

Unexpected insularity effects in invasive plant mating systems: the case of *Carpobrotus* (Aizoaceae) taxa in the Mediterranean Basin

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Although biological invasions are currently recognized as being especially severe on islands, little attention has been given to detecting parameters influencing this pattern. This study tested the common perceptions that uniparental reproductive modes are associated with invasive and/or island plant populations due to a lack of pollinator vectors and/or small initial population sizes, and that pollinator services and biparental seed production modes will subsequently be associated with adjacent mainland sites. Using controlled pollination and germination experiments on invasive *Carpobrotus edulis* and *C. aff. acinaciformis* populations in both island and mainland habitats in south-east France, we found no evidence to support these hypotheses. All significant mean differences found between locations for reproductive indices describing uniparental reproductive modes were significantly smaller in island populations. In contrast, seedling sizes issuing from manual outcrossing and manual hybridization experiments, regardless of taxon, as well as *C. aff. acinaciformis* hybridization indices, were larger in island populations. The presence of significant, though limited, pollinator service was detected for all populations, and stressed the importance of such mutualisms. We suggest that invasive plant reproductive traits could be highly contextual, and that islands may have a potential role in the acceleration of the invasion process through the production of highly variable populations. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, **85**, 65–79.

ADDITIONAL KEYWORDS: agamospermy – hybrid vigour – inbreeding depression – island invasion – pollinator limitation – self fertilization.

INTRODUCTION

Present-day island invasions are frequent and severe as compared with their mainland counterparts, though few studies have attempted to pinpoint empirically factors underlying this pattern (D'Antonio & Dudley, 1995; MacDonald & Cooper, 1995; Lonsdale, 1999). The mating system of plants is one such crucial factor determining their success in insular and invasive contexts. Island theory has asserted that uniparental reproductive modes are associated hypothetically with colonization processes, since they ensure reproduction in spite of a lack of outcrossing opportunities associated with small population size and/or a lack of pollination vectors (McMullen, 1987;

McMullen, 1993a; Barrett, 1996; Barrett, 1998). This idea targets primarily oceanic islands due to their extreme isolation, but supporting results have been found for offshore islands (see Inoue & Amano, 1986; Glover & Barrett, 1987; Spears, 1987). The same hypotheses are also often extended to invasive plant species, i.e. uniparental modes should favour invasion via reproductive insurance (Baker, 1955; Baker, 1986; Brown & Burdon, 1987; Roy, 1990; Meyer, 1998; Cadotte & Lovett-Doust, 2001). Empirical studies have detected concordant pollinator limitation for non-native shrubs on the Pacific coast of the United States (Parker, 1997; Parker & Haubensak, 2002) and Tasmania (Stout, Kells & Goulson, 2002). However, intraspecific studies specifically designed to compare the reproductive traits of island and mainland plant populations remain rare, and the only study, to our

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knowledge, specifically studying invasive plant mating systems in function of insularity has demonstrated a switch from sexual seed production in a native range to apomictic seed production in an invasive, island range (Amsellem, Noyer & Hossaert-McKey, 2001).

It seems logical, therefore, to predict that an invasive plant species will differ in the success of its reproductive mode when introduced on adjacent island and mainland habitats, and that insularity will subsequently select for certain reproductive syndromes associated with small population sizes or a lack of pollinators. In order to test these hypotheses, we initiated a study which examined reproductive differences in island and mainland habitats for two South African succulents introduced into the Mediterranean Basin: *Carpobrotus edulis* (L.) N. E. Br. and *C. aff. acinaciformis* (L.) L. Bol. These species have been naturalized along the Provençal coasts of south-east France since the early 1900s (Albert & Jahandiez, 1908), where they have been reported to menace several threatened species (Suehs, Médail & Affre, 2001) and are associated with a decrease in plant diversity (Vilà *et al.*, 2004).

Previous studies have demonstrated that despite their very similar appearance and habit, these two taxa differ dramatically in their reproductive strategies and thus provide an ideal model for studying the effects of extrinsic parameters, such as insularity, on plant mating-system characteristics. *C. edulis* has been shown to be slightly agamospermic, completely self-fertile (Vilà, Weber & D'Antonio, 1998; Suehs *et al.*, 2001; Suehs, Affre & Médail, 2004b) and self-compatible, without inbreeding depression, and is equally able to produce seed when crossed with *C. aff. acinaciformis* (Suehs *et al.*, 2001, 2004b). The mating system of *C. aff. acinaciformis* is characterized by extremely weak agamospermy, low self-fertility and self-compatibility, a slight inbreeding depression, and seed production is maximized when it is hybridized with *C. edulis* (Suehs *et al.*, 2001, 2004b). We assumed that if consistent reproductive syndromes associated with island populations exist despite these taxon differences, this would be a good indication that insularity is affecting the mating-system characteristics of these plants. Within this context, we assessed agamospermy, self-fertility, self-compatibility, outcrossing, hybridization and free pollination for these two taxa in both insular and mainland habitats, using controlled pollination experiments. The resulting seed production, germination data and reproductive mode indices were used to test the hypotheses that: (1) uniparental reproductive modes (agamospermy, self-fertility, and self-compatibility) will have higher performance in island habitats, and (2) pollinator service will be higher in mainland habitats, which in turn will lead to (3) higher biparental reproductive

mode (outcrossing and hybridization) performance in mainland habitats.

MATERIAL AND METHODS

FOCAL SPECIES AND STUDY SITES

The *Carpobrotus* (Aizoaceae) species studied are robust, trailing succulents, which can form mats up to 10 m in diameter and 40 cm deep (D'Antonio & Mahall, 1991). The flowers are large (50–120 cm in diameter), actinomorphic and hermaphroditic, and can produce hundreds of seeds per flower (Blake, 1969; Wisura & Glen, 1993). *C. edulis* (L.) N. E. Br. is the only member of its genus to have distinctly yellow flowers (Blake, 1969; Wisura & Glen, 1993), while *C. aff. acinaciformis* typically has magenta flowers. Pollinators include *Bombus terrestris*, *Halictus* sp. and *Anthidium* sp. (C. Suehs, unpubl. data).

The *Carpobrotus* populations studied occur on Bagaud island and the adjacent mainland on the Provençal coast of France, as presented in Figure 1. The island, with a surface area of 45 ha and a maximum altitude of 59 m, is 7.5 km from the adjacent mainland and 500 m from the nearest island (Port Cros) within the French National Park of Port Cros. Population Caa-I (*C. aff. acinaciformis* – Island) consists of a 1500-m² mat of *C. aff. acinaciformis* spreading over the low coastal matorral on the eastern side of the Bagaud island. Population Ce-I (*C. edulis* – Island) corresponds to a 2020-m² population of *C. edulis* on the western side of the same island. Populations Caa-M (400 m²; *C. aff. acinaciformis* – Mainland) and Ce-M (1000 m²; *C. edulis* – Mainland) are dispersed on the thin littoral belt of the French mainland near the locality of Brégançon. Both island and mainland sites are characterized by a mediterranean climate, silicious bedrock and a typical mediterranean coastal matorral formation. In addition, Bagaud island only recently separated from the mainland (8500–9000 years BP

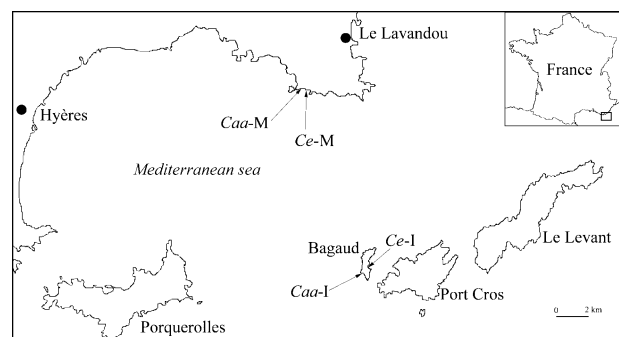


Figure 1. Locations on the south-east coast of France of *Carpobrotus aff. acinaciformis* (Caa-I and Caa-M) and *C. edulis* (Ce-I and Ce-M) populations studied.

Sartoretto, Verlaque & Laborel, 1996), resulting in highly similar native communities and abiotic factors between insular and mainland communities.

CONTROLLED POLLINATION EXPERIMENTS AND SEED PRODUCTION

In April 1999 and 2000, flower buds were manipulated in order to evaluate seed production as follows: (1) agamospermy [stamen and style removal, plus veiling (0.5×0.5 nylon mesh)], (2) spontaneous selfing (veiling only), (3) manual selfing (hand self-pollination plus veiling), (4) manual outcrossing (hand, intraspecific cross-pollination plus veiling), (5) manual hybridization (hand, interspecific cross-pollination plus veiling), and (6) free pollination (the flower bud was marked, but was otherwise left unmanipulated). The compact nature of buds necessitated petal removal, but previous experiments have demonstrated no negative effect as a result of this manipulation (Suehs *et al.*, 2004b). Hand pollinations were performed using cotton swabs on fully receptive stigmas on two consecutive days. Pollen donors separated from pollen receivers by as great a distance as possible (minimum 7–10 m) were selected. In total, the six controlled pollination experiments were performed on 38, 32, 25 and 30 individuals for populations *Caa-I*, *Ce-I*, *Caa-M* and *Ce-M*, respectively. Individual plants were known to be genetically different due to a previous isozyme study (Suehs, Affre & Médail, 2004a) or belonged to spatially and visually separate, non-overlapping clones separated by a minimum of 5 m. All six pollination treatments were applied in a random fashion on each individual so that no phenological difference among the flowers of one individual could be confused with experimental effects. Fruits were collected at the end of each season (June to July), and total seed production mass (mg) was quantified and seed counts per fruit were estimated using the weight of 100 hand counted seeds from each fruit. The mean seed mass (the average mass of one seed per fruit, mg) was then calculated by taking the mass of 100 seeds, or the total number of seeds if there were less than 100, and dividing by the number of seeds; this later served for calculation of relative performance indices (see below).

In order to evaluate taxon, pollination treatment, and island–mainland differences at the seed production level, seed counts were analysed as recommended by Manly (1997) using two-group, distribution free randomization tests due to distributions that were naturally non-normal (counts) and whose large amounts of ties in the small-integer range resulted in zero-skewed data, non-normality, heteroscedascity and non-transformability. Significance was assessed by comparing the mean seed count difference observed between two groups with the one-tailed distribution

generated from 5000 random samplings without replacement of those two groups, with Bonferroni adjustment (Manly, 1997). *C. aff. acinaciformis* seed count means were compared with those of *C. edulis* within each pollination treatment, and island vs. mainland seed count means were compared within each taxon and pollination treatment. Pollination treatment performance, within taxa but both across and within sites, was evaluated using analogous tests comparing manual outcrossing with each of the remaining treatments since manual outcrossing was assumed to maximize the quantity of progeny.

SEED GERMINATION AND SEEDLING SIZE PARAMETERS

Manual selfing, manual outcrossing and manual hybridization progeny were chosen for continued study by germination experiments because this allowed subsequent determination of relative performance indices (see biparental or mixed indices, below). Thirty seeds were selected from each fruit resulting from each pollination experiment for both taxa and locations. If a fruit contained less than 30 seeds (only nine of the 293 available fruits), all seeds were selected. Each lot of seeds was scarified and was allowed to germinate in Petri dishes prepared with a 30-g layer of Fontainebleau sand at room temperature (18–20 °C). Benlate solution (1 g/L) was added to each Petri dish to prevent fungal infection, and sand was kept moist with demineralized water on a daily basis. Petri dishes were arranged randomly to reduce position and edge effects. The number of germinations (determined when both cotyledons were distinguishable) in each Petri dish was counted every 2–3 days for 1 month, and every 4 days for an additional 17 days. After a total of 47 days, final cumulative per cent germinations were assessed to estimate seed viability, and ten germinations were removed from each Petri dish in order to measure cotyledon width, the length of cotyledon spread, and stem length using callipers precise to 0.1 mm. Cotyledon surface area (mm^2) was estimated as $0.5 \times \text{cotyledon width (mm)} \times \text{cotyledon spread (mm)}$.

Three way ANOVAs (ANOVA with repeated measures) were used to test for taxon, insularity and treatment effects for cumulative germination percentages and also for germination speeds (Δ percentage germination/ Δ days) occurring throughout the duration of the study. Because of a lack of sphericity, Greenhouse–Geiser corrections on significance values were used (Stevens, 1992). Post-hoc Scheffé tests were used to pinpoint differences between groups within days.

A three-way MANOVA was used to test for taxon, insularity and treatment effects on cotyledon surface areas (mm^2) and stem lengths (mm) of seedlings. Cotyledon surface area was square-root transformed

to eliminate heteroscedasticity during analysis (Sokal & Rohlf, 1995). Post-hoc Scheffé tests were used to detect overall differences between treatments, between taxa for each treatment and between treatments within each taxa, as well as location differences within each taxon-treatment group. Statistica 6.0 (StatSoft, 2001) was used to perform ANOVAs, MANOVAs and posthoc Scheffé tests.

INDICES DESCRIBING UNIPARENTAL REPRODUCTIVE MODES

Reproductive mode indices were used to describe the ability of an individual to perform in a given mode relative to a standard, which maximizes theoretical performance. They therefore characterized an individual's capacity in a given reproductive mode, incorporating maternal effects.

Relative agamospermic capacities (AC) were estimated using the following equation: $AC = a/(a + R_{max})$, where a represents the seed count in agamospermy, and R_{max} represents the highest seed count chosen from among all other pollination treatments performed. When $AC = 0$, no agamospermic capacity was detected. When $0 < AC < 0.5$, agamospermic capacity was detected, but it was weak and did not maximize seed production. When $0.5 \leq AC \leq 1$, preferential agamospermic capacity was detected.

We calculated a self-fertility index (SF) for each individual as $SS/(SS + MO)$, where SS is the seed set of spontaneously selfed fruits, and MO that of manually outcrossed fruits. In a similar fashion, we calculated a self-compatibility index (SC) as $MS/(MS + MO)$, where MS is the seed set of manually selfed fruits (Lloyd & Schoen, 1992). Sterile individuals, where numerators and denominators both equalled zero, were scored as zero (self-infertile/self-incompatible). Index values under 0.5 indicated partial self-fertility or self-compatibility, 0.5 was the value obtained for equal performances in selfing and outcrossing, and thus complete self-fertility or self-compatibility, and values above 0.5 indicated preferentially self-fertile or self-compatible individuals.

INDICES DESCRIBING POLLINATOR SERVICE AND BIPARENTAL REPRODUCTIVE MODES

In order to quantify to what extent in situ pollination maximizes seed production, a pollinator service index (PS) was created for each individual. When free pollination seed counts were less than that for spontaneous selfing, $PS = 0$ and no evidence of pollinator service was detected. Otherwise, PS was equal to $(f - s)/(f + R_{max} - 2s)$, where f represents the seed count resulting from free pollination, s the seed count resulting from spontaneous selfing, and R_{max} the largest seed

count from amongst spontaneous selfing, manual selfing, manual outcrossing and manual hybridization experiments. When $0 \leq PS \leq 0.5$, evidence of pollinator service was present, but this service did not maximize seed counts. When $0.5 \leq PS \leq 1$, evidence of pollinator service was detected and this service was considered as 'efficient', or as maximizing seed counts.

Inbreeding (RP_I) and hybridization (RP_H) indices are based on the relative performances of manual selfing and manual hybridization compared with that of manual outcrossing, where performance is multiplicative across life-history stages (Agren & Schemske, 1993). For an individual within a pollination treatment, performance was thus calculated by multiplying seed count, seed mass (mg), % seed viability, cotyledon width (mm), cotyledon length (mm) and stem length (mm). The inbreeding index was then calculated as $RP_I = (W_o - W_s)/W_{max}$, where W_o is the performance in manual outcrossing, W_s the performance in manual selfing, and W_{max} the larger of W_o and W_s . Similarly, the hybridization index was calculated as $RP_H = (W_h - W_o)/W_{max}$, where W_h is the performance in manual hybridization, and W_{max} the larger of W_o and W_h . Positive values for these two indices indicated inbreeding or outbreeding depressions corresponding to outbreeding or hybridization vigours, and negative values indicated outbreeding or hybridization depressions, respectively.

Index means were first tested against relevant thresholds in order to determine overall reproductive capacities, and then compared between taxa and between island and mainland sites within taxa. Due to large amounts of ties resulting in non-normality, heteroscedasticity and non-transformability, this was accomplished using distribution free randomization tests as recommended by Manly (1997). Overall reproductive capacities were determined by comparing index means to their nearest 0.5 increment threshold using two-tailed, 5000 repeat, Fisher's randomization tests (Manly, 1997), both over and within each location for each taxon. Two-group randomization tests identical to those used at the seed count level were then chosen to compare index mean differences between *Carpobrotus* taxa, and between sites within *Carpobrotus* taxa.

RESULTS

SEED COUNTS

Seed count distributions are presented in Figure 2. Seed counts for *C. edulis* were significantly higher than were those of *C. aff. acinaciformis* at the $P < 0.001$ level for all controlled pollination experiments with the exception of agamospermy. Among pollination treatment comparisons, agamospermy resulted in significantly smaller seed counts than did

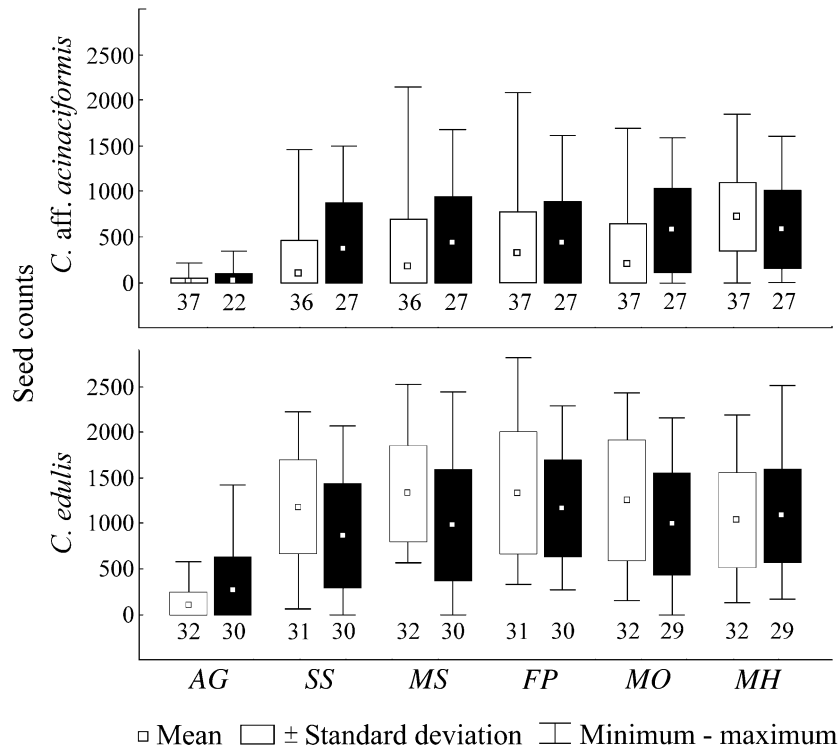


Figure 2. Means, standard deviations, minima and maxima for seed counts per fruit resulting from controlled pollination experiments on *Carpobrotus* aff. *acinaciformis* and *C. edulis* on Bagaud island (white) and the mainland (black). The sample size per experiment is given below each box. AG, agamospermy; SS, spontaneous selfing; MS, manual selfing; FP, free pollination; MO, manual outcrossing; MH, manual hybridization.

manual outcrossing (*C. aff. acinaciformis* agamospermy vs. outcrossing: $P < 0.01$; *C. edulis* agamospermy vs. outcrossing: $P < 0.001$). *C. edulis* performed equally well in the remaining experiments. *C. aff. acinaciformis*, however, maximized seed counts in hybridization (hybridization vs. outcrossing: $P < 0.01$). Significantly smaller seed counts in agamospermy compared with manual outcrossing also persisted within populations for *C. edulis* on both Bagaud island (agamospermy vs. outcrossing: $P < 0.001$) and the mainland (agamospermy vs. outcrossing: $P < 0.001$), and for *C. aff. acinaciformis* on the mainland (agamospermy vs. outcrossing: $P < 0.01$). The capacity of *C. aff. acinaciformis* to maximize seed counts through hybridization existed at the within population level only for the Bagaud island population (hybridization vs. outcrossing: $P < 0.001$). No significant differences were found when comparing Bagaud island and mainland seed count means.

CUMULATIVE GERMINATION PERCENTAGES AND SPEED

Cumulative germination percentages and germination speeds are presented in Figures 3 and 4, respectively. A three-way ANOVA revealed only a significant day

effect ($P < 0.001$), and a significant day–taxon interaction ($P < 0.01$) for cumulative germination percentages, indicating that site location and treatment did not affect this life-history stage (Table 1). Post-hoc Scheffé tests indicated that the day–taxon interaction resulted in significantly higher ($P < 0.05$) cumulative germination percentages for *C. edulis* as compared with *C. aff. acinaciformis* for days 6–28.

For germination speeds, a three-way ANOVA detected a significant day effect ($P < 0.001$) and day–taxon ($P < 0.001$), day–location ($P < 0.01$) and day–taxon–location interactions ($P < 0.001$; Table 2). No treatment effects were found at this life-history stage. Post-hoc Scheffé tests between the four taxon–location groups within each day (Table 3) suggested a complex pattern dominated by higher germination speeds for *C. edulis* on Bagaud island during the first 14 days of the germination trial, and higher germination speeds for *C. aff. acinaciformis* on the continent and then switching to Bagaud island between 18 and 30 days.

SEEDLING SIZE

Means and standard deviations for cotyledon surface areas and stem lengths are presented in

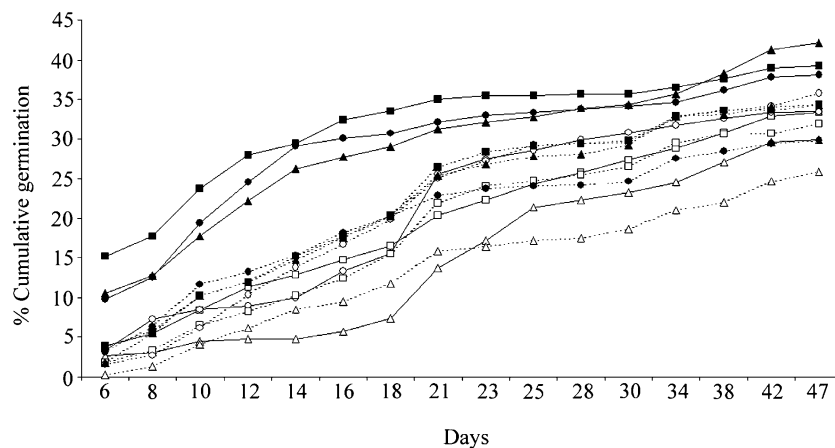


Figure 3. Per cent cumulative germinations for *Carpobrotus* aff. *acinaciformis* (white) and *C. edulis* (black) from Bagaud island (solid lines) and the mainland (dotted lines) and issuing from manual selfing (triangles), manual outcrossing (circles) and manual hybridization (squares).

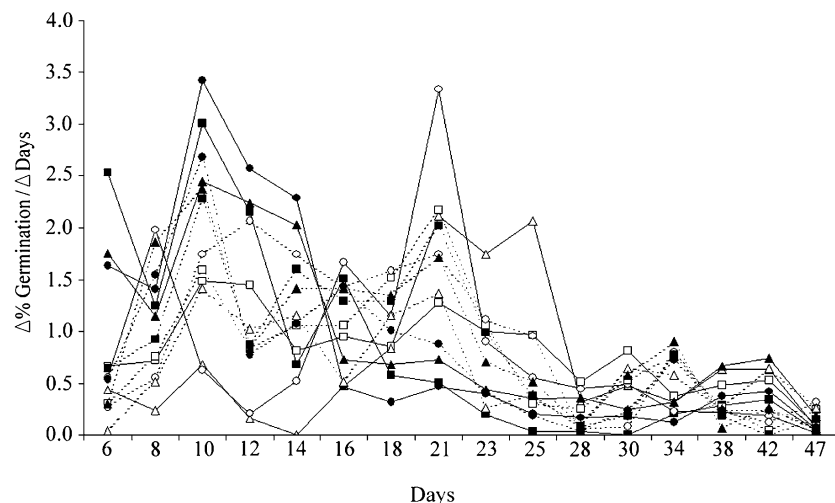


Figure 4. Germination speeds (Δ percentage germination/ Δ days) for *Carpobrotus* aff. *acinaciformis* (white) and *C. edulis* (black) on both Bagaud island (solid lines) and the mainland (dotted lines) and issuing from manual selfing (triangles), manual outcrossing (circles) and manual hybridization (squares).

Figure 5. A three-way MANOVA detected significant taxon ($F = 8.51$, d.f. = 2, $P < 0.001$), insularity ($F = 113.98$, d.f. = 2, $P < 0.001$) and treatment effects ($F = 13.10$, d.f. = 4, $P < 0.001$), as well as taxon by location ($F = 4.45$, d.f. = 2, $P < 0.05$), taxon by treatment ($F = 5.08$, d.f. = 4, $P < 0.001$) and treatment by location ($F = 9.57$, d.f. = 4, $P < 0.001$) interactions (Table 4). Post-hoc Scheffé tests detected that, in general, only cotyledon area ($P < 0.001$) was significantly different between the two taxa. However, this difference was most likely due to the number of individuals within each treatment as no significant differences were detected between the two taxa within treatments. Overall manual hybridization cotyledon

surface areas were significantly larger than were those of manual outcrossing and manual selfing at the $P < 0.001$ level, and all three treatments were significantly different for stem lengths at the $P < 0.05$ level (manual selfing < manual outcrossing < manual hybridization). Within each taxon, this pattern persisted at the $P < 0.05$ level with the exception that no significant differences were found for manual selfing vs. manual outcrossing, nor for *C. aff. acinaciformis* manual selfing vs. manual hybridization. When comparing sites, island values were significantly larger than were mainland values for all manual outcrossing comparisons, with the exception of *C. aff. acinaciformis* stem lengths, and

Table 1. Repeated analysis of variance results for per cent cumulative germinations for *Carpobrotus* aff. *acinaciformis* and *C. edulis* issued from insular and mainland sites and three reproductive mode treatments, with Greenhouse–Geiser significance values (P_{GG}) corrected for a lack of sphericity

Source	d.f.	SS	MS	F	$P <$	$P_{GG} <$
Days	15	320965	21398	304.19	0.001	0.001
Days \times taxon	15	6218	415	5.89	0.001	0.004
Days \times location	15	990	66	0.94	0.520	0.381
Days \times treatment	30	1014	34	0.48	0.993	0.726
Days \times taxon \times location	15	3025	202	2.87	0.002	0.065
Days \times taxon \times treatment	30	3013	100	1.43	0.062	0.229
Days \times location \times treatment	30	1983	66	0.94	0.560	0.432
Days \times taxon \times location \times treatment	30	1263	42	0.60	0.959	0.642
Error	4215	296491	70			

SS, sum of squares; MS, mean squares.

Table 2. Repeated analysis of variance results for germination speeds for *Carpobrotus* aff. *acinaciformis* and *C. edulis* issued from insular and mainland sites and three reproductive mode treatments, with Greenhouse–Geiser significance values (P_{GG}) corrected for a lack of sphericity

Source	d.f.	SS	MS	F	$P <$	$P_{GG} <$
Days	15	961.05	64.07	24.91	0.001	0.001
Days \times taxon	15	327.33	21.82	8.48	0.001	0.001
Days \times location	15	119.33	7.96	3.09	0.001	0.002
Days \times treatment	30	59.79	1.99	0.77	0.804	0.714
Days \times taxon \times location	15	192.90	12.86	5.00	0.001	0.001
Days \times taxon \times treatment	30	76.23	2.54	0.99	0.485	0.467
Days \times location \times treatment	30	102.33	3.41	1.33	0.110	0.173
Days \times taxon \times location \times treatment	30	111.62	3.72	1.45	0.052	0.112
Error	4215	10841.72	2.57			

SS, sum of squares; MS, mean squares.

all manual hybridization comparisons at the $P < 0.05$ level.

UNIPARENTAL REPRODUCTIVE MODES

Reproductive index distributions are presented in Figure 6. *C. edulis* had significantly higher agamospermic capacity ($P < 0.001$), self-fertility ($P < 0.001$) and self-compatibility ($P < 0.001$) compared with *C. aff. acinaciformis*. Fisher's randomization tests (Table 5) detected the presence of weak agamospermic capacities across sites for *C. aff. acinaciformis*, though this effect disappeared at the within-location level due to the corresponding drop in observation numbers. Both across and within locations, *C. aff. acinaciformis* was also partially self-fertile and self-compatible while *C. edulis* was weakly agamospermic, completely self-fertile and self-compatible. The relative levels of these uniparental capacities were significantly higher on the mainland than they

were on Bagaud island at the $P < 0.05$ level for *C. edulis* agamospermy and *C. aff. acinaciformis* self-fertility and self-compatibility.

POLLINATOR SERVICE AND BIPARENTAL REPRODUCTIVE MODES

Comparing indices between the two taxa, the only differences found were that *C. aff. acinaciformis* had significantly higher outbreeding ($P < 0.05$) and hybridization ($P < 0.01$) vigours compared with *C. edulis*. Fisher's randomization tests (Table 5) detected significant pollinator service for both taxa across and within locations, though this service did not maximize seed counts. Mean differences between island and mainland pollinator services were also not significant. Inbreeding indices indicated outbreeding vigour for *C. aff. acinaciformis*, and neither vigour nor depression for *C. edulis* both across and within locations. In contrast, island–mainland differences were apparent

Table 3. Post-hoc Scheffé test probability values on germination speeds within days and between four taxon-location groups

	<i>Caa-I</i> vs. <i>Ce-I</i>	<i>Caa-M</i> vs. <i>Ce-I</i>	<i>Ce-I</i> vs. <i>Ce-M</i>	<i>Caa-I</i> vs. <i>Ce-M</i>	<i>Caa-I</i> vs. <i>Caa-M</i>	<i>Caa-M</i> vs. <i>Ce-M</i>
Day 6	0.001	0.001	0.001	NS	NS	NS
Day 8	NS	NS	NS	NS	NS	NS
Day 10	0.001	0.05	NS	NS	NS	NS
Day 12	0.001	0.05	0.001	NS	NS	NS
Day 14	0.05	NS	NS	NS	NS	NS
Day 16	NS	NS	NS	NS	NS	NS
Day 18	NS	0.05	NS	NS	NS	NS
Day 21	0.01	0.05	NS	NS	NS	NS
Day 23	0.01	NS	NS	NS	NS	NS
Day 25	0.001	NS	NS	0.01	NS	NS
Day 28	0.01	NS	NS	0.001	0.01	NS
Day 30	0.001	NS	NS	NS	NS	NS
Day 34	NS	0.05	0.01	NS	NS	NS
Day 38	NS	NS	0.05	NS	NS	NS
Day 42	NS	NS	0.05	NS	NS	NS
Day 47	NS	0.05	NS	NS	0.05	0.05

Caa-I = *Carpobrotus* aff. *acinaciformis* on Bagaud island; *Ce-I* = *C. edulis* on Bagaud island; *Caa-M* = *C. aff. acinaciformis* on the mainland; *Ce-M* = *C. edulis* on the mainland. NS, not significant.

for hybridization indices for both taxa, with hybrid vigour being found in island populations. This insular hybrid vigour was strong enough in *C. aff. acinaciformis* to induce an across-sites hybrid vigour, which was not the case for *C. edulis*. The only significant difference found between insular and mainland biparental reproductive mode means was that *C. aff. acinaciformis* had a higher hybrid vigour mean ($P < 0.001$) on Bagaud island than it did on the adjacent mainland.

DISCUSSION

The plant reproductive characters of the *Carpobrotus* taxa studied are consistent with previous work (Vilà *et al.*, 1998; Suehs *et al.*, 2001, 2004b). The overall greater seed production capacities and greater uniparental capacities of *C. edulis* compared with *C. aff. acinaciformis* help to explain its larger distribution in south-east France (Suehs *et al.*, 2001). As regards the effects of insularity on plant reproductive characters, one must first keep in mind the very important factor that, aside from using two different taxa, our experiment was pseudoreplicated, and therefore subject to interference from common maternal effects. In addition, the weak agamospermic capacities

Table 4. Multiple analysis of variance results for cotyledon areas and stem lengths of *Carpobrotus* aff. *acinaciformis* and *C. edulis* seedlings issued from insular and mainland sites and three reproductive mode treatments, with cotyledon areas square-root transformed before analysis

Source	d.f.	<i>F</i>	<i>P</i> <
Taxon	2	8.512	0.001
Location	2	113.984	0.001
Treatment	4	13.101	0.001
Taxon × location	2	4.450	0.013
Taxon × treatment	4	5.083	0.001
Location × treatment	4	9.566	0.001
Taxon × location × treatment	4	1.703	0.148
Error	229		

(Fig. 6) detected may participate in the seed production of other reproductive modes. Keeping these caveats in mind, we found varying results among the life-history stages studied (indicating the importance of investigating as many stages as possible), which nevertheless suggested certain insularity patterns. No island–mainland differences were detected at the raw seed production or cumulative seed germination (seed viability) levels. However, at the germination speed level, complex taxon–insularity interactions (Fig. 4) indicate a potential role played by insularity, though a clear-cut conclusion remains elusive. The seedling-size stages and reproductive indices, which take into account the relative performance among reproductive modes, provide the most insight into the potential effects of insularity on plant reproductive systems.

THE IMPORTANCE OF POLLINATORS IN PREDICTING INVASIVE PLANT MATING SYSTEMS

We hypothesized that pollinator services for invasive species will be greater in mainland habitats than they are on islands. Contrary to this prediction, though we did detect significant pollination service in all populations, we did not detect significant differences due to insularity. Previous studies using fluorescent powders have also contradicted this prediction by demonstrating significantly smaller pollen dispersal distances for *C. edulis* and a paucity of pollinator visits for *C. aff. acinaciformis* on the mainland vs. Bagaud island (Suehs, Médail & Affre, 2003). The presence of a pollinator vector substantially alters the predictions that can be made about the reproductive characters of the ‘ideal’ invasive or island plant. Both the colonization and naturalization/adaptation stages of the invasion process are likely to be affected by the availability of pollinator services. We should expect an overall

Table 5. Results for Fisher's randomization tests comparing in *Carpobrotus* aff. *acinaciformis* and *C. edulis* mean reproductive indices to their nearest 0.5 increment threshold, which defines reproductive categories

	<i>C. aff. acinaciformis</i>			<i>C. edulis</i>		
	Across locations	Island	Mainland	Across locations	Island	Mainland
Agamospermic capacity						
Mean \pm SD	0.01 \pm 0.04	0.01 \pm 0.02	0.02 \pm 0.06	0.09 \pm 0.12	0.06 \pm 0.09	0.12 \pm 0.13
<i>P</i> <	0.01	NS	NS	0.001	0.001	0.001
Category	Weak	None	None	Weak	Weak	Weak
Self-fertility						
Mean \pm SD	0.21 \pm 0.34	0.14 \pm 0.31	0.31 \pm 0.37	0.48 \pm 0.19	0.51 \pm 0.13	0.46 \pm 0.24
<i>P</i> <	0.001	0.01	0.01	NS	NS	NS
Category	Partial	Partial	Partial	Complete	Complete	Complete
Self-compatibility						
Mean \pm SD	0.19 \pm 0.31	0.11 \pm 0.28	0.28 \pm 0.32	0.50 \pm 0.19	0.54 \pm 0.12	0.47 \pm 0.23
<i>P</i> <	0.001	0.01	0.001	NS	NS	NS
Category	Partial	Partial	Partial	Complete	Complete	Complete
Pollinator service						
Mean \pm SD	0.22 \pm 0.25	0.18 \pm 0.19	0.26 \pm 0.31	0.28 \pm 0.27	0.28 \pm 0.28	0.29 \pm 0.25
<i>P</i> <	0.001	0.001	0.001	0.001	0.001	0.001
Category	Present	Present	Present	Present	Present	Present
Outcrossing						
Mean \pm SD	0.31 \pm 0.09	0.23 \pm 0.10	0.39 \pm 0.15	0.01 \pm 0.09	- 0.02 \pm 0.10	0.04 \pm 0.14
<i>P</i> <	0.01	0.001	NS	NS	NS	NS
Category	Vigour	Vigour	Vigour	No preference	No preference	No preference
Hybridization						
Mean \pm SD	0.38 \pm 0.09	0.83 \pm 0.10	- 0.07 \pm 0.13	0.14 \pm 0.09	0.21 \pm 0.10	0.08 \pm 0.15
<i>P</i> <	NS	0.001	NS	NS	0.05	NS
Category	Vigour	Vigour	No preference	No preference	Vigour	No preference

NS, not significant.

negative correlation between the degree of pollinator service and invasive-plant dependence on uniparental reproductive modes, regardless of the invasion stage being studied. Conversely, we expect highly outcrossing invasive plants to demonstrate a positive relationship between the degree of pollinator service and fruit/seed set (e.g. Parker & Haubensak, 2002; Stout *et al.*, 2002). Indeed, simulations by Parker (1997) suggested potentially large effects of increasing pollinator visitation in rapidly expanding populations of highly outcrossing invaders.

Restricted pollinator guilds, and a corresponding high dependence on uniparental reproductive modes, are most likely to occur on rather isolated islands (Barrett, 1998), such as the Galapagos (McMullen, 1993b; McMullen, 1994) or the Izu islands off the coast of Japan (Inoue & Amano, 1986). Otherwise, many areas, including offshore islands such as that studied, may have a generalist guild readily adaptable to the flowers of incoming colonists (Valentine, 1978; Richardson *et al.*, 2000), though this guild may be limited in diversity according to insularity, habitat fragmen-

tation or other factors. For example, British aliens are more likely than not to be pollinated by insects (Crawley, Harey & Purvis, 1996). Native bumble bees were important pollinators of invasive *Cytisus scoparius* and *Genista monspessulana* populations in California (Parker *et al.*, 2002). *Impatiens glandulifera* is another good example of a highly invasive species that has had no problem in attracting native pollinators in its adventive range (Valentine, 1978; Thompson, Hodgson & Rich, 1995; Chittka & Schürkens, 2001). Such is also likely the case for the island habitat studied, which is only 7.5 km from the mainland (Fig. 1) and where a generalist pollinator guild servicing *Carpobrotus* is represented by *Bombus terrestris*, *Apis mellifera* and *Halictus* sp. (C. M. Suehs, unpubl. data). In addition, though such insular guilds may lack diversity, the abundance of certain species, such as *B. terrestris* on Bagaud island (C. M. Suehs, unpubl. data), could ensure pollinator services.

The ubiquity of generalist pollinator guilds has led to the conclusion that pollinator mutualisms are widely available to invasive plants (Valentine, 1978;

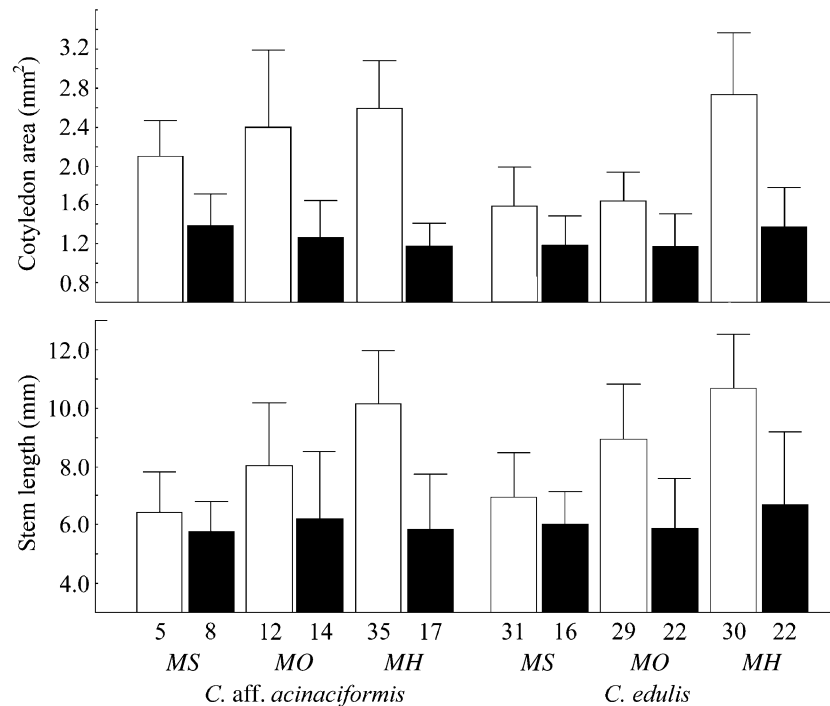


Figure 5. Cotyledon area (mm²) and stem length (mm) means for *Carpobrotus* aff. *acinaciformis* and *C. edulis* seedlings resulting from manual selfing (MS), manual outcrossing (MO) and manual hybridization (MH) experiments on Bagaud island (white) and the mainland (black). The sample size per experiment is given below each set of boxes. Bars indicate standard deviations.

Richardson *et al.*, 2000) and perhaps generally do not restrict modern invasions. However, one should note that though we detected significant pollinator service, this service was not maximizing seed counts, and therefore *Carpobrotus* seed production in the study area seems to be pollinator limited. Pollinator limitation can be expected for invasive species because their recent introduction may not have allowed enough time for mutualisms to develop with the entire available pollinator guild. Pollinator limitation has also been found for invasive *Cytisus scoparius* and *Genista monspessulana* populations along the Pacific coast of the United States (Parker, 1997; Parker & Haubensak, 2002), as well as *Lupinus arboreus* in Tasmania (Stout *et al.*, 2002). This stresses the importance played by pollinator services in the invasion process, which should not be ignored. At what point a limitation in pollinator service restricts the expansion of outcrossing plant populations merits further investigation.

THE LACK OF ASSOCIATION BETWEEN UNIPARENTAL REPRODUCTIVE MODES AND INSULARITY

Uniparental reproductive modes were hypothesized to strongly characterize exotic plant taxa invading island

habitats. However, our results do not support this prediction. Though raw seed count performance for *C. aff. acinaciformis* agamospermy on Bagaud island was not significantly different from manual outcrossing (the reproductive mode theoretically maximizing progeny number and quality), and may therefore be interpreted as a strong indicator of agamospermic capacity in this island population, this result was due to distributions highly skewed towards zero for both of these experiments (Fig. 2). Otherwise, the only differences found between island and mainland populations regarding uniparentality were found among the relative reproductive mode indices. Weaker uniparental capacities, when they were found, were associated with Bagaud island and not with the adjacent mainland (see *C. edulis* agamospermic capacities, and *C. aff. acinaciformis* self-fertility and self-compatibility; Fig. 6). This lack of reproductive assurance via seed production may be compensated for in island habitats by clonality. Aggressive vegetative reproduction is often reported for introgressed or hybridized plants (Vilà, Weber & D'Antonio, 2000), as is the case for *C. aff. acinaciformis*. Indeed, we have previously shown that *C. aff. acinaciformis* relies more on clonality than it does on sexual reproduction (Suehs *et al.*, 2004a). Clonality has also been observed in *C. edulis*

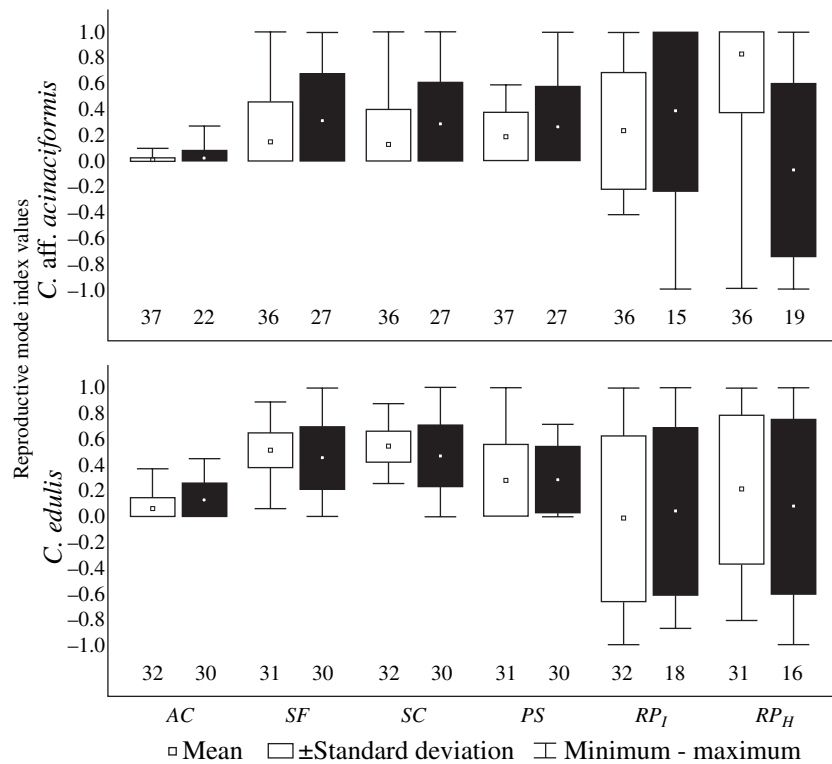


Figure 6. Means, standard deviations, minima and maxima for reproductive mode indices for *Carpobrotus* aff. *acinaciformis* and *C. edulis* on Bagaud island (white) and the mainland (black). The sample size per experiment is given below each box. AC, agamospermic capacity; SF, self-fertility; SC, self-compatibility; PS, pollinator service; RP_I , inbreeding; RP_H hybridization.

(Suehs *et al.*, 2003, 2004a), and though vegetative growth is non-significantly different between insular and mainland matorral habitats similar to those studied (Suehs *et al.*, 2003), its existence may compensate for diminished self-fertility and self-compatibility within populations. In addition, self-infertility and self-incompatibility may be associated with meiotic perturbations found within the insular populations (both *C. aff. acinaciformis* and *C. edulis*) studied (K. Diadema, unpubl. data) due to the putative hybrid origin of these populations (Suehs *et al.*, 2004a). Further studies describing resource allocation to vegetative and sexual modes of reproduction in insular and mainland habitats, as well as in relation to introgression, are needed to evaluate the role that clonality and hybridization may play in the uniparental seed production patterns found in the populations studied.

Lack of evidence supporting the active selection of uniparental modes in island habitats may be due to a corresponding lack of conditions, such as small initial population sizes, which render such modes necessary for population survival. In fact, previous studies demonstrating (1) higher than average clonal and genetic variability for both the island populations studied here

(Suehs *et al.*, 2001, 2004a) and for *C. edulis* populations in California (Gallagher, Schierenbeck & D'Antonio, 1997), as well as (2) the fact that we found high outcrossing vigour (inbreeding depression) for *C. aff. acinaciformis* in this study, suggest that small initial population size or bottlenecks is not associated with these invasions. Evidence that sufficiently large initial population sizes may avoid selection for uniparentality has also been found for oceanic island floras, with the association between grouped seed dispersal via bird ingestion, fleshy fruits and floral dimorphism having been used to explain the high incidence of dioecy on Hawaii (Sakai *et al.*, 1995a). In addition, large initial populations are likely to arise frequently in invasions because they are often vehicled by man in large numbers and/or with multiple introductions (Noble, 1989). The resulting high propagule pressure may provide a sufficient number of individuals at the onset of invasion so as to provide ample opportunities for outcrossing, and no need for uniparental modes for population survival and expansion.

A third explanation for the weaker uniparental capacities associated with island habitats in this study is that once the colonization stage of the inva-

sion process has been surpassed, either naturally or by human intervention, the mating system of the species in question may respond to requirements other than reproductive assurance. The need for genetic recombination providing the variation necessary for the adaptive evolution thought to be important to invasive or weedy species (Baker, 1986; Bazzaz, 1986; Brown & Burdon, 1987; Roy, 1990; Pantone, Pavlik & Kelley, 1995; Ellstrand & Schierenbeck, 2000; Sakai *et al.*, 2001) may quickly outweigh the advantages of uniparentality. Evidence that a lack of uniparentality is not limiting in island habitats is provided by Sakai *et al.* (1995b), who demonstrated that dioecy has not been a severely limiting factor in dispersal and colonization of the Hawaiian Islands. The example of a sexual species of *Cortaderia* in California being more expansive and invading a greater diversity of habitats compared with a similar, apomictic congener supports this idea (Lambrinos, 2001). The situation of Californian *Carpobrotus* congeners is also exemplary, with invasive taxa (*C. edulis* and hybrids) having greater genetic variability compared with a putative, nonexpansive native taxa (Gallagher *et al.*, 1997).

POSSIBLE INTERACTIONS BETWEEN INSULARITY AND BIPARENTALITY

Our results also refute our third proposed hypothesis that outcrossing and hybridization should be relatively highly represented in mainland invasions compared with adjacent islands. We found significantly higher performances in the island habitat studied for outcrossed and hybridized seedling sizes (Fig. 5) and the presence of significant hybrid vigour only in island populations (Table 5), regardless of taxon. The significantly high seed counts in hybridization compared with outcrossing for *C. aff. acinaciformis* on Bagaud island (Fig. 2), as well as the highly significant differences between its hybridization indices on island and mainland populations (Fig. 6), reinforce this last trend. The higher than average clonal and genetic diversities found for the Bagaud island populations, as well as the introgression detected for *C. aff. acinaciformis* (Suehs *et al.*, 2004a), concord with in situ outcrossing and hybridization. While these results may be related to the hybridization histories of the populations involved (Suehs *et al.*, 2003), this outbreeding tendency agrees with studies documenting a high frequency of dioecy on oceanic islands, though a substantial part of this trend may be linked to an avian dispersal mechanism at colonization (Sakai *et al.*, 1995a), and also the observation that hybridization frequently occurs on islands (Barrett, 1996; Francisco-Ortega *et al.*, 2000; Crawford *et al.*, 2001).

High degrees of outcrossing, and especially hybridization, can exacerbate the invasion process through

the generation of advantageous genotypes/genetic novelty (Ellstrand & Schierenbeck, 2000). In addition, backcrossing and introgression subsequent to hybridization can contribute to adaptive evolution within populations (Rieseberg & Carney, 1998), and thus to increased invasion (Ellstrand & Schierenbeck, 2000). A similar process has already been exemplified in California where hybrids contribute to the successful invasion of *Carpobrotus* due to the formation of additional spreading genotypes (Vilà & D'Antonio, 1998; Weber *et al.*, 1998). We have previously demonstrated that such introgression is also occurring within Bagaud island *Carpobrotus* populations (Suehs *et al.*, 2004a). This study now reinforces this trend, as demonstrated by the high seedling sizes and frequent hybrid vigours resulting from our controlled pollination experiments (Figs 5, 6). This may be especially true in island habitats, given that the largest seedling sizes were found for hybrid issue in insular habitats (Fig. 5) and hybrid vigour was detected in island populations for both taxa (Table 5), and significantly so for *C. aff. acinaciformis*. This latter taxon also maximized its island seed production when manually hybridized, or when left in free pollination (Fig. 2). In contrast, its island seed production was quite poor in all uniparental modes and even in manual outcrossing, suggesting that in situ seed production results primarily from hybridization. As evolution/adaptation is thought to occur rapidly on islands compared with adjacent continents (Berry, 1983; Barrett, 1985, 1996), the results of this study thus underline a potential role of island invasions in accelerating the invasion process should they prove to be associated with biparental reproductive modes. Island invasions may result in highly variable and/or introgressed individuals on which selection can act to form new invasive populations. The potential for change is of special concern since contemporary evolution is increasingly thought to be a factor behind the aggressiveness of certain invasions (García-Ramos & Rodríguez, 2002; Hänfling & Kollman, 2002; Stockwell, Hendry & Kinnison, 2003).

CONCLUSIONS

In the context of plant invasions, we have outlined the association of uniparental reproductive modes (agamosperry, self-fertility and self-compatibility) with insularity, and the association of pollinator services, outcrossing and hybridization with mainland habitats as common perceptions present in island and invasion ecology. However, this study unexpectedly detected ubiquitous pollination vectors and an association between biparental reproductive modes and insularity. These results may be complicated by maternal effects sampled insufficiently due to pseudoreplica-

tion, the potential participation of agamospermy in other reproductive modes, and other parameters not taken into account, such as clonality and the degree of introgression present. Furthermore, though insularity syndromes have been detected in the archipelago in question (Médail & Vidal, 1998), its youth (c. 10 000 years BP Sartoretto *et al.*, 1996) and the recent nature of the invasion (c. 150 years BP) may influence the strength of the insularity syndrome present. Variation in invasive plant propagule pressure provided by man, variation in pollinator service guilds with location, and a possible need for increased genetic variability on islands are also proposed as additional, possible explanations for our results. These last factors may also help explain the lack of overall predictive value for invasiveness found in studies treating invasive plant mating syndromes where the invasive range context is unknown (e.g. Crawley *et al.*, 1996; Williamson & Fitter, 1996). Finally, the potential for island habitats to accelerate adaptive evolution in invasive plant populations is also evoked. Should insularity affect the gene flow and adaptation rates of invasive species on a general basis, lag times before rapid expansion could be diminished and invasive spread rates increased due to the rapid development of highly invasive populations.

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REFERENCES

- Agren J, Schemske DW. 1993. Outcrossing rate and inbreeding depression in two annual monoecious herbs, *Begonia hirsuta* and *B. semiovata*. *Evolution* **47**: 125–135.
- Albert A, Jahandiez E. 1908. *Catalogue des plantes qui croissent naturellement dans le département du Var*. Muséum d'Histoire Naturelle de Toulon reprints, 1985. Paris: Klincksieck.
- Amsellem L, Noyer J-L, Hossaert-McKey M. 2001. Evidence for a switch in the reproductive biology of *Rubus alceifolius* (Rosaceae) towards apomixis, between its native range and its area of introduction. *American Journal of Botany* **88**: 2243–2251.
- Baker HG. 1955. Self-compatibility and establishment after 'long-distance' dispersal. *Evolution* **9**: 347–349.
- Baker HG. 1986. Patterns of plant invasion in North America. In: Mooney HA, Drake JA, eds. *Ecology of biological invasions of North America and Hawaii*. New York: Springer-Verlag, 45–57.
- Barrett SCH. 1985. Floral trimorphism and monomorphism in continental and island populations of *Eichhornia paniculata* (Spreng.) Solms. (Pontederiaceae). *Biological Journal of the Linnean Society* **25**: 41–60.
- Barrett SCH. 1996. The reproductive biology and genetics of island plants. *Philosophical Transactions of the Royal Society of London B* **351**: 725–733.
- Barrett SCH. 1998. The reproductive biology and genetics of island plants. In: Grant PR, ed. *Evolution on islands*. New York: Oxford University Press, 18–34.
- Bazzaz FA. 1986. Life history of colonizing plants: some demographic, genetic, and physiological features. In: Mooney HA, Drake JA, eds. *Ecology of biological invasions of North America and Hawaii*. New York: Springer-Verlag, 96–110.
- Berry RJ. 1983. Diversity and differentiation: the importance of island biology for general theory. *Oikos* **41**: 523–529.
- Blake ST. 1969. A revision of *Carpobrotus* and *Sarcozona* in Australia, genera allied to *Mesembryanthemum* (Aizoaceae). *Contributions to the Queensland Herbarium* **7**: 1–65.
- Brown AHD, Burdon JJ. 1987. Mating systems and colonizing success in plants. In: Gray AJ, Crawley MJ, Edwards PJ, eds. *Colonization, succession and stability. The 26th symposium of the British Ecological Society held jointly with the Linnean Society of London*. Oxford: Blackwell Scientific Publications, 115–131.
- Cadotte MW, Lovett-Doust J. 2001. Ecological and taxonomic differences between native and introduced plants of southwestern Ontario. *Écoscience* **8**: 230–238.
- Chittka L, Schürkens S. 2001. Successful invasion of a floral market. *Nature* **411**: 653.
- Crawford DJ, Ruiz E, Stuessy TF, Tepe E, Aqueveque P, Gonzalez F, Jensen RJ, Anderson GJ, Bernardello G, Baeza CM, Swenson U, Silva MO. 2001. Allozyme diversity in endemic flowering plant species of the Juan Fernandez Archipelago, Chile: ecological and historical factors with implications for conservation. *American Journal of Botany* **88**: 2195–2203.
- Crawley MJ, Harey PH, Purvis A. 1996. Comparative ecology of the native and alien floras of the British Isles. *Philosophical Transactions of the Royal Society of London B* **351**: 1251–1259.
- D'Antonio CM, Dudley TL. 1995. Biological invasions as agents of change on islands versus mainlands. In: Vitousek

- PM, Loope LL, Adersen H, eds. *Islands: biological diversity and ecosystem function*. Berlin: Springer, 103–121.
- D'Antonio CM, Mahall BE. 1991.** Root profiles and competition between the invasive, exotic perennial, *Carpobrotus edulis*, and two native shrub species in California coastal scrub. *American Journal of Botany* **78**: 885–894.
- Ellstrand NC, Schierenbeck KA. 2000.** Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Sciences, USA* **97**: 7043–7050.
- Francisco-Ortega J, Santos-Guerra A, Kim S-C, Crawford DJ. 2000.** Plant genetic diversity in the Canary Islands: a conservation perspective. *American Journal of Botany* **87**: 909–919.
- Gallagher KG, Schierenbeck KA, D'Antonio CM. 1997.** Hybridization and introgression in *Carpobrotus* spp. (Aizoaceae) in California II. Allozyme evidence. *American Journal of Botany* **84**: 905–911.
- García-Ramos G, Rodríguez D. 2002.** Evolutionary speed of species invasions. *Evolution* **56**: 661–668.
- Glover DE, Barrett SCH. 1987.** Genetic variation in continental and island populations of *Eichhornia paniculata* (Pontederiaceae). *Heredity* **59**: 7–17.
- Hänfling B, Kollman J. 2002.** An evolutionary perspective of biological invasions. *Trends in Ecology and Evolution* **17**: 545–546.
- Inoue K, Amano M. 1986.** Evolution of *Campanula punctata* Lam. in the Izu Islands: changes in pollinators and evolution of breeding systems. *Plant Species Biology* **1**: 89–97.
- Lambrinos JG. 2001.** The expansion history of a sexual and asexual species of *Cortaderia* in California, USA. *Journal of Ecology* **89**: 88–98.
- Lloyd DG, Schoen DJ. 1992.** Self- and cross-fertilization in plants. I. Functional dimensions. *International Journal of Plant Science* **153**: 358–369.
- Lonsdale WM. 1999.** Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**: 1522–1536.
- MacDonald IAW, Cooper J. 1995.** Insular lessons for global biodiversity conservation with particular reference to alien invasions. In: Vitousek PM, Loope LL, Adersen H, eds. *Islands: biological diversity and ecological function*. Berlin, Heidelberg: Springer-Verlag, 189–203.
- Manly BFJ. 1997.** *Randomization, bootstrap and Monte Carlo methods in biology*. Boca Raton, London, New York, Washington, D. C.: Chapman & Hall.
- McMullen CK. 1987.** Breeding systems of selected Galápagos Islands angiosperms. *American Journal of Botany* **74**: 1694–1705.
- McMullen CK. 1993a.** Angiosperm breeding systems and pollination ecology in the Galápagos Islands. *Research and Exploration* **9**: 380–382.
- McMullen CK. 1993b.** Flower-visiting insects of the Galápagos Islands. *Pan-Pacific Entomologist* **69**: 95–106.
- McMullen CK. 1994.** Pollinator availability: a possible explanation of inter-island floral variation in *Justicia galapagana* (Acanthaceae). *Noticias de Galapagos* **54**: 22–27.
- Médail F, Vidal E. 1998.** Organisation de la richesse et de la composition floristiques d'îles de la Méditerranée occidentale (sud-est de la France). *Canadian Journal of Botany* **76**: 321–331.
- Meyer J-Y. 1998.** Observations on the reproductive biology of *Miconia calvescens* DC (Melastomataceae), an alien invasive tree on the island of Tahiti (South Pacific Ocean). *Biotropica* **30**: 609–624.
- Noble IR. 1989.** Attributes of invaders and the invading process: terrestrial and vascular plants. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmanek M, Williamson M, eds. *Biological invasions; a global perspective*. Chichester: John Wiley & Sons, 301–313.
- Pantone DJ, Pavlik BM, Kelley RB. 1995.** The reproductive attributes of an endangered plant as compared to a weedy congener. *Biological Conservation* **71**: 305–311.
- Parker IM. 1997.** Pollinator limitation of *Cytisus scoparius* (Scotch Broom), an invasive exotic shrub. *Ecology* **78**: 1457–1470.
- Parker IM, Engel A, Haubensak KA, Goodell K. 2002.** Pollination of *Cytisus scoparius* and *Genista monspessulana*, two invasive shrubs in California. *Madroño* **49**: 25–32.
- Parker IM, Haubensak KA. 2002.** Comparative pollinator limitation of two non-native shrubs: do mutualisms influence invasions? *Oecologia* **130**: 250–258.
- Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmanek M. 2000.** Plant invasions – the role of mutualisms. *Biological Reviews* **75**: 65–93.
- Rieseberg LH, Carney SE. 1998.** Tansley Review, 102. Plant hybridization. *New Phytologist* **140**: 599–624.
- Roy J. 1990.** In search of the characteristics of plant invaders. In: di Castri F, Hansen AJ, Debussche M, eds. *Biological invasions in Europe and the Mediterranean Basin*. Dordrecht: Kluwer Academic Publishers, 335–352.
- Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG. 2001.** The population biology of invasive species. *Annual Review of Ecology and Systematics* **32**: 305–332.
- Sakai AK, Wagner WL, Ferguson DM, Herbst DR. 1995a.** Biogeographical and ecological correlates of dioecy in the Hawaiian flora. *Ecology* **76**: 2530–2543.
- Sakai AK, Wagner WL, Ferguson DM, Herbst DR. 1995b.** Origins of dioecy in the Hawaiian flora. *Ecology* **76**: 2517–2529.
- Sartoretto S, Verlaque M, Laborel J. 1996.** Age of settlement and accumulation rate of submarine 'coralligène' (–10 to –60 m) of the northwestern Mediterranean Sea; relation to Holocene rise in sea level. *Marine Geology* **130**: 317–331.
- Sokal RR, Rohlf FJ. 1995.** *Biometry*. New York: Freeman.
- Spears EE. 1987.** Island and mainland pollination ecology of *Centrosema virginianum* and *Opuntia stricta*. *Journal of Ecology* **75**: 351–362.
- StatSoft. 2001.** *STATISTICA for Windows [Computer program manual]* 6.0 edn. Tulsa, OK: Statsoft Inc.
- Stevens J. 1992.** *Applied multivariate statistics for the social sciences*. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Stockwell CA, Hendry AP, Kinnison MT. 2003.** Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution* **18**: 94–101.

- Stout JC, Kells AR, Goulson D. 2002.** Pollination of the invasive exotic shrub *Lupinus arboreus* (Fabaceae) by introduced bees in Tasmania. *Biological Conservation* **106**: 425–434.
- Suehs CM, Affre L, Médail F. 2004a.** Invasion dynamics of two alien *Carpobrotus* (Aizoaceae) taxa on a Mediterranean island: I. Genetic diversity and introgression. *Heredity* **92**: 31–40.
- Suehs CM, Affre L, Médail F. 2004b.** Invasion dynamics of two alien *Carpobrotus* (Aizoaceae) taxa on a mediterranean island: II. Reproductive strategies. *Heredity* **92**: 550–556.
- Suehs CM, Médail F, Affre L. 2001.** Ecological and genetic features of the invasion by the alien *Carpobrotus* plants in Mediterranean island habitats. In: Brundu G, Brock J, Camarda L, Child L, Wade M, eds. *Plant invasions: species ecology and ecosystem management*. Leiden: Backhuys Publishers, 145–158.
- Suehs CM, Médail F, Affre L. 2003.** Invasion by South African *Carpobrotus* (Aizoaceae) taxa in the Mediterranean Basin: the effects of insularity on plant reproductive systems. In: Child L, Brock JH, Brundu G, Prach K, Pyšek P, Wade PM, Williamson M, eds. *Plant invasions: ecological threats and management solutions*. Backhuys Publishers, 247–263.
- Thompson K, Hodgson JG, Rich TCG. 1995.** Native and alien invasive plants: more of the same? *Ecography* **18**: 390–402.
- Valentine DH. 1978.** The pollination of introduced species, with special reference to the British Isles and the genus *Impatiens*. In: Richards AJ, ed. *The pollination of flowers by insects*. London: Academic Press, 117–123.
- Vilà M, D'Antonio CM. 1998.** Fitness of invasive *Carpobrotus* (Aizoaceae) hybrids in coastal California. *Ecoscience* **5**: 191–199.
- Vilà M, Tessier M, Gimeno I, Moragues E, Traveset A, de la Bandera MC, Suehs CM, Médail F, Affre L, Galanidis A, Dalias P, Petsikos B, Carta L, Manca M, Brundu G. 2004.** Impacts of plant invasion on species diversity in Mediterranean islands. In: Arianoutso M, Papanastasis VP, eds. *Proceedings of the 10th MEDECOS Conference, Ecology, conservation and management of mediterranean climate ecosystems*. Rotterdam: Millpress Science Publishers, 1–7.
- Vilà M, Weber E, D'Antonio CM. 1998.** Flowering and mating system in hybridizing *Carpobrotus* (Aizoaceae) in coastal California. *Canadian Journal of Botany* **76**: 1165–1169.
- Vilà M, Weber E, D'Antonio CM. 2000.** Conservation implications of invasion by plant hybridization. *Biological Invasions* **2**: 207–217.
- Weber EF, Vilá M, Albert M, D'Antonio CM. 1998.** Invasion by hybridization: *Carpobrotus* in coastal California. In: Starfinger U, Edwards K, Kowarik I, Williamson M, eds. *Plant invasions: ecological mechanisms and human responses*. Leiden: Backhuys Publishers, 275–281.
- Williamson MH, Fitter A. 1996.** The characters of successful invaders. *Biological Conservation* **78**: 163–170.
- Wisura W, Glen HF. 1993.** The South African species of *Carpobrotus* (Mesembryanthema – Aizoaceae). *Contributions to the Bolus Herbarium* **15**: 76–107.