Invasional meltdown potential: Facilitation between introduced plants and mammals on French Mediterranean islands[1]

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Abstract: In the increasingly important domain of insular invasion ecology, the role of facilitation between different introduced taxa has been mentioned, but rarely studied. This paper outlines facilitation between introduced mammals and the invasive succulents *Carpobrotus edulis* and *C.* aff. *acinaciformis* on offshore islands in southeast France. Rats and rabbits are the primary seed dispersers of *Carpobrotus* sp. on the islands studied. No such dispersal activity was detected on the adjacent mainland. Seed digestion by rats and rabbits also enhanced percent seed germination and speed, in spite of an associated reduction in seed size. In return, *Carpobrotus* provides a water/energy-rich food source during the dry summer season, thus demonstrating a clear case of mutualism between invaders.
Keywords: Carpobrotus, endozoochory, insularity, *Oryctolagus cuniculus*, *Rattus rattus*, seed dispersal.

Résumé : Dans le domaine en plein essor de l'écologie des invasions biologiques insulaires, le rôle de la facilitation entre plusieurs taxons introduits a souvent été évoqué mais rarement étudié. Cet article met en évidence le phénomène de facilitation qui existe entre des mammifères introduits et deux plantes grasses envahissantes, *Carpobrotus edulis* et *C.* aff. *acinaciformis*, sur des îles littorales du sud-est de la France. Les rats et les lapins sont des agents de dissémination primaires des graines de *Carpobrotus* sur les îles étudiées. Aucune dissémination de graines de cette nature n'a été détectée dans la zone continentale adjacente. La digestion des graines par les rats et les lapins hausse également le pourcentage de germination des graines et accélère la vitesse de germination, malgré une réduction de la taille des graines. En retour, les *Carpobrotus* fournissent une source de nourriture riche en eau et en énergie au cours de la saison sèche estivale, ce qui constitue un cas évident de mutualisme entre espèces envahissantes.
Mots-clés : Carpobrotus, dissémination des graines, endozoochorie, insularité, *Oryctolagus cuniculus*, *Rattus rattus*.

Introduction

Biological invasions have been multiplying for several decades as international traffic increases, and they are now recognized as detrimental to biodiversity on a planetary scale and a primary threat to biodiversity on islands (Vitousek *et al.*, 1996; Williamson, 1999). As more and more species are transported to new areas, the probability that entire "invasive communities" will develop increases. Of great concern is the potential for two or more invasive taxa to facilitate one another's invasion. In this context, Simberloff and Van Holle (1999) suggested "the term 'invasional meltdown' for the process by which a group of non-indigenous species facilitate one another's invasion in various ways, increasing the likelihood of survival and/or of ecological impact, and possibly the magnitude of impact." Richardson *et al.* (2000) also recently emphasized the role that mutualistic interactions (*i.e.*, relationships in which both partners derive some benefit from their participation) may play in invasion success. For example, animal plant-dispersers can benefit from the increased food availability produced by a highly productive exotic plant in exchange for the movement of exotic seeds they provide (Richardson *et al.*, 2000; Herrera, 2002).

The Mediterranean Basin has been characterized by multiple invasions for many centuries, particularly on islands (di Castri, Hansen & Debussche, 1990). Among the plants introduced on Mediterranean coasts, several South African taxa from the genus *Carpobrotus* (Wisura & Glen, 1993) are considered major pests. Two taxa are particularly known to invade the littoral ecosystems of southeast France: *C. edulis* and *C.* aff. *acinaciformis* (Suehs, Médail & Affre, 2001), where potential frugivores are present. In their native range, the indehiscent and fleshy fruits of these plants are readily eaten by native vertebrates such as ungulates and baboons (C. Suehs, pers. observ.). Outside its native range, *C. edulis* has also been observed to be dispersed by non-specialized, native mammals up to 1 km from the nearest adult plant. Uneaten fruits otherwise remained on plants for several years (D'Antonio, 1990). In addition, gut passage enhanced the germination of *C. edulis* seeds, thus indicating that mammal dispersers facilitate invasive spread in California (D'Antonio, 1990; Vilà & D'Antonio, 1998).

Such endozoochory has frequently been documented for native plants, and it can be a very efficient seed dis-

persal vector. Specifically, it permits relatively long-distance plant dispersal, particularly when fruits are heavy, indehiscent, or fleshy (Debussche & Isenmann, 1989). Endozoochory is affected by dispersal distance, the effect of ingestion on seed germination and viability, the number of seeds transported, and the place where they are dropped (Traveset, 1998; Kollmann, 2000; Calviño-Cancela, 2002). However, despite the obvious potential of such interactions to greatly accelerate the invasion process, case studies specifically documenting plant-disperser facilitation in the invasion process remain few (Simberloff & Von Holle, 1999; Richardson et al., 2000; Adams, Pearl & Bury, 2003; O'Dowd, Green & Lake, 2003), and it is therefore difficult to assume the importance of such interactions in invasion ecology.

We therefore aim to determine whether or not Mediterranean mammal communities, consisting of both native and introduced species, are implicated in the spread of invasive Carpobrotus taxa. Specifically, we address three goals relative to C. edulis and C. aff. acinaciformis and their potential seed-dispersing mammals in five sites situated on the Provençal coast of France: i) to identify introduced and/or native mammals active in Carpobrotus dispersal, ii) to determine the distances and the amounts of seeds dispersed depending on the animal species involved, and iii) to assess the effects of seed digestion on Carpobrotus seed size and germinative abilities.

Methods

STUDY SPECIES AND SITES

Carpobrotus edulis and C. aff. acinaciformis are fleshy-fruited, succulent, and mat-forming perennial Aizoaceae. These taxa were introduced into southeast France in the early 1800s at the Marseille botanical garden (Gouffé de la Cour, 1813) and were subsequently mentioned as naturalized on the Hyères coastline and archipelago in the early 1900s (Albert & Jahandiez, 1908). They are now invading backdunes, coastal rocky slopes, maritime cliffs, coastal scrubs, grasslands, and matorrals. Their rapid vegetative growth threatens native plant communities considered of high conservation value (Suehs, Médail & Affre, 2001).

This study took place on the siliceous coast of southeast France, where three insular sites (MC on Porquerolles, BG1 and BG2 on Bagaud) and two continental sites (TC for Taillat Cape and BC for Brégançon Cape) were selected for their large invasions by one or both Carpobrotus taxa (Figure 1). Sites TC, MC, BG1, and BG2 all occur within nature reserve areas (the French Conservatoire Littoral or Parc National de Port-Cros). Site BC occurs on the coastline of a private domain with poor accessibility and is preserved from anthropogenic disturbance due to its remoteness.

Several mammals have been deliberately or accidentally introduced into the study region. Cats (Felis catus) and rabbits (Oryctolagus cuniculus) have been present on Porquerolles since at least 1751 (Pasqualini, 1995). Rats (Rattus rattus) have also been present at least as long on the islands, and probably well beforehand, as they have invaded other islands in the Mediterranean as early as

2400 BP (Audoin-Rouzeau & Vigne, 1994; Martin, Thibault & Bretagnolle, 2000). Rats and rabbits have also been reported on Bagaud Island (Cheylan, 1984), but now only rats are present (K. Bourgeois, pers. observ.). On Porquerolles Island, five more introduced mammals are also present: the feral cat, the eastern house mouse (Mus musculus), the wood mouse (Apodemus sylvaticus), the lesser white-toothed shrew (Crocidura suavolens), and the western hedgehog (Erinaceus europaeus) (Cheylan, 1984). All five of these mammals are also considered native on the adjacent mainland (sites BC and TC).

SEED DISPERSAL

Feces prospection was carried out each month between July and December 2001 for each of the study sites. Care was taken to collect only fresh feces at varying distances from Carpobrotus plants, aiming to determine the maximum dispersal distance possible for each site. All fecal collections were independent of each other with the exception of rabbit feces at MC, which were restricted to latrines. There also, care was taken to use only fresh feces and to well-represent each latrine during each collection time. Feces from site BC may contain either C. edulis or C. aff. acinaciformis seeds, as both taxa are present at this site. Otherwise, feces were considered to contain seeds of only one Carpobrotus taxon. With the exception of cat feces, which were immediately dissected, feces were dried to constant mass, weighed, and then dissected to determine the presence/absence of seed remains and the number of intact seeds per feces (FIS).

The percentage of feces containing seeds or seed remains (%FS) was calculated for each disperser and site, and these feces were also used to calculate the mean number of intact seeds per g of feces. In addition, separate generalized linear models (GLM) with mixed factorial options, normal distributions, and identity link functions were used to examine the relationship between FIS and dispersal distance (m) and Carpobrotus taxa on Bagaud Island, and between FIS and dispersal distance (m) and disperser species on Porquerolles Island.
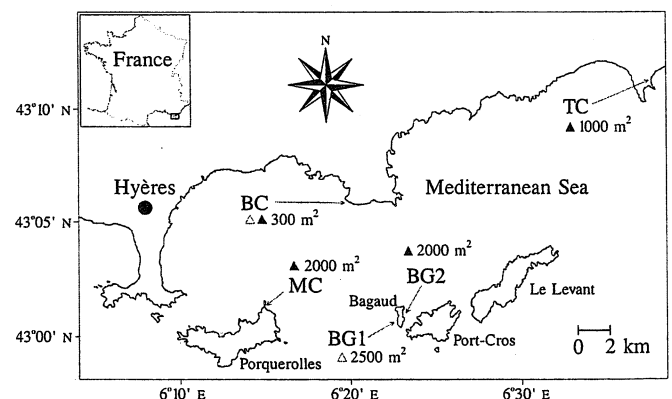

FIGURE 1. Study site map indicating Carpobrotus taxa present (black triangles: C. edulis; white triangles: C. aff. acinaciformis) and their approximate population sizes (m²) at the five study sites: Medes Cape (MC), Bagaud 1 (BG1), Bagaud 2 (BG2), Brégançon Cape (BC), and Taillat Cape (TC).

EFFECT OF INGESTION ON SEED GERMINATION AND SIZE SELECTION

Germination rates were studied only for sites BG1, BG2 and MC because FIS was far too small in the remaining sites. The germination rates of digested seeds were compared to those of dried fruits removed from the same site (Nogales, Valido & Medina, 1995; Vilà & D'Antonio, 1998). Depending on seed origin, at least 15 sets of 15 seeds (from feces) or 30 sets of 50 seeds (from fruits) were sown on 20 g of Fontainebleau sand in Petri dishes. The temperature was stabilized between 18 and 20 °C. Benlate $(1 \ g \cdot L^{-1})$ was added fortnightly to each Petri dish to prevent fungal infection, and sand was kept moist with demineralized water every 3 d (Suehs, Médail & Affre, 2001; Suehs, Affre & Médail, 2004b). Seeds were considered germinated when cotyledons were distinguishable; germinated seeds were then counted and removed each week for 105 d (15 weeks). Petri dishes were randomized fortnightly to reduce position and edge effects.

Final, cumulative percent germination, germination speeds across 7-d intervals $(\Delta\% \ \text{germination} \cdot \Delta \ d^{-1})$, and the average time to germination (d) were analyzed separately for Bagaud (sites BG1 and BG2) and Porquerolles Islands (MC). Generalized linear model ANOVAs (analyses of variance) using normal error distributions and identity link functions were used to test Carpobrotus taxon and digestion group (rat-digested and undigested) effects on Bagaud Island and only digestion group (rat digested, rabbit-digested, and undigested) effects on Porquerolles Island for final, cumulative percent germination. When a factor with more than two levels was significant, the statistical significance of comparisons between levels of the factor was estimated by the likelihood ratio statistic. The same factors and groups were also tested for germination speeds across time (day intervals) using repeated measure ANOVAs (ANOVAR) with Greenhouse-Geiser corrections for sphericity. Data were arcsin (square root) transformed to minimize heteroscedasticity. For Porquerolles data, post-hoc Tukey tests were used to pinpoint significant differences between digestion groups. Finally, the number of days between sowing and seedling emergence for each individual seed was analyzed using Cox proportional hazard regression on germination failure times.

In order to determine whether seed-size selection subsequent to mammal ingestion exists, and therefore possibly influences the germination process, we compared the average masses of intact seeds extracted from feces and from fruits removed from the same site. The average mass of intact seeds extracted from feces was obtained by weighing at least 15 sets of 15 seeds for each mammal species in each site, each set being extracted from one scat. The average seed mass for fruits was obtained from each Carpobrotus taxon in each site by weighing at least 30 sets of 100 seeds, each set being extracted from one fruit. We compared the average masses of seeds extracted from feces and extracted from fruit within each Carpobrotus taxon on Bagaud Island and within each disperser taxon on Porquerolles Island by using one-way ANOVAs. When the assumptions of ANOVAs were not fulfilled, the masses were log-transformed (Sokal &

Rohlf, 1995). Due to tied values, we tested the correlation between the seed mass and the percentage or the time of germination by using the γ correlation test (StatSoft, 2001).

Results

PATTERNS OF SEED DISPERSAL

Carpobrotus seeds were found in R. rattus, O. cuniculus, F. catus, and A. sylvaticus feces. The disparity between sites for seed dispersal events was severe: only two intact seeds dispersed by wood mice and one intact seed dispersed by rabbits were found for sites BC and TC, respectively. In stark contrast, the remaining island sites (BG1, BG2, MC) exhibited frequent seed ingestion (see Table I), with FIS ranging from 0 to 260 for rats, 0 to 30 for rabbits, and 0 to 650 for cats. All of the above-mentioned seed dispersers are introduced species on the islands. Feces of western hedgehog, red fox (Vulpes vulpes), wild boar (Sus scrofa), and at least one unidentified Mustelid species were also collected, but didn't contain Carpobrotus seeds or remains.

The relationships between FIS and dispersal distances for rats and rabbits on insular sites are presented in Figure 2, and maximum dispersal distances predicted by GLM are given in Table I. On Bagaud Island, the GLM fit the data well (scaled Pearson $\chi^2 = 609.0$, df = 605, $P > 0.44$), with no evidence of over- or under-dispersion $(\phi = 1.0)$. Distance and Carpobrotus taxon factors were both significant (GLM $\chi^2 = 26.8$, df = 1, $P < 0.001$ and GLM $\chi^2 = 8.4$, df = 1, $P < 0.01$, respectively), with no interaction between the two, indicating that C. aff. acinaciformis seeds occurred in larger numbers in feces than C. edulis, and that the number of seeds·feces^{-1} decreased with distance for both Carpobrotus taxa in the same manner. On Porquerolles Island, the GLM also fit well (scaled Pearson $\chi^2 = 257.0$, df = 253, $P > 0.41$) with no evidence of over- or under-dispersion $(\phi = 1.0)$. Significant distance (GLM $\chi^2 = 27.5$, df = 1, $P < 0.001$) and disperser (GLM $\chi^2 = 137.7$, df = 1, $P < 0.001$) effects were detected, as well as a distance × disperser-group interaction (GLM $\chi^2 = 26.2$, df = 1, $P < 0.001$), indicating that in general, rat feces contained more seeds than rabbit feces, that the number of seeds·feces^{-1} significantly decreased with distance, and that this relationship with distance was significantly different between the two disperser species (i.e., rabbits dispersed to longer distances than rats).

EFFECTS OF SEED INGESTION ON GERMINATION RATES, SPEED, AND SEED SIZE

Seeds extracted from rat, rabbit, cat, and wood mouse feces conserved their ability to germinate after gut passage (Table I). On Bagaud Island, the model to analyze final, cumulative percent germination fit the data well (scaled Pearson $\chi^2 = 95.0$, df = 92, $P > 0.39$), with no evidence of over- or under-dispersion $(\phi = 1.0)$. Only a significant digestion group effect was detected by the model (GLM $\chi^2 = 29.0$, df = 1, $P < 0.001$), indicating that rat digestion significantly increased final, cumulative percent germination (Figure 3). A two-way ANOVAR detected a significant day effect $(F = 128.6$, df = 13, $P < 0.001)$ and significant day × taxon $(F = 3.9$, df = 13, $P < 0.01)$, day ×

digestion ($F = 28.1$, df = 13, $P < 0.001$), and day × digestion × taxon ($F = 5.8$, df = 13, $P < 0.001$) interactions, indicating that germination speeds differed over time, and that all four groups reacted differently to day intervals (Figure 4). *Post-hoc* Tukey tests (Table II) supported that, in general, germination speeds were significantly higher for rat-digested seeds in the first 2 day intervals (0 to 14 d) compared to fruits, and significantly lower between 21 and 35 d. The *Carpobrotus* taxon interaction resulted in a reversal of the trend in fruit data for *C. aff. acinaciformis* to peak after *C. edulis*, leading instead to a trend in the rat data where *C. aff. acinaciformis* immediately had a higher germination speed in the first day interval. Cox proportional hazard regression detected only a digestion effect (Wald $\chi^2 = 381.7$, df = 1, $P < 0.001$); *i.e.*, rat-digested seeds germinate earlier than non-digested seeds.

On Porquerolles Island, the GLM for final, cumulative percent germination fitted the data well (scaled Pearson $\chi^2 = 75.0$, df = 72, $P > 0.38$) and there was no evidence of over- or under-dispersion ($\phi = 1.0$). The model detected a significant digestion effect (GLM $\chi^2 = 80.6$, df = 2, $P < 0.001$). Rat-digested seeds had final, cumulative percent germination higher than those of both fruits ($\chi^2 = 107.4$, df = 1, $P < 0.001$) and rabbit-digested seeds ($\chi^2 = 23.2$, df = 1, $P < 0.001$), and rabbit-digested seeds had final, cumulative percent germination significantly higher than those of fruits as well ($\chi^2 = 6.1$, df = 1, $P < 0.05$; Figure 3). The ANOVAR on Porquerolles detected a significant day effect ($F = 63.6$, df = 14, $P < 0.001$) and a significant day × digestion-group interaction ($F = 20.3$, df = 28, $P < 0.001$) for germination speeds across day intervals (Figure 4). *Post-hoc* Tukey tests (Table II) supported that rat-digested seeds had faster germination rates for the first 4 day intervals (days 0 to 28) than both rabbit-digested seeds and fruits, and that rabbit-digested seeds had higher germination speeds than fruits on days 7-14. Cox proportional hazard regressions detected digestion effects for germination failure where rat-digested seeds germinated earlier than both rabbit-digested seeds (Wald $\chi^2 = 68.1$, df = 1, $P < 0.001$) and fruits (Wald $\chi^2 = 473.9$, df = 1, $P < 0.001$), and rabbit-digested seeds also germinated earlier than fruits (Wald $\chi^2 = 70.7$, df = 1, $P < 0.001$).

The average seed masses for fruits were significantly higher than those extracted from the feces of rats (ANOVAs, Bagaud Island: *C. aff. acinaciformis* $F = 50.4$, df = 1, $P < 0.001$, *C. edulis* $F = 4.4$, df = 1, $P < 0.05$; Porquerolles Island: $F = 24.1$, df = 1, $P < 0.001$) and of rabbits (Porquerolles Island: $F = 54.4$, df = 1, $P < 0.001$) across both sites and *Carpobrotus* taxa (Figure 5). Fruit seed masses were positively correlated with percent germination ($\gamma = 0.10$, n = 213, $P < 0.05$) and negatively correlated with time to germination ($\gamma = -0.10$, n = 197, $P < 0.05$). γ correlation tests did not detect significant correlations between feces seed masses and percent germination ($\gamma = 0.07$, n = 75, $P = 0.41$) or between feces seed masses and time to germination ($\gamma = 0.05$, n = 66, $P = 0.57$).

Discussion

IMPACTS ON *CARPOBROTUS* INVASION

Among the sites studied, dispersal was anecdotal for BC and TC (Figure 1), but included two native mammals:

TABLE I. The number of feces collected (n), the percentage of feces containing seeds or seed remains (%FS), the number of intact seeds per feces containing seed remains (No. seeds·feces^{-1}, mean ± SD [maximum]), the number of intact seeds per g of feces containing seed remains (No. seeds·g feces^{-1}, mean ± SD [maximum]), maximum seed dispersal distances predicted by GLM models (MDD; maximum seed dispersal distances predicted by GLM models are given in parentheses), and seed germination ability after gut passage by mammal dispersers (G) at the five study sites (see Figure 1). Cat (*Felis catus*) MDDs were determined not only in relation to Medes Cape site, but also to *Carpobrotus* populations elsewhere on Porquerolles Island due to the overlap between potential cat territory and multiple *Carpobrotus* zones.

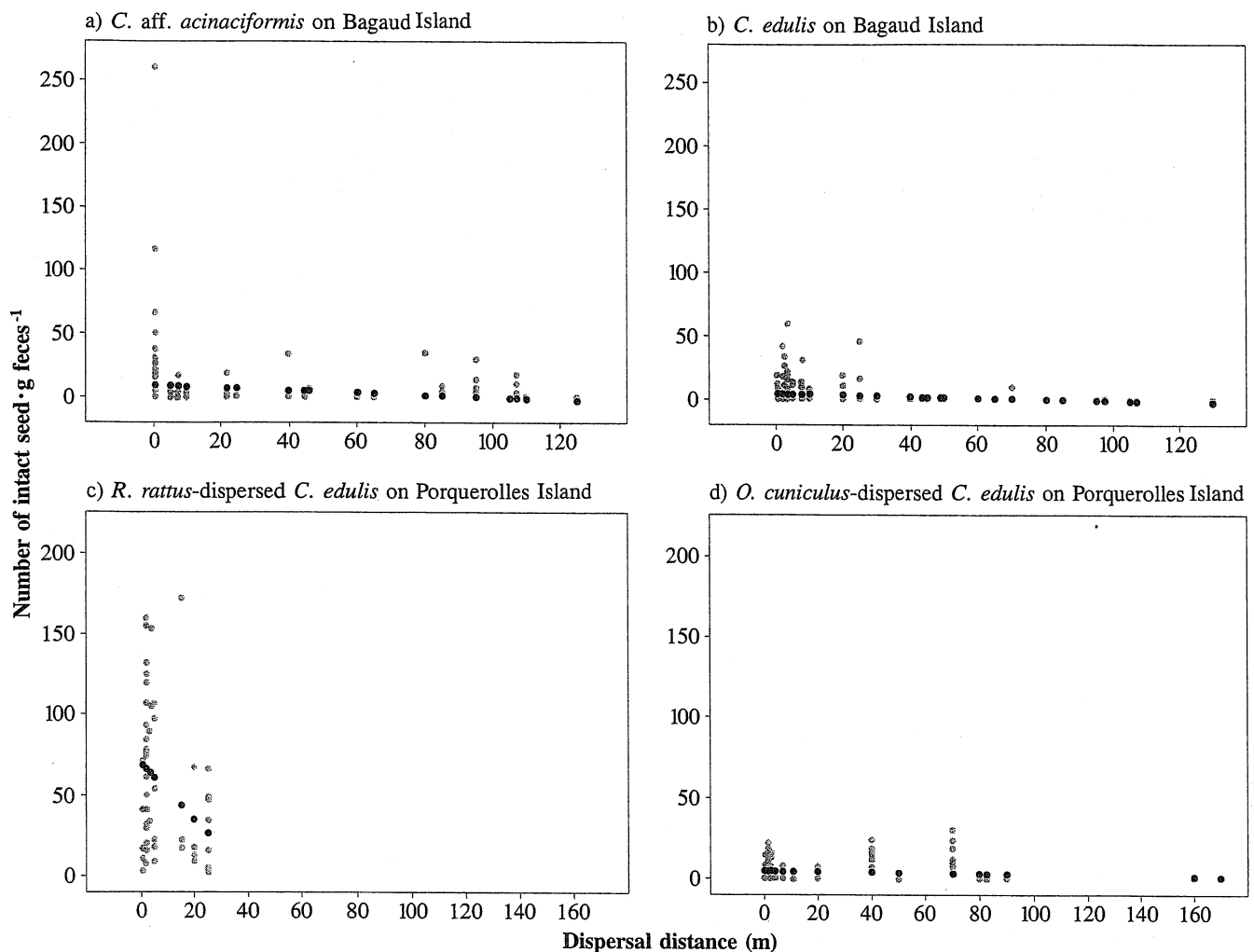| Seed disperser	Bagaud 1 (BG1)						Brégançon Cape (BC)						Bagaud 2 (BG2)						Taillat Cape (TC)						Medes Cape (MC)					
	n	%FS	No. seeds·feces^{-1}	No. seeds·g feces^{-1}	MDD (m)	G	n	%FS	No. seeds·feces^{-1}	No. seeds·g feces^{-1}	MDD (m)	G	n	%FS	No. seeds·feces^{-1}	No. seeds·g feces^{-1}	MDD (m)	G	n	%FS	No. seeds·feces^{-1}	No. seeds·g feces^{-1}	MDD (m)	G	n	%FS	No. seeds·feces^{-1}	No. seeds·g feces^{-1}	MDD (m)	G
Erinaceus europaeus	0	0	0	—	—	—	—	—	—	—	—	—	0	0	—	—	—	—	—	—	—	—	—	—	81	0	—	—	—	—
Felis catus	0	0	—	—	—	—	—	—	—	—	—	—	0	0	—	—	—	—	—	—	—	—	—	—	93	4.3	184.0 ± 310.8 [650]	7.4 ± 6.6 [30]	62.8 ± 55.1 [195.3]; 70 [209]	yes
Oryctolagus cuniculus	0	0	—	—	—	—	—	—	—	—	—	—	0	0	—	—	—	—	—	—	—	—	—	—	192	55.0	—	—	> 500	yes
Rattus rattus	240	46.3	10.2 ± 8.4 [260]	72.9 ± 148.3 [1154.5]	115 [96]	yes	—	—	—	—	—	—	369	50.1	4.9 ± 8.4 [60]	44.8 ± 59.57 [229.5]	98 [80]	yes	—	—	—	—	—	—	65	100.0	54.4 ± 51.4 [30]	359.7 ± 225.5 [1044.5]	25 [40]	yes
Apodemus sylvaticus	6	100.0	0.3 ± 0.5 [1]	17.2 ± 26.8 [55.6]	2	yes	—	—	—	—	—	—	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mustelidae	35	0	—	—	—	—	—	—	—	—	—	—	0	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Oryctolagus cuniculus	0	0	—	—	—	—	—	—	—	—	—	—	92	6.5	0.2 ± 0.4 [1]	1.7 ± 4.3 [10.4]	20	yes	—	—	—	—	—	—	—	—	—	—	—	—
Sus scrofa	0	0	—	—	—	—	—	—	—	—	—	—	30	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Vulpes vulpes	0	0	—	—	—	—	—	—	—	—	—	—	10	0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

FIGURE 2. The relationship between the number of intact seeds·g feces^{-1} (FIS) and dispersal distance for a) *Carpobrotus* aff. *acinaciformis* and b) *C. edulis* seeds dispersed by *Rattus rattus* on Bagaud Island and for c) *R. rattus*-dispersed and d) *Oryctolagus cuniculus*-dispersed *C. edulis* seeds on Porquerolles Island. Grey circles represent observed values and black circles represent GLM-predicted values.

A. sylvaticus and *O. cuniculus*. At sites BG1, BG2, and MC, seeds were commonly dispersed by *R. rattus* and *O. cuniculus*, and more rarely by *F. catus*. All three of these species were introduced at these insular sites, and are on a world's worst island invader list (Courchamp, Chapuis & Pascal, 2003). Combined with other observations of *Carpobrotus* seed dispersers, which include deer and kangaroos (D'Antonio, 1990; Parsons, 1997), this study indicates that seed dispersal can occur via a large range of animals. In addition, *Rattus* spp. are prolific, globally widespread, and maintain high insular densities (Cheylan & Granjon, 1985; Sarà & Morand, 2002; Courchamp, Chapuis & Pascal, 2003). Thus, the likelihood that at least one efficient disperser is present at an introduction site is quite high. As regional differences in frugivore diversity can affect seed dispersal (Bleher & Böhning-Gaese, 2001), this likelihood could be important in determining plant invasiveness.

Our observed and GLM-predicted dispersal distances (Figure 2; Table I) via endozoochory are large compared to a Californian study where rabbits dispersed seeds 0-10 m and long-distance dispersal up to 1 km was done by the much-larger mule deer (D'Antonio, 1990); they are also large compared to typical rodent dispersal values, which average 14-15 m, with maximums between 9 and 60 m, as noted in Price and Jenkins (1986). These distances are sufficient for new habitat colonization and to increase establishment/survival by moving seedlings away from competitive adult plants (D'Antonio, 1990; Howe & Miriti, 2000; Kollmann, 2000). Improved dispersal can also increase invasion by "thickening" seed shadow tails, a critical parameter in plant spread (Levin *et al.*, 2003), and the probability that a seed will fall in appropriate, unoccupied microsites (Calviño-Cancela, 2004). Furthermore, models suggest that increasing the propagule-producing loci in an invasion front greatly speeds the invasion process (Moody & Mack, 1988).

Regarding seed size, ingested seeds are significantly smaller than non-digested seeds, suggesting that smaller seeds are escaping mastication (Nogales, Valido & Medina, 1995). Size selection may affect invasion, since seed size has been linked to germination and growth (Eriksson, 1999; Susko & Lovett-Doust, 2000; Traveset, Riera & Mas, 2001). However, in tests of the relationship between

252

seed mass and percent germination/speed, the smaller digested seeds germinated more and earlier than non-digested seeds. Seed coat abrasion and/or pulp removal via gut passage (Traveset, 1998) may explain the combination of enhanced germination and reduced seed size.

Finally, *C.* aff. *acinaciformis* germination rates are approximately doubled via rat digestion (Figure 3).
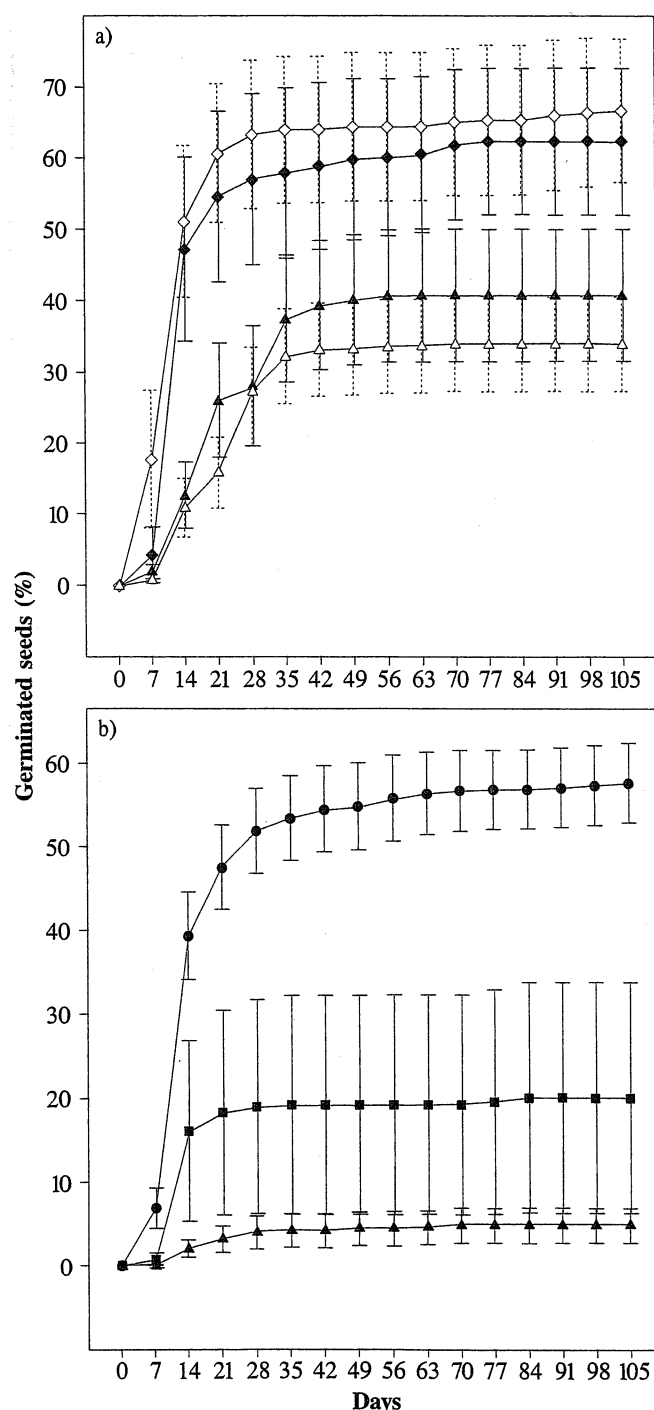
Carpobrotus edulis germination rates are similarly increased 1.5 to 11 times by rat digestion, and ~4 times by rabbit digestion. A similar phenomenon has been documented in California, where deer and rabbit digestion augmented *C. edulis* germination rates ~3 to 4 times that of non-digested rates (D'Antonio, 1990; Vilà & D'Antonio, 1998). We also found that digestion by either rats or rabbits decreased the time to germination for both *Carpobrotus* taxa studied. Thus, introduced mammals enhance the likelihood of *Carpobrotus* establishment and spread, and the time to germination is shortened. This may represent a favourable strategy on Mediterranean islands, where digested seeds are likely to take advantage of the first autumn rainfalls, thus increasing their competitive abilities with regard to the colonization of available space.

Overall, mammal seed dispersal appears to play a large role in the studied *Carpobrotus* invasion and may favour *C.* aff. *acinaciformis* over *C. edulis* on Bagaud due to the higher number of seeds of this taxon per feces (Table I). Both predicted and observed dispersal distances vary greatly with site and disperser, but nevertheless result in tens of metres of movement away from adult *Carpobrotus* plants. Increased dispersal distances and augmented germination rates and speed all increase the prob-
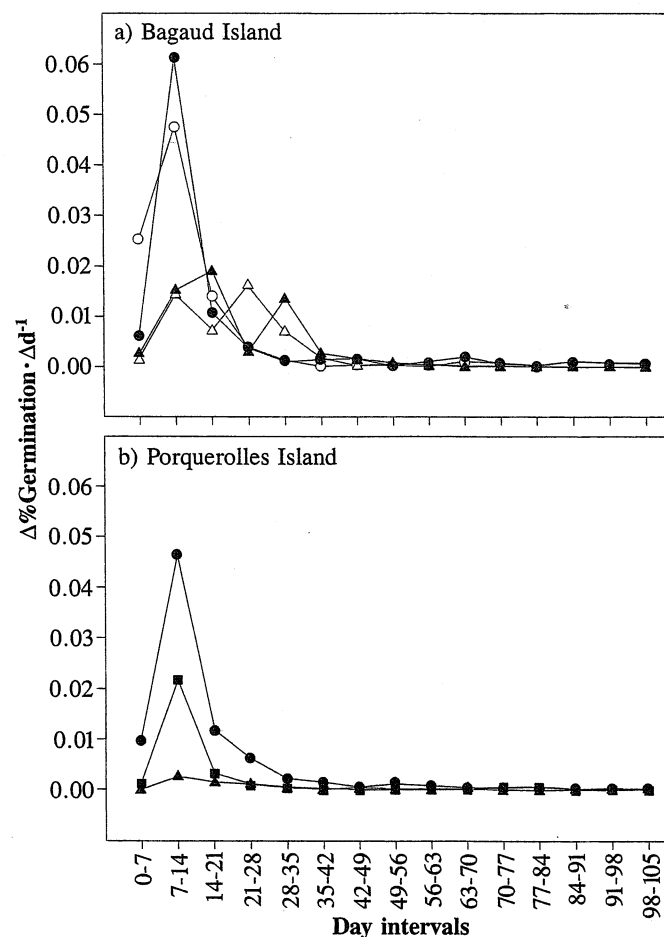

FIGURE 3. Mean percent germination curves for *Carpobrotus* seeds extracted from fruits and mammal feces on a) Bagaud Island and b) Porquerolles Island (black: *C. edulis*; white: *C.* aff. *acinaciformis*; triangles: seeds from fruits; diamonds and circles: seeds from rat feces; squares: seeds from rabbit feces; bars indicate 95% confidence intervals).

FIGURE 4. Mean germination speed curves ($\Delta\%$ germination$\cdot\Delta$ d^{-1}) for *Carpobrotus* seeds extracted from fruits and mammal feces on a) Bagaud Island and b) Porquerolles Island (black: *C. edulis*; white: *C.* aff. *acinaciformis*; triangles: seeds from fruits; circles: seeds from rat feces; squares: seeds from rabbit feces).

TABLE II. *Post-hoc* Tukey test probability values (*P*) between *Carpobrotus* digestion groups on Bagaud Island and *Carpobrotus edulis* digestion groups on Porquerolles Island following repeated measures ANOVA on germination speeds (Δ % germination·Δ d^{-1}) within the first 5 day intervals. The remaining day intervals were insignificant.

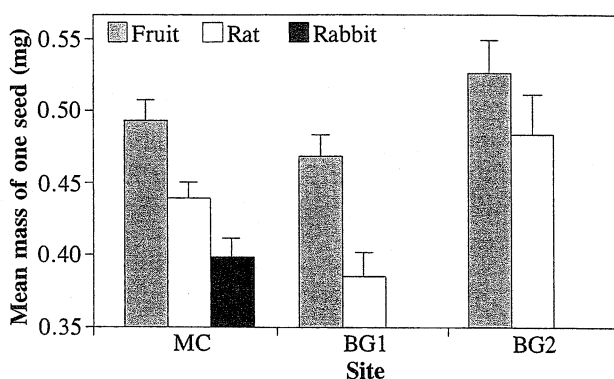| Comparison	Day intervals				
	0-7	7-14	14-21	21-28	28-35
BAGAUD					
C. aff. *acinaciformis* fruit versus rat	0.001	0.001	ns	0.001	0.01
C. edulis fruit versus rat	ns	0.001	ns	ns	0.001
Rat *C.* aff. *acinaciformis* versus *C. edulis*	0.001	ns	ns	ns	ns
Fruit *C.* aff. *acinaciformis* versus *C. edulis*	ns	ns	0.05	0.001	ns
PORQUEROLLES (*C. EDULIS* ONLY)					
Rat versus fruit	0.001	0.001	0.001	0.01	ns
Rabbit versus fruit	ns	0.01	ns	ns	ns
Rat versus rabbit	0.01	0.001	0.001	0.01	ns

FIGURE 5. Mean *Carpobrotus* seed masses of seeds extracted from fruits and from mammal feces (MC: Medes Cape on Porquerolles Island, anti-transformed values; BG1: *C.* aff. *acinaciformis* area on Bagaud Island; BG2: *C. edulis* area on Bagaud Island). Bars indicate 95% confidence intervals.

ability that a *Carpobrotus* seed will be deposited in an appropriate site and then successfully germinate.

INVASIONAL MELTDOWN POTENTIAL

Three points demonstrate that mammal dispersers are actively searching for *Carpobrotus*. First, rats are known to forage ~50 m from their burrows (Cheylan & Granjon, 1985), and the daily activity of rabbits averages 80-140 m, with maximum movements of 100-200 m during summer and autumn (Moreno *et al.*, 2004). Thus, the maximum *Carpobrotus* seed dispersal distances found (see Table I) suggest long distances covered to reach fruits. Second, these dispersers eat *Carpobrotus* frequently, as indicated by the > 46% FS values in Table I. Third, feces contained a high number of seeds·g^{-1} compared to other reports of Mediterranean endozoochory (Malo, Jiménez & Suárez, 1995). These three points stress the value of this resource for introduced mammals. In fact, *Carpobrotus* fruits are large (~19 × 26 mm; Suehs, Affre & Médail, 2004a) and energy- (310 kJ·100 g dry mass^{-1}) and water-rich (79% water; K. Bourgeois, unpubl. data; see also Vilà & D'Antonio, 1998), and they ripen between June and July, a drought season on Mediterranean islands. They also occur in large numbers, with ~25 fruits·m^{-2} (C. Suehs, unpubl. data), resulting, for example, in ~750 kg for site MC (Figure 1). Typical fruits in Mediterranean areas are 6-10 mm in diameter and rarely larger than 14 mm (Herrera, 1987). Dispersers therefore benefit from a large energy/water resource not provided by native vegetation during a drought and starvation period. Indeed, Cheylan (1988) has also noted that rats select *Carpobrotus* fruits during this time, supposedly for water content.

Interestingly, *Carpobrotus* seeds were also found in cat scats, though this rare dispersal is probably not of great quantitative importance. However, it is likely to drive sporadic, long-distance dispersal, increasing the potential to colonize sites that would not have been reached otherwise. Again, increasing dispersal loci within an invasion front, even rarely, is known to greatly augment invasion speed (Moody & Mack, 1988).

Interestingly, seed dispersal was nearly absent for the mainland sites BC and TC (Figure 1; Table I). This site pattern of *Carpobrotus* seed dispersal is confounded by the site pattern of mammal guilds (introduced or native), but does not exclude the following hypothesis: *Carpobrotus* endozoochory is linked to introduced mammal dispersers, which are linked to insularity. Although one must keep in mind the limited size of our study as a caveat, a plausible explanation for this pattern is that community-assembly rules varying with insularity are affecting the invasion process. Indeed, insularity is currently one of the most consistent predictors of biological invasion occurrence (Lonsdale, 1999).

Overall, we clearly demonstrated mutualism/facilitation between *R. rattus*/*O. cuniculus* and *Carpobrotus* taxa at three sites (BG1, BG2, and MC; Figure 1). Although further data are needed to evaluate the response of survivorship to these interactions, we hypothesize that all three species benefit from their new relationships: *Carpobrotus* gains seed dispersers and increased germination capacities, and *R. rattus* and *O. cuniculus* gain a food and water resource. Therefore, we conclude that there is a high potential for invasional meltdown in Mediterranean sites where these taxa coexist.

Conclusion

Simberloff and Von Holle (1999) have called "invasional meltdown" a process by which introduced species facilitate one another's invasion. The demonstrated synergism between introduced plants and seed dispersers undoubtedly favours invasion on the Mediterranean islands studied and illustrates the importance of mutualisms. Furthermore, these relationships have developed over a short time-scale, since *Carpobrotus* is mentioned on the Hyères archipelago only since the early 1900s (Albert & Jahandiez, 1908). While certain authors (Simberloff & Von Holle, 1999; Richardson *et al.*, 2000) have hypothesized the importance of multi-species relationships in invasions, this study is one of the few that documents this phenomenon empirically (but see Adams, Pearl & Bury, 2003), especially for terrestrial environments (O'Dowd, Green & Lake, 2003). In addition, we have evidence indicating that islands might be especially susceptible to invasional meltdown.

Acknowledgements

Literature cited

Adams, M. J., C. A. Pearl & R. B. Bury, 2003. Indirect facilitation of an anuran invasion by non-native fishes. Ecology Letters, 6: 343-351.

Albert, A. & E. Jahandiez, 1908. Catalogue des plantes qui croissent naturellement dans le département du Var. Museum d'Histoire Naturelle de Toulon reprints, 1985, Toulon.

Audoin-Rouzeau, F. & J.-D. Vigne, 1994. La colonisation de l'Europe par le rat noir (*Rattus rattus*). Revue de Paléobiologie, 13: 125-145.

Bleher, B. & K. Böhning-Gaese, 2001. Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. Oecologia, 129: 385-394.

Calviño-Cancela, M., 2002. Spatial patterns of seed dispersal and seedling recruitment in *Corema album* (Empetraceae): The importance of unspecialized dispersers for regeneration. Journal of Ecology, 90: 775-784.

Calviño-Cancela, M., 2004. Ingestion and dispersal: Direct and indirect effects of frugivores on seed viability and germination of *Corema album* (Empetraceae). Acta Oecologica, 26: 55-64.

Cheylan, G., 1984. Les mammifères des îles provençales. Travaux Scientifiques du Parc national de Port-Cros, France, 10: 13-25.

Cheylan, G., 1988. Les adaptations écologiques de *Rattus rattus* à la survie dans les îlots méditerranéens (Provence et Corse). Bulletin d'Écologie, 19: 417-426.

Cheylan, G. & L. Granjon, 1985. Écologie d'une population de rats noirs *Rattus rattus* à Port Cros (Var) méthodologie et premiers résultats obtenus sur quadrat. Travaux Scientifiques du Parc national de Port-Cros, France, 11: 109-130.

Courchamp, F., J.-L. Chapuis & M. Pascal, 2003. Mammal invaders on islands: Impact, control and control impact. Biological Reviews, 78: 347-383.

D'Antonio, C. M., 1990. Seed production and dispersal in the non-native, invasive succulent *Carpobrotus edulis* (Aizoaceae) in coastal strand communities of central California. Journal of Applied Ecology, 27: 693-702.

Debussche, M. & P. Isenmann, 1989. Fleshy fruit characters and choice of bird and mammal seed dispersers in a mediterranean region. Oikos, 56: 327-338.

di Castri, F., A. J. Hansen & M. Debussche (eds.), 1990. Biological Invasions in Europe and the Mediterranean Basin. Kluwer Academic Publishers, Dordrecht.

Eriksson, O., 1999. Seed size variation and its effect on germination and seedling performance in the clonal herb *Convallaria majalis*. Acta Oecologica, 20: 61-66.

Gouffé de la Cour, M., 1813. Mémoire sur les végétaux exotiques qui peuvent être naturalisés dans les départements méridionaux de la France, suivi de la liste des plantes rares qui ont fleuri et de celles qui ont fructifié dans divers jardins de Marseille principalement dans le jardin de botanique et de naturalisation de cette ville. Mémoires de l'Académie de Marseille, 11: 149-259.

Herrera, C. M., 1987. Vertebrate-dispersed plants of the Iberian Peninsula: A study of fruit characteristics. Ecological Monographs, 57: 305-331.

Herrera, C. M., 2002. Seed dispersal by vertebrates. Pages 185-208 in C. M. Herrera & O. Pellmyr (eds.). Plant-Animal Interactions: An Evolutionary Approach. Blackwell Publishing, Oxford.

Howe, H. F. & M. N. Miriti, 2000. No question: Seed dispersal matters. Trends in Ecology and Evolution, 15: 434-436.

Kollmann, J., 2000. Dispersal of fleshy-fruited species: A matter of spatial scale? Perspectives in Plant Ecology, Evolution and Systematics, 3: 29-51.

Levin, S. A., H. C. Muller-Landau, R. Nathan & J. Chave, 2003. The ecology and evolution of seed dispersal: A theoretical perspective. Annual Review of Ecology and Systematics, 34: 575-604.

Lonsdale, W. M., 1999. Global patterns of plant invasions and the concept of invasibility. Ecology, 80: 1522-1536.

Malo, J. E., B. Jiménez & F. Suárez, 1995. Seed bank build-up in small disturbances in a Mediterranean pasture: The contribution of endozoochorous dispersal by rabbits. Ecography, 18: 73-82.

Martin, J.-L., J.-C. Thibault & V. Bretagnolle, 2000. Black rats, island characteristics and colonial nesting birds in the Mediterranean: Consequences of an ancient introduction. Conservation Biology, 14: 1452-1466.

Mitchell-Jones, A. J., G. Amori, W. Bogdanowicz, B. Krystufek, P. J. H. Reijnders, F. Spitzenberger, M. Stubbe, J. B. M. Thissen, V. Vohralík & J. Zima (eds.), 1999. The Atlas of European Mammals. T & AD Poyser Natural History, London.

Moody, M. E. & R. N. Mack, 1988. Controlling the spread of plant invasions: The importance of nascent foci. Journal of Applied Ecology, 25: 1009-1021.

Moreno, S., R. Villafuerte, S. Cabezas & L. Lombardi, 2004. Wild rabbit restocking for predator conservation in Spain. Biological Conservation, 118: 183-193.

Nogales, M., A. Valido & F. M. Medina, 1995. Frugivory of *Plocama mendula* (Rubiaceae) by the rabbit (*Oryctolagus cuniculus*) in xerophytic zones of Tenerife (Canary islands). Acta Oecologia, 16: 585-591.

O'Dowd, D. J., P. T. Green & P. S. Lake, 2003. Invasional 'meltdown' on an oceanic island. Ecology Letters, 6: 812-817.

Parsons, R. F., 1997. *Carpobrotus modestus* (Aizoaceae), a post-fire pioneer in semi-arid southern Australia. Journal of Arid Environments, 37: 453-459.

Pasqualini, M., 1995. Aux sources du peuplement récent des îles d'Hyères. Les archives du génie. Travaux Scientifiques du Parc national de Port-Cros, France, 16: 81-92.

Price, M. V. & S. H. Jenkins, 1986. Rodents as seed consumers and dispersers. Pages 191-236 in D. R. Murray (ed.). Seed Dispersal. Academic Press, San Diego, California.

Richardson, D. M., N. Allsopp, C. M. D'Antonio, S. J. Milton & M. Rejmánek, 2000. Plant invasions: The role of mutualisms. Biological Reviews, 75: 65-93.

Sarà, M. & S. Morand, 2002. Island incidence and mainland population density: Mammals from Mediterranean islands. Diversity and Distributions, 8: 1-9.

Simberloff, D. & B. Von Holle, 1999. Positive interactions of nonindigenous species: Invasional meltdown? Biological Invasions, 1: 21-32.

Sokal, R. R. & F. J. Rohlf (eds.), 1995. Biometry, 3rd Edition. Freeman and Company, New York, New York.

StatSoft, 2001. STATISTICA for Windows [Computer program manual]. 6.0 Edition. Tulsa, Oklahoma.

Suehs, C. M., L. Affre & F. Médail, 2004a. The invasion dynamics of two introduced succulents, *Carpobrotus affine acinaciformis* and *C. edulis* (Aizoaceae), on a Mediterranean Island: I. Taxonomy, clonality and introgression. Heredity, 92: 31-40.

Suehs, C. M., L. Affre & F. Médail, 2004b. The invasion dynamics of two introduced succulents, *Carpobrotus affine acinaciformis* and *C. edulis* (Aizoaceae), on a Mediterranean Island: II. Reproductive alternatives. Heredity, 92: 550-556.

Suehs, C. M., F. Médail & L. Affre, 2001. Ecological and genetic features of the invasion by the alien *Carpobrotus* plants in Mediterranean island habitats. Pages 145-158 *in* G. Brundu, J. Brock, L. Camarda, L. Child & M. Wade (eds.). Plant Invasions: Species Ecology and Ecosystem Management. Backhuys Publishers, Leiden.

Susko, D. J. & L. Lovett-Doust, 2000. Patterns of seed mass variation and their effects on seedling traits in *Alliaria petiolata*. American Journal of Botany, 87: 56-66.

Traveset, A., 1998. Effect of seed passage through vertebrate frugivores' guts on germination: A review. Perspectives in Plant Ecology, Evolution and Systematics, 1: 151-190.

Traveset, A., N. Riera & R. E. Mas, 2001. Ecology of fruit-colour polymorphism in *Myrtus communis* and differential effects of birds and mammals on seed germination and seedling growth. Journal of Ecology, 89: 749-760.

Vilà, M. & C. M. D'Antonio, 1998. Fruit choice and seed dispersal of invasive *versus* noninvasive *Carpobrotus* (Aizoaceae) in coastal California. Ecology, 79: 1053-1060.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope & R. Westbrooks, 1996. Biological invasions as global environmental change. American Scientist, 84: 468-478.

Williamson, M., 1999. Invasions. Ecography, 22: 5-12.

Wisura, W. & H. F. Glen, 1993. The South African species of *Carpobrotus* (Mesembryanthema - Aizoaceae). Contributions to the Bolus Herbarium, 15: 76-107.