



Original article

Exploring local borders of distribution in the shrub *Daphne laureola*: Individual and populations traits

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ABSTRACT

Biogeographic models predict that marginal populations should be more geographically isolated and smaller than central populations, linked to more stressful conditions and likely also to a reduction in density of individuals, individual growth, survival and reproductive output. This variation in population features could have important consequences for different aspects of plant ecology such as individual reproductive success, population genetic structure or plant-animal interactions. In this study, we analyze if individuals of the evergreen shrub *Daphne laureola* at disjunct populations in a local border of its distribution area in southern Iberian Peninsula differ in individual size, shoot growth, reproductive output and the pollination environment from central continuous populations within the area. Plants of central continuous populations were larger and produced more flowers and fruits than plants of marginal disjunct populations suggesting more optimal conditions, although they had lower annual shoot growth. In contrast, fruit set was higher in plants at the local border, suggesting a more efficient pollinator service in these populations where the main pollinator in central continuous populations, the pollen beetle *Meligethes elongatus*, was not present. Our results do not support strong differences in the ecological stress between marginal disjunct and central continuous populations of *D. laureola* in the south of the Iberian Peninsula but indicate some changes in plant-pollinator interactions that could be relevant for the sexual polymorphism in this gynodioecious species.

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1. Introduction

Distinguishing the factors that determine the limits in the distribution of species has been one of the most important issues both in ecology (e.g. Caughley et al., 1988; Lawton et al., 1994; Brown and Lomolino, 1998) and evolutionary biology (Jablonski, 1987; Sexton et al., 2009). According to niche-based conception of geographical range limits, the spatial variation in the biotic and abiotic factors that define a species' ecological niche determine where the species does or does not occur (Samis and Eckert, 2009). Therefore, along any ecological gradient, a species will be most abundant where the conditions allow maximum survival and reproduction and will be progressively less abundant away from this point until a geographic limit is reached (Hengeveld and Haec, 1982; Brown, 1984; Lawton, 1993). However, several studies have shown that some species do not present lower fitness in marginal populations (e.g. Jump and Woodward, 2003; Kluth and Bruelheide, 2005; Samis and Eckert, 2007) suggesting that marginal

populations may be locally adapted to sub-optimal conditions at the range edge (Caughley et al., 1988; Barton, 2001) and other mechanisms such as dispersal limitation or unstable meta-population dynamics, rather than departure from ecological optimum, could be also important in limiting geographic distributions of some species (Kawecki and Holt, 2002; Holt, 2003).

Evolutionarily stable range limits are established when marginal populations cannot adapt to conditions beyond the limit because genetic variance is too low to allow adaptation to local conditions on the margin (Kawecki, 2008) or gene flow from central populations recurrently introduces genes adapted to ecological optimum in the center of range and therefore it prevents local adaptation on the distribution borders ("gene swamping"; García-Ramos and Kirkpatrick, 1997; Alleaume-Benharira et al., 2006). Otherwise, genetic drift in combination with responses to local selection pressures could promote genetic divergence, non-reduced fitness, and rapid evolution in marginal populations (Lesica and Allendorf, 1995; Alleaume-Benharira et al., 2006).

Plant-pollinator interactions are an example of selection pressures expected to vary geographically following spatial changes in the abundance and identity of the floral visitors (Moeller, 2005, 2006; Thompson, 2005). In general, small and/or isolated

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populations attract fewer and less diverse pollinators (Groom, 1998; Sih and Baltus, 1987). Also, marginal populations have been found to have poorer pollinator faunas than central populations (Silva-Montellano and Eguiarte, 2003; Stone and Jenkins, 2008). Pollination regimes differing in composition and abundance of pollinators can in turn lead to differential reproductive success (Herrera et al., 2006; Pérez-Barrales et al., 2007), and in the specific context of the comparison between central and marginal populations, could lead to a higher reproductive success in central populations.

In the present study, we compared central continuous and marginal disjunct populations of *Daphne laureola* within its distribution range in the south of the Iberian Peninsula. We used a broad array of population features and plant fitness correlates, in addition to consideration of the main pollinator identity and abundance of co-flowering species. *D. laureola* is an evergreen shrub with a wide distribution range within Europe, growing in the understory of mountain forests and presenting distribution patches on the main calcareous mountain ranges of southern Europe and north of Africa (Meusel et al., 1978). In our study area, most populations are gynodioecious with hermaphrodite and female plants coexisting within populations (Alonso et al., 2007). The main pollinator of *D. laureola* in the central area is a small pollen beetle, *Meligethes elongatus* Rosenhauer (Alonso, 2004), but its role as pollinator in marginal populations was uncertain. We analyzed population features such as population size, density of reproductive and non-reproductive individuals within population, identity of main pollinators and alternative floral resources for the pollinators, and individual life-history traits including plant size, shoot growth, flower and fruit production, fruit-set, and mortality. We further studied differences between females and hermaphrodites in size and reproductive traits presuming the existence of more stressful conditions in marginal populations that would allow to test the “sex-differential plasticity hypothesis” (Case and Ashman, 2007; Dorken and Mitchard, 2008). A considerable number of studies support that females are more abundant under stressful conditions because by investing in one only sex function, females have more available resources for other functions thus increasing their relative fitness compared to hermaphrodites (reviewed in Ashman, 2006).

However, according to the sex-differential plasticity hypothesis (Dorken and Mitchard, 2008), if hermaphrodites are plastic in their investment in female reproduction, they will allocate fewer resources to seed production under stressful conditions counteracting the females’ advantages. Specifically, we addressed the following questions: (1) do population size and density of individuals differ between central continuous and marginal disjunct populations? (2) do plants in central continuous and marginal disjunct populations differ in size, growth, flower and fruit production? (3) do the identity of main pollinator and the abundance and diversity of other co-flowering species vary in central continuous and marginal disjunct populations? and (4) do hermaphrodite plants present a lower seed output than females in the marginal disjunct populations?

2. Material and methods

2.1. Study species

D. laureola L. (Thymelaeaceae) is an evergreen shrub with a disjunct Palaearctic distribution associated to the main calcareous mountain ranges of Europe, and north of Africa. In the Iberian Peninsula it shows a disjunct distribution, being abundant in the northern Cantabrian Range and the Pyrenees, and also in the southern Baetic Ranges (Alonso et al., 2007; Fig. 1a). This study was conducted in 2007–2009 in the Baetic Ranges.

Plants of *D. laureola* present a variable number of branches that elongate over several consecutive growing seasons without any secondary branching. Leaves occur only at the distal end of branches, where they form a well-defined rosette, termed “leaf whorl” hereafter. It has a broad winter-flowering period (January–April) and produces a large number of small, tubular, green-yellowish flowers aggregated into several compact axillary inflorescences per stem. *D. laureola* presents gynodioecious populations where female and hermaphrodite individuals coexist, and populations having exclusively hermaphrodite plants, the last ones being rare in our study area (Alonso et al., 2007). Fructification begins in June, presenting one only seed per fruit.

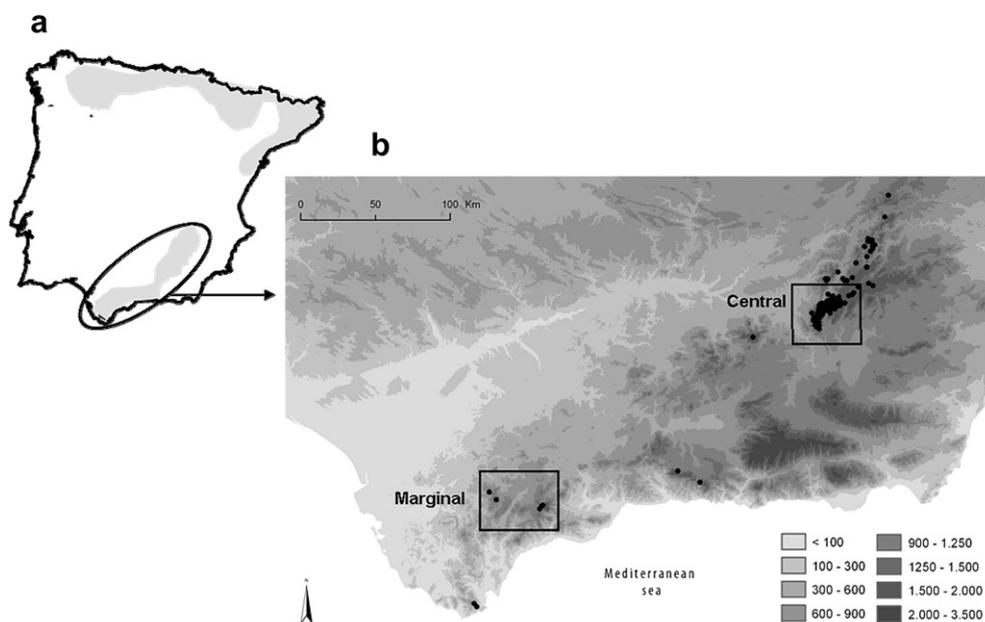


Fig. 1. (a) Distribution range of *Daphne laureola* in the Iberian Peninsula. (b) More detailed distribution of populations in the study area and location of central and marginal regions defined in this study. Intervals of altitude (m.a.s.l.) in the study area are represented with grey scale (see legend).

The main pollinator of *D. laureola* in populations of the Sierra de Cazorla, which constitute the center of abundance of the species within the studied southern Iberian region (Fig. 1b), is *M. elongatus* Rosenhauer, a small pollen beetle that moves frequently among flowers of the same individual (Alonso, 2004).

2.2. Study area

Across the Baetic Ranges, *D. laureola* is especially abundant in the Sierra de Cazorla, with at least 88 populations highly connected among them located along a broad altitudinal range. In fact, considering population as a discrete group of individuals distant from other groups of individuals by at least 1 km, most populations of Cazorla have >60 neighbouring populations in a radius of 25 km (Castilla et al., unpublished data). The geographic isolation among population increases towards eastern and western regions of the Baetic Ranges, being isolation more marked in the western populations here analyzed (Castilla et al., unpublished data). In particular, western populations of *D. laureola* have on average <3 neighbouring populations in a radius of 25 km. Therefore, in this study we considered the Sierra de Cazorla as the local continuous center (“central region”, hereafter) and populations at the western edge as a local disjunct margin (“marginal region”, hereafter) of the species’ distribution patch in southern Iberian Peninsula (Fig. 1b).

We studied three accessible populations per region. In the central region we used Valdecuevas, Cañada del Espino and Fuente Bermejo, the distance among them being 2–5 km. In the marginal region we used two different mountain ranges. Two populations (Fuente Molina and Cañada de las Animas) were located in the Sierra de las Nieves, with a distance between them <3 km. The third marginal population was located in the Sierra de Grazalema, distant from the other two populations about 35 km. All study populations were gynodioecious, and the proportion of female and hermaphrodite individuals determined during the flowering period of 2007 by examining 100 randomly chosen individuals was ca. 20% in all of them (Table 1). At the beginning of the study we haphazardly marked 25 hermaphrodite and 15 female plants in each study population, to avoid potential artefacts due to uncontrolled variation on sample sex ratio.

2.3. Population features: size, plant density and mortality of individuals

Populations were classed into one of the following size categories: <500, 500–1000, 1000–1500, 1500–2000, >2000 reproductive individuals. Densities of reproductive and non-reproductive individuals within each population were estimated using 20 randomly located circular areas of 10 m diameter in which the number of

reproductive and non-reproductive individuals were counted. In 2009 summer, the mortality of marked individuals was recorded.

2.4. Individual features: size, annual shoot growth, floral display and seed production

Four measures related to individual size were obtained for every marked plant: height of the tallest branch (“plant height” hereafter), total number of leaf whorls (“number of leaf whorls” hereafter) and the major and the minor diameter of the plant vertical projection, used to estimate the area of the plant assimilating it to an ellipse (“plant area” hereafter).

Three measures related to floral display were also obtained for every marked plant: proportion of stems bearing flowers; number of inflorescences/stem (based on counts of five stems per plant) and number of flowers/inflorescence (counted in one inflorescence per sampled stem). Total flower production per plant was then estimated as the number of flowering stems \times average number of inflorescences/stem \times average number of flowers/inflorescence. The annual shoot growth was estimated by measuring the shoot elongation at the end of the growing season in the five stems per plant used for the floral display (“shoot growth” hereafter). In addition, the total number of fruits produced per individual was counted (“fruit production” hereafter) and the proportion of fruits per flower (“fruit set” hereafter) was estimated using the five marked inflorescences.

2.5. Main pollinator and alternative floral resources

Previous studies showed that the pollen beetle *M. elongatus* (Nitidulidae) is the main pollinator of *D. laureola* in Sierra de Cazorla, determining important aspects of species’ reproductive biology (Alonso, 2004; Medrano et al., 2005). However, occasional observations on *D. laureola* flowers during the flowering period of 2007 (A.C. personal observation) indicated that pollen beetles were apparently absent from marginal populations, where several species of Hymenoptera, mainly *Bombus terrestris* L., *Xylocopa violacea* L. and *Apis mellifera* L., and another beetle *Tachyporus nitidulus* Fabricius (Staphylinidae) were observed. Therefore, in 2009 censuses were conducted to determine the abundance of *M. elongatus* in marginal populations of *D. laureola*. The censuses were done in sunny days. In each census, the observer was close to the plant and counted the number of *M. elongatus* individuals systematically by examining all the flowering stems of the plant during a maximum interval of three minutes. The number of flowering stems, the time spent and whether the plant was in sun or shade during the observation were recorded. Forty individuals per population were censused in all cases. In marginal populations, censuses were conducted in three different dates covering all the flowering period (early, peak and late flowering) to exclude the possibility of a mismatch between the presence of *M. elongatus* and the *D. laureola*’s flowering peak. For comparison within the same season, plants in central populations were similarly censused although only in a single date at flowering peak. We censused the same number of individuals in marginal and central populations, investing 168 min in marginal populations during the flowering peak and altogether 539 and 304 min in marginal and central populations, respectively.

In addition, the abundance of other flowering species which could potentially share pollinators with *D. laureola* was estimated by counting the number of flowering individuals of each species within five meters around every censused plant.

Table 1
Population features of the six *Daphne laureola* populations studied.

Population	Coordinates	Region	Altitude (m.a.s.l.)	Size (No. reproductive individuals)	Female frequency (%)
Valdecuevas	37° 54' N 2° 52' W	Central	1380	>2000	25.5
Cañada del Espino	37° 55' N 2° 53' W	Central	1575	500–1000	20
Fuente Bermejo	37° 55' N 2° 50' W	Central	1513	>2000	21
Grazalema	36° 46' N 5° 25' W	Marginal	1229	1500–2000	10
Fuente Molina	36° 41' N 5° 1' W	Marginal	1380	1000–1500	20
Cañada de las Animas	36° 42' N 5° 1' W	Marginal	1333	500–1000	18.5

2.6. Data analyses

All statistical analyses were performed using the SAS statistical package (SAS Institute, 2002). In order to compare marginal and central populations, tests considering the effects of region (central vs. marginal) and sex (female vs. hermaphrodite) as fixed factors and the effect of population as random, were conducted. Density of reproductive and non-reproductive individuals, plant area, plant height, number of leaf whorls, flower production, shoot growth, fruit production and fruit set were the response variables analyzed separately. Fruit set was normally distributed and plant height was normalized after being log transformed. Both responses were analyzed by mixed models (Procedure MIXED). We analyzed all the other variables with generalized linear mixed models (Procedure GLIMMIX), using the negative binomial function. Differences among regions in the relationship between flower production and individual size (plant area and number of leaf whorls per plant) were studied with an analysis of covariance (ANCOVA). Flower production was the response variable, plant area, and number of leaf whorls were the explanatory variables and region was the categorical effect. In addition, we explored potential trade-offs between reproduction and shoot growth with an analysis of covariance, distinguishing shoot growth as the response variable, flower and fruit production as the explanatory variables and region as the categorical effect. Finally we used Fisher's exact test to analyze differences in the frequency of dead individuals between central and marginal populations. Means are given ± 1 SE.

3. Results

3.1. Population features: size, plant density and mortality of individuals

All the populations studied had more than 500 reproductive individuals (Table 1). The two largest populations occurred in the central region, with >2000 reproductive plants. The two smallest populations, with 500–1000 reproductive individuals were found one in the central region and the other in the marginal region.

There was marginally significant variation among regions for plant density within population ($F_{1,106} = 3.86$, $P = 0.05$). Marginal populations were denser than central populations (0.09 ± 0.01 and 0.06 ± 0.01 individuals/100 m² respectively). Density of reproductive individuals did not differ significantly between regions ($F_{1,118} = 2.48$, $P > 0.1$; Fig. 2). However, density of non-reproductive individuals in marginal populations was larger than in central populations ($F_{1,118} = 13.84$, $P < 0.001$; Fig. 2). The percentage of dead individuals after two years was also larger in marginal than in central populations (17% and 2% respectively; Fisher's exact test: $P < 0.0001$).

3.2. Individual features: plant size, shoot growth, floral display and fruit production

Plants of central populations were larger than those growing in marginal populations. The average area of individuals in central populations was more than twice the area of plants in marginal populations ($F_{1,232} = 17.65$, $P < 0.0001$; Fig. 3a). Also the number of leaf whorls was more than three times larger in central populations ($F_{1,232} = 16.92$, $P < 0.0001$; Fig. 3b). Plants in marginal populations tended to be taller than those in central populations but their height averages did not differ significantly (84.72 ± 2.44 cm vs. 80.22 ± 2.28 cm; $F_{1,232} = 0.71$, $P = 0.40$). Shoot growth was significantly larger in marginal populations (5.9 ± 0.2 cm vs. 3.9 ± 0.1 cm; $F_{1,229} = 24.07$, $P < 0.0001$). Also, shoot growth was negatively related to flower and fruit production ($F_{1,235} = 36.21$, $P < 0.0001$ and $F_{1,235} = 9.01$, $P < 0.01$, respectively). The ANCOVA revealed that

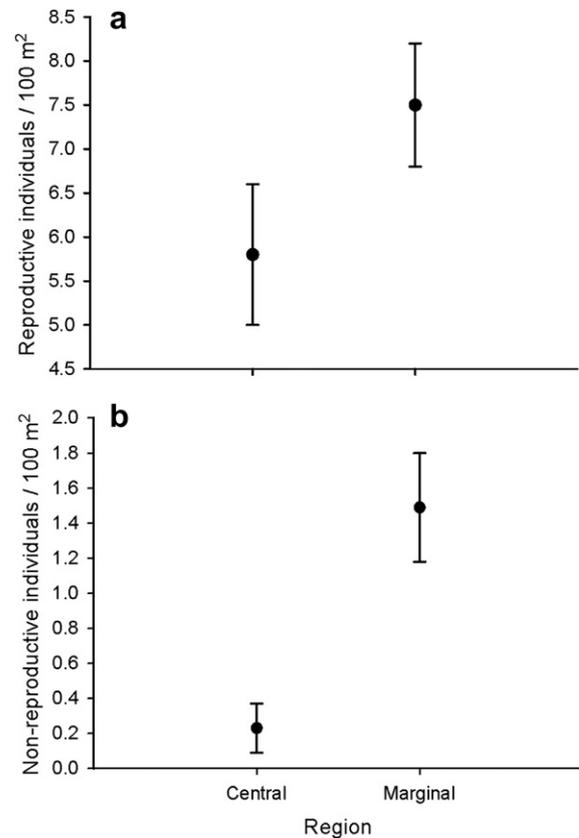


Fig. 2. Regional differences in the density of reproductive (a) and non-reproductive (b) individuals of *Daphne laureola* based on data of three populations per region and 20 plots per population. In each plot, reproductive and non-reproductive individuals were counted in a circular area with a diameter of five meters. Bars represent the least-square means (\pm s.e.).

negative relationships between growth and flower and fruit production were consistent in the two study regions ($P = 0.28$ and $P = 0.29$ for the interaction between region and flower and fruit production, respectively). Furthermore, there were not significant differences between hermaphrodite and female plants in any size-related variable ($P > 0.5$ in all cases). Absence of differential size between sexes was consistent between the two study regions ($P > 0.5$ in the interaction region \times sex for all size variables).

Floral display was larger in plants of central populations (Table 2). They produced more reproductive stems/individual, more inflorescences/stem and more flowers/inflorescence, and consequently many more flowers than plants in marginal populations (Table 2). No significant differences were found between female and hermaphrodite individuals in any of these reproductive parameters ($P > 0.5$). Absence of differences in any of reproductive parameters between sexes was consistent between the two study regions ($P > 0.5$ in the interaction region \times sex for all variables).

Flower production was directly related to plant area in both central and marginal populations ($R^2 = 0.43$, $F_{1,118} = 90.48$, $P < 0.0001$ and $R^2 = 0.28$, $F_{1,118} = 46.87$, $P < 0.0001$, respectively). Nevertheless there was a regional difference in the slope of the relationship between these variables ($F_{1,236} = 6.44$, $P < 0.05$; Fig. 4a). Flower production was also positively related to number of leaf whorls in both regions ($R^2 = 0.56$, $F_{1,118} = 142.46$, $P < 0.0001$ and $R^2 = 0.56$, $F_{1,118} = 142.47$, $P < 0.0001$ in central and marginal populations, respectively) and there was a regional difference in the slope of the relationship between flower production and number of leaf whorls ($F_{1,236} = 40.61$, $P < 0.0001$; Fig. 4b). In both cases, the

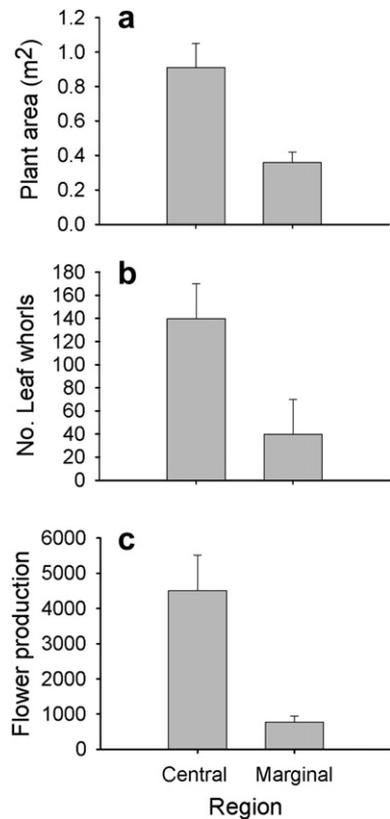


Fig. 3. Differences in average plant area (a), number of leaf whorls (b) and flower production per plant (c) in central and marginal populations of *Daphne laureola*, based on data of three populations per region and 40 individual per population. Bars represent the least-square means (+s.e.) after accounting for sex (fixed effect) and population (random effect) variation.

slope of the relationship between flower production and individual size variables was steeper in central populations.

Fruit production was greater in central populations ($F_{1,231} = 8.36$, $P < 0.01$; Fig. 5a). No effect of sex on fruit production was detected ($P > 0.1$). Absence of differential fruit production between sexes was consistent between the two study regions ($P > 0.5$ region \times sex interaction). The proportion of flowers setting fruit, however, was larger in marginal populations ($F_{1,231} = 5.13$, $P < 0.05$; Fig. 5b). Fruit set was the only variable for which a significant difference was detected between plants of different sex, with hermaphrodite plants having a larger fruit set than females ($F_{1,231} = 7.33$, $P < 0.01$; 0.46 ± 0.04 and 0.52 ± 0.03 fruits/flower in female and hermaphrodite plants respectively). This difference in fruit set between sexes was consistent in central and marginal populations ($P > 0.5$ region \times sex interaction). Note that all sampled populations showed female frequencies ca. 20% except one, the marginal population of Grazalema with 10% females (Table 1). Therefore, the average fruit set of this population with more hermaphrodites was expected to be even larger, increasing the average fruit set of marginal populations and their difference with respect to central populations.

Table 2

Reproductive parameters analyzed (mean \pm S.E.) in the marginal and central *Daphne laureola* populations studied.

	Central	Marginal	$F_{1,232}$	P
No. reproductive stems	97 \pm 24	30 \pm 7.4	11.14	<0.01
No. inflorescences /stem	5 \pm 0.3	4 \pm 0.2	19.78	<0.0001
No. flowers /inflorescence	9 \pm 0.5	7 \pm 0.4	10.18	<0.01

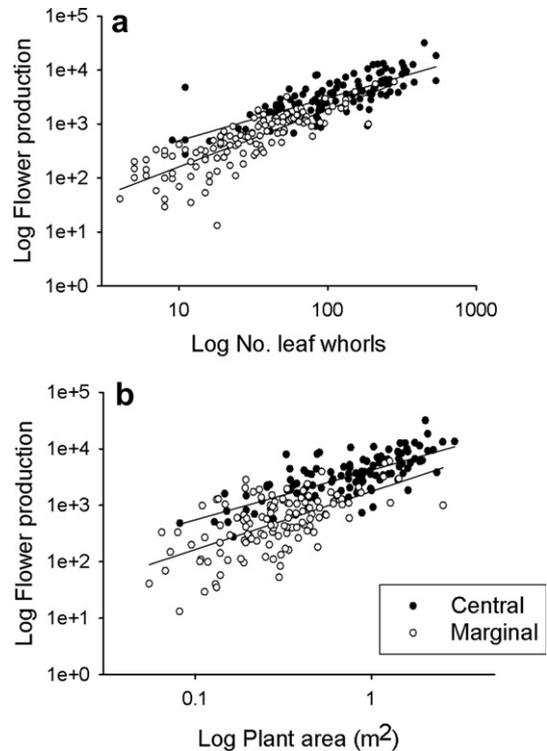


Fig. 4. The total number of flowers per individual related to plant area (a) and number of leaf whorls (b). Each circle corresponds to an individual. The axes were transformed to a logarithmic scale.

3.3. Pollination environment

In central populations, *M. elongatus* was observed in all censuses and its average abundance at flowering peak in this region was 0.8 beetles /min equivalent to 2 individuals /plant. In contrast, this species was not observed in any of the censuses in marginal populations conducted at early, peak and late flowering (Table 3).

A marked regional difference was found in the number of local plant species co-flowering with *D. laureola* (Appendix 1). Nine herbaceous species were blooming in the three central populations combined: *Helleborus foetidus*, *Viola odorata*, *Lobularia maritima*, *Primula vulgaris*, *Narcissus cuatrecasii*, *Bellis perennis*, *Ranunculus ficaria*, *Scilla reverchonii*. However, one central population (Cañada del Espino) presented a poor flowering community with only *Crocus nevadensis* flowering with *D. laureola* at low density (Appendix 1). In marginal populations, in contrast only *Helleborus foetidus* was flowering together with *D. laureola*, and its abundance was four times lower than in central populations (2.8 and 0.6 individuals /100 m² in central and marginal populations respectively). Thus, *D. laureola* was almost the only floral resource available for pollinators in marginal populations, while a broader array of species co-flowered with *D. laureola* in most central populations.

4. Discussion

4.1. Population features: size, plant density and mortality of individuals

Empirical evidence for the hypothesized reduction of population size towards limits of distribution is quite limited (Gaston, 2009). Ongoing studies with *D. laureola*, based on an intensive sampling of 111 populations, revealed a decrease of the frequency of populations and an increase of the geographic isolation of populations towards the geographic limits of the study area (Castilla et al., unpublished

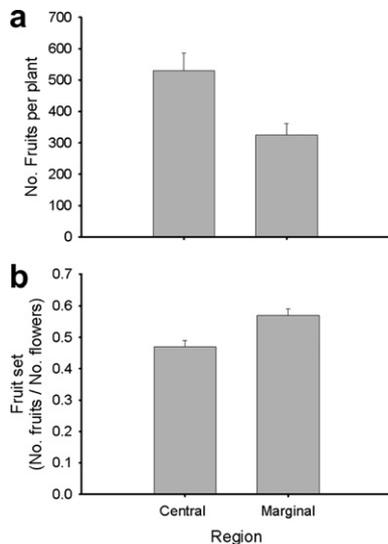


Fig. 5. Regional differences in fruit production per plant (a) and fruit set (b). Bars represent the least-square means (\pm s.e.) after accounting for sex (fixed effect) and population (random effect) variation, and are based on three populations per region and 40 individual per population.

data); both trends were more marked on the western border, examined in this study. However differences in population size between central and marginal populations were not detected (Castilla et al., unpublished data). In the present study, we found that relatively large populations of *D. laureola* occurred indistinctly in central and marginal locations. In fact, two of the three marginal populations had more than 1000 reproductive individuals, supporting that high quality habitats do exist in both marginal and central locations although likely at different frequency.

A lower density of individuals associated with stressful conditions in marginal populations has been also hypothesized (Brown, 1984; Brussard, 1984; Lawton, 1993). Nevertheless, tests of this hypothesis have provided contradictory results, particularly in plants for which there are a reduced number of studies (Sagarin and Gaines, 2002; Sagarin et al., 2006). A decrease in the density of individuals in marginal populations has been found in only five out of 13 plant species for which this pattern has been analyzed (Carey et al., 1995; Jump and Woodward, 2003; Lönn and Prentice, 2002; Moore, 2009). In other cases, the density of individuals either did not vary between central and marginal populations (Herlihy and Eckert, 2005; Ribeiro and Fernandes, 2000; Samis and Eckert, 2007) or even was higher in marginal populations (Kluth and Bruelheide, 2005; Yakimowski and Eckert, 2007). In the present study, the density of reproductive individuals did not differ significantly between central and marginal populations of *D. laureola* suggesting the absence of strong difference in ecological stress between central and marginal populations. However, we

Table 3

Abundance of *Meligethes elongatus* in central and marginal populations of *Daphne laureola*. Censuses were conducted in three different dates at early, peak and late flowering in marginal populations and only at flowering peak in the central region.

Population	<i>Meligethes elongatus</i> (individuals/min)	Total time per population (min)
<i>Center</i>		
Cañada del Espino	1.6 \pm 0.3	109
Fuente Bermejo	0.8 \pm 0.2	95
Valdecuevas	0.1 \pm 0.03	100
<i>Marginal</i>		
Fuente Molina	0	125
Cañada de las Animas	0	194
Grazalema	0	220

found differences in the density of non-reproductive individuals (Fig. 2) and the frequency of dead individuals. Non-reproductive individuals were always smaller than reproductive ones, therefore suggesting they were younger plants. Assuming this, the combination of larger mortality of adults and higher density of non-reproductive individuals in marginal populations would suggest a higher turnover in these populations. A higher demographic variability in marginal populations of plant species has been found by several studies (Lönn and Prentice, 2002; Moore, 2009; Nantel and Gagnon, 1999). However, more demographic analyses are required to determine if this is a common pattern in plants and to investigate the possible underlying factors.

4.2. Individual features: plant size, annual growth, floral display and reproductive output

Adult plants of *D. laureola* vary widely in size and architecture through the Iberian Peninsula (Alonso et al., 2007). The present study found that in its southern distribution area, individuals of central populations were larger than those in marginal populations, which had as a direct consequence a huge variation in flower production. Plants in central populations produced one order of magnitude more flowers per individual than in marginal populations, because they consistently produced more reproductive stems, more inflorescences per stem and more flowers per inflorescence. These results suggested more optimal conditions for the species in the central locations, further supported by the steeper slope of the relationship between flower production and individual size in central populations. We must point out, however, that shoot growth was lower in central populations, likely showing a trade-off between reproduction and growth within the season with different outcomes in central and marginal populations (Obeso, 2002 and references therein; but see also Knops et al., 2007). Shoot growth was negatively related to flower and fruit productions. Plants of central populations produced more flowers and fruits than plants of marginal populations, which could have constrained more the shoot growth in individuals of central populations.

Ecological stress in distribution borders can also result in differential reproduction between central and marginal populations (Hengeveld and Haeck, 1982; Brown, 1984; Lawton, 1993). We found that *D. laureola* individuals of central populations produced more fruits than those on marginal populations, associated to the differences in size and flower production mentioned above. The connection between the number and density of adult individuals in populations and their reproductive output was not, however, supported because central and marginal populations did not differ in size or density of adult plants (see also Samis and Eckert, 2007). The expectation that population size and density of individuals are mainly determined by individual seed production, however, could be unrealistic in some circumstances. Likely there are other factors constraining seedling establishment, such as abundance and quality of available sites for establishment and further postdispersal factors that affect seed survival, germination and seedling survival (Harper, 1997; Clark et al., 2007) that could be more determinant for population size and density of individuals.

Finally, according to the sex-differential plasticity hypothesis (Dorken and Mitchard, 2008), if the hermaphrodites are plastic in their investment on female reproduction they will allocate fewer resources to the seed production under more stressful conditions, and subsequently their relative female fitness should change. Our results, however, indicated that hermaphrodite individuals did not produce less fruits than female individuals in *D. laureola* central or marginal populations, suggesting either the absence of ecological stress in both study regions or a similar response of the two sexes.

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