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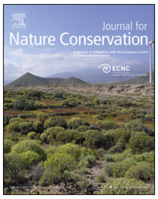

Comprehensive population viability study of a rare endemic shrub from the high mountain zone of the Canary Islands and its conservation implications

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ABSTRACT

Oceanic island ecosystems harbour many endemic plant and animal species, which are often threatened because they have only a few small populations. Many factors contribute to the biological viability of such populations, such as demography and population dynamics, breeding system and pollination ecology, seed dispersal and genetic variation. In a collaborative project, all these factors were studied in the rare endemic, predominantly monoecious shrub *Bencomia exstipulata* Svent. (Rosaceae), which grows exclusively in the national parks of El Teide (Tenerife) and La Caldera de Taburiente (La Palma). Demography was monitored through annual censuses of individual plants in a natural and an augmented population on Tenerife. The breeding system and reproductive success were studied through bagging and pollination experiments, and insect visitation censuses. Seed dispersal by animals was assessed using cafetaria experiments. With matrix projection models and stochastic simulations, we show that the Tenerife population was demographically stable. This was largely explainable by the high survival of adult individuals. Despite frequent germination, successful seedling recruitment was very rare. Male and female flowers occurred in separate inflorescences within individuals, although some inflorescences were mixed and some shrubs were entirely male or female. Despite frequent visits by honeybees, the species is predominantly wind pollinated. Insect-proof bags reduced seed set by 12.5%, and pollen-proof bags by 44%. Large quantities of airborne pollen were detected on unbagged sticky microscope slides, this was 56% reduced by insect-proof and 96% by pollen-proof bags. Hence, some self-pollination also seems to occur. Cafetaria experiments showed that the local lizards (*Gallotia galloti* Oudart) readily eat the fruits and that the seeds pass through their intestines unharmed and germinable. Since other dispersal vectors are unknown, saurochory seems the most likely mode of dispersal. Our study strongly suggests that the population of *B. exstipulata* on Tenerife is viable, and that there are no significant threats associated with its breeding system, pollination or seed dispersal. To alleviate the natural extinction risk typical of narrow endemics, five main conservation measures are proposed.

1. Introduction

Oceanic islands are hotspots of biodiversity, and harbour many endemic species. In some cases, these endemics have very narrow distributions, being restricted to single mountains, volcanoes, rock outcrops or ravines. The low number of populations and their small size render such species prone to extinction (O'Grady, Reed, Brook, & Frankham, 2004)

An important question in ecology, evolutionary biology and conservation biology is to what extent the populations of these 'old rares' suffer from the same problems observed in small, fragmented 'island' populations of formerly common mainland species, the 'new rares' (Huenneke, 1991). Evidence is increasing that the latter populations show loss of genetic diversity, skewed sex-ratios, inbreeding and inbreeding depression, and reduced reproductive success (Allee-effects) (Dai, Vorselen, Korolev, & Gore, 2012). It can be expected that island

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endemics with a very restricted distribution had to adapt to living in small, isolated populations or they would have become extinct a long time ago (Frankham, 1996). Hence, although we know that (narrow) endemics generally have lower genetic diversity, there is little evidence that they show detrimental inbreeding depression or Allee-effects (Frankham, 1997).

Yet, many plant species of high mountains or volcanoes on tropical and subtropical islands such as the Canary archipelago are considered threatened, e.g. *Cistus osbaeckiifolius* Web *ex* Christ (Batista et al., 2001), *Echium acanthocarpum* Svent. (Marrero-Gómez, Arévalo, Bañares, & Carqué, 2000), *Helianthemum juliae* Wildpret (Marrero-Gómez, Oostermeijer, Carqué, & Bañares, 2007), *Limonium dendroides* Svent. (Suárez, Pérez de Paz, Febles, & Caujapé-Castells, 2009), *Sambucus nigra* L. subsp. *palmensis* (Link) R. Bolli (Sosa, González-Pérez, Moreno, & Clarke, 2010) and *Stemmacantha cynaroides* (C. Sm. *in* Buch) Dittrich (Carqué, Durbán, Marrero-Gómez, & Bañares, 2004). Direct threats to island endemics can range from non-native herbivore damage, invasive species, and habitat destruction or degradation to climate change (Berglund, Järemo, & Bengtsson, 2009; Carqué et al., 2004; Fordhamm & Brook, 2010; Marrero-Gómez et al., 2007; Oostermeijer, 2000). Low genetic diversity and high inter-population differentiation have been shown in several, but certainly not all, species studied (Batista et al., 2001; Batista, Bouza, González-Pérez, & Sosa, 2004; Batista & Sosa, 2002; Bouza, Caujapé-Castells, González-Pérez, Batista, & Sosa, 2002; Kim, Lee, & Santos-Guerra, 2005; Sosa et al., 2010; Suárez et al., 2009). Although the fixation index sometimes suggests inbreeding (Batista & Sosa, 2002; Suárez et al., 2009), the opposite, i.e. heterozygote excess, is also reported (Batista et al., 2001; Suárez et al., 2009; Sosa et al., 2010). Inbreeding depression under environmental stress occurs in *Echium wildpretii* Pearson *ex* Hook. *f.* (Sedlacek, Schmid, Matthies, & Albrecht, 2012) and is evident from inbreeding coefficients declining from seed to adult cohorts in *Silene nocteolens* Webb & Berthel. (González-González, 2011). Skewed flower morph ratios and low reproductive success have been demonstrated for *L.dendroides* (Suárez et al., 2009). Low levels of seedling recruitment affect several species (Marrero-Gómez et al., 2000, 2007; Suárez et al., 2009) and may be particularly correlated with drought years (Marrero-Gómez et al., 2007; Sedlacek et al., 2012).

The current study focuses on and compiles existing information on various aspects of the biology and population viability of one of the rarest narrow-endemic plants on the Canary Islands, *Bencomia exstipulata* (Rosaceae). This shrub to small tree grows exclusively on the islands of La Palma and Tenerife and the two natural island populations are located within the boundaries of two national parks, with 57 plants inhabiting the area of Tiro del Guanche, Tenerife (González-Pérez et al., 2009) and 113 individuals distributed across four subpopulations in La Caldera de Taburiente (La Palma) (Fig. 1). The fact it is currently relegated to two national parks affords protection from important pressure factors. However, we do not know with certainty to what extent past threat factors could have affected it. In fact, in the territory nowadays protected as a national park, there was livestock activity (mainly goats) up until the mid-twentieth century.

Once stock was excluded on the declaration of the national parks, the high mountain vegetation underwent a progressive improvement. Nowadays, other problems may be affecting the species, e.g. the introduction at the end of the 20th century of other allochthonous herbivores for hunting purposes (mouflons, *Ovis orientalis* Gmelin, on Tenerife and barbary sheep, *Ammotragus lervia* Pallas, on La Palma), presence of feral goats, expansion of introduced rabbits and habitat destructuring by coniferous (*Pinus canariensis* Sweet *ex* Spreng.) plantations.

Due to the low number of individuals, *Bencomia exstipulata* has been the focus of conservation efforts for the past 15 years to reduce its extinction probability, accompanied by various research projects. The main strategy has been based on the storage of seeds in germplasm banks to later replenish individuals in cases of population collapse, and in the reinforcement of natural subpopulations with specimens grown in nurseries. Precisely these reinforcements have led to a substantial increase in abundance (nº plants) and area of occupancy (Fig. 1). As a result, the species' IUCN category was re-evaluated and changed from critically endangered to vulnerable (Bilz, Shelag, Maxted, & Lansdown, 2011; Marrero-Gómez, Bañares, Carqué, & Palomares, 2003; Moreno, 2008). Nevertheless, it was included as endangered species in both the Canary Islands Catalogue of Protected Species (B.O.I.C., 2010) and the National Catalogue of Threatened Species (B.O.E., 2011). The latter regulations officially require the responsible administrations to implement a recovery plan based on the best possible science. This requirement specifically justifies undertaking conservation biology studies such as the present one to clarify key ecological aspects of the taxon and predict whether the efforts made to date are sufficient or not. These studies are aimed at obtaining the necessary information to resolve the conservation problems of the species and develop such a recovery plan.

The overall aim of our study is to determine to what extent this very rare, disjunct species is threatened by A) external factors: reduction of habitat quality, disturbance and introduced species and B) internal factors likely deriving from its extreme rarity: genetic diversity, reproductive success, seed dispersal and demographic stochasticity.

More specifically, we aimed to: 1) conduct a demographic population viability analysis to (a) identify the most important life cycle stages, and (b) use a stochastic simulation to forecast the future development of the natural population on Tenerife; to determine, 2) the breeding system of the species; 3) the main pollen vectors; 4) the main seed dispersers and their effectiveness; and 5) the importance of seedling herbivory for recruitment success. These allow us to evaluate the conservation status of the species and prepare a conservation strategy to ensure its long term population viability.

To our knowledge, this is the first study regarding the population viability of an officially threatened insular plant species, in which a wide scope of biological aspects have been considered. *B. exstipulata* is recognized as endangered by the Canary Islands Catalogue of Endangered Species, and by the National Catalogue of Endangered Species, and principal among these aspects are demography and population dynamics, breeding system, pollination ecology and seed dispersal. Additionally we provide some genetic considerations based on the results and conclusions previously published (González-Pérez et al., 2009).

2. Material and methods

2.1. The species

Bencomia is included in a group (*Bencomia* alliance) that comprises three genera of tall shrubs endemic to the Macaronesian Archipelago: *Bencomia* Webb & Berth., *Dendriopoterium* Svent. and *Marcetella* Svent. Together with 14 other genera, they constitute the tribe Sanguisorbae within the subfamily Rosoideae of Rosaceae. As with other members of the Macaronesian flora, they have long been considered a relictual fragment of the widespread Tertiary subtropical flora, but other studies suggest they are a recently derived group that has evolved woodiness on the islands (Carine, Russell, Santos-Guerra, & Francisco-Ortega, 2004; Helfgott, Francisco-Ortega, Santos-Guerra, Janzen, & Simpson, 2000). The genus *Bencomia* is represented by four species (*B. exstipulata*, *B. caudata* Webb & Berth., *B. brachystachia* Svent. and *B. sphaerocarpa* Svent.), which mainly grow on cliff-walls in different non-overlapping ecological zones. Except *B. caudata*, all these species comprise only a few small populations (typically < 100 individuals) and have been listed as critically endangered (VV.AA., 2000). The Macaronesian group of the *Bencomia* alliance is clearly monophyletic, all species are tetraploid with 2n = 28 and a base chromosome number x = 7 and have similar ecological, biogeographical and reproductive-biological characteristics (González-Pérez et al., 2009; Pérez de Paz, 2004). Their island origin is an example of wide diversification and evolution to

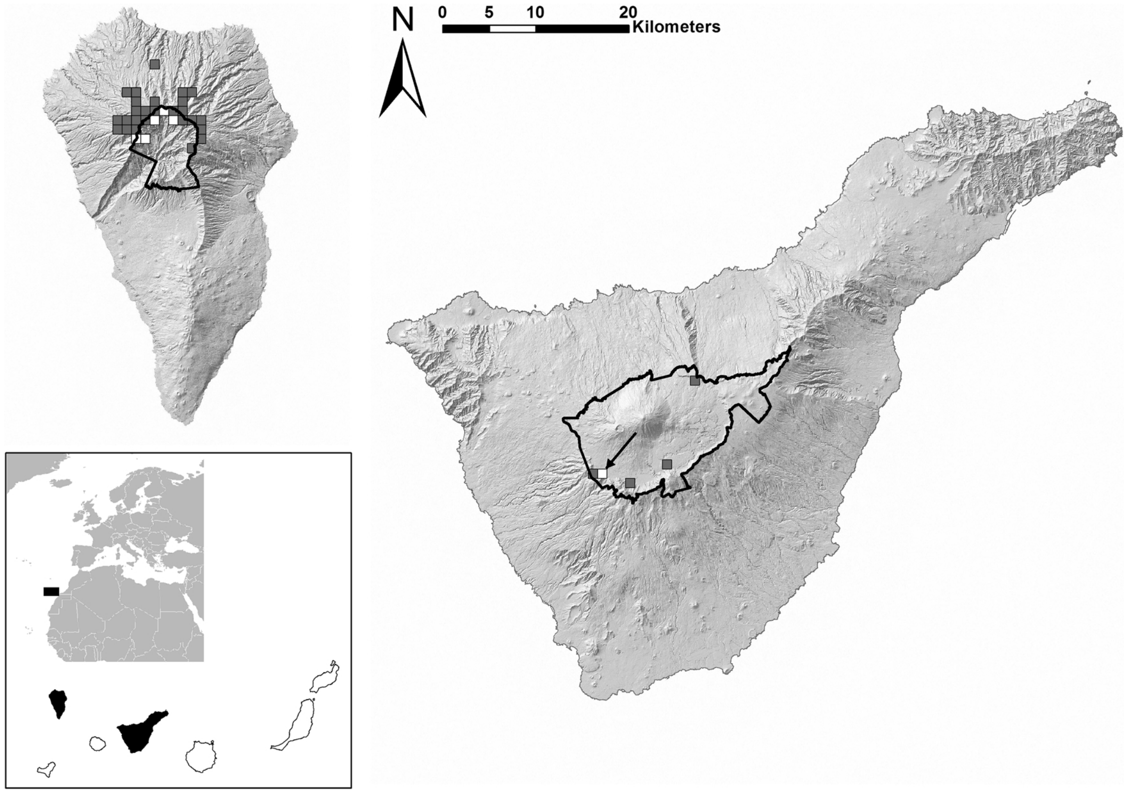

Fig. 1. Distribution of *Bencomia exstipulata* in 1 km^2 squares. Gray squares indicate planted populations and white squares indicate natural populations. Thick black lines show the boundaries of the Teide and Caldera de Taburiente national parks. Arrow indicates de location of the studied population in Tenerife island.

dioecy from a continental monoecious and gynomonoecious ancestor (Helfgott et al., 2000; Pérez de Paz, 2004). This sexual differentiation increases the genetic diversity of the population, especially after colonization; it is a common feature in tropical habitats and oceanic islands, although specific studies are lacking.

Both natural and reinforced localities have been previously analysed genetically using microsatellite loci (González-Pérez, Lledó, Fay, Lexer, & Sosa, 2004, 2009). Like many species from oceanic islands (Batista et al., 2001, 2004; Bouza et al., 2002; Francisco-Ortega, Santos, Kim, & Crawford, 2000), *B. exstipulata* exhibits strong genetic differentiation between populations, since they are located on different islands. The natural population on Tenerife had very low levels of genetic diversity while the natural locality on La Palma was highly polymorphic.

In recent years, the results of the genetic studies previously cited were used to perform reinforcements with selected genotypes, with the intention of increasing the genetic variability by raising the frequencies of the alleles that were rare in the natural populations, especially in El Teide National Park. Seeds from mother plants belonging to each identified genotype were used to obtain new individuals in the nursery, then planting them in an adequate proportion to create an additional set of individuals at a locality adjacent to the natural nucleus.

Demographically, populations of *B. exstipulata* are differently structured and their dynamics are very slow. Adult stages prevail, and plant size depends strongly on the depth of the substrate. Individuals growing on cliffs are quite small compared with those growing at the cliff-base, especially on Tenerife (Marrero-Gómez et al., 2003). Their longevity is notable and they commonly flower after 4–5 years, from February to May.

Bencomia exstipulata is monoecious, although some individuals carry exclusively male or female flowers during their entire lifetime. The 10–15 cm long inflorescences can be either uni- or bisexual and very rarely flowers are hermaphroditic. The sex ratio of the natural populations is variable, also because considerable changes in allocation to male or female structures occur within plants from one year to the next, possibly as a result of habitat variability. Judging from the long filaments, dangling stamens and feathery stigmas, pollination seems to occur mainly by wind. Fleshy fruits appear in summer, and dispersal occurs largely by endozoochory, barochory and lastly, anemochory, at the end of its fructification cycle. Additionally, seeds of *B. exstipulata* have been found in droppings of the endemic lizard *Gallotia galloti* (Valido, 1999), although the role of the lizard as seed disperser has not been quantitatively evaluated. Native bird species are other candidates, as they are known to disperse seeds of other plant species in this high-altitude environment (Rumeu et al., 2009).

2.2. Study area

Data was collected in the only natural subpopulation on Tenerife, due to its better accessibility. The La Palma population is highly inaccessible in a very small location, and sampling implies a high risk of damaging specimens of the taxon.

The Tenerife natural subpopulation is formed by a small group of *B. exstipulata* individuals located at Tiro del Guanche in the southwest sector of El Teide National Park. They grow preferentially on a cliff oriented to the northeast, limited to cracks and small platforms. However, a minimal number of individuals are located in flatter areas associated with the nearby piedmont. The area of dispersion is seriously limited by the lava flows arising from the eruption of Narices del Teide in 1798, which make an unsuitable substrate for the germination and establishment of new individuals. So the expansion of the subpopulation is limited to a small area with moderate slope (45°) in a geological environment dominated by traquibasalts and relatively poor soils. In these environments a subalpine continental climate regime is dominant, with average temperature values between 3 °C and 15 °C that frequently fall below 0 °C in the winter nights. The annual total precipitation ranges between 250 and 550 mm usually falling in autumn and winter, when snow is also frequent. Away from the cliff, the dominant vegetation is a Canary Islands high-mountain shrubland with high levels of endemicity. This is composed mainly of species of the Fabaceae family, especially *Spartocytisus supranubius* (L. f.) Christ *ex* G. Kunkel and *Adenocarpus viscosus* (Willd.) Webb & Berthel. subsp. *viscosus*. Taxa of the families Brassicaceae, Dipsacaceae, Asteraceae, Boraginaceae and Lamiaceae are also common. However, this shrubland is highly modified since there were some plantations of *Pinus canariensis* in the second half of the 20th century in more accessible terrain surrounding the natural subpopulation.

2.3. Demography and population dynamics

Several abseil lines were installed to conduct demographic censuses for 10 years (1999–2008) on the natural population on the cliff face at Tiro del Guanche, Tenerife. The rope lines allowed a trained climber access to most individuals, while from the base of the cliff the work was supported by an observer with a high magnification telescope. Censuses were annual, coinciding with the peak flowering period of the species in spring. The position of the plant was recorded with a high quality photograph. Each individual was assigned to one of the following life-stages (Lefkovitch, 1965; Werner, 1975): (1) *juvenile* (individuals too small for reproduction, lacking remains of reproductive structures); (2) *vegetative adult* (non-flowering individuals that seemed large enough for reproduction, or had remains of reproductive structures from previous years); (3) *male adult* (flowering individuals in which at least 75% of the flowers were male); (4) *female adult* (flowering individuals with at least 75% female flowers); and, (5) *bisexual adult* (flowering individuals with a more or less equal proportion of male and female flowers). In the first sampling, the cliff face population comprised 51 individuals (4 juvenile, 8 vegetative, 21 male, 11 female and 7 bisexual).

Transition probabilities were obtained by calculating the proportion of individuals in each category undergoing each specific fate, from one year to the next. Relative fecundity was based on the number of male and female inflorescences on each plant, from which we calculated the proportional contribution of each of the three reproductive stages to the total reproductive effort. Subsequently, the number of juveniles observed in the following year was proportionally assigned to a particular reproductive stage. The transitions between the five different life stages are shown in the life-cycle diagram (Fig. 2).

The demographic data were integrated into Lefkovitch matrices (Caswell, 2001), where the basic matrix model is determined by $n(t + 1) = An(t)$, in which nt and $n(t + 1)$ are vectors whose elements a_{ij} constitute the number of individuals in each stage class at time t and $t + 1$. A is a non-negative square matrix whose elements a_{ij} consist of annual contributions or transitions from individuals in the j^{th} class to the i^{th} class (Caswell, 2001). To process the data we used Poptools 3.0 for MS Excel (Hood, 2002). To determine the 95% confidence intervals of λ, the bootstrap method was used (Caswell, 2001; Kalisz & McPeek, 1992), using the R package Popbio (Stubben & Milligan, 2007).

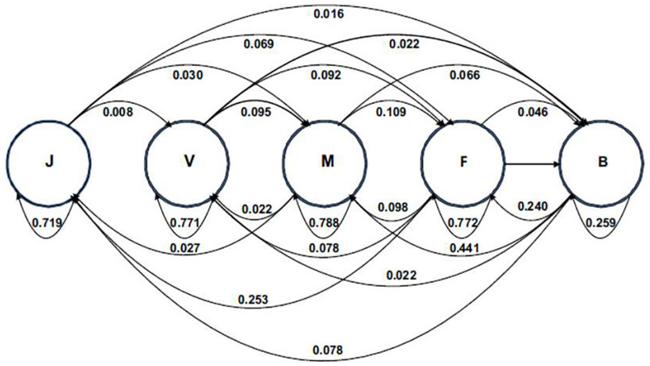

Fig. 2. Life cycle graph for *Bencomia exstipulata* and the corresponding average transition matrix. Circles indicate life stages, arrows represent the possible transitions among them, and numbers show the different transition values on the average matrix. J: Juvenile, V: Vegetative, M: Male, F: Female, B: Bisexual.

Stochastic simulations. To avoid potential problems of colinearity, environmental stochasticity was simulated by random selection of a matrix (from the total set of 9) for each year of the simulation into the future (the Independently and Identically Distributed, or IID, approach, cf. Morris & Doak, 2002). The process was carried out by a Monte Carlo analysis available in Poptools 3.0, with a time horizon of 100 years and 100 iterations. The correlation between λ and the climatic variables obtained from the Parador AEMET Station for the studied period (1999–2008) and the vital rates were analysed using the Spearman Coefficient developed with R using the function: cor.test(x,y, method = "spearman").

To calculate the stochastic growth rate, numerical values for population size generated for each year of a simulation were used. It was obtained from the average growth rate over a long simulation (Caswell, 2001; Dennis, Munhollland, & Scott, 1991; García & Iriondo, 2002) as follows: $\log \lambda_s = (\log n_t - \log n_0)/t$, in which n_t and n_0 are the population size at the end and start of the simulation, respectively, and t is the time interval of the simulation (100 years).

2.4. Pollination system and pollen vectors

The roles of insects and wind in the pollination of *B. exstipulata* were determined in 2008 by experiments and observations on a total of 23 randomly chosen individuals in the reinforced population at the cliff-base at Tiro del Guanche, Tenerife. Insect visitation rates were determined using the standardized method first employed by Arroyo, Armesto, and Primack (1985) (see also Kearns & Inouye, 1994; McCall & Primack, 1992). Individual plants were observed for 10 min during six periods over the course of the day (9:00 – 16:30 h). Any insects contacting anthers or stigmas were recorded. For each plant we determined the proportion of male and female flowers, the number of inflorescences, whether or not the inflorescences were bisexual, the percentage of open flowers, and the distance to the nearest other individual.

At least two exclusively female immature inflorescences were used per individual and per treatment. The treatments consisted of placing an entire inflorescence in either (1) an insect-proof gauze bag with a 1.0 mm mesh width, or (2) a microperforated plastic 'pollen-proof' bag (pore diameter 0.4 mm). Per individual, at least two inflorescences in the same stage of development as the bagged ones were used as an unbagged control treatment. To account for a possible positive or negative effect of the bagging, control inflorescences were also provided with a pollen-proof bag (treatment 2) after they had finished flowering. The pollen-proof bags remained in position until the fruits had ripened. Fruits were collected to determine seed set (i.e. number of developed, hard seeds relative to the sum of developed and shrivelled, aborted seeds or ovules) and seed weight. To test the ability for spontaneous self-pollination, a series of mixed male-female inflorescences was also placed in a pollen-proof bag. In addition, fruits of a single (planted) individual growing several km from the nearest reproductive *B. exstipulata* individual were collected to determine seed set. Mature seeds from the pollination treatments were harvested in June.

In order to test the effectiveness of each type of bag used for the treatments, an altitudinal transect with ten sampling sites approximately 4 m apart was established within the *B. exstipulata* population. Three microscope slides covered with a thin layer of fuchsin gel (Kearns & Inouye, 1993) were suspended in either a pollen-proof bag, an insect-proof bag, or without any bag. After a period of two weeks, slides were collected and the number of pollen grains captured on a fixed area of the sticky gel counted under a light microscope. The insect-proof bags were expected to hinder putative wind-pollination to some extent and a small fraction of the seed set was expected in the inflorescences enclosed in the pollen-proof bags. The experiment described above allowed us to correct for this ‘leakage’ if necessary.

To investigate the diversity of plant species visited by *B. exstipulata* pollinators, insects visiting its flowers were caught with a standard insect-net and tranquillized in a jar with ethyl acetate. Pollen carried on the body of the insect was collected by dabbing the insect with a $2 \times 2 \times 2\,\text{mm}^3$ cube of fuchsin gel. Directly after all pollen was collected from the body, the gel cube was placed on a glass microscope slide and subsequently molten with a cigarette lighter and fixed with a cover slide. The slides prepared in the field were later examined under a light microscope in the laboratory. Pollen grains were counted and the ratio of *B. exstipulata* pollen grains to the total number of grains (from all species) was calculated.

2.5. Temporal variation in gender expression

The gender expression of a total of 51–71 individual plants in the natural population of Tiro del Guanche, Tenerife, was monitored between 1999 and 2007. On each reproductive individual, the relative proportion of male and female inflorescences was recorded annually. Data were analysed by calculating the change in the proportion of male inflorescences from one year to the next, then counting the proportion of plants in the population that show an overall increase or decrease in male flowering. Based on the proportion of male inflorescences, the change in gender was classified into three different categories: no major change; a *decrease* in the proportion of male inflorescences; and, an *increase* in the proportion of male inflorescences. In this way, insight into the sex-change behaviour of the entire population was obtained. We analysed the synchronicity in changes in gender expression among individuals within the population, and correlated the observed changes to weather variables from the Izaña meteorological station in El Teide National Park.

2.6. Frugivory, seed dispersal and seedling herbivory

To census the percentage of plants in and around Tiro del Guanche that produced fruits and seeds, we counted all accessible individuals. Recent droppings from the endemic lizard *Gallotia galloti* were collected in the field in 2009, along with pellets from the birds of prey that might act as secondary seed dispersers (mainly the kestrel, *Falco tinnunculus* Linnaeus). We also collected droppings from rabbits (*Oryctolagus cuniculus* Linnaeus), mouflons (*Ovis orientalis*), rock pigeons (*Columba livia* Gmelin) and partridges (*Alectoris barbara* Bonnaterre) to test for the presence of *Bencomia* seeds or fruits. We also installed two mist nets (7 and 10 m in length), during a 60 h fruiting period, to evaluate fruit consumption by passerine birds. Droppings and pellets were individually conserved in aluminium foil in order to maintain the unit of analysis. This material was analysed to establish the frequency of occurrence and number of seeds per sample, using a dissecting microscope (16x). Any seeds damaged in the digestive processes were noted.

In total, 200 seeds were tested for viability using 2,3,5 triphenyltetrazolium chloride (hereafter TTC test; Marrero, Padilla, Valdés, & Nogales, 2007; Scharpf, 1970; Tanaka, 1984). We distinguished between the natural (in the steepest area) and reinforced localities (in the more accessible area at the cliff base), analysing 100 seeds (50 control and 50 lizards, respectively) from each location. After opening seeds manually, the state of the embryo was morphologically classified as (1) healthy (apparently intact), and (2) damaged (aborted, in bad condition – considered non-viable). Embryos of healthy seeds were immersed in an aqueous 0.1 TTC solution with pH 7 phosphate buffer for 24 h in total darkness at room temperature (Scharpf, 1970; Tanaka, 1984). The viability was classified into three categories (1) viable (entire embryo surface stained red), (2) potentially viable (partially stained in critical zones such as cotyledons and radicle) and (3) non-viable (no sign of staining). Apart from viability, seed germination was another main variable investigated in the study of seed dispersal effectiveness; the strong dormancy of *B. exstipulata* hindered such an experiment, however.

The seed coat was measured for both control seeds and those previously consumed by lizards. A total of 200 seeds were cut transversally and examined under a binocular lens (16x). Seeds were photographed at 8x enlargement (ZEISS Stemi 2000) and three measurements of the endocarp thickness were taken for each seed (IMAGE J 1.42 program).

Seed viability for the different treatments (lizard and control) and seedling fate was evaluated using categorical data analysis (likelihood ratio tests/G-tests). Comparison of mean seed coat thickness among control seeds and seeds consumed by lizards was analysed by a Student *t*-test. All statistical analyses were carried out using the SPSS statistical package (version 21.0).

There are no bibliographical references or field observations that allow us to infer any *Bencomia* seed consumption by invertebrates in the natural environment, and we never observed damage of this type to stored seeds.

In 2010, we located and individually marked all seedlings ($n = 63$) within the natural population of Tiro del Guanche to monitor their fate and study predation by the main potential herbivores (invertebrates and lizards, rabbits and mouflons). We established three treatments: (1) total exclosure (using a 0.5 cm grade metal grid fence) to test whether factors other than herbivory affected seedling survival; (2) partial exclosure (only permitting the access of native lizards and invertebrates); and, (3) control (a treatment permitting access by all potential predators, including the human-introduced rabbits and mouflons). The dimensions of the exclosures were $13 \times 24 \times 13$ cm ($l \times w \times h$).

3. Results

3.1. Population dynamics

3.1.1. Deterministic analysis

The dominant eigenvalue of the average matrix (λ) was 1.030. There was very low variation in λ among the nine year-to-year transitions (Table 1; Fig. 2), since values ranged between 1.064 (2002–2003) and 0.990 (2007–2008), with no specific pattern.

Overall, the highest elasticities (Table 1) are associated with the survival of the reproductive plants, especially the females. In some years however, juvenile (2001, 2002, 2003) and vegetative adult survival (2000, 2003, 2005, 2007) also contributes to the overall elasticity. A triangular ordination diagram of the relative contribution of Growth (G), Survival (L) and Fecundity (F) to the λ of each matrix (Silvertown, Franco, Pisanty, & Mendoza, 1993) (Fig. 3) shows that all matrices are concentrated towards the bottom right section of the triangle (i.e. low fecundity and growth, and high survival). The net reproduction rate (R_0) was 3.32, the average age of reproductive adults was 72 years and the mean generation time is 40 years. Analysis of the fundamental matrix obtained from the average matrix reveals that the life span for each new recruitment was 34 years and the sum of the elements of the fundamental diagonal matrix is 81 years.

The correlation analysis between λ and the principal climatic variables reveal a negative correlation with winter precipitation ($\rho = -0.8$; $p = 0.013$) and a positive relation with autumn temperature ($\rho = 0.95$; $p = 0.001$).

3.1.2. Stochastic analysis

When environmental stochasticity is simulated by a random selection of the nine available annual matrices, the resulting stochastic growth rate (λs) is 1.007, indicating demographic stability and a very low risk of extinction. In fact, calculations for several series of simulations performed under Monte Carlo analysis indicated a slow and progressive increase in individuals with a risk of extinction of less than 5% in 100 years. During the nine-year period, the proportion of vegetative adults and bisexual reproductive individuals in the population decreased significantly, while the proportion of juveniles increased (J: $r = 0.852$, $p = 0.002$; V: $r = -0.820$, $p = 0.004$; B: $r = -0.740$, $p = 0.014$). The proportions of female and male reproductive plants did

Table 1

Projection and elasticity matrices for the annual transitions from 1999 to 2008 and the average matrix for the population of *Bencomia exstipulata* and their dominant eigenvalues (λ), confidence intervals (C.I.), reproductive value and stable stage distribution. J: Juvenile, V: Vegetative, M: Male, F: Female, B: Bisexual.

λ	C.I.		Demographic matrix					Stable-stage distribution	Reproductive value	Elasticity matrix				
1.057	0,976–1,137	**1999–2000**	J	V	M	F	B			J	V	M	F	B
		J	0.500	0.000	0.056	0.333	0.167	0.187	0.134	0.091	0.000	0.002	0.094	0.006
		V	0.000	1.000	0.000	0.091	0.000	0.458	0.000	0.000	0.000	0.000	0.000	0.000
		M	0.000	0.000	0.714	0.000	0.286	0.030	0.271	0.000	0.000	0.042	0.000	0.020
		F	0.250	0.000	0.238	0.818	0.429	0.289	0.300	0.101	0.000	0.015	0.514	0.033
		B	0.000	0.000	0.048	0.091	0.286	0.036	0.296	0.000	0.000	0.003	0.056	0.022
1.063	0,965–1,162	**2000–2001**	J	V	M	F	B			J	V	M	F	B
		J	0.429	0.000	0.050	0.300	0.150	0.182	0.115	0.040	0.000	0.005	0.050	0.004
		V	0.000	0.889	0.059	0.056	0.200	0.233	0.187	0.000	0.173	0.010	0.015	0.009
		M	0.000	0.000	0.882	0.056	0.400	0.212	0.188	0.000	0.000	0.157	0.015	0.017
		F	0.143	0.111	0.059	0.833	0.200	0.323	0.293	0.034	0.034	0.016	0.354	0.013
		B	0.143	0.000	0.000	0.056	0.200	0.051	0.218	0.025	0.000	0.000	0.018	0.010
0.979	0,856–1,077	**2001–2002**	J	V	M	F	B			J	V	M	F	B
		J	0.700	0.000	0.050	0.298	0.149	0.383	0.106	0.151	0.000	0.004	0.054	0.003
		V	0.000	0.727	0.000	0.105	0.000	0.134	0.107	0.000	0.055	0.000	0.019	0.000
		M	0.000	0.000	0.722	0.105	0.000	0.132	0.273	0.000	0.000	0.138	0.049	0.000
		F	0.100	0.091	0.056	0.737	0.667	0.321	0.296	0.060	0.019	0.011	0.372	0.031
		B	0.000	0.000	0.222	0.000	0.000	0.030	0.218	0.000	0.000	0.034	0.000	0.000
1.064	0,975–1,143	**2002–2003**	J	V	M	F	B			J	V	M	F	B
		J	0.714	0.000	0.057	0.340	0.170	0.229	0.132	0.114	0.000	0.021	0.025	0.009
		V	0.071	0.600	0.000	0.053	0.000	0.047	0.193	0.017	0.029	0.000	0.006	0.000
		M	0.071	0.100	0.933	0.105	0.500	0.542	0.170	0.015	0.004	0.453	0.010	0.034
		F	0.071	0.100	0.000	0.684	0.250	0.106	0.284	0.024	0.007	0.000	0.109	0.029
		B	0.000	0.200	0.067	0.158	0.250	0.077	0.220	0.000	0.011	0.042	0.019	0.022
1.019	0,839–1,093	**2003–2004**	J	V	M	F	B			J	V	M	F	B
		J	0.889	0.000	0.022	0.131	0.066	0.254	0.102	0.122	0.000	0.002	0.015	0.001
		V	0.000	0.910	0.000	0.188	0.000	0.366	0.191	0.000	0.337	0.000	0.040	0.000
		M	0.000	0.090	0.700	0.000	0.286	0.134	0.231	0.000	0.040	0.114	0.000	0.012
		F	0.056	0.000	0.150	0.813	0.286	0.212	0.238	0.018	0.000	0.025	0.218	0.012
		B	0.000	0.000	0.150	0.000	0.429	0.034	0.238	0.000	0.000	0.025	0.000	0.018
0.947	0,891–1,009	**2004–2005**	J	V	M	F	B			J	V	M	F	B
		J	0.947	0.000	0.000	0.000	0.000	0.000	0.990	0.000	0.000	0.000	0.000	0.000
		V	0.000	0.455	0.000	0.053	0.000	0.014	0.003	0.000	0.008	0.000	0.009	0.000
		M	0.053	0.273	0.875	0.368	0.667	0.840	0.002	0.000	0.004	0.757	0.051	0.008
		F	0.000	0.273	0.063	0.526	0.000	0.134	0.003	0.000	0.005	0.063	0.084	0.000
		B	0.000	0.000	0.000	0.053	0.333	0.011	0.002	0.000	0.000	0.000	0.008	0.004
0.999	0,911–1,073	**2005–2006**	J	V	M	F	B			J	V	M	F	B
		J	0.882	0.000	0.004	0.406	0.003	0.622	0.000	0.000	0.000	0.000	0.000	0.000
		V	0.000	0.857	0.033	0.083	0.000	0.122	0.250	0.000	0.276	0.006	0.039	0.000
		M	0.000	0.142	0.733	0.000	0.666	0.074	0.250	0.000	0.046	0.144	0.000	0.006
		F	0.000	0.000	0.200	0.916	0.000	0.178	0.250	0.000	0.000	0.039	0.433	0.000
		B	0.000	0.000	0.033	0.000	0.333	0.004	0.250	0.000	0.000	0.006	0.000	0.003
1.018	0,957–1,081	**2006–2007**	J	V	M	F	B			J	V	M	F	B
		J	0.650	0.000	0.007	0.401	0.000	0.155	0.058	0.029	0.000	0.001	0.015	0.000
		V	0.000	0.750	0.040	0.000	0.000	0.085	0.234	0.000	0.073	0.026	0.000	0.000
		M	0.100	0.125	0.880	0.176	0.500	0.570	0.214	0.016	0.011	0.525	0.024	0.031
		F	0.000	0.125	0.040	0.764	0.000	0.132	0.287	0.000	0.015	0.032	0.141	0.000
		B	0.000	0.000	0.040	0.058	0.500	0.059	0.207	0.000	0.000	0.023	0.008	0.030
0.990	0,906–1,089	**2007–2008**	J	V	M	F	B			J	V	M	F	B
		J	0.761	0.000	0.003	0.066	0.002	0.135	0.043	0.020	0.000	0.000	0.006	0.000
		V	0.000	0.750	0.068	0.071	0.000	0.194	0.248	0.000	0.165	0.016	0.037	0.000
		M	0.047	0.125	0.655	0.071	0.666	0.203	0.211	0.006	0.023	0.128	0.032	0.004
		F	0.000	0.125	0.172	0.857	0.333	0.462	0.266	0.000	0.029	0.042	0.481	0.003
		B	0.000	0.000	0.034	0.000	0.000	0.007	0.231	0.000	0.000	0.007	0.000	0.000
1.030		**Average matrix**	J	V	M	F	B			J	V	M	F	B
		J	0.719	0.000	0.027	0.253	0.078	0.265	0.098	0.091	0.000	0.004	0.034	0.002
		V	0.008	0.771	0.022	0.078	0.022	0.120	0.194	0.002	0.088	0.006	0.021	0.001
		M	0.030	0.095	0.788	0.098	0.441	0.285	0.212	0.008	0.012	0.234	0.029	0.023
		F	0.069	0.092	0.109	0.772	0.240	0.280	0.274	0.025	0.015	0.042	0.291	0.016
		B	0.016	0.022	0.066	0.046	0.259	0.050	0.222	0.005	0.003	0.021	0.014	0.014

not change significantly.

The elasticities of fecundity, growth, survival and retrogression also changed significantly during the nine-year monitoring period. Elasticities for survival and retrogression increased over time, although only marginally significantly for the latter (L: $r = 0.726$, $p = 0.027$; R: $r = 0.597$, $p = 0.090$). However, those for fecundity and growth declined significantly (F: $r = -0.888$, $p = 0.001$; G: $r = -0.736$, $p = 0.024$). Higher λ were associated with higher elasticity for fecundity and growth and lower elasticity for survival (Pearson correlation λ and F: $r = 0.653$, $p = 0.057$; λ and G: $r = 0.771$, $p = 0.015$; λ and L: $r = -0.735$, $p = 0.024$).

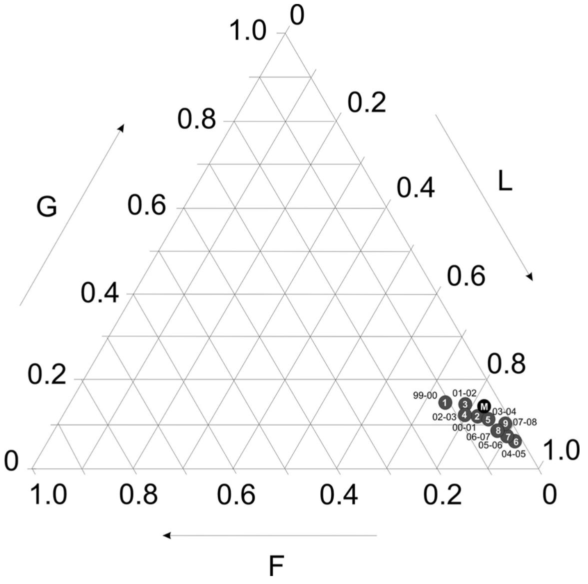

Fig. 3. Triangular ordination diagram representing the position of the nine matrices for *Bencomia exstipulata* between 1999 and 2008 with respect to their relative contribution (summed elasticities) of fecundity (F), Growth (G) and Survival (L) to the population growth rate, λ. The matrices have been chronologically numbered from 1, 1999–2000 to 9, 2007–2008. Black circle with "M" denotes the position of the average matrix.

3.2. Pollination

Bencomia individuals were frequently visited by honey-bee workers (*Apis mellifera* Linnaeus). Most of the observed bees visited male inflorescences (77% of all 9315 visits), and fewer visits were paid to mixed inflorescences (23%). The large corbicular loads of most workers showed that they foraged mainly for pollen, which explains their preference for male inflorescences. The pollen loads sampled from the bodies of 12 captured bees showed that by far the largest proportion of pollen grains belonged to *B. exstipulata*. Very few grains (< 1%) belonged to other species. Visitation rates showed high temporal variation (Fig. 4). At the peak flowering period in early March, the average inflorescence received about 0.25 visits per day.

Sufficient numbers of airborne pollen grains of *Bencomia* were captured on the slides with sticky gel to enable a good test of the bagging treatment (Fig. 5). On average, the insect-proof bags kept out 41% of the pollen grains, whilst the pollen-proof bags kept out most (96%) of them. Hence, it was concluded that the bagging treatments worked as planned.

No significant differences in seed set were observed between the control treatment, that with insect-proof bags, or that with pollen-proof bags in which the female flowers were cross-pollinated either at peak flowering or just after opening (Fig.6). Only female or mixed inflorescences covered with a pollen-proof bag showed significantly lower mean seed set per fruit. There was no difference in seed set between female and mixed inflorescences enclosed in pollen-proof bags.

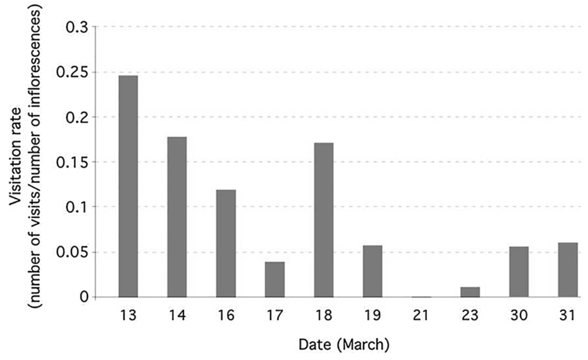

Fig. 4. Mean daily visitation rate (by honey bees) per inflorescence on different observation days throughout the main flowering period of *B. exstipulata* in March 2008.

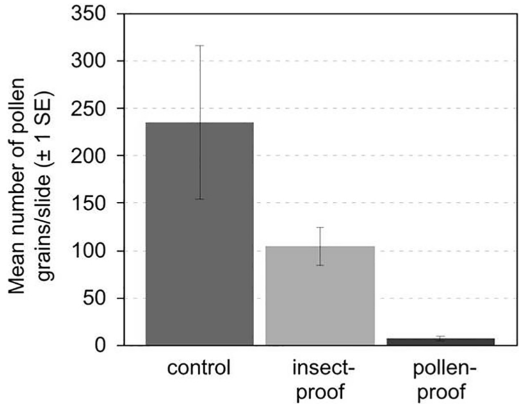

Fig. 5. Mean number of pollen grains of *B. exstipulata* captured on microscope slides with sticky gel covered with either insect-proof or pollen-proof bags or without bag (control treatment).

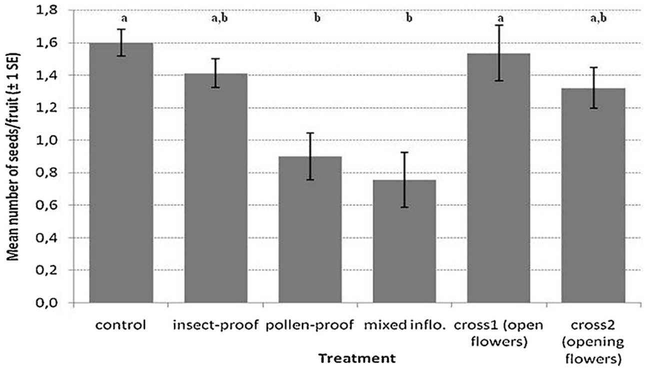

Fig. 6. Mean (± 1 SE) seed set for each pollination treatment for *B. exstipulata*. Different letters on top of the bars indicate significant differences between means (Bonferroni Posthoc test P < 0.05).

The seed set of a single isolated shrub, growing approx. 1 km from the main population in El Teide National Park, was examined to check for self-compatibility. The average number of seeds per fruit on this individual was 3.0 ($n = 123$), higher than the control plants in our experiment. Hence, at least this plant seemed highly self-compatible, and more so than those at Tiro del Guanche, of which mixed inflorescences (allowing within-inflorescence pollen transfer) showed significantly reduced seed set after being covered with pollen-proof bags.

3.3. Temporal variation and gender expression

The sex ratio in the population of *B. exstipulata* varies around a male:female ratio of 1:1, with the deviation not exceeding 10% (Fig. 7). Most deviations were towards a slight male bias. A small proportion of all individuals showed the same gender during the entire monitoring period, whereas most plants changed their gender to a minor or a major extent. An interesting pattern can be observed after 2002, when there seems to be an annual alternation between predominantly male and predominantly female flowering (Fig. 8).

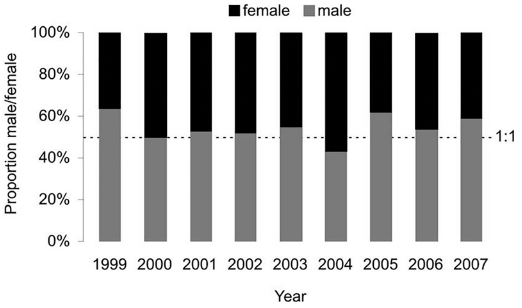

Fig. 7. Sex ratio of the *B. exstipulata* population in the Teide National Park between 1999 and 2007.

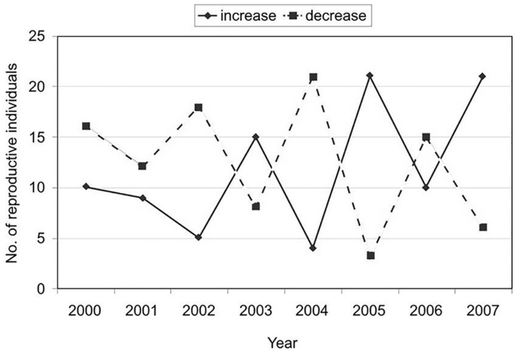

Fig. 8. Trends in gender change among individuals of *B. exstipulata* in the in the Teide National Park between 1999 and 2007. The line representing “increase” is the number of reproductive individuals that showed an increase in proportion of male flowers between one years and the next; the reverse is true for the line “decrease”.

3.4. Seed dispersal

While 124 of the 170 individuals (73%) in the planted locality produced fruits, this was only 18 of 77 individuals (23%) in the natural population. This difference in fruiting between sites was significant ($G_1 = 54.60$; $p < 0.001$).

Seeds of *B. exstipulata* were only found in 67% of droppings from the lizard *G. galloti*. From a total of 4688 seeds counted in 818 droppings collected in the field, only 131 (2.8%) were visually damaged. A significant correlation was noted between dropping width (which is proportional to lizard body length; see Valido & Nogales, 2003) and the number of seeds they contained ($r_s = 0.45$; $p < 0.001$). Only two species of partially frugivorous passerine birds were captured in the mist nets: *Erithacus rubecula* Linnaeus and *Sylvia melanocephala* Gmelin, but no *B. exstipulata* seeds were detected in their droppings.

The external appearance of the control seed embryos differed between the two sites, with significantly more aborted embryos in the natural (21%) than in the planted locality (7%) ($G_1 = 5.50$; $p = 0.019$). No significant difference in mean viability of undamaged seeds was observed between the two sites (95% viability in both populations; $G_1 = 0.066$; $p = 0.96$). Lizard gut passage significantly decreased seed viability relative to the control treatment in both populations. Viability declined by 22% in the natural ($G_2 = 9.43$; $p = 0.009$), and by 26% in the restored population ($G_2 = 9.90$; $p = 0.007$). Seed coats of the seeds that passed through lizard guts were clearly thinner at both sites, with a 16% difference between the two treatments (Table 2).

The monitored seedlings showed a high mortality rate of 97%, comprising 6% by herbivory and 91% from other causes (Table 3), although the observation of dry seedling remains points to this high percentage being due to the summer drought. No significant differences in seedling fate were recorded between the three treatments (the two herbivore exclosures and the control, $G_3 = 2.09$; $p = 0.719$).

Table 2

Seed coat of *B. exstipulata* after passing throughout the lizard *G. galloti* digestive tract compared to uneaten control seeds.

	Natural subpopulation			Restored subpopulation		
	Seed coat (mean ± SD)	n	Reduction (%)	Seed coat (mean ± SD)	n	Reduction (%)
Control	0.27 ± 0.04	50	–	0.24 ± 0,03	50	–
Gallotia	0.23 ± 0.03	50	16.1	0.20 ± 0.01	50	15.8
	$t = 5.68$; $P < 0.001$			$t = 5.40$; $P < 0.001$		

Table 3

B. exstipulata seedling fate in the three different treatments (two exclosures: total and partial, and the control). Partial exclosure only permits access by lizards.

	Seedling status		
	Survival	Death (without predation)	Death by predation
Total exclosure	1	19	1
Partial exclosure	1	19	1
Control	0	19	2

4. Discussion

4.1. Internal factors

4.1.1. Population dynamics

Judging from the demographic censuses and the projection matrices obtained between 1999 and 2008, the natural population of *B. exstipulata* in Tenerife is relatively stable, even though there was an interesting trend in stage structure during the study period. None of the dominant eigenvalues deviated significantly from unity, and there was no significant trend in λ over time either. Yet, during the sampling period, the initial population (in 1999) of 51 individuals increased to 72 plants. At the same time, the proportion of juveniles increased, and proportions of vegetative and also bisexual adults declined significantly. Even though this change in structure suggests that recruitment became more important, elasticities for fecundity as well as growth transitions declined significantly over the study period, whilst the importance of survival transitions for λ increased. As previously observed for a perennial herb (Oostermeijer, Berholz, & Poschlod, 1996, see also Caswell, 2001), high λ were associated with high elasticities for fecundity and growth. This population is therefore probably relying heavily on survival of adult shrubs to maintain demographic stability. The population received an increasing number of new recruits, which only manage to survive and progress to their following stages in years that sustain sufficient growth.

Although seedlings are normally sensitive to summer drought (Eriksson & Ehrlen, 1992), survival and growth of *B. exstipulata* seedlings seemed positively associated with low precipitation and high temperatures. Most seedlings were found in shaded conditions at the cliff base, which might generally be too cold and also too wet in winters with high precipitation. In this particular environment, drier and warmer conditions (as recorded at Izaña weather station, 19.8 km away) might promote rather than inhibit seedling growth.

The life span (34 years) and the average age of parents (72 years for reproductive individuals) of *B. exstipulata* is similar to other shrub species of the subalpine ecosystems of Tenerife, like *Spartocytisus supranubius* (Kyncl, Suda, Wild, Wildová, & Herben, 2006) or *Adenocarpus viscosus* and *Chamaecytisus proliferus* (L.f.) Link (observed comparing aerial photographs since 1964). Its lower half-life contrasts with most of the taxa present in the national park (mainly herbaceous and chamaephytic plants). This relatively long life span can be considered an adaptive strategy in habitats where conditions are rarely favourable to recruitment (Eriksson, 1992; García, Zamora, Hódar, & Gómez, 1999).

Given the stability observed over the study period, the stochastic simulations unsurprisingly suggest that the demographic viability of the Tenerife population is high, with an extinction probability lower than 5% for the next 100 years. In fact, field observations in the last decade (2008–2017) reveal a slow but constant population increase. Apparently, this demographic stability suggests that intervention to increase its numerical strength is not necessary. However, there are several potential risks discussed below derived from external factors and the limited colonization capacity of *Bencomia exstipulata.* These point to the need to establish new populations in those areas of the summit of Tenerife with appropriate microsites for its germination and recruitment, similar to the natural locality and away from pine forests.

Using demographic results, we can revalue the conservation status of the species following the guidelines provided by Caswell (2001) and the IUCN Criteria (UICN, 2012). Considering a generation time of 40 years, and values for λ and R_0 of 103 and 332 respectively, we cannot apply the A and C criteria for any of the IUCN threat categories. Application of criterion B is also difficult, because we have not detected evidence of extreme fluctuations and the present chorology of the species (considering natural and planted localities) exceeds the thresholds to consider it as threatened. At present, the number of mature individuals is higher than 1000 and the occupation area, calculated as 2×2 km cells (IUCN Standards and Petition Subcommittee, 2017) is 76 km^2, which makes it difficult to apply criteria D1 and D2. Finally, it is not possible to apply criterion D because the probability of extinction in the wild is lower than 10% within 100 years. Although with these data the species should not be qualified as threatened (CR, EN or VU), we propose maintaining it provisionally as VU D2, coinciding with Bilz et al. (2011), until long-term survival in its distribution area is fully guaranteed. For this purpose, it should be confirmed that the progressive increase in number of individuals (produced by natural recruitment, not plantations) predicted in the present paper is fulfilled, and that this is sufficient to compensate the mortality processes that may occur in the future when the life expectancy of the planted individuals is attained.

Similarly, we can evaluate the species' conservation status according to the criteria established for the Canary Islands Catalogue of Endangered Species (B.O.I.C., 2010). According to these, the species could be listed as Vulnerable following the criterion B1b because the area of occupation is lower than 80 km^2. However, to apply this criterion we must assume that it could be subject to some decline, which is not supported by the results obtained, but this would be possible in the absence of conservation measures.

4.1.2. Pollination system

Although *B. exstipulata* has morphological characteristics suggesting a predominant wind-pollination syndrome (cf. Faegri & van der Pijl, 1979), visitation by honey bees is highly frequent in the flowering season. Since bees were occasionally observed visiting mixed male-female inflorescences, some insect-pollination probably occurs. Nonetheless, bagging female inflorescences with insect-proof gauze did not reduce seed set significantly. Hence, we conclude that flower characteristics matching the wind-pollination syndrome, i.e. unisexual flowers, catkin-like inflorescence architecture, many stamens with long filaments, dry pollen and feathery stigmas (Faegri & van der Pijl, 1979) correctly predicted predominant wind pollination for this species.

Typically for wind-pollinated taxa (Charlesworth, 1993; Friedman & Barret, 2009), *B. exstipulata* has unisexual flowers, and shows monoecy and protogyny, with most individuals bearing both male and female flowers/inflorescences. Some of the studied individuals were unisexual during their entire lifetime, but on most plants the frequency of male and female flowers changed from one year to the next. At the population level, monitoring since 1999 shows that sex allocation occurs as an alternation between mainly male and mainly female years. The reasons for this behaviour are not yet clear. Significant trends in sex allocation and climatic variables were not detected, other than the years with cold winters (< 9 °C) having a higher proportion of male plants ($> 50\%$), which fits with a theoretical model in which sex allocation reflects resource availability (Masaka & Takada, 2006; Masaka, 2000). Since water availability is the factor most likely to affect demography, it may well influence sex allocation in *B. exstipulata.* This needs to be studied in more detail.

A study on the genetic population structure of *Sanguisorba officinalis* L., a relative of *Bencomia* with similar floral morphology, but with shorter filaments and a globular instead of linear inflorescence, showed very low genetic differentiation ($F_{ST} = 0.008$), suggesting a high level of gene flow between its populations (Musche, Settele, & Durka, 2008). Looking at the high number of insects visiting the flowers, the authors concluded that this species is insect pollinated and that highly mobile insects are responsible for the low genetic variation. However, it could also be the result of a mating system like that observed in *B. exstipulata*, with predominant wind pollination in combination with frequent, but relatively ineffective, insect visitation.

4.1.3. Seed dispersal

It seems there is a tendency for some individuals of *B. exstipulata* to change sex allocation. So, the data obtained in 2009 on the proportion of plant fruit producers are similar to those recorded in 2007, and there is possibly a periodic change in their sex proportion. Fruit production was clearly higher in the restored population than in the natural area. It is not easy to identify the main causes of this difference; however, the variable local soil conditions could be a determinant factor. The soil in the restored area is clearly deeper and better developed than on the steep cliff refuge occupied by the natural population. In *Juniperus cedrus* Webb & Berthel., another fleshy-fruited plant of the Tenerife high-mountain zone, cone production was also higher in the more benign environment at the cliff base than on top of the cliff (Rumeu et al., 2009).

A considerable number of lizard droppings contained *B. exstipulata* seeds, and a high proportion of these passed through their guts undamaged, which strongly suggests that lizards are important seed dispersers. Furthermore, the close relationship between lizard body size and number of seeds consumed (Valido & Nogales, 2003) was confirmed. Hence, as previously suggested by Valido (1999), saurochory is both qualitatively and quantitatively the only dispersal mechanism recorded for *B. exstipulata.* In addition to invertebrates, the diet of lizards on islands chiefly consists of plants (Cooper & Vitt, 2001; Van Damme, 1999), which is why many of their species function as effective seed dispersers (Olesen & Valido, 2003).

Lizards are mainly short distance dispersers (Bauwens, Garland, Castilla, & Van Damme, 1995); the maximum recorded for *B. exstipulata* seeds was 40 m from the nearest mother plant. Some studies have shown that birds of prey can increase seed dispersal distances, i.e. when they capture animals that have consumed fruits and seeds (Dean & Milton, 1998; Nogales, Padilla, Nieves, Illera, & Traveset, 2007). Although we did not record any seeds in the total of 94 kestrel (*Falco tinnunculus*) pellets analysed in this study, some *B. exstipulata* seeds were found in such pellets in the spring of 2008 (Padilla, González-Castro, & Nogales, 2012). Hence, this complex ecological process is potentially important for seed dispersal of this threatened plant over longer distances, and thus might lead to the foundation of new populations in the future. However, as will be discussed later in the analysis of external factors, this process may be affected by the presence of introduced predators (e.g. *Felis silvestris* Schreber).

Two of the most important factors in zoochory are embryo viability and seed coat thinning, after digestion by frugivores and the passage through their intestinal tracts. Embryo viability had only decreased slightly after passing through lizard guts, but seed coats became significantly thinner. The latter generally increases the permeability to water and enhances germination (Traveset, 1998; Traveset, Riera, & Mas, 2001). This did not occur in *B. exstipulata* however, because its seed viability declined after gut passage by 22–26% in the natural as well as the restored population.

The high seedling mortality observed in the field confirms that natural recruitment is extremely rare. The apparently low incidence of vertebrate herbivory on the seedlings suggests that other factors are negatively affecting them. Drought is probably the main cause of seedling death in this population, as it generally is at high altitudes (Kajimoto, 2002). Rainfall rarely exceeds 430 mm per year (Bustos & Delgado, 2004) and is also one of the main factors controlling seedling fate and population growth rates in the small woody perennial *Helianthemum juliae* (Marrero-Gómez et al., 2007). However, in the future, germination and survival tests should be carried out on seedlings subjected to different levels of humidity, in order to definitely confirm that seedling survival depends on soil moisture.

4.1.4. Genetic structure

Stochastic processes such as genetic drift (Bouzat, 2010) can have different outcomes in terms of retaining diversity, and consequently regarding the adaptive potential of populations following bottlenecks. This also highlights how the outcome of an individual bottleneck tends to be population-specific, and depends on the specific lineage and genetic background of the population.

From previously published articles (González-Pérez et al., 2009), we can add some considerations. The genetic diversity of the Tenerife population of *B. exstipulata* is extraordinarily low compared to that observed on the island of La Palma. If the microsatellite results are extrapolated to the whole genome of the species, it ought to be close to extinction on Tenerife. They give it little chance of medium or long-term survival and a great risk of falling into what has come to be called a 'local extinction vortex'. Alternative solutions must in that case be found to widen diversity, avoiding endogamy-derived processes. However, these results are based on a low number of molecular markers which greatly conditions decision-making. The markers are mostly neutral, but see García-Verdugo et al. (2015). Nevertheless, *B. exstipulata* on Tenerife does not present symptoms of being in a vortex of extinction; it shows neither diminished biological efficiency nor a low reproductive rate (Allee effect). This is a reason why the possible effects of a high rate of inbreeding were not detected. On the contrary, its spread and demographic stability are beyond doubt, with a healthy generation of fruits and seeds dependent more on the seasonal climatic conditions than its biological state. It therefore shows low (or zero) levels of genetic variability, but with demographic and reproductive stability. However, the genetic variability among La Palma natural populations is much higher using the same molecular markers. Obviously, it is necessary to include other types of studies to assess the degree of endogamy and biological fitness of the species and elucidate how endangered it is from a genetic point of view.

The possible effect of the volcanic eruption of Narices del Teide (1798) cannot be forgotten. They may have influenced the numerical strengths of the species, since the lava flowed alongside the current natural population of the species. It is possible that these lava currents buried a good part of the individuals and that only those on the cliff survived. In fact, there is some evidence that the species was more abundant in the past. Archaeological studies at sites close to the natural locality on Tenerife (Machado Yanes & Galván Santos, 1998) indeed show charcoal remnants belonging to the family Rosaceae. Such proximity allows us to ascribe such remains to *B. exstipulata* more easily than to other species of the genus present on Tenerife, which have either been introduced in historical times, or have much more remote natural locations. This indicates that with much more humid climatic conditions in the past, the bush was possibly abundant enough for use as firewood.

Nowadays, conservation biology presents two essential, but opposite, approaches. These are the 'Jekyll and Hyde' of conservation. In theory, the adverse effects of genetic isolation can often be reversed by re-establishing gene flow between populations (Frankham, Ballou, & Briscoe, 2010). Experimental studies have documented the rapid spread of immigrant genomes within inbred populations due to heterosis (Saccheri & Brakefield, 2002; Willi, van Kleunen, Dietrich, & Fischer, 2007) and increased biological efficacy of plants (Newman & Tallmon, 2001; Tallmon, Luikart, & Waples, 2004). Indeed, Willi et al. (2007) confirmed that large numbers of immigrants are not necessary to increase the genetic diversity of new generations. This means that low levels of immigration (even just 2–3 individuals) could be effective in the Tenerife population without affecting local adaptation.

On the other hand, management actions to accomplish genetic recovery involve facilitating gene flow between populations to reverse inbreeding, recover genetic diversity, and improve reproductive fitness. These are sometimes limited by concerns about outbreeding depression (Edmans, 2007; Frankham et al., 2011), since such processes can imply a loss of local adaptability. Therefore, the translocation of individuals between populations should be avoided. However, some research has appeared questioning the strength and importance of outbreeding depression in plants (Rousselle, Thomas, Galic, Bonnin, & Goldringer, 2011). These authors consider that scepticism towards the development of artificial genetic flow is not justified in those cases where populations are small and show a significant reduction in efficacy due to endogamous depression, fixed mutational load or reduced cross-compatibility.

Before the present study, the biological efficacy of the different generations of *B. exstipulata* on the same island had not been measured. As already mentioned, more research is necessary to ascertain the extent of possible genetic deterioration in the Tenerife populations. Efforts should particularly be made to raise their low level of genetic diversity, through outbred progeny. Indeed, the possibility has even been raised of transferring specimens of *B. exstipulata* from La Palma, where its populations present wider genetic diversity. Handicaps to this are the wide genetic differentiation between the populations of the two islands (González-Pérez et al., 2004) and the difficulty in homogenizing and integrating alleles exclusive to each island. Caution is therefore necessary for the moment, given that the species does not appear to be under extreme extinction pressure in El Teide National Park. The actions performed so far seem to be ensuring the survival of *Bencomia exstipulata* on Tenerife, but it is still necessary to thoroughly monitor its real genetic diversity, using new molecular markers (NGS). Despite this, in attempting to increase the population it would perhaps be advisable to cross the largest possible number of genetically diverse individuals. However, since individuals are not simply 'boxes of genes' (Tallmon et al., 2004), until clear effects of the expected impaired biological efficacy are perceived, demographic and environmental monitoring and related actions also remain important in such experimental work.

4.2. External factors

4.2.1. Disturbances and reduction in habitat quality

The demographic stability of the Tenerife natural population suggests that intervention to increase its numerical strength is not necessary. However, the steep slopes and their geological instability make for a potential risk of serious rockfalls, leading to a loss of individuals. This is accentuated by the proximity of *P. canariensis* plantations, which shed considerable combustible litter that increases the risk of wild-fires. In fact, in 2012 fire came near to causing the extinction of this entire *Bencomia* natural population. Therefore, one of the aims should be to remove these planted stands of *Pinus*, relatively alien to the non-conifer potential of this habitat. Moreover, the risks referred to and the limited colonization capacity of *B. exstipulata* would support establishing new populations in those areas of the summit of Tenerife that have appropriate microsites for its germination and recruitment, similar to the natural locality and away from pine stands. Other feasible actions are the inclusion of seeds in germplasm banks for future recovery efforts, in case stochastic events such as those mentioned cause the loss of populations or their collapse.

4.2.2. Allochthonous species

The results suggest that the presence of rabbits, mouflons and other introduced herbivores have no special impact on the recruitment of new individuals or on the planted or natural adults. However, feral cat populations are undergoing a significant increase in El Teide National Park, and the sightings and captures of felines have risen substantially in recent years. The presence of this introduced species could affect the seed dispersal of *B. exstipulata*, since the presence of lizards in the feral cat diet in El Teide is one of the most important at a global scale (Nogales, Abdola, Alonso, & Quilis, 1990). So it would be convenient to assess the real effect on this prey interaction, and if necessary, to develop effective control of *Felis silvestris* around the plant populations in order to reduce its effect.

5. Conclusion

Although in the present study we describe the case of a single insular endemic species whose status could be considered as threatened, this species certainly represents the case of many plants in several archipelagos. Therefore, the integrative view set out here is applicable to many other species with a delicate conservation status. On assessing the results, a general strategy has been compiled for the recovery of *Bencomia exstipulata*, that complements the conservation efforts carried out in previous years. This general strategy implies five main goals.

1) Establishment of new localities in El Teide and La Caldera de Taburiente National Parks, with appropriate microsites for germination and recruitment, similar to or with more precipitation than the natural localities, and away from pine forests.
2) Inclusion of seeds in germplasm banks for use in the case of stochastic events. These accessions must be carried out in a specific way for each individual, covering all or most of the mother plants.
3) Assess the impact of introduced *Felis silvestris* on native lizard dispersers within and nearby the populations of *B. exstipulata* localities (natural and planted) and, if necessary, to control the population of this carnivore.
4) The plantations made to create new populations must harbour all genotypes present in natural populations, especially on Tenerife.
5) Genetic studies should be continued with the aim of evaluating the suitability of introducing individuals from La Palma on Tenerife.

Author contributions

Ángel Bañares coordinated the study generally as well as helping in the data collection and demographic analysis, which were carried out jointly with Manuel Marrero and Eduardo Carqué. Gerard B. Oostermeijer contributed with the conceptualization of the study, supervising demographic analysis, and together with Thomas Van Hengstum focused on the study of the pollination system and the variation in gender expression. Frugivory, seed dispersal and seedling herbivory were assessed by Manuel Nogales and Isabel Saro, and finally Pedro Sosa and I. Saro contributed genetic considerations to the study.

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