merging of gametes produced by gametophytic shoots grown-up from the same protonema, and hence, originating from the same spore), which results in a fully homozygous sporophyte generation (Taylor, Eppley & Jesson 2007). Bisexual species can thus rapidly purge recessive deleterious mutations through intragametophytic selfing and avoid the demographic effect of inbreeding depression found in the diploid phase of unisexual species (Szövényi, Ricca & Shaw 2009), which may further promote the application of Baker's law in bryophytes.

In this study, we combined an extensive literature survey with actual observations to determine whether the island syndromes apply to bryophytes. Contrasting continents; continental islands (including islands which are located on the continental shelf and may have been connected to a continent during the Quaternary ice ages, and islands formed by ancient continental fragments); and oceanic islands (islands which are of volcanic origin and have never been connected to continents) (see Whittaker & Fernández-Palacios 2007 for review), we address the following questions: (i) Does Baker's law apply to bryophytes, that is, is there a higher number of bisexual species on islands than on continents owing to the severe constraints imposed on fertilization after LDD? (ii) Do LHTs related to dispersal differ on islands and on continents? Is there, in particular, a tendency towards increased asexual reproduction and decreased sexual reproduction on islands? And (iii) are the LHTs observed in continental island floras more similar to those observed on continents or on oceanic islands, pointing to differences in the origin of continental and oceanic islands?

Materials and methods

SELECTION AND SCORING OF LIFE-HISTORY TRAITS

We explored variation in LHTs related to reproduction and dispersal depending on two factors. The factor GEO accounted for the geographical origin of the species surveyed, including oceanic islands, continental islands and continents. The few cases of island groups with a mixed continental and oceanic origin (i.e. Japan and Western Indies) were included in the continental island category. The factor TAXON accounted for the difference between mosses and liverworts, and offered independent tests of the underlying hypotheses. Hornworts should, for consistency, have been analysed separately. They are, however, a small group of about 300 species whose diversity pales in comparison with liverworts (ca. 6000 species) and mosses (ca. 10 000 species). The number of hornwort species in our data set did not warrant separate analyses, and because hornworts exhibit a suite of functional vegetative traits and ecological features that are similar to those of liverworts, the data from the two groups were merged.

The LHTs studied were the mating system, the production of sporophytes and specialized vegetative diaspores. These LHTs were

chosen because (i) the combination of mating systems and dispersal traits can help to explain reproductive constraints on islands (but see Cheptou & Massol 2009); and (ii) much information about these particular traits is available in the literature of bryophytes for different geographical regions. Mating systems included four categories: (i) unisexual (separate sexes; dioecious *s.l.*); (ii) bisexual (combined sexes; monoecious *s.l.*); (iii) unisexual and bisexual (when exhibiting both mating systems); and (iv) unknown because gametangia were never observed. A fifth group, namely functionally bisexual species (i.e. unisexual species with dwarf males growing on female plants), could potentially have been identified. The proportion of functionally bisexuals ranged, however, from 0% to 6.7% in the surveyed floras (see below), and this rare category was therefore excluded.

Species with bisexual gametophytes were considered as selfers because of the almost complete absence of constraint on fertilization and the negligible cost of inbreeding depression (Eppley, Taylor & Jesson 2007; Taylor, Eppley & Jesson 2007). This assumption has been confirmed genetically by inbreeding coefficients (F_{is}) values close to 1 in the bisexual species investigated to date (Eppley, Taylor & Jesson 2007; Hutsemékers, Hardy & Vanderpoorten 2013).

A species was considered as reproducing sexually when there was an explicit statement in the literature surveyed and/or when frequency data and descriptions or measurements of sporophytic characters were provided. Because information on seta length and spore size was often missing or incomplete, we did not include these traits in the analyses. We considered plants to produce specialized asexual propagules if they were described as having deciduous shoot apices, deciduous flagelliform shoots, bulbils, gemmae, branchlets, rhizoid gemmae, caducous or fragile leaves (following Longton & Schuster 1983). Dispersal traits were scored as 'none' when there was an explicit statement that a species lacks diaspores.

DATA COLLECTION

Information on mating systems and production of sporophytes and specialized asexual diaspores was collected in three data sets. Data set 1 resulted from the scoring of LHTs for island (considering both the endemic and non-endemic element) and continental floras world-wide. Sixty-three moss and liverwort floras were selected on the basis of the availability of recent, critical and/or updated information on species lists and reproductive traits (Data set 1, Appendix S1 in Supporting Information).

For Data set 2, we scored from the available literature the three LHTs in pairs of conspecific populations between islands and the nearest continent. Because sexual expression and production of diaspores are strongly controlled by macroclimatic factors (Schuster 1988), the choice of the closest continental areas to perform comparisons with islands was critical to ensure that all areas belong to the same biome. We assumed that the nearest continent was the main source area for islands. This assumption is supported in Macaronesia, a biogeographical region comprised of the Azores, Canary Islands and Madeira, where the bryophyte flora exhibits closer affinities with the European flora than with any of the other floras world-wide (Vanderpoorten, Carine & Rumsey 2007). Because island species are assumed to originate from a continental ancestor, and because island taxa are expected to evolve syndromes in response to the specificities of the island environment (see Whittaker & Fernández-Palacios 2007; for review), we further assumed that character states observed in islands are derived. Four pairwise comparisons, two between continental islands and nearest continent (Germany & Belgium vs. British Isles; Central America including Mexico vs. West Indies) and two between

oceanic islands and nearest continent (Iberian Peninsula vs. Madeiran & Canarian archipelagos; Scandinavia vs. Iceland), were performed in pleurocarpous mosses (Appendix S1; Data set 2). In total, we made 606 comparisons of traits documented, for each species, in floras of island and continental areas.

In Data set 3, we selected four unisexual moss species broadly distributed in Madeira, the Canaries and the Iberian Peninsula to contrast their LHTs on islands and on continents based on actual specimen observations. We selected two species known to produce sporophytes but not specialized asexual diaspores (*Isoetecium myosuroides* and *Leptodon smithii*) and two species capable of producing both sporophytes and specialized asexual diaspores (*Leucodon sciuroides* and *Orthotrichum lyellii*). Specimens were sampled from nine herbaria to cover the complete distribution of the species in the study area. Species descriptions and voucher specimens studied are provided in Appendix S2. Our sampling included 43 collections from Macaronesia and 56 from the Iberian Peninsula for *I. myosuroides*; 52 and 74 for *L. smithii*; 45 and 64 for *L. sciuroides*; and 47 and 64 for *O. lyellii*. We recorded (i) how many of the investigated collections included at least one shoot exhibiting either sporophytes or specialized asexual diaspores and (ii) the relative abundance of shoots with sporophytes and specialized vegetative diaspores (I = 1–5 shoots with sporophytes/asexual diaspores; II = 6 shoots to 50% of shoots; III > 50% of shoots; IV = absent) within each of the approximately 100 cm² (10 × 10 cm) collections.

DATA ANALYSIS

Character states observed across species may lack independence due to their phylogenetic relatedness, requiring a phylogenetic correction (Harvey & Pagel 1991). Mating systems and dispersal traits were, however, shown to shift states very quickly along moss and liverwort phylogenies (Devos *et al.* 2011; McDaniel, Atwood & Burleigh 2013). This suggests that the phylogenetic component of trait evolution is low, decreasing the chance of type I errors (Hardenberg & Gonzalez-Voyer 2013).

The variables mating system (i.e. the proportion of unisexual, bisexual or unisexual & bisexual species) and dispersal traits (i.e. the proportion of species producing specialized vegetative diaspores and sporophytes) met the criteria of normality and homoscedasticity after arcsine-square root transformation. Variation in those variables depending on the factors GEO and TAXON was explored in the 63 bryophyte floras world-wide (Data set 1) by multivariate analysis of variance (MANOVA).

Two-way analyses of variance (ANOVAS) were then carried out for each life-history trait independently depending on the factors GEO, TAXON and GEO × TAXON. Because of the trade-offs between mating systems and dispersal traits, we further explored whether production of sporophytes and asexual diaspores depended on GEO, TAXON and GEO × TAXON for each mating system separately by two-way ANOVAS. When the interaction between GEO and TAXON was significant, the two-way ANOVAS were split into two one-way ANOVAS, one for each taxon (i.e. liverworts and mosses) independently, using GEO as a factor. Average values for each LHT were then computed within each factor combination and ranked using Tukey's honestly significant difference (HSD) for multiple post hoc comparisons.

We employed Pearson's chi-squared tests to seek for differences in the proportion of unisexual and bisexual species on continents, continental islands and oceanic islands. This analysis was repeated for the endemic element in a subset of 21 floras. Chi-squared tests were also employed to seek for differences in LHTs among conspecific

populations in each of the continental and island settings (Data sets 2 and 3). The statistical analyses were carried out in R 2.14.1 (R Development Core Team 2011).

Results

GLOBAL ANALYSES OF MATING SYSTEMS AND DISPERSAL TRAITS DEPENDING ON THE FACTORS GEO AND TAXON (DATA SET 1)

Significant differences in mating systems and dispersal traits were observed depending on the factors GEO and TAXON and their interaction (Table 1a), indicating that LHT variation may change in a different way among taxa depending on their occurrence on islands or continents.

The proportion of unisexual and bisexual species varied significantly with GEO, but not with TAXON (Table 1b). There were significantly more unisexual species on continents than on continental islands, and significantly more on continental islands than on oceanic islands (Table 1b). The number of bisexual species was higher on both oceanic and continental islands than on continents (Table 1b). There was a significantly higher proportion (2/3) of unisexual than bisexual species on continents (Fig. 1). A lower, but significant bias was observed in continental islands, whereas the difference in the proportion of unisexual and bisexual species on oceanic islands was not significant (Fig. 1). The results for the endemic element of bryophyte floras were similar (Fig. S1).

The proportions of bryophyte species producing sporophytes, specialized asexual diaspores, or none of them significantly differed depending on the factors GEO and TAXON (Table 1b). Approximately 50% of oceanic island species produced sporophytes, but this proportion was significantly higher on continents and continental islands. Contrastingly, the proportion of species producing specialized asexual diaspores or failing to produce any dispersal trait was significantly higher on oceanic islands for both native and endemic species (Table 1b; Fig. S1). There was a significant interaction between GEO and TAXON for the proportion of species producing specialized asexual diaspores, which was significantly higher on oceanic islands in liverworts, but only marginally so in mosses (Table S1).

When variation in dispersal traits was analysed within each mating system individually, the proportion of species producing sporophytes was significantly higher on continents and continental islands than on oceanic islands for both unisexual and bisexual species. The proportion of species lacking both sporophytes and specialized asexual diaspores was significantly higher on oceanic islands than on continents and continental islands for both unisexual and bisexual species (Table 2). There was a significant GEO × TAXON interaction in the production of asexual diaspores in unisexual species. In fact, there was a significantly higher proportion of unisexual species producing specialized asexual diaspores on oceanic islands than on continents in mosses, but not in liverworts (Table S1). The TAXON factor also accounted for significant differences in the proportion of species producing specialized asexual diaspores between liverworts and mosses (Tables 1b and 2).

Table 1. (a) MANOVA (above) and (b) two-way ANOVA (below) of mating systems (proportion of unisexual, bisexual and unisexual & bisexual bryophyte species) and dispersal traits (proportion of species producing only sporophytes, only specialized asexual diaspores or none of them) depending on the factors GEO (continent, continental island, oceanic island) and TAXON (mosses, liverworts) in 63 bryophyte floras world-wide. Average (\pm SD) proportions of species for each mating system depending on the factors GEO and TAXON are shown in Table 1(b)

(a)								
Factor	d.f.							
GEO	12, 102							
TAXON	6, 50							
GEO × TAXON	12, 102							
	F							
	5.099***							
	3.406***							
	3.323***							
(b)								
Reproductive traits	GEO		TAXON		TWO-WAY ANOVA (F)			
	Continent (n = 29)		Continental is. (n = 14)		Oceanic is. (n = 20)		Liverwort (n = 12)	
Mating system	61.5 ± 5.3 ^a		51.0 ± 12.6 ^b		38.3 ± 12.8 ^c		49.1 ± 11.7	
	28.7 ± 5.7 ^a		34.5 ± 12.5 ^b		38.1 ± 11.8 ^b		30.8 ± 15.3	
	4.1 ± 1.3		3.6 ± 3.4		6.5 ± 9.8		6.5 ± 8.1	
Dispersal trait	87.9 ± 5.4 ^a		81.5 ± 16.1 ^a		56.6 ± 12.1 ^b		66.04 ± 22.6	
	22.6 ± 8.7 ^a		20.3 ± 16.4 ^a		32.7 ± 24.7 ^b		48.5 ± 23.2 ^b	
	5.6 ± 5.8 ^a		7.9 ± 12.8 ^a		16.7 ± 14.9 ^b		12.5 ± 17.4	
Specialized asexual diaspores only	10.694***		10.694***		10.694***		10.694***	
	3.037*		3.037*		3.037*		3.037*	
	0.204		0.204		0.204		0.204	
None	18.088***		18.088***		18.088***		18.088***	
	16.910***		16.910***		16.910***		16.910***	
	4.046*		4.046*		4.046*		4.046*	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Superscript letters indicate significant pairwise differences based on the Tukey HSD test at the 0.05 significance level. d.f., degrees of freedom; is., island.

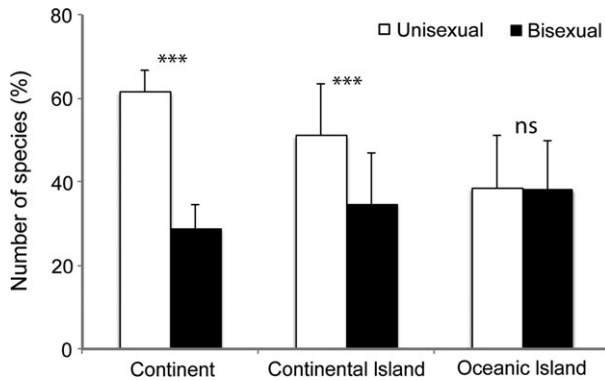


Fig. 1. Number of unisexual and bisexual bryophyte species (in percentage) on continents, continental islands and oceanic islands in 63 bryophyte floras world-wide, and associated Pearson's chi-squared test (χ^2). *** $P < 0.001$, ns = $P \geq 0.05$.

DIFFERENCES IN MATING SYSTEMS AND DISPERSAL TRAITS BETWEEN CONSPECIFIC ISLAND AND CONTINENTAL POPULATIONS (DATA SETS 2 AND 3)

There was a higher frequency of shifts from the 'unisexual and bisexual' condition to the bisexual condition in oceanic island/continent comparisons than in continental island/continent comparisons (2×2 contingency table; $\chi^2 = 7.77$, $P = 0.005$;

Table 3). Similarly, the proportion of species exhibiting shifts from known to unknown sporophyte production was significantly higher in oceanic island/continent comparisons than in continental island/continent comparisons (2×2 contingency table; $\chi^2 = 36.35$, $P < 0.001$; Table 3). The opposite trend was marginally more frequent in continental island/continent than in oceanic island/continent (2×2 contingency table; $\chi^2 = 6.99$, $P = 0.054$; Table 3) comparisons.

In *Leptodon smithii* and *Leucodon sciuroides*, the proportion of collections with a least one sporophyte was higher in collections made in the Iberian Peninsula than on the Macaronesian islands (2×2 contingency table; $\chi^2 = 6.74$, $P < 0.01$ and $\chi^2 = 6.74$, $P < 0.01$). The reverse trend was observed in *Orthotrichum lyellii* (2×2 contingency table; $\chi^2 = 30.72$, $P < 0.001$) (Fig. 2a). The relative abundance of sporophytes within the collections was significantly higher for the four species in collections made on Macaronesian islands than on Iberian regions (4×2 contingency table; from $P \leq 0.05$ to $P < 0.001$) (Fig. 2b). The proportion of collections with specialized asexual diaspores did not differ on islands and on the continent in *Orthotrichum lyellii* and *L. sciuroides* (Fig. 2a). The relative frequency of specimens producing specialized asexual diaspores within the collections was, however, significantly higher on oceanic islands in *O. lyellii* (4×2 contingency table; $\chi^2 = 56.31$, $P < 0.001$) (Fig. 2c).

Table 2. Two-way anova of the proportion of species producing both sporophytes and specialized asexual diaspores; only sporophytes; only specialized asexual diaspores; and none of these depending the factors GEO (continent, continental island, oceanic island) and TAXON (mosses, liverworts) in 63 bryophyte floras world-wide, for each of the mating systems investigated (unisexual, bisexual and both unisexual and bisexual). Average (\pm SD) proportions of species for each dispersal trait per mating system type depending on the factors GEO and TAXON are shown

Reproductive traits	GEO			TAXON		TWO-WAY ANOVA (F)		
	Continent ($n = 29$)	Continental is. ($n = 14$)	Oceanic is. ($n = 20$)	Moss ($n = 51$)	Liverwort ($n = 12$)	GEO	TAXON	GEO x TAXON
Unisexual								
Sporophyte and specialized asexual diaspores	13.6 \pm 5.5	7.2 \pm 4.8	7.1 \pm 8.1	9.2 \pm 6.7	12.4 \pm 8.2	1.405	3.523	3.957
Sporophytes only	33.9 \pm 5.9 ^a	32.8 \pm 14.1 ^a	14.0 \pm 8.2 ^b	29.2 \pm 12.7	27.3 \pm 9.5	12.533***	3.261	2.698
Specialized asexual diaspores only	4.2 \pm 2.4 ^a	4.2 \pm 4.7 ^a	7.2 \pm 7.0 ^b	4.3 \pm 4.6 ^a	8.9 \pm 5.5 ^b	3.725*	5.215*	3.785*
None	6.0 \pm 3.6 ^a	7.1 \pm 4.4 ^a	13.9 \pm 8.4 ^b	8.8 \pm 6.8	9.1 \pm 6.9	6.112**	0.858	0.755
Bisexual								
Sporophyte and specialized asexual diaspores	3.2 \pm 1.9	3.3 \pm 3.6	6.3 \pm 7.9	3.0 \pm 3.1 ^a	10.0 \pm 8.3 ^b	0.513	7.729**	0.152
Sporophytes only	26.7 \pm 9.6 ^a	30.2 \pm 11.7 ^a	20.8 \pm 9.5 ^b	26.6 \pm 9.6	19.2 \pm 12.9	3.809*	2.738	1.828
Specialized asexual diaspores only	0.1 \pm 0.8	0.1 \pm 0.4	1.4 \pm 2.6	0.4 \pm 1.2 ^a	1.9 \pm 2.7 ^b	1.813§	4.263*	1.233
None	0.9 \pm 0.8 ^a	1.2 \pm 1.0 ^a	7.0 \pm 7.9 ^b	3.2 \pm 5.7	1.9 \pm 2.2	4.051*	3.553	0.183
Unisexual and bisexual								
Sporophyte and specialized asexual diaspores	5.7 \pm 15.3 ^a	0.9 \pm 2.3 ^b	1.3 \pm 2.9 ^b	0.7 \pm 0.7 ^a	11.6 \pm 24.7 ^b	9.345***	26.625***	5.713**
Sporophytes only	—	—	—	—	—	—	—	—
Specialized asexual diaspores only	0.04 \pm 0.1	0.08 \pm 0.2	0.6 \pm 1.3	0.1 \pm 0.5	0.09 \pm 0.2	0.847	0.258	0.258
None	0.2 \pm 0.1	0.1 \pm 0.2	0.3 \pm 0.7	0.1 \pm 0.4	0.09 \pm 0.2	0.978	0.021	0.021

§ $P < 0.06$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Superscript letters indicate significant pairwise differences based on the Tukey HSD test at the 0.05 significance level. is., island.

Table 3. Number (%) of pleurocarpous moss species showing differences in mating systems and production of sporophytes and specialized asexual diaspores between islands and nearest continental areas

	Continent→Continental island		Continent→Oceanic island		χ^2 (P-value)
	Central America→Western Indies (212) (%) [†]	Belgium→Germany→UK (151) (%) [†]	Iberian Peninsula→Macaronesia (98) (%) [†]	Scandinavian Peninsula→Iceland (145) (%) [†]	
Mating system					
Unisexual and Bisexual→Unisexual	2 (1.88)	6 (3.97)	3 (4.08)	2 (1.37)	0.03
Unisexual and Bisexual→Bisexual	4 (1.88)	3 (1.98)	11 (9.18)	6 (3.44)	7.77**
Sporophytes					
Known→None	26 (12.26)	11 (7.28)	26 (26.53)	61 (44.82)	36.35***
None→Known	13 (6.13)	12 (7.94)	4 (4.08)	0 (0)	6.99[§]
Specialized asexual diaspores					
Known→None	6 (2.83)	5 (3.31)	3 (3.06)	4 (2.75)	0.02 (0.888)
None→Known	1 (0.47)	11 (7.28)	5 (5.10)	1 (0.68)	0.11 (0.739)

[†]The total number of species considered for each pairwise comparison is provided between brackets. χ^2 statistics are reported and significant differences are highlighted in bold ($\S P < 0.06$, $**P < 0.01$, $***P < 0.001$).

Discussion

DO BRYOPHYTES EXHIBIT ISLAND SYNDROMES?

Significant differences in LHTs were observed between continental and oceanic island bryophyte floras (Table 1). This finding parallels evidence for structured morphological variation in bryophytes across large geographical scales (Pereira, Zartman & Dambros 2013). These observations do not challenge the well-supported notion that bryophytes are capable of LDD (Muñoz *et al.* 2004; Sundberg 2013; Patiño *et al.* 2013a). They suggest, however, that migration rates between oceanic islands and continents are not sufficient to prevent the effects of genetic drift and particularly contradict the view that the sea is not a major impediment for migration in bryophytes (Patiño *et al.* 2013b). In fact, while recurrent colonization events were reported on islands close to continental sources in Mediterranean (Grundmann *et al.* 2007) and Canary Islands (Hutsemékers *et al.* 2011; Laenen *et al.* 2011), the limited evidence available for more remote archipelagos like Hawaii points to single colonization events (Karlin *et al.* 2011). Except for specialized asexual diaspores, which are produced by a larger number of liverwort than moss species (Longton & Schuster 1983), differences in LHTs were not explained by the TAXON factor, indicating that reproductive and dispersal traits varied in a homogeneous way in the two groups and providing independent evidence of the influence of geographical isolation on those traits.

Globally, the LHTs observed in the oceanic island bryophyte floras were statistically different from those observed in both continental islands and continents, suggesting that typical island syndromes affect the bryophyte floras on oceanic islands, but not on continental ones. Two hypotheses could explain this difference. First, the bryophyte flora of continental

islands did not originate from dispersal but from a common species pool (vicariance hypothesis), when the island was connected to the continent in a sufficiently recent past, such as the last glacial maximum, preventing divergence by genetic drift. Secondly, the comparatively short distance separating continental islands as compared to oceanic ones does not impede migration, erasing the effects of genetic drift (dispersal hypothesis). The latter hypothesis is supported in Mediterranean islands, where the short distances between islands and the continent are not an impediment for migration (Grundmann *et al.* 2007). These two hypotheses are, however, not mutually exclusive and the biota of continental islands was indeed shown to originate from a complex mix of vicariance and dispersal (Wilmé, Goodman & Ganzhorn 2006; Goldberg, Trewick & Paterson 2008; Mansion *et al.* 2009).

DOES BAKER'S LAW APPLY TO BRYOPHYTES?

The proportions of unisexual and bisexual species were similar on oceanic islands (Fig. 1). On continents and continental islands, conversely, a significantly higher proportion of unisexual species was found, reflecting the notion that about 2/3 of the moss and liverwort species are unisexual (Longton & Schuster 1983). The proportion of bisexual species in individual island floras was also significantly higher than that in continental floras (Table 1b), and significantly higher levels of bisexuality were observed among endemic species as compared to continental ones (Fig. S1). Finally, there was a higher proportion of species that are either bisexual or unisexual on continents but exclusively bisexual on oceanic islands than on continental ones (Table 3). Altogether, these observations suggest that Baker's law applies to bryophytes.

In situ selection for selfing, which has been identified as the main mechanism behind Baker's law in angiosperm

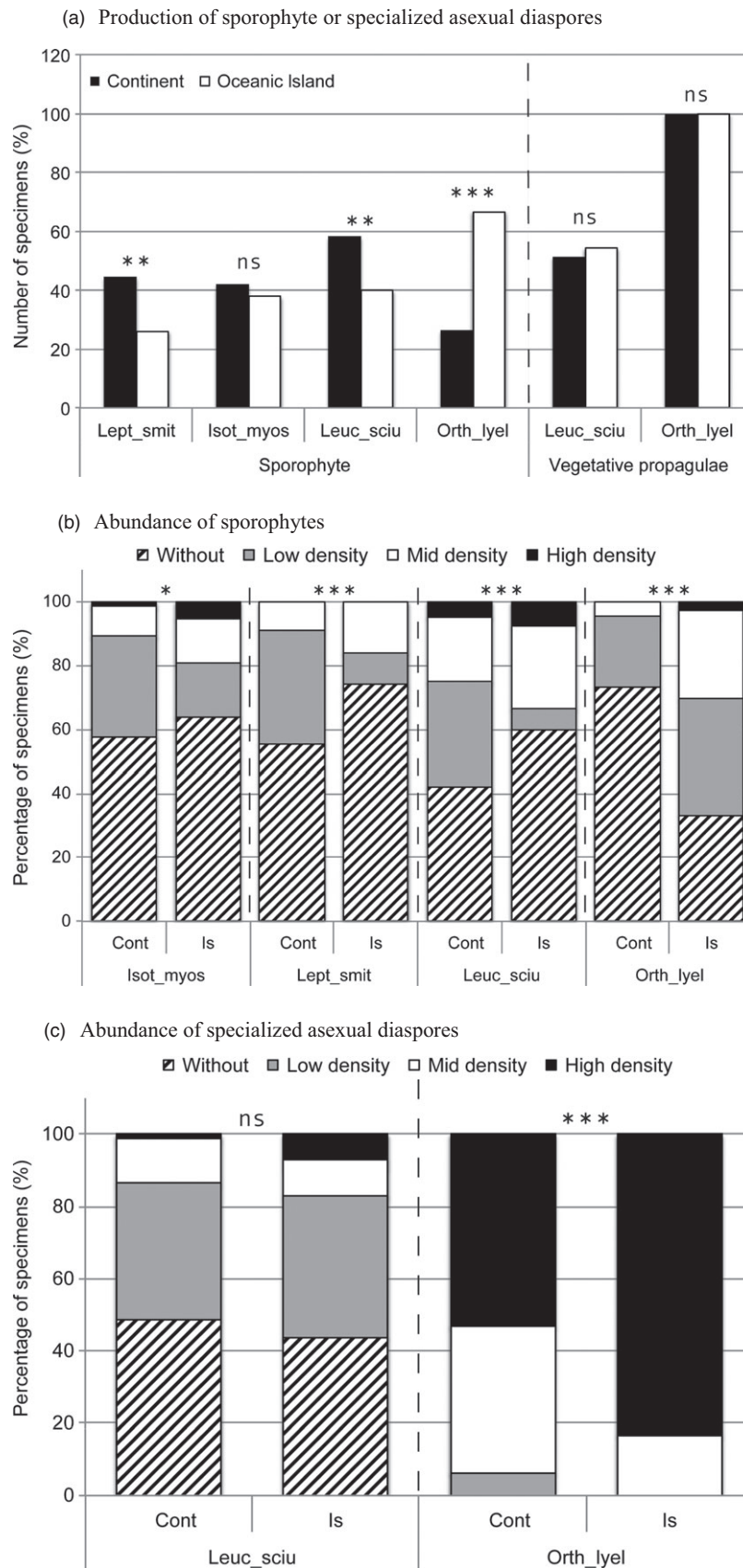


Fig. 2. Proportion of 10×10 cm colonies producing sporophytes or specialized asexual diaspores (a) and frequency of specimens within colonies with sporophytes (b) or specialized asexual diaspores (c) in the mosses *Leptodon smithii* (Lept_smit; $n = 79$), *Isoetes myosuroides* (Isot_myos; 93), *Leucodon sciuroides* (Leuc_sciu; 107) and *Orthotrichum lyellii* (Orth_lyel; 99) on continental (cont in b and c; Iberian Peninsula) and oceanic island regions (is in b and c; Madeira and the Canary Islands). Pearson's chi-squared analyses were used to test whether the percentages were significantly different.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = $P \geq 0.05$.

(Barrett 1996; Cheptou 2012) and fern (De Groot *et al.* 2012) populations with extremely weak densities following LDD might, however, not be the only underlying process in bryophytes. Living bryophyte diaspores can be found in (see Boch *et al.* 2013 for review) or on (Lewis-Smith 1999; Heinken *et al.* 2001) animals by chance, but the significance of zoochorous dispersal of specialized vegetative diaspores in explaining patterns of genetic variation has been questioned (Korpelainen *et al.* 2011). Therefore, wind has long been identified as the main vector for LDD in bryophytes (Muñoz *et al.* 2004; Sundberg 2013). The wind-dispersed units in bryophytes are the spores, which are on average smaller than asexual diaspores (Longton 1997; but see Pohjamo *et al.* 2006). A small diaspore size has in fact been identified as a critical condition for efficient wind LDD, with diaspores bigger than 20 µm in diameter becoming increasingly unlikely to be wind-dispersed (Wilkinson *et al.* 2012). As opposed to green asexual diaspores, spores further exhibit a higher resistance to frost and drought that prevail in high-altitude air currents (van Zanten 1978a,b). In bryophytes, spore production involves that the sperm swims to the archegonia via a continuous film of water, although microarthropods might locally enhance the process (Cronberg, Natcheva & Hedlund 2006). This strict reliance on water for fertilization imposes a severe constraint in the reproductive biology of unisexual species, leading to substantially lower rates of sexual reproduction in the latter. In a study on the reproductive biology of British mosses, Longton (1997) found, for instance, that 77% of the species, for which sporophytes are unknown, are unisexual, whereas sporophytes are commonly found in 30% of the bisexual species. Therefore, bisexual species may be overrepresented on islands because they produce more capsules, and hence, larger number of spores potentially able to reach oceanic islands after LDD than unisexual ones.

DO ISLAND BRYOPHYTES LOSE DISPERSAL POWER?

The proportion of species producing specialized asexual diaspores was higher on islands than on continents (Table 1b). Furthermore, oceanic island populations of *Orthotrichum lyellii* produced significantly more specialized asexual diaspores than continental ones (Fig. 2c). Conversely, a significantly higher proportion of species failed to produce sporophytes on islands than on continents (Table 2). In the moss *Syrrhopodon involutus*, similarly, a significant negative correlation between the presence of gametangia and the distance from mainland S.E. Asia was documented (Fischer 2011).

Failure to produce sporophytes on islands might merely reflect the necessity, in unisexual species, for both sexes to occur within the close vicinity of each other following LDD (Cronberg 2002). The proportion of bisexual species lacking sporophytes was, however, also higher on islands than on continents.

Environmental conditions have repeatedly been reported to affect sexual reproduction (Longton 1997), so that the observed shifts in reproductive strategies could be interpreted in terms of a more humid and buffered climate on islands. Water availability conditions sex expression and, in unisexual

species, the development of female-only populations (Benassi *et al.* 2011 for review). An oceanic island climate would hence, at first sight, promote sexual reproduction, which is not compatible with the general trend towards decreased sporophyte production reported here. Furthermore, we still found differences in LHTs between the Iberian Peninsula, Madeira and the Canary Islands, which belong to the same biome and exhibit a comparable range of climatic conditions, from arid environments to evergreen cloud forests. The interpretation that the observed shifts in LHTs are caused by differences in climatic conditions between islands and continents therefore seems insufficient to explain the observed patterns. Experimental studies under controlled conditions would, however, be necessary to disentangle the potential role of climate in the observed shifts in LHTs.

Alternatively, the observed increase in production of specialized asexual diaspores and decrease in the proportion of species reproducing sexually on islands might be adaptive. Clonal reproduction ensures rapid population growth following founding events. In fact, establishment rates in bryophytes were experimentally shown to be higher from asexual diaspores than from spores (Löbel, Snäll & Rydin 2009; Löbel & Rydin 2010). Asexual diaspores allow for early reproduction and, as compared to spores, are less sensitive to habitat quality (Löbel, Snäll & Rydin 2009). Asexual reproduction also results in the production of new gametophytes at a faster rate than sexual reproduction (Mishler & Newton 1988). These features might be crucial for establishment on islands, where the abundance of empty niches might select for fast and efficient dispersal mechanisms at the local scale (Bushakra *et al.* 1999; Lhuiller, Butaud & Bouvet 2006; Franks 2009; but see Franks *et al.* 2004).

In this hypothesis, two mechanisms might account for the lower proportion of species producing sporophytes on oceanic islands than on continents. First, although empirical confirmation is lacking in bryophytes (Algar-Hedderston, Söderström & Hedderston 2013; but see Fuselier & McLetchie 2002), theoretical models predict a negative trade-off in resource allocation between asexual and sexual reproduction (Sutherland & Vickery 1988). This idea is somewhat weakened by theoretical models predicting that, if dispersal traits are plastic, an increase in dispersal rate, and hence, of spore production should be observed (Ronce *et al.* 2005). Alternatively, recent evidence indicates that sex expression is under genetic control (Horsley, Stark & McLetchie 2011), raising the hypothesis that 'vegetative' ecotypes might be selected on islands.

While a clear pattern of decrease in sexual reproduction and increase in asexual propagation emerges from the analysis of LHTs in oceanic island bryophytes, approximately 50% of the species, however, still produce sporophytes (Table 1b). In species that are fertile in Madeira and the Canarian Islands, the density of fertile shoots per 100 cm² was even higher on islands than on the continent and in *O. lyellii*, the frequency of fertile collections exhibited the same trend (Fig. 2a,b). Altogether, these observations suggest that a substantial proportion of species maintain the potential for LDD on oceanic islands. In fact, migration rates from and towards the Macaronesian islands

derived from population genetic estimators were balanced in the moss *Rhynchostegium riparioides* (Hutsemékers *et al.* 2011). European populations of the liverwort *Radula lindenbergiana* were shown to derive from Macaronesian ancestors (Laenen *et al.* 2011). Macaronesia, with its comparatively stable climate and larger area size during the last glacial periods (Fernández-Palacios *et al.* 2011), was hence identified as a refugium where bryophyte species exhibit higher genetic diversity than on the continent (Freitas & Brehm 2001; Laenen *et al.* 2011). Altogether, these observations support mounting evidence that oceanic islands are not necessarily the 'end of the colonization road' (Bellemain & Ricklefs 2008; Harbaugh *et al.* 2009; Fernández-Mazuecos & Vargas 2011), but instead increasingly appear as reservoirs for continental floras.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Geographical regions, taxonomic group, number of species and literature sources used in Data sets 1 and 2.

Appendix S2. Description of the model species (*Isoetecium myosuroides*, *Leptodon smithii*, *Leucodon sciuroides*, *Orthotrichum lyellii*) and voucher specimens studied (Data set 3).

Figure S1. Proportion of endemic species for each mating system and dispersal trait on continents, continental islands, and oceanic islands for a subset of 21 floras.

Table S1. One-way ANOVA of the proportion of liverwort and moss species for the combinations of reproductive traits with a significant interaction of GEO and TAXON (see two-way ANOVAS results).