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Disruption of a Plant-Lizard Seed Dispersal System and Its Ecological Effects on a Threatened Endemic Plant in the Balearic Islands

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Abstract: *The introduction of exotic species to an island can have significant effects on the population density and distribution of native species and on the ecological and evolutionary interactions among them (e.g., plant-animal mutualisms). The disruption of these interactions can be dramatic, significantly reducing the reproductive success of the species and even leading to their extinction. On Menorca Island (Balearic Islands, western Mediterranean), we examined the consequences of the disruption of the mutualism between two endemic species: a perennial shrub, (*Daphne rodriguezii* [Texidor]) and a frugivorous lizard (*Podarcis lilfordi* [Günther]). The lizard became extinct from this island (as well as from Mallorca) as a result of the introduction of carnivorous mammals, which has continued since Roman times. The relict mutualism between *D. rodriguezii* and the lizard currently persists only in an islet (60 ha) where *P. lilfordi* is still abundant. We hypothesized that the absence of this lizard from most Menorcan populations is the factor causing the regression of this plant, currently considered at risk of extinction. Through observation and experimentation in the field and laboratory, we found strong evidence that a lack of seed dispersal in Menorca is the main cause of the low seedling recruitment. First, the population with greatest seedling recruitment was that in the islet where lizards were abundant. Second, lizards appeared to be the only dispersers of *D. rodriguezii*. Lizards consumed large amounts of fruits, without affecting either germination or seedling growth, and moved seeds to sites suitable for plant establishment. Seedlings in Menorca, in contrast, recruited almost exclusively under the parent plants. Third, the effect of other factors that may influence plant population growth (a low fruit set and a high postdispersal seed predation) was similar between the islet and the Menorcan populations. To our knowledge, our results are the first that quantitatively show that a biological invasion can cause a disruption of a specialized plant-vertebrate mutualism that sets the plant partner on the road to extinction.*

Key Words: *Daphne rodriguezii*, mutualism disruption, plant-lizard interaction, *Podarcis lilfordi*, saurochory, western Mediterranean

Interrupción de un Sistema de Dispersión de Semillas Planta-Lagartija y sus Efectos Ecológicos sobre una Planta Endémica Amenazada en las Islas Baleares

Resumen: *La introducción de especies exóticas a una isla puede tener efectos significativos sobre la densidad y distribución de especies nativas y sobre sus interacciones ecológicas y evolutivas (e.g. mutualismos planta-animal). La alteración de estos mutualismos puede ser dramática, altera significativamente el éxito reproductivo y puede provocar la extinción de las especies. Examinamos las consecuencias de la interrupción del mutualismo en dos especies endémicas en la isla Menorca (Islas Baleares, Mediterráneo occidental): un arbusto perenne, (*Daphne rodriguezii* [Texidor]) y una lagartija frugívora (*Podarcis lilfordi* [Günther]). La lagartija se extinguió en esta isla (así como en Mallorca) debido a la introducción de mamíferos carnívoros desde tiempos Romanos. Actualmente, el mutualismo relicto entre *Daphne rodriguezii* y la lagartija solo persiste en un islote (60 ha), donde *P. lilfordi* aún es abundante. Probamos la hipótesis que la ausencia de esta lagartija*

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en la mayoría de las poblaciones de Menorca es lo que está causando la regresión de esta planta, actualmente considerada en riesgo de extinción. Mediante observación y experimentación en el campo y laboratorio, encontramos fuerte evidencia de que la falta de dispersión de semillas en Menorca es la principal causa del bajo reclutamiento de plántulas. Primero, porque la población con el mayor reclutamiento de plántulas fue la del islote, donde la lagartija abunda. Segundo, parece que las lagartijas son el único dispersor de *D. rodriguezii*. Las lagartijas consumieron grandes cantidades de frutos, sin afectar a la germinación ni al crecimiento de plántulas, y movieron semillas a sitios adecuados para el establecimiento de plántulas. En contraste, plántulas en Menorca reclutaron casi exclusivamente debajo de las plantas parentales. Tercero, el efecto de otros factores que pueden influenciar al crecimiento de la población de plantas (baja de frutos y alta depredación de semillas post dispersión) fueron similares entre el islote y las poblaciones de Menorca. Hasta donde sabemos, nuestros resultados son los primeros que muestran cuantitativamente que una invasión biológica puede provocar la interrupción de un mutualismo planta-vertebrado especializado que coloca a la planta asociada en el camino a la extinción.

Palabras Clave: *Daphne rodriguezii*, interacción planta-lagartija, interrupción de mutualismo, Mediterráneo occidental, *Podarcis lilfordi*, saurocoria

Introduction

An invasive species can have a direct effect on native species (e.g., by being competitively superior and displacing them from the habitat) but can also affect them indirectly by altering species interactions (e.g., plant-animal mutualisms) that are sometimes very specific. Researchers have documented mutualistic disruptions resulting from invasive species, mostly in island ecosystems such as New Zealand (e.g., Webb & Kelly 1993; Ladley & Kelly 1995), Hawaii, Samoa, Easter Island (Cox & Elmqvist 2000 and references therein), Tonga (Meehan et al. 2002), Mauritius (Hansen et al. 2002), the Azores and Canary islands (Olesen et al. 2002; Valido et al. 2002), and the Balearic Islands (Riera et al. 2002; Traveset 2002). A number of researchers have also reported mutualistic disruptions (specifically pollination disruptions, mostly caused by the introduction of honeybees) in Australia, a continent with traits similar to those of a large island (e.g., Paton 2000 and references therein). Little information on this subject is available from continental areas, except in the case of the South African fynbos, where the Argentine ant (*Linepithema humile*) has had a detrimental effect on the plant community composition by altering the patterns of seed dispersal by native ants (Christian 2001). An example of a plant-avian disperser disruption (in this case resulting from forest fragmentation in Tanzania) and its consequences has recently been reported by Cordeiro and Howe (2003).

Because of the intrinsic traits of insular ecosystems, mainly low population sizes and isolated evolution (Vitousek et al. 1995; Simberloff 2000), both ecological and evolutionary interactions may be particularly vulnerable to biological invasions compared with continental areas. Such an interaction between plants and lizards appears to have evolved mainly on islands (reviewed in Olesen & Valido 2003) and may be threatened by the introduction of new species. In this relationship lizards act as the

plant's pollinators or seed dispersers. Few researchers have examined these mutualisms; thus, for most systems, the data needed to predict the consequences of a disruption of such interactions are lacking. In general, the fate of a plant species deprived of its animal mutualists is determined, among other factors, by the amplitude of the pollinator and disperser assemblage and by the mechanisms the plant possesses to compensate for such a loss (Bond 1994). Although generalist plants (interacting with many pollinator or disperser species) are presumed to be less sensitive to disturbance than specialized plants (Cox et al. 1991; Bond 1994; Kearns et al. 1998), there is little evidence to date that supports this contention (e.g., Steiner & Whitehead 1996).

We examined the consequences of the disappearance of a lizard, *Podarcis lilfordi* (Lacertidae), from some of the Balearic Islands (western Mediterranean Sea) on the reproductive success of an endemic shrub, *Daphne rodriguezii* Texidor (Thymelaeaceae). Although the development of tourism and coastal urbanization have contributed to the regression of this species (Gómez-Campo 1987), we hypothesize that the disappearance of this lizard and the subsequent lack of seed dispersal has been the major force limiting seedling recruitment and, ultimately, plant regeneration in the remnant populations. According to the fossil record, *P. lilfordi* began vanishing from the large Balearic Islands, Mallorca and Menorca, about 2000 years ago, presumably after the human introductions of predators such as weasels (*Mustela nivalis*), pine martens (*Martes martes*), genets (*Genetta genetta*), and cats (*Felis catus*; Pleguezuelos et al. 2002). This lizard persists only in the small islands around the two larger ones and is an important seed disperser for a number of plant species (Sáez & Traveset 1995; Traveset 1995; Pérez-Mellado & Traveset 1999). It consumes the fruits of *D. rodriguezii* at the only site (Colom Islet) where these two species still coexist (Traveset 2002). If our hypothesis is true, we expect that (1) seeds dispersed by

lizards would have a greater probability of recruitment and establishment and (2) other biotic or abiotic factors limiting population growth of *D. rodriguezii* would be less important than seed dispersal. Through field observations and experiments, we studied the plant breeding system and the pollinator assemblage, assessed whether lizards are the main legitimate dispersers of the plant, quantified the levels of postdispersal seed predation, and determined the germination and establishment requirements of seeds and seedlings.

Methods

Study Plant

D. rodriguezii is a small, evergreen, long-lived shrub, usually <80 cm tall, with abundant, intricate, and usually sharp lateral woody branches. It is a paleoendemic species of the Balearic Islands, and its present distribution is restricted to a few populations on the island of Menorca (702 km²) and on Colom Islet (60 ha), which is approximately 200 m offshore of Menorca. The species is considered at risk of extinction by the Spanish Ministry of Environment Real Decret 439/1990. *D. rodriguezii* occurs in the coastal shrubland, usually growing under shrubs of *Pistacia lentiscus* L., *Phillyrea angustifolia* L., *Phillyrea latifolia* subsp. *media* L., *Rosmarinus officinalis* L., or *Erica multiflora* L.

D. rodriguezii flowers from late February through mid April, and the flowering peak occurs from mid to late March. Inflorescences are fascicles, bearing an average of 2–3 flowers located at the leaf axes. Flowers are tubular, 9.25 mm (± 1.06 SD; $n = 33$) long, 7.26 mm (± 1.03 SD; $n = 30$) wide, 1.77 mm (± 0.17 SD; $n = 30$) in diameter, and white or yellowish, with conspicuous orange pollen when anthers dehisce. They produce a small amount of nectar and release a weak, sweet odor during the day. Flowers are hermaphroditic, with a unilocular ovary and eight stamens, and their lifespan is 7–10 days. The stigma becomes receptive after stamens dehisce, although there is some overlap in the two functional genders. A pilot study showed us that no apomixis occurs (i.e., pollination is needed for seed production). Fruits develop from May through June and are orange-red drupes, approximately 5.0 mm long and 3.0 mm wide, that weigh an average of 40.0 mg ($n = 148$). The single seed is 3.96 mm long and 2.5 mm wide and weighs 18.0 (± 11.0 SD; $n = 149$) mg. The pulp has high water content (86.4%) and contains a relatively large amount of phenolic compounds (7.69 mg/g dry weight). *D. rodriguezii* does not have vegetative propagation and thus depends entirely on seeds for its reproduction.

Study Sites and Population Densities

We examined four populations (Porter, Cala Mesquida, Pudent, and Favàritx) of *D. rodriguezii* on Menorca Is-

land and one on Colom Islet. Except for Mesquida (close to a small town), the Menorcan populations are found in open shrublands in nonurbanized areas. Colom Islet is included in a preserved area (Parc de S'Albufera des Grau) and has by far the highest population density of *D. rodriguezii* (up to 18,000 individuals have been recorded, 329 individuals/ha; Parc de S'Albufera des Grau 1996, unpublished data). The density of *P. lilfordi* on this islet is also very high (approximately 10,000 individuals/ha; Pérez-Mellado 1989). The entire archipelago was declared a Biosphere Reserve in 1992. Mean annual temperature is 17° C, with the maximum occurring in August (24° C) and the minimum in January (11° C). Total annual precipitation is 600 mm on average (1970–1990). The years 1999 and 2000 were especially dry, with a total precipitation in the study areas of 308 mm and 371 mm, respectively. Rainfall in 2001 and 2002 was much greater: 530 and 653 mm, respectively (data from the National Institute of Meteorology, Palma de Mallorca).

An intensive exploration of the Menorcan sites was made from 1999 through 2002 in an attempt to detect most individuals (often under shrub species) in the populations. We marked each plant and measured height, maximum crown diameter, flower crop, and distance to closest conspecific. At the southwest of this islet, we set up a permanent plot of approximately 100 m², marking and measuring all its *D. rodriguezii* individuals. We examined differences in soil composition among populations (pH, carbonates, total nitrogen [N; Kjeldahl's method], organic matter, phosphorus [P], and potassium [K]). Soil samples (up to 5 cm in depth) were collected arbitrarily from each site.

Sexual System and Pollination

From 17–19 March 1999, we bagged flower buds at Porter and Mesquida to determine (1) the capacity of selfing (cloth bags through which pollen cannot pass were left until flowers were shed); (2) whether wind is a relevant pollen vector (flowers were emasculated and covered with cloth bags that allowed pollen but not insects to pass through); and (3) whether pollen limits fruit set (previously emasculated flowers were hand pollinated with xenogamous pollen). Another group of flower buds was used as control. We monitored 18 individuals, 11 from Porter and 7 from Mesquida, although we hand pollinated only 5 plants from each population. We recorded the number of fruits produced on 25 May 1999. Experiments were repeated the next flowering season (14–15 March 2000). Fruit set was recorded from 35 individuals at Porter and from 18 at Mesquida. To determine spatial and temporal variation in fruit set, we monitored flowers and fruits from a minimum of 10 reproductive individuals in the different populations and years. On sunny days during the flowering peak (1999–2002), we observed insects visiting flowers at different times of day and at dusk.

Dispersal System

We assessed seed dispersal mainly in an indirect manner by intensively searching for seed-containing vertebrate feces in the four Menorcan populations and on Colom Islet. We invested less time in censusing frugivore visits to *D. rodriguezii* in Menorca because of the (1) relatively low fruit production, (2) scarcity of frugivorous birds during the fruiting period of this plant (early summer), and (3) absence of frugivorous lizards on the island. Ripe fruits on Colom Islet are rapidly removed by lizards, and most evidence of dispersal in the islet comes from collected feces.

We periodically monitored fruiting phenology and the rate at which mature fruits dropped on Menorca in 1999 (25 May–12 June) at Porter and Mesquida and in 2000 (5 April–2 June) at Porter, Mesquida, and Pudent. At each visit, we recorded the number of green and mature drupes on all branches.

Seed Predation Experiments

No predispersal seed predation was detected in *D. rodriguezii* in any study year. Experiments to determine the importance of postdispersal seed predation were carried out at Pudent, Porter, Favàritx, and Colom Islet. In each population we randomly established various numbers of stations (number depended on fruit availability) consisting of two pairs of petri dishes with five fruits per dish. A pair of dishes was placed under a fruiting *D. rodriguezii* shrub, and the other pair was located in the open at least 3 m away. Half the dishes of each pair were covered with wire mesh (1 × 1 cm) to discriminate between seed removal by ants and by vertebrates (rodents or birds). We began the experiment on 22–24 May 2002 and examined seed removal on 16 July. On Colom Islet fruit pulp was manually removed to prevent fruits from being consumed by lizards.

Seed Germination Experiments

From 18–19 May 2000, we haphazardly collected ripe fruits from a minimum of 10 fruiting plants from Porter ($n = 60$), Pudent ($n = 30$), and Colom Islet ($n = 30$) (no fruits were produced in Cala Mesquida). On Colom Islet we collected lizard feces containing *D. rodriguezii* seeds ($n = 50$). We manually depulped fruits, dry cleaned seeds in feces, and kept all seeds in the refrigerator until sowing time. On 10 October 2000, all these seeds were individually planted (5 mm deep) in pots filled with horticultural potting soil (4 × 4 cm). Five trays of 60 pots each were placed in a germination chamber at 16° C and a humidity level of 75–80% with a photoperiod of 12 hours, optimum conditions for the germination of this species (Servicios Forestales de Baleares 1992). Every 3–7 days, we recorded the time elapsed from sowing until germination for each emerged seedling. For each population and

treatment, we also recorded the final percent germination (i.e., germinability).

In 2001 we again collected ripe fruits from the same populations, manually removed seeds, and planted the seeds—on the same collection date—in their respective populations. We planted 250 seeds at Pudent and Porter and 200 seeds on Colom Islet. Seeds were grouped in five replicate units, each consisting of two groups of seeds: one planted under vegetation (either *D. rodriguezii* or other shrubs such as *Pistacia*, *Phillyrea*, or *Juniperus*) and the other in uncovered soil (open). Each sowing unit thus consisted of 25 seeds (20 in the case of Colom) equally spaced and separated from each other by 5 cm, planted at a depth of 0.5–1.0 cm, and covered with a cage (30 × 20 × 2.5 cm) of wire mesh to prevent rodent predation. Previously, we removed all naturally occurring seeds in these sites. On Colom Islet we simultaneously planted, under vegetation, 100 *D. rodriguezii* seeds gathered from fresh lizard feces. At all sites, germination was monitored on 15 March and on 25 April 2002.

We also tested germination in a common garden (mainly to obtain seedlings for future experiments) with seeds gathered in 2001. In November, we planted—in the same type of trays used in the previous year—50 seeds from each population (Colom Islet, Pudent, Porter, and Favàritx) and an additional group of seeds extracted from lizard scats in Colom. Trays were watered weekly and seed germination was monitored every 7–10 days until June 2002, after which no more seedlings emerged.

Seedling Survival and Growth

We transplanted individual seedlings that emerged in the germination chamber in 2000 to pots (12 cm in diameter) filled with the horticultural soil mixture and placed them in the experimental garden in shady conditions. Seedling growth rates were compared among populations and treatments (ingested versus controls). We measured seedling length on 19 September 2001 and three more times (after 3, 6, and 12 months).

For the seeds planted in 2001 in natural conditions, we monitored seedling emergence and annual survival. Beginning in 1999, we also marked, measured, and monitored all naturally occurring seedlings we found in the populations (or in the permanent plot on Colom Islet). Annual survival was subsequently monitored from 2000 to 2003.

Data Analysis

Analyses of variance (ANOVA) (general linear model [GLM] procedure in SAS [SAS Institute, Cary, North Carolina]) were performed to test for differences among populations in plant size and distance to the nearest reproductive conspecific. We compared fecundities from all monitored individuals compared among populations with non-parametric tests (Mann-Whitney and Kruskal-Wallis tests). We used Spearman correlations to test the consistency

among years in flower and fruit crops and fruit set for each population.

Fruit set among treatments and populations in the pollination experiments and levels of seed predation were analyzed with generalized linear modeling (GENMOD procedure in SAS) with a binomial distribution and a logit link function. Pollination treatment, population, microhabitat, and exclusion treatment were included as fixed effects. For the pollination analysis, treatment was a within-subject factor (i.e., repeated measure) as all treatments were applied to all individuals. For the seed predation analysis, station was considered a random effect.

In all germination experiments, we compared the rate of germination among populations and treatments (ingested versus not ingested by lizards) with failure-time analyses by fitting a Cox proportional hazards regression model (e.g., Allison 1995) to the number of days between sowing and seedling emergence for each individual seed. Population and treatment were categorical fixed effects, and seed weight was a continuous variable. We included only data for seeds germinated by the end of the germination experiments. Germinability in the experimental garden was analyzed with two chi-square tests: one tested only for control seeds from different populations and the other compared ingested versus uningested seeds from Colom Islet. We tested germinability and seedling survival in the field with two-way ANOVA, with population and microhabitat as fixed effects and proportion of seeds germinated or proportion of surviving seedlings (both normalized with the angular transformation) as the dependent variables.

We compared seedling growth among populations with a repeated-measurement analysis of covariance (ANCOVA) in which the dependent variable was seedling length (logarithmically transformed). Two covariates were included in the analysis after we determined that there was homogeneity of slopes for each: time elapsed between seedling emergence and measurement and seed weight.

Results

Current Status of the Populations

The distribution of size classes differed among populations (Fig. 1). The number of seedlings was much higher on Colom Islet than at any of the Menorcan populations. In Menorca the densest population of *D. rodriguezii* was at Pudent, where we detected and measured 132 individuals (there were more individuals in scattered patches along the coast nearby, but we did not measure those). Porter and Favàritx had 82 and 68 individuals, respectively, whereas Mesquida had only 34 individuals, all located on a low and narrow hill near a beach. Mesquida and Pudent, with the most individuals of the largest sizes, had the lowest recruitment (Fig. 1). Distances between individual *D. rodriguezii* at Pudent and Favàritx were larger

than in other populations, where this species had a more clumped distribution ($F_{4,401} = 52.58, p < 0.001$; Table 1). Plant height and crown and trunk diameter were all positively correlated (all $p < 0.001, n = 136$, all populations pooled).

Breeding System, Plant Fecundity, and Pollinators

The proportion of flowers that set fruit in *D. rodriguezii* was consistently low (never $>20\%$ and usually $<10\%$). The plant may eventually self-pollinate, although this occurs infrequently (selfing was 1.4% at Mesquida and 0% at Porter over 2 years; Fig. 2). The anemogamy treatment yielded a negligible fruit set ($<3\%$) in both populations. This fruit set could be the result of small insects such as thrips or small ants that passed through the bags. For hand pollinations, pollen somewhat limited fruit set in 1999 ($\chi^2_1 = 4.74, p = 0.03$); there were no differences between the two populations ($\chi^2_1 = 0.02, p = 0.89$) and the interaction between population and treatment was not significant ($\chi^2_1 = 1.29, p = 0.26$). In 2000 most flower buds at Mesquida aborted before anthesis; thus, pollinations could not be performed. Fruit set at Porter was not pollen limited in 2000 ($F_{1,12} = 2.26, p = 0.13$).

In 2001 Pudent had a higher fruit set than the other sites ($\chi^2_3 = 23.89, p < 0.001$), and in 2002 Porter and Colom Islet had higher fruit sets than the other sites ($\chi^2_4 = 12.32, p = 0.02$; Table 1). Fruit set was inconsistently correlated among years in any of the populations (all $p \gg 0.05$). Flower and fruit crops varied considerably among populations and years (Table 1), and the most fecund individuals one year were not necessarily the most productive in successive years. Neither plant size nor distance to the nearest flowering conspecific appeared to influence either fecundity or fruit set (no correlations were significant; $p > 0.05$). Mean annual rainfall in each population did not explain any of the variation in fecundity or fruit set. Likewise, none of the parameters measured in the soil analyses from the five different populations showed any significant association with either plant size or fecundity.

Direct observations of pollinators were extremely rare. We only observed small ants (*Plagiolepis pygmaea*) within the flowers in some individuals at Porter and, on a single occasion, we found a small unidentified beetle and an unidentified species of butterfly on the flowers. Additional observations in Sóller Botanical Garden, in contrast, showed a great abundance of thrips (*Thrips vulgatissimus*; Thysanoptera) inside the flowers, which might explain, at least partly, the relatively higher fruit set observed in those cultivated individuals.

Dispersal System

We found no evidence of animals removing the fruits from plants and dispersing seeds in any of the Menorcan populations. Only at Favàritx did we occasionally observe the endemic beetle *Pimelia criba* moving dropped fruits a short distance from the parent plant, consuming

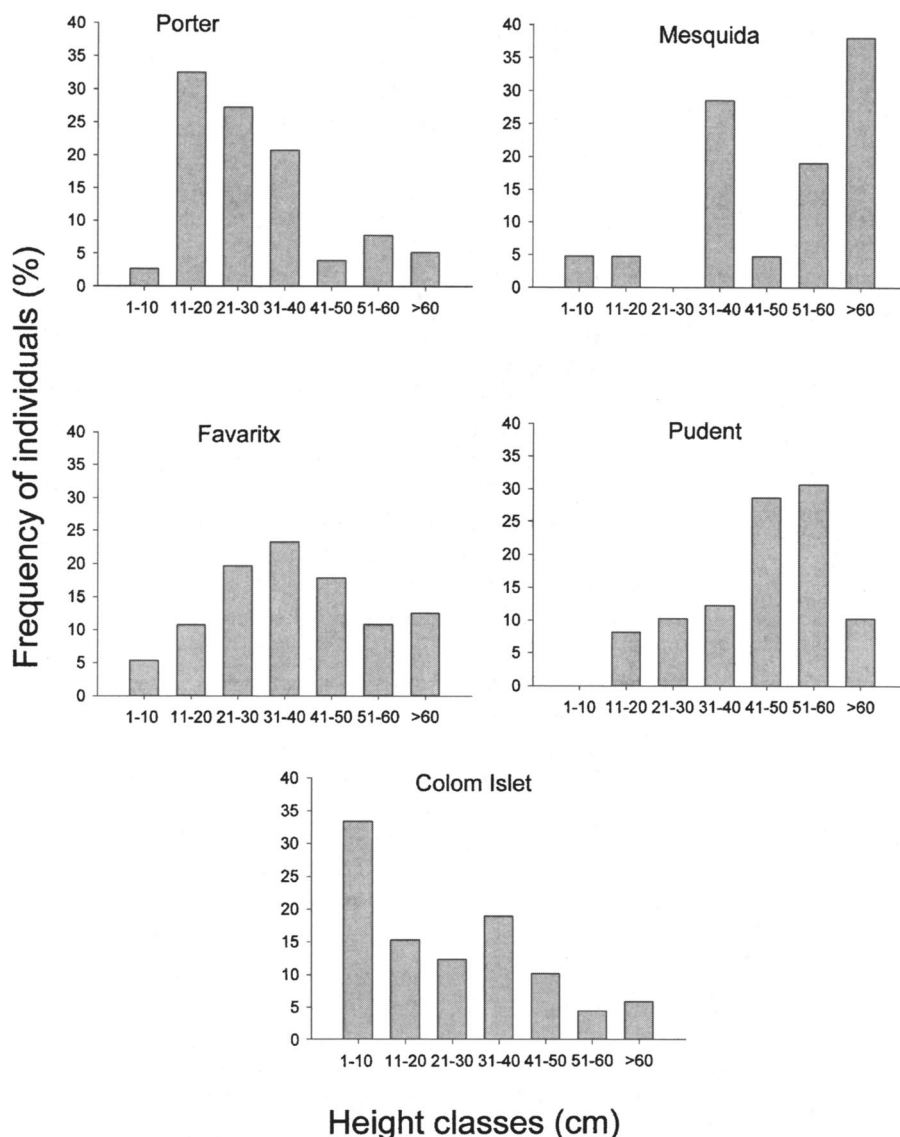


Figure 1. Plant size distributions for the five studied populations of *Daphne rodriguezii*.

the pulp, and leaving the seeds intact. Even though some frugivorous birds such as Sardinian Warblers (*Sylvia melanocephala*) are common in Menorca, we did not observe them on *D. rodriguezii*. The usually scarce fruit production, along with the intricate branching, which diminishes accessibility to fruits, suggests that avian fruit removal is negligible. Furthermore, during the fruiting period of this plant (May–June), the number of avian frugivores is low, and birds seem to invest more energy in feeding on the insects present at this time of year than in searching for fruits. Fruits were often observed drying on the branches or dropped below the shrubs (although these were rapidly removed by ants or rodents).

On Colom Islet, in contrast, fruit removal from the shrubs was intense. As soon as drupes were ripe, they were rapidly consumed by lizards, which climbed through the branches. Lizard scats, containing 1–4 *Daphne* seeds, were often found in the area underneath

shrubs and on or near the abundant rocky walls present on the islet.

Fruit and seed size were similar among populations in 2000 and 2002 (data not shown). In 2001, however, fruits from Porter and Favàritx were larger and heavier than those from Pudent and Colom Islet.

Seed Predation

The levels of seed predation were rather high in all study areas. On Menorca no significant differences existed among populations ($\chi^2_2 = 4.34$, $p = 0.11$), and on Colom Islet, most seeds were also removed by predators (Fig. 3). Seed predation was not significantly influenced by microhabitat (underneath vegetation versus open) on either Menorca or Colom Islet ($\chi^2_2 = 0.001$, $p \gg 0.05$), so we pooled data to test for differences between vertebrate-excluded and open treatments. Seeds in Menorca were

Table 1. Traits and fecundity (mean \pm SE) in four populations of *Daphne rodriguezii* on Menorca Island and Colom Islet.^a

Population	Plant height (cm) ^a	Canopy diameter (cm) ^a	Trunk diameter (cm) ^a	Distance to conspecific (cm) ^a	Flower crop ^b	Fruit crop ^b	Fruit set (%)
Mesquida	53.43 \pm 3.86a (20)	40.28 \pm 4.74a (20)	0.97 \pm 0.14a (20)	79.25 \pm 34.88b (20)	1999: 181 \pm 170 (18) 2000: 162 \pm 168 (20) 2001: 53 \pm 111 (20) 2002: 199 \pm 253 (19)	5 \pm 8 (19) 1 \pm 1 (20) 0 (20) 4 \pm 6 (19)	3.7 \pm 5.7 (18) 0.2 \pm 0.5 (17) 0 (20) 2.1 \pm 3.7 (18)
Porter	30.69 \pm 1.80b (71)	21.94 \pm 2.15b (69)	0.69 \pm 0.08b (71)	61.11 \pm 29.46b (71)	1999: 182 \pm 430 (46) 2000: 86 \pm 273 (51) 2001: 72 \pm 160 (35) 2002: 106 \pm 290 (48)	7 \pm 13 (45) 1 \pm 3 (35) 21 \pm 59 (37) 7 \pm 16 (36)	6.0 \pm 8.5 (32) 5.7 \pm 10.3 (21) 3.5 \pm 9.4 (19) 12.6 \pm 14.0 (25)
Favàritx	38.04 \pm 2.14ab (68)	42.28 \pm 3.68a (67)	1.19 \pm 0.10a (68)	252.80 \pm 39.35a (65)	2001: 53 \pm 105 (48) 2002: 97 \pm 136 (64)	2 \pm 4 (81) 8 \pm 41 (38)	7.6 \pm 8.3 (4) 1.5 \pm 2.6 (46)
Pudent	44.11 \pm 1.60a (108)	35.53 \pm 1.58a (108)	1.14 \pm 0.06a (106)	163.51 \pm 30.56a (106)	2000: 113 \pm 284 (37) 2001: 70 \pm 167 (96) 2002: 306 \pm 494 (104)	13 \pm 22 (104) 2 \pm 4 (111) 4 \pm 11 (81)	3.8 \pm 7.3 (27) 20.4 \pm 24.4 (54) 2.2 \pm 9.1 (88)
Colom Islet	25.01 \pm 1.72c (138)	19.64 \pm 1.65b (106)	—	21.19 \pm 2.51c (144)	2002: 21 \pm 46 (73)		17.0 \pm 18.4 (20)

^aFor each variable, means with the same letter are not significantly different (Tukey's test). Numbers in parentheses are sample sizes.
^bOnly reproductive individuals are considered.

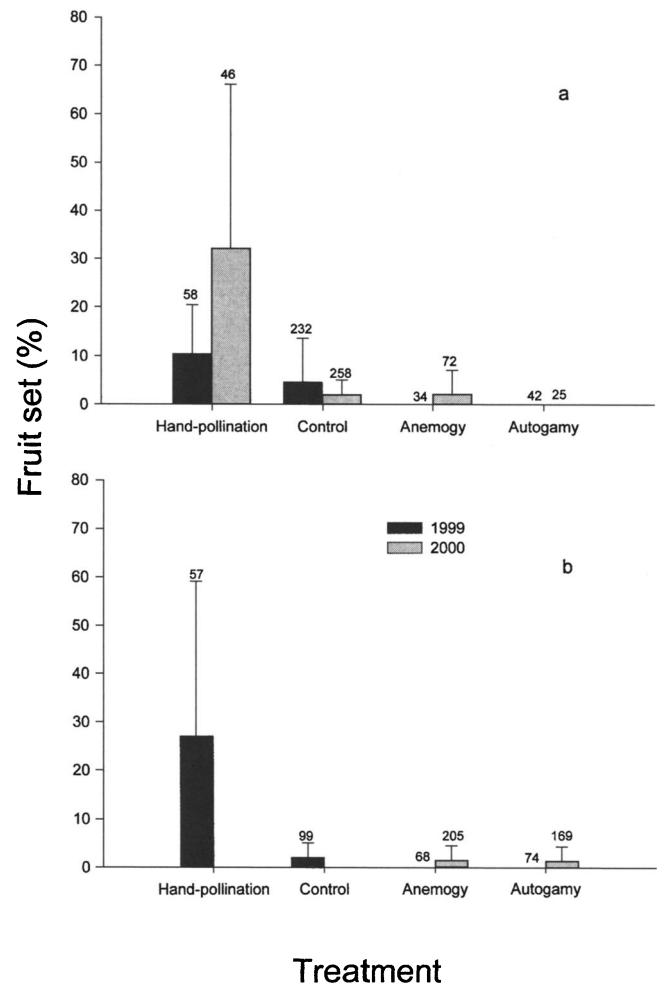


Figure 2. Proportion of flowers that set fruit after various pollination treatments (see text for details) in two populations—(a) Porter and (b) Mesquida—of *Daphne rodriguezii*. In 2000 most flower buds in Mesquida aborted before anthesis and pollinations could not be performed. Numbers above each column are sample sizes. Bars represent standard deviations.

removed more frequently from open dishes than from vertebrate-excluded dishes ($\chi^2_1 = 9.17$, $p = 0.002$), and a marginally significant interaction between population and treatment was found ($\chi^2_2 = 5.38$, $p = 0.07$). Differences between treatments were larger at Favàritx than at Porter or Pudent (Fig. 3). At Colom all seeds in open dishes disappeared, whereas about 30% remained in the covered dishes.

Seed Germination

Germination took place toward the end of winter and in early spring. The survival analysis performed with seeds planted in fall 2000 in the germination chamber showed that germination rate did not differ between seeds from Colom Islet and Porter ($\chi^2_2 = 0.98$, $p = 0.61$; $\beta = -0.30$,

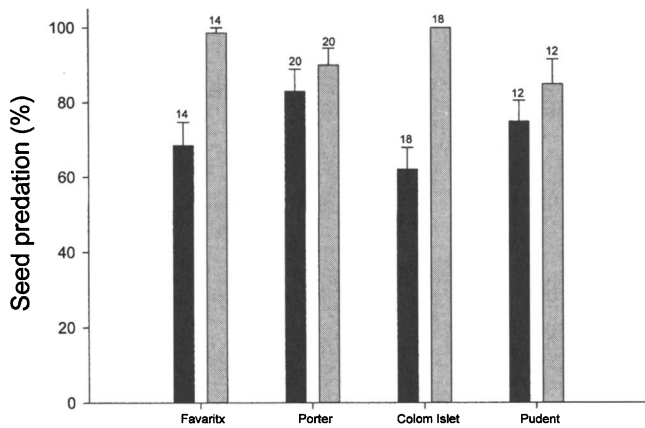


Figure 3. Postdispersal seed predation (mean \pm SE) in four populations of *Daphne rodriguezii* obtained by comparing vertebrate-excluded petri dishes (black bars) with dishes open to all predators (rodents and ants; gray bars). On Colom Islet, fruit pulp was manually removed to prevent fruits being consumed by lizards. Numbers above each bar are sample sizes.

$p = 0.34$, Wald's statistic = 0.91, $n = 57$; Fig. 4a). Seeds from Pudent were not included in the analysis because only a few (<5%) germinated that year. In the experimental garden, seeds planted in 2001 germinated at a similar rate in all populations ($\chi^2_2 = 0.99$, $p = 0.61$; $\beta = -0.09$, $p = 0.33$, Wald's statistic = 0.95, $n = 113$; Fig. 4b). Seed weight was included in the two Cox regression models but had no effect in either case ($p \gg 0.05$).

Final percent germination in the chamber differed among populations ($\chi^2_3 = 32.4$, $p < 0.0001$; Fig. 4a): the percentage was highest for Colom (63.3%), lowest for Pudent (3.3%), and intermediate for Porter (54.3%). Although no seeds were available in 2000 from Mesquida, a pilot study performed in 1999 showed that seeds from that population had a germinability similar to those from Porter (69%, $n = 50$ versus 72%, $n = 55$, respectively). In the garden, final germination was also higher for Colom seeds (82.6%) than for the other populations (Porter, 59.2%; Favàritx, 64.4%; Pudent, 39.1%; $\chi^2_3 = 18.61$, $p < 0.0001$; Fig. 4b). In the field, in contrast, seeds germinated in similar proportions in all populations ($F_{2,20} = 0.49$, $p = 0.62$). There was no effect of microhabitat ($F_{1,20} = 0.91$, $p = 0.35$) and no interaction between those two factors ($F_{2,20} = 0.43$, $p = 0.66$). Germination was $34.4 \pm 7.8\%$ (mean \pm SE; $n = 8$ stations, two were disturbed) at Colom, $33.0 \pm 9.3\%$ ($n = 8$; two disturbed) at Porter, and $25.6 \pm 4.6\%$ ($n = 10$) at Pudent. Both in the field and the garden, most seeds germinated in 2002, but a small proportion (<5%) germinated in the winter of 2003.

Seed passage through lizards' guts had no significant effect on germination. An average of $42.5\% (\pm 11.6 \text{ [SE]}\%)$; $n = 4$ stations) of seeds ingested by lizards germinated in the field, not significantly different from germination of control seeds ($F_{1,10} = 2.91$, $p = 0.12$). In the garden, ger-

mination of ingested seeds was higher than in the field (76%), but again it was not significantly different from that of controls ($\chi^2_1 = 0.38$, $p \gg 0.05$) and germination rate was also similar between ingested and control seeds ($\chi^2_2 = 1.90$, $p = 0.39$; $\beta = 0.37$, $p = 0.23$, Wald's statistic = 1.44, $n = 54$; Fig. 4b). In the germination chamber, however, even though ingested seeds germinated at a rate similar to that of control seeds ($\chi^2_2 = 2.27$, $p = 0.32$; $\beta = 0.65$, $p = 0.14$, Wald's statistic = 2.16, $n = 31$), their germinability was lower ($\chi^2_1 = 12.22$, $p < 0.001$; Fig. 4a). One possible reason for such a result could be that ingested seeds weighed slightly less than controls ($10.87 \pm 0.33 \text{ mg} [\pm]$ versus $12.67 \pm 0.35 \text{ mg}$, respectively; $t_{78} = 3.58$, $p = 0.001$), perhaps because seeds collected from lizard scats the first year (2000), mostly in sites exposed to sun, were not as fresh as those collected directly from the plant. Another possibility was that lizards might have

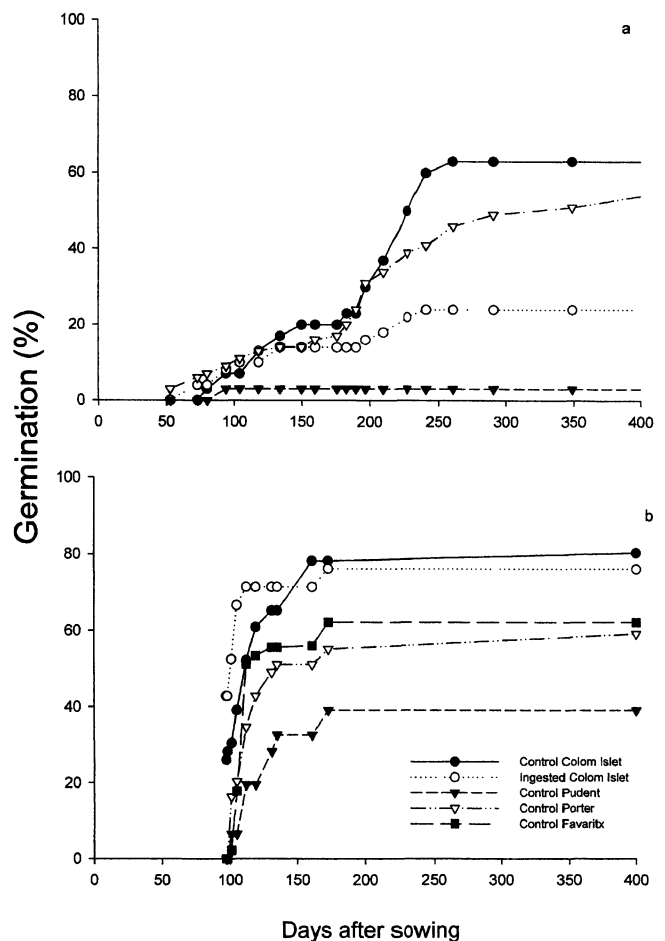


Figure 4. Cumulative germination of *Daphne rodriguezii* seeds from Menorcan populations and from the Colom Islet in (a) a germination chamber (data from 2000–2001) and (b) an experimental garden (data from 2001–2002). For Colom Islet, germination of lizard-ingested seeds is also shown. Control seeds refer to uningested seeds collected directly from the plant.

Table 2. Mean proportion (\pm SE) of seedlings surviving in the field after 1 year of emergence in three different populations of *Daphne rodriguezii*.

Population	Microhabitat ^a	Seedling survival ^b
Porter	covered	0.93 \pm 0.08 (4)
	open	0.10 \pm 0.10 (4)
Pudent	covered	0.75 \pm 0.11 (5)
	open	0.19 \pm 0.09 (4)
Colom	covered	0.63 \pm 0.24 (4)
	open	0.35 \pm 0.23 (4)

^aSeeds were planted in two microhabitats ("covered" by vegetation and in open interspaces) in summer 2001 and emerged in winter 2002.

^bRecorded in spring 2003. Numbers in parentheses represent the number of stations placed at each microhabitat and site.

selected smaller fruits (seeds), but we discarded this because seed size was slightly greater for defecated than for control seeds (seed diameter: 2.54 ± 0.03 [\pm] mm versus 2.42 ± 0.04 mm, $n = 30$, respectively).

Seedling Survival and Growth

One-year seedling survival in the field was similar among populations ($F_{2,19} = 0.01$, $p = 0.99$) but was higher under vegetation than in the open ($F_{1,19} = 16.13$, $p = 0.001$) in all populations ($F_{2,19} = 1.51$, $p = 0.25$; Table 2). Moreover, seedlings from ingested seeds on Colom Islet were as likely to survive as controls ($t_6 = 0.97$, $p = 0.37$).

Greater survival at covered microsites is consistent with the observation that the majority (approximately 95%) of naturally emerged seedlings (all populations pooled, $n = 381$ seedlings during the period from 1999 to 2003) were found under vegetation. A striking difference did exist between Colom Islet and the Menorcan populations in the frequency distribution of seedlings in different microhabitats ($\chi^2 = 83.20$; $p < 0.0001$; Table 3). Whereas approximately 50% of seedlings were found outside the canopy projection of *D. rodriguezii* on Colom, nearly all seedlings on Menorca were located under the parent plants. Moreover, the mean distance of seedlings to other conspecifics was greatest at Colom (Table 3).

Although seedling survival was high (more than 50% of the seedlings that naturally emerged in the field and were marked in 1999 were still alive in 2003) regardless of the microsite in which they were located, it is likely that a relevant proportion of seedlings had already died at very early stages before we detected and marked them in the field. Of the seeds we planted in the field in 2001, though, 75% of the seedlings that emerged were alive in 2003.

Seedling growth (length), measured in the experimental garden during the first year after germination, did not differ among populations ($F_{2,19} = 1.45$, $p = 0.26$; no significant time \times population interaction) or treatments on Colom Islet (ingested versus uningested: $F_{1,11} = 0.26$, $p = 0.62$; no time \times treatment interaction) after con-

Table 3. Number of seedlings found in different microhabitats in Colom Islet and in the four Menorcan populations examined, and mean (\pm SD) distance from seedling to the nearest adult conspecific.

Population	Under Daphne rodriguezii	Under other shrubs*	Open interspaces	Distance to nearest (cm)
Colom Islet	99	98	9	40.0 \pm 62.0
Porter	9	1	0	6.1 \pm 9.1
Mesquida	21	0	0	19.2 \pm 15.1
Faváritx	24	0	0	10.7 \pm 11.2
Pudent	14	1	0	5.6 \pm 6.6

*Refers to Pistacia, Phillyrea, Erica, or Helichrysum, which are common in the habitat where *D. rodriguezii* is found.

trolling for both seed weight and date of germination. When relative growth rates (based on exponential fits of size over time) were compared, we obtained similar results (data not shown). These data, however, must be considered with caution because of the small number of seedlings (5–18) from which we could gather data from some populations.

Discussion

Our data strongly support the hypothesis that seed dispersal is the critical stage that limits population expansion of the Menorcan populations of *D. rodriguezii*. First, the population with greatest seedling recruitment occurred where lizards are still present and abundant. Second, lizards appear to be the exclusive dispersers of *D. rodriguezii*, consuming large amounts of fruits without affecting either germination or seedling growth and moving seeds to sites suitable for plant establishment, as indicated by the fraction of seedlings found below shrubs of other species. Seedlings in the Menorcan populations, in contrast, recruited almost exclusively under the parent plants. Third, the effect of other factors that may influence plant population growth was similar between the islet and the Menorcan populations.

The plant-lizard disruption probably began to take place when carnivorous mammals were introduced into Menorca. Later on, introduced snakes (*Macropododon cucullatus* and *Elaphe scalaris*) may have had a detrimental effect on lizard populations (Pleguezuelos et al. 2002). Fossil evidence shows that *P. lilfordi* was present mainly at elevations <500 m asl (Alcover et al. 1981). Menorca's highest peak is 358 m; thus, this species probably occupied the entire island, at least the coastal habitats where *D. rodriguezii* lives. Other recently introduced lizard species in Menorca are *Podarcis sicula* and *Lacerta perspicillata*, which are almost exclusively insectivores (V. Pérez-Mellado, personal communication) and appear to resist the presence of predators.

D. rodriguezii had a low fruit set in all populations studied. This species is largely self-incompatible and fruit set depends almost exclusively on insect visits to flowers.

Pollinator limitation has been reported for other Mediterranean woody species that, like *D. rodriguezii*, are remnants of a tropical Tertiary flora (Traveset 1995). Even with hand pollinations, fruit set remained low, which suggests that factors other than lack of pollen limit seed production. One of these factors could be "pollen clogging" on the stigmas, reported for *Daphne kamtchatica* (Kikuzawa 1989). Another factor might be inbreeding depression because of the small size of populations. Fruit set is also influenced by water and nutrient supply in some species (Herrera 1990); indeed, *D. rodriguezii* plants in the Botanical Garden (where water is not limiting) have a higher fruit set (A.T. & N.R., unpublished data). Alternatively, a low fruit set might actually be a characteristic of the genus. Other *Daphne* species have low fruit set (Herrera 1987; Kikuzawa 1989), although *D. laureola* has shown a rather high fruit set, at least in one population in southern Spain (32.5%; Alonso & Herrera 2001). Some *Daphne* species are gynodioecious, meaning that a low fruit set might indeed be associated with a low density of hermaphrodites in the populations. This does not seem to be the case, however, in *D. rodriguezii*. Further research is needed on pollen viability analyses.

The high levels of postdispersal seed predation contributed to the low seedling recruitment of *D. rodriguezii* on Menorca. We believe seed predation is consistently high in such populations because of the accumulation of undispersed seeds beneath reproductive individuals, which probably attracts predators, either rodents or granivorous ants. On Colom Islet seed predation was also high, but a fraction of the seeds may have escaped predators once seeds were embedded in lizard feces and scattered over a larger area. Seeds disappeared more frequently from the open than from the vertebrate-exclusion treatment only at Colom Islet and Favàritx, suggesting that vertebrate seed predators were more common there than at Porter and Pudent. On Colom Islet, in particular, *Rattus rattus* is very common (as indicated by the great number of rat scats observed) and *Apodemus sylvaticus* is also present. Several species of granivorous ants, such as *Messor structor*, *M. bouvieri*, and *Crematogaster scutellaris*, are also found on this islet (Comín & De Haro 1980). The latter was observed removing the seeds from the dishes in some of the Menorcan populations.

Germinability in the growth chamber and common garden was highest for seeds from Colom, suggesting an effect of inbreeding depression in the Menorcan populations that results from much smaller population densities. Germination was lowest, however, in Pudent, the largest Menorcan population. In the field, in contrast, germinability was similar in all populations, which shows the relevance of performing this type of experiments in situ rather than exclusively in the laboratory or under semi-natural conditions (e.g., Traveset & Verdú 2002).

Seedling survival was also similar between Colom and the other populations, which negates the possibility of a differential herbivory or effect of abiotic factors on

seedlings. At all sites survival was lower in open interspaces than under vegetation, where seedlings were better protected from solar radiation and drought. This differential seedling survival was consistent with the greater recruitment of *D. rodriguezii* seedlings observed under shrubs. Moreover, lizards usually spend most of the time under shrubs, using them as refuges from high temperatures and predators, and this behavior enhances recruitment under vegetation because most seeds are defecated at such microsites.

Retention time for seeds in the digestive tracts of lizards is usually 2–3 days (A.T. & N.R., personal observation with captive lizards), which may increase the probability that seeds move far away from parent plants. *P. lilfordi*, however, is territorial and thus has a limited home range. Seedlings of *D. rodriguezii* on Colom Islet were sometimes located up to 4 m away from any reproductive adult, indicating that lizards were spreading seeds, whereas seeds on Menorca remained below the parent plant (<50 cm away).

Our results represent an example of the potential of a disturbance (the introduction of exotic species, in particular) to a vulnerable system, such as an island, to disrupt species interactions. The disappearance of such interactions, which may have existed for millions of years, is likely to result in a detrimental effect on the species that most strongly depends on the interaction. In our case, there seems to be no species able to replace the dispersal services provided by the extinct *P. lilfordi*. This contrasts with our findings with *Cneorum tricocon* L., another shrub species with seeds that are mainly dispersed by lizards in the Balearics. On Mallorca and Menorca, however, this plant is currently dispersed by introduced carnivores, mainly pine martens. These animals consume large quantities of fruits, effectively dispersing the seeds, and appear to have prevented population decreases and extirpation from those islands (Traveset 1995; Riera et al. 2002). Therefore, our data support the argument that specialized plants (with few species of animal mutualists) are more sensitive to disturbance than generalists. Given that *D. rodriguezii* strongly depends on lizards for its dispersal and that the plant has no mechanism to compensate such dispersal loss, we predict that the only natural population likely to survive in the (near) future is the one on the islet, where lizards persist. Fortunately, Colom Islet is inside a preserved area, which ensures a certain degree of control on new introductions that might threaten either the lizard or the plant. Other islets around Menorca have *P. lilfordi*, but the plant has not been found in them. A recommendation for improving the conservation of this unique plant-animal interaction might be to introduce the plant to such islets. The preservation of *D. rodriguezii* on Menorca may be more difficult because the eradication of invasive mammals and the reintroduction of *P. lilfordi* into this highly disturbed island would likely be unsuccessful. The only possibility for maintaining the populations that we can see is to plant seeds in suitable microsites.

Monitoring seedlings and saplings in the natural sites where the plant is present would allow confirmation of whether their recruitment is consistently impaired or if it might be compensated in the long run (e.g., in favorable years with high recruitment).

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