Plant performance in central and northern peripheral populations of the widespread Plantago coronopus

Jesús Villellas, Johan Ehrlén, Jens M. Olesen, Rita Braza and María B. García

Peripheral populations have long been predicted to show lower vital rates, higher demographic fluctuations, and lower densities than central populations. However, recent research has questioned the existence of clear patterns across species’ ranges. To test these hypotheses, we monitored five central and six northern peripheral populations of the widespread herb Plantago coronopus along the European Atlantic coast during 5 yr. We estimated population density, and calculated main values and temporal variability of four vital rates (survival, individual growth, fecundity and recruitment) in hundreds of plants in permanent plots. Central populations showed higher fecundity, whereas peripheral populations had higher recruitment per reproductive plant, indicating a higher overall reproductive success in the periphery. Central populations showed a marginally significant tendency for higher growth, and there were no differences between range positions in survival. Fecundity and growth were affected by intraspecific competition, and recruitment was affected by precipitation, highlighting the importance of local environmental conditions for population performance. Central and peripheral populations showed no significant differences in temporal variability of vital rates. Finally, density was significantly higher in peripheral than in central populations, in discrepancy with the abundant-centre model. Density was correlated to seedling recruitment, which would counterbalance in peripheral populations the lower fecundity and the tendency for lower growth of established plants. Such compensations among vital rates might be particularly common in widespread plants, and advise against simplistic assumptions of population performance across ranges. The whole species’ life cycle should be considered, since different arrangements of vital rates are expected to maximize fitness in local environments. Our results show also the importance of discerning between geographical periphery and ecological marginality. In a context of climate-induced range shifts, these considerations are crucial for the reliability of niche-models and the management of plant peripheral populations.

Peripheral populations are a popular topic of research in ecology, evolutionary biology and genetics (Eckert et al. 2008, Sexton et al. 2009). These studies provide insight into critical phenomena such as speciation, adaptive radiation, and natural selection (Grant and Antonovics 1978, Holt and Keitt 2005), and there is a strong debate about their evolutionary potential (Lesica and Allendorf 1995), particularly in the context of global warming and its effects on range-margin dynamics (Hampe and Petit 2005). For example, northern populations often constitute leading edges in species’ distribution shifts in the northern hemisphere (Travis and Dytham 2004). Additionally, it is important to evaluate intraspecific variation in population performance across ranges, to improve the reliability of comparative analyses across taxa (Frederiksen et al. 2005) and of niche-based models forecasting biodiversity responses in future ecological scenarios (Lavergne et al. 2010).

The abundant-centre model predicts higher densities in central than in peripheral populations due to more favourable conditions in the core of species’ ranges (Hengeveld and Haekc 1982, Brown 1984). This model has been a tenet in much theoretical and empirical research, e.g. in the central-marginal model, which predicts decreasing genetic diversity towards the range periphery (Brussard 1984). In a demographic context, lower density, greater isolation and lower habitat suitability at the periphery are often referred as the main causes to expect lower values in vital rates, higher variability in abundance or higher vulnerability to stochastic events in peripheral populations (Lawton 1993, Lesica and Allendorf 1995, Vucetich and Waite 2003). However, although some studies have reported an actual decrease in abundance towards range margins (Carey et al. 1995, Curnutt et al. 1996, Jump and Woodward 2003), the abundant-centre theory has received weak support in recent reviews (Sagarin and Gaines 2002, Gaston 2003, Sagarin et al. 2006), which inequitably questions some of the above predictions based on the model (Eckert et al. 2008).
Demographic performance of populations seems to be indeed rather variable across many species’ ranges (Carey et al. 1995, Nantel and Gagnon 1999, García et al. 2000, Kluth and Bruelheide 2005a, Purves 2009), probably reflecting specific local environmental conditions. In addition, populations at the range margin may or may not be considered marginal from an ecological point of view (Grant and Antonovics 1978, Herrera and Bazaga 2008). Although both concepts often overlap, not all ecologically marginal populations are peripherally located, and not all geographically peripheral populations are ecologically marginal (Soule 1973). Peripheral populations may occur in locally favourable conditions (Lennon et al. 2002), such as high water availability, high soil organic matter content or low competition. Thus, there is no reason to expect that individuals in peripheral populations will always under-perform relative to those in central populations. While some studies have found lower fecundity (Garcia et al. 2000, Jump and Woodward 2003), recruitment (Tremblay et al. 2002) or survival (Carey et al. 1995) in peripheral populations, others have reported increased values in different vital rates towards range edges (Kluth and Bruelheide 2005a, Angert 2009, Samis and Eckert 2009). Moreover, many widespread plants are exposed to different environments across their distribution, yet appear to be well adapted to these varied conditions (Joshi et al. 2001). In these cases, different fitness components such as survival, growth, fecundity or recruitment may show different patterns across the range. For example, Doak and Morris (2010) illustrated how life histories of two tundra plants change in the southern limit, where higher individual growth counteracts lower survival and recruitment rates, and Suryan et al. (2009) reported intraspecific trade-offs between survival and fecundity in marine taxa present both in the Atlantic and the Pacific Ocean. Thus, a correct assessment of population performance across species’ distributions should analyze the full spectrum of vital rates and consider variation in local environmental conditions.

Variability in vital rates may also be very important when analyzing demography across species’ ranges (Gould and Nichols 1998, Morris and Doak 2004), as it usually reduces long-term population growth (Gillespie 1977). Populations seem to fluctuate more in peripheral than in central areas (Gaston 2009, Sexton et al. 2009), although most research on this topic has been done with animals (Carnett et al. 1996, Williams et al. 2003). In plants, few range-wide studies have specifically analyzed temporal variation of vital rates. Some of them confirmed the expected higher variability in peripheral areas (Nantel and Gagnon 1999, Gerst et al. 2011), but others did not (Volis et al. 2004, Kluth and Bruelheide 2005a, Angert 2009). However, many of these studies lasted no more than 3 yr, analyzed few populations per species and did not consider the effects of sampling error, which can artificially increase the real variability found in nature (Gould and Nichols 1998). Thus, multi-population approaches with accurate measurements of the variation in vital rates are needed to reach general conclusions about plant dynamics across ranges.

Recent reviews of population performance in central and peripheral areas of species’ distributions (Gaston 2009, Sexton et al. 2009) show that generalizations are difficult to establish, partly because few studies are designed to cover a significant fraction of species spatio-temporal variability. In the present work we analyze variation in vital rates and density in the widespread Plantago coronopus subsp. coronopus, a circum-Mediterranean short-lived herb also present in the coasts of northern Europe. We collected demographic data over 5 yr from ca 11 000 individuals in five central and six northern peripheral populations along the European Atlantic coast. Using this spatially and temporally extensive dataset, we tested the following hypotheses: 1) peripheral populations show lower average vital rates, i.e. survival, individual growth, fecundity and recruitment, than central populations; 2) peripheral populations exhibit higher temporal variability in vital rates; and 3) peripheral populations show lower density. We also analyze the effects of intraspecific competition, precipitation and soil richness, to account for differences in vital rates across the species’ range, and we discuss our results in the context of geographical periphery vs ecological marginality.

**Material and methods**

**Species and populations studied**

Plantago coronopus (Plantaginaceae) is a widespread, short-lived herb that occurs from north Africa and the Iberian Peninsula to SE Asia. It reaches north Europe through a narrow strip along the Atlantic coast (Huloten and Fries 1986; Fig. 1). We have focused on the subspecies coronopus, which is present throughout the whole species’ distribution and differs from other much less widespread subspecies in the morphology of the bracts (Chater and Cartier 1976). Hereafter, we will refer to it as P. coronopus. Individuals have one or a few basal rosettes, and produce several spikes with wind-pollinated flowers. Spontaneous autogamy is possible but very variable among and within populations, and fruit set is very high (between 80 and 100%; Villelles et al. unpubl.).

Plantago coronopus is present in a wide variety of environmental conditions across its range, in terms of climate, soil richness and vegetation cover. In central areas, the species is found in coastal and inland locations, in contrasting habitats such as sand dunes, shurblands or human-disturbed areas, and as annual or short-lived perennial life-forms (Chater and Cartier 1976). In contrast, northern populations are restricted to coastal areas, such as seashore meadows or salt marshes, and present a short-lived perennial life-form. For our study, we chose 11 perennial populations along the Atlantic coast (Fig. 1, Table 1) to minimize habitat differences across the species’ distribution. We spanned more than two thirds of the whole subspecies latitudinal range (Huloten and Fries 1986), encompassing a substantial part of its ecological variation in coastal environments. We monitored five central populations in sand dunes of S and NW Spain, and NW France, along a latitudinal transect of ca 1500 km; we also monitored six peripheral populations in coastal meadows of S Denmark, SW Sweden and N Scotland, along a longitudinal transect of ca 1500 km. All populations contained thousands of individuals.
Table 1. Characterization of central and peripheral populations of *Plantago coronopus* in the study area. See methods for details on the estimation of plant size (cm), population density (ind m$^{-2}$), percentage vegetation cover (by other plant species), SOM (percentage of soil organic matter content), mean annual precipitation (mm) and its coefficient of variation (CV).

<table>
<thead>
<tr>
<th>Position</th>
<th>Population</th>
<th>Location</th>
<th>Years of study</th>
<th>Plant size</th>
<th>Population density</th>
<th>Vegetation cover (%)</th>
<th>SOM (%)</th>
<th>Precipitation (and CV)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central</td>
<td>Tarifa (T)</td>
<td>36°02′N, 5°38′W</td>
<td>5</td>
<td>91.3</td>
<td>10.3 ± 2.9</td>
<td>0–25</td>
<td>0.7</td>
<td>634 (0.18)</td>
</tr>
<tr>
<td></td>
<td>Camposoto (CA)</td>
<td>36°25′N, 6°13′W</td>
<td>4</td>
<td>152.4</td>
<td>13.2 ± 2.8</td>
<td>0–25</td>
<td>0.4</td>
<td>608 (0.25)</td>
</tr>
<tr>
<td></td>
<td>Corrubedo (C)</td>
<td>42°33′N, 9°01′W</td>
<td>5</td>
<td>36.0</td>
<td>212.1 ± 43.5</td>
<td>0–25</td>
<td>1.1</td>
<td>1003 (0.29)</td>
</tr>
<tr>
<td></td>
<td>Traba (TB)</td>
<td>43°11′N, 9°03′W</td>
<td>4</td>
<td>28.2</td>
<td>145.8 ± 39.1</td>
<td>25–50</td>
<td>1.4</td>
<td>842 (0.20)</td>
</tr>
<tr>
<td></td>
<td>Pen Bron (F)</td>
<td>47°18′N, 2°30′W</td>
<td>5</td>
<td>56.2</td>
<td>182.6 ± 112.6</td>
<td>25–50</td>
<td>0.9</td>
<td>680 (0.37)</td>
</tr>
<tr>
<td>Peripheral</td>
<td>Helnaes (DH)</td>
<td>55°8′N, 9°59′E</td>
<td>4</td>
<td>62.9</td>
<td>112.4 ± 20.6</td>
<td>75–100</td>
<td>5.6</td>
<td>757 (0.17)</td>
</tr>
<tr>
<td></td>
<td>Skallingen (DS)</td>
<td>55°29′N, 8°15′E</td>
<td>5</td>
<td>48.9</td>
<td>175.8 ± 71.0</td>
<td>75–100</td>
<td>17.9</td>
<td>906 (0.17)</td>
</tr>
<tr>
<td></td>
<td>Glommen (SG)</td>
<td>56°23′N, 12°21′E</td>
<td>5</td>
<td>25.1</td>
<td>579.5 ± 173.1</td>
<td>75–100</td>
<td>0.8</td>
<td>962 (0.24)</td>
</tr>
<tr>
<td></td>
<td>Torekov (ST)</td>
<td>56°23′N, 12°38′E</td>
<td>5</td>
<td>41.9</td>
<td>268.3 ± 63.7</td>
<td>75–100</td>
<td>6.1</td>
<td>733 (0.21)</td>
</tr>
<tr>
<td></td>
<td>Aberdeen (EA)</td>
<td>57°20′N, 1°55′W</td>
<td>4</td>
<td>40.8</td>
<td>388.4 ± 19.1</td>
<td>75–100</td>
<td>18.1</td>
<td>840 (0.13)</td>
</tr>
<tr>
<td></td>
<td>Skye (ES)</td>
<td>57°30′N, 6°26′W</td>
<td>4</td>
<td>27.1</td>
<td>498.5 ± 17.9</td>
<td>75–100</td>
<td>17.7</td>
<td>2020 (0.16)</td>
</tr>
</tbody>
</table>

Figure 1. Location of central and peripheral populations of *Plantago coronopus* in this study (black dots). The distribution range of the species and the subspecies *coronopus* is highlighted in grey (including the coastal outlines) according to Hultén and Fries (1986). Notice the species is restricted to coastal locations in the northern periphery. See Table 1 for population acronyms.

**Monitoring and data collection**

Field data were collected in the period 2007–2010, except for the population F, which was monitored in the period 2003–2006. However, we verified that the average and the variance of climatic variables at site F were similar between both sampling periods. To calculate vital rates, we monitored all the populations over 4 yr, yielding three annual transitions. An additional fifth year of data was collected in a subset of three central and three peripheral populations (2006 for T, C, DS, SG and ST, and 2007 for F), and used for the analysis of temporal variability in vital rates (Table 1; see below). In the first year of study for each population, we established randomly-distributed permanent plots that...
varied in number (3 to 10) and size (0.25 to 5 m²) depending on local plant density. Annual censuses were done during fruit maturation and before seed dispersal. Due to regional differences in phenology, central populations were monitored in July and peripheral populations in August. In each census, we recorded between 100 and 400 individuals older than 1-yr seedlings within the plots, which we relocated the following year with the aid of tags and hand-drawn maps showing the position of plants. For each individual, we recorded life stage as vegetative (V) or reproductive (R), the number of leaves and inflorescences, and the length of an average leaf and an average inflorescence. We also counted and mapped new seedlings in each census.

Growth, fecundity and survival rates of *P. coronopus* were then calculated annually for all non-seedling individuals monitored in the plots. We estimated plant growth rate as the ratio between plant size in a given year and that in the previous year. Plant size was defined as number of leaves × length of an average leaf. We estimated fecundity in reproductive individuals as number of inflorescences × length of an average inflorescence × number of seeds per unit of inflorescence length (calculated with a regression equation for each population). We also calculated the total number of reproductive years and the lifetime fecundity (total seed production over the lifespan) of those reproductive individuals that were monitored for their entire lives. Recruitment was estimated within each plot as the number of new seedlings in a given year divided by the number of reproductive individuals present in the previous year (the seed bank contribution is negligible in this species).

Plant density (D) was estimated annually from linear transects (Strong 1966) using the equation $D = \frac{L}{d}$, where $L$ is total transect length (it varied from 10 to 200 m depending on local density), and $d$ is the diameter perpendicular to the transect of non-seedling plants intercepting the transect.

Environmental factors were estimated as follows. In all populations, we collected 10 cm deep soil cores the first year, to estimate soil organic matter content from the organic carbon (Heanes 1984). We obtained annual precipitation data for the sampling period from public databases: Spanish National Meteorological Agency (T and CA); MeteoGalicia (C and TB); MeteoFrance (F); Danish Meteorological Inst. (SG and ST); and Met Office (EA and ES). For each population, we also calculated the mean annual precipitation and the coefficient of variation (CV) for the sampling period. Intraspecific competition was estimated the first year scanning the maps with the position of each plant within plots, and measuring Voronoi polygons with Arc-GIS (ver. 9.3). These polygons contain the area closer to each plant than to any other conspecific, and thus represent individual resource availability (thereafter ‘resource area’). Resource area mainly allowed us to analyze the effects of intraspecific competition on per capita vital rates but, averaged across individuals, constituted an additional estimate of population density. We also measured the abundance of other plant species as percentage of vegetation cover in plots, by using the categories 0–25, 25–50, 50–75 and 75–100%.

### Statistical analyses

Statistical analyses were made with SPSS (ver. 17.0) unless specified otherwise. To test for differences in mean vital rates between central and peripheral populations, we used linear mixed models (LMM) for continuous variables, i.e. growth, fecundity and recruitment (log-transformed), and a generalized linear mixed model (GLMM; GLIMMIX procedure, SAS ver. 9.1) for the binomial variable, i.e. survival (Table 2). The central or peripheral position of populations was a fixed factor, and year and population (nested within position) were random factors. The factor plot was not included in the models because according to preliminary analyses it did not affect the significance of position and population. Likewise, interactions between position and year were removed from the analyses when their effect was not significant. Life stage and plant size (log-transformed) were also included in models as a fixed factor and a covariate, respectively. The significance of random factors in the GLMM was evaluated by testing whether $z$-values (the covariance parameter estimates divided by the standard errors) significantly differed from zero (Juenger and Bergelson 2000). Additionally, we tested for differences between range positions in lifetime fecundity and in mean plant size with LMMs, including plant stage as a fixed factor and year as a random factor in the analysis of plant size.

To analyze the role of environmental factors in the differences in vital rates between range positions (Results), we

### Table 2. Comparison of mean vital rates between central and peripheral populations of *Plantago coronopus*. Results from analyses (linear mixed models for fecundity, recruitment and growth, and generalized linear mixed model for survival) and average values per position (± SE).

<table>
<thead>
<tr>
<th>Effects in analyses</th>
<th>F</th>
<th>p</th>
<th>F</th>
<th>p</th>
<th>F</th>
<th>p</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Fecundity</strong></td>
<td></td>
<td></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Position</td>
<td>13.60,17</td>
<td>0.007</td>
<td>5.07,19</td>
<td>0.050</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Population</td>
<td>39.60,3</td>
<td>&lt;0.001</td>
<td>4.69,0,001</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year</td>
<td>1.83,3</td>
<td>0.353</td>
<td>7.86,0,001</td>
<td>0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Recruitment</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Position × year</td>
<td>38.29,2</td>
<td>&lt;0.001</td>
<td>4.97,2</td>
<td>0.007</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Plant size</td>
<td>1685.97,1</td>
<td>&lt;0.001</td>
<td>388.17,1,4099</td>
<td>&lt;0.001</td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td>Life stage</td>
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<td></td>
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<tr>
<td><strong>Growth</strong></td>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Central</td>
<td>1089.5 ± 200.0</td>
<td>2.4 ± 0.7</td>
<td>1.7 ± 0.1</td>
<td>42.7 ± 5.1</td>
<td></td>
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</tr>
<tr>
<td>Peripheral</td>
<td>203.1 ± 33.0</td>
<td>6.6 ± 1.8</td>
<td>1.3 ± 0.1</td>
<td>53.7 ± 5.7</td>
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<td></td>
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</tr>
</tbody>
</table>

*Values correspond to covariance parameter estimates ± SE, instead of F statistic.
tested with a set independent analyses (LMMs) the effect of resource area (as an estimate of intraspecific competition), annual precipitation and soil organic matter on vital rates, and if the effect of position remained significant after controlling for those explanatory variables. First, we analyzed the effect of resource area, including population as a random factor and plant size as a covariate, because of its potential influence on resource area. Second, we tested the effect of annual precipitation, using annual population averages of vital rates and including year as a random factor. Third, the effect of soil organic matter was tested on average population vital rates across all years (here we used a linear model instead of a LMM). In addition, we tested for differences in resource area and in annual precipitation between central and peripheral positions with LMMs (including population as a random factor), and for differences in soil organic matter and in CV in precipitation with t tests.

Temporal variability in vital rates was analyzed in a subset of three central (T, C, F) and three peripheral (DS, SG, ST) populations monitored during 5 yr (four transitions). To accurately estimate this variability, we firstly accounted for sampling error: for each vital rate, we fitted a model with an intercept and a random factor of year, and we obtained the corrected annual population averages from the coefficients of the random factor (Altwegg et al. 2007, Morris et al. 2011). The analyses applied for such corrections were LMMs for fecundity, growth and recruitment and a GLMM for survival (lme and lmer procedures, respectively, R Development Core Team 2010). Variability in vital rates was then estimated from the CV of the corrected annual values. Survival has a binomial distribution with an inherent limit in variance, so we estimated its relative CV instead: CV/CV\text{max}. We calculated CV\text{max} from the square root of the ratio between (1−p) and p, where p is mean survival rate (Morris and Doak 2004). For each vital rate we tested for differences between central and peripheral populations in variability (CV) with t tests. We also analyzed overall differences in variability between range positions considering all vital rates together (except for survival), by performing a LMM with position as a fixed factor and vital rate as a random factor.

We finally compared density between central and peripheral populations with a LMM. The position of populations was included as a fixed factor and population as a random factor. We also tested with a linear model whether density was correlated to recruitment, using average population values across years, and including position as a fixed factor.

Results

Mean vital rates in central and peripheral populations

Plants had significantly higher fecundity in central than in peripheral populations of \textit{P. coronopus} (Table 2, Fig. 2). There were no differences between range positions, however, in the average number of reproductive years per individual: between 1.12 (population F) and 1.40 (T) in central populations, and between 1.14 (DH) and 1.44 (ST) in peripheral ones. The analysis of lifetime fecundity confirmed a higher total seed production in central areas (F\text{1.2617} = 35.67, Figure 2. Annual averages of vital rates in central (dark bars) and peripheral (light bars) populations of \textit{Plantago coronopus} (± SE). Vital rates are (a) fecundity, measured as number of seeds per year and reproductive plant; (b) recruitment, measured as number of seedlings in a given year divided by number of reproductive plants in the previous year; (c) plant growth, measured as size in a given year divided by size in the previous year; and (d) survival, measured as percentage of surviving individuals. Notice the logarithmic scale of the vertical axis in (a) and (b).
Effects of competition and environmental factors on vital rates

Plants in central populations had a significantly larger resource area ($F_{1,9} = 30.60, p < 0.001$) and lower soil organic matter content ($t_{9} = -2.89, p = 0.018$) than in peripheral populations. Precipitation was lower on average in central locations (754 mm) than in peripheral ones (1036 mm), although not significantly ($F_{1,9} = 1.50, p = 0.252$), and variability in precipitation was marginally higher in central populations ($t_{4} = 2.21, p = 0.055$). In addition, vegetation cover was consistently higher in peripheral populations (Table 1). Resource area was positively and significantly correlated to growth ($F_{1} = 4.81, p = 0.030$). Since the effect of position on growth found in previous analyses was not significant after controlling for resource area ($F_{1} = 0.08, p = 0.784$), this factor explained differences in growth between central and peripheral populations. Resource area was also positively and significantly correlated to fecundity ($F_{1} = 68.01, p < 0.001$), but the effect of position on fecundity remained significant after controlling for resource area ($F_{1} = 12.90, p < 0.001$). Precipitation had no significant effect in fecundity ($F_{1,28} = 1.18, p = 0.287$) or growth ($F_{1,28} = 0.34, p = 0.563$), but did have a significant effect in recruitment ($F_{1,28} = 8.32, p = 0.007$). Since the effect of position was not significant after controlling for precipitation ($F_{1,28} = 2.37, p = 0.135$), this environmental variable explained differences in recruitment between central and peripheral populations. Finally, soil organic matter had no significant effect in mean values of fecundity ($F_{1} = 0.03, p = 0.879$), recruitment ($F_{1} = 0.17, p = 0.691$) or growth ($F_{1} = 0.06, p = 0.815$). The effect of environmental variables on survival was not analyzed because central and peripheral populations did not differ in this vital rate.

Temporal variability in vital rates

Considering vital rates independently, central populations showed on average higher temporal variability in fecundity and growth, and peripheral populations were more variable on average in recruitment and survival (Fig. 3), but these differences were not significant (fecundity: $t_{4} = 0.71, p = 0.519$; growth: $t_{4} = 0.96, p = 0.391$; recruitment: $t_{4} = -1.68, p = 0.168$; survival: $t_{4} = -1.20, p = 0.296$). Central and peripheral populations showed no significant differences in overall variability when three of the vital rates (fecundity, growth and recruitment) were analyzed together ($F_{1,2} = 0.28, p = 0.647$).

Density in central and peripheral populations

Peripheral populations showed significantly higher densities ($F_{1,9} = 7.73, p = 0.021$) than central populations. Density was significantly correlated to recruitment ($F_{1} = 7.19, p = 0.028$). Since the effect of position was no longer significant after including recruitment in the model ($F_{1} = 1.72, p = 0.226$), this factor explained differences in density between range positions.

Discussion

Peripheral populations have long been predicted to show lower vital rates, higher demographic fluctuations, and lower densities than central populations (Hengeveld and Haecck 1982, Brown 1984, Lawton 1993, Vucetich and Waite 2003). In our comparative analysis of _P. coronopus_, we found higher fecundity and a tendency for higher growth in central populations. However, northern peripheral populations showed higher recruitment, resulting in higher population density, and exhibited similar temporal variability in vital rates. Thus, our findings diverge from classical predictions, in agreement with other recent studies (Sagarin and Gaines 2002, Angert 2009, Doak and Morris 2010). Differences in demographic performance between central and peripheral populations of this widespread herb seem to be explained by local precipitation and intraspecific competition. We now discuss the main results.

Mean vital rates in central and peripheral populations

Peripheral populations of _P. coronopus_ showed a much lower fecundity than central ones. This result agrees with other studies reporting reduced seed production or seed quality at the species' range margin (Pigott and Huntley 1981, García et al. 2000, Jump and Woodward 2003), although the...
pattern does not seem to be general (Kluth and Bruelheide 2005a, Yakimowski and Eckert 2007). Fecundity was positively correlated with size in _P. coronopus_, a common pattern in plants (Hendriks and Mulder 2008). However, we found no significant differences in plant size between range positions. Fecundity was also negatively affected by intraspecific competition, attending to the significant correlation between seed production and resource area (Waite and Hutchings 1982), and this effect might have been further increased in peripheral locations by a higher vegetation cover. Thus, to some extent, competition for resources seems to limit seed production in northern peripheral populations of _P. coronopus_, although only removal experiments would confirm such hypothesis. However, differences in fecundity between central and peripheral populations seem to be also determined by factors not considered in this study, since the effect of position remained significant after controlling for plant size and intraspecific competition.

In contrast to fecundity, recruitment rate was higher in peripheral populations, in agreement with the pattern reported by Samis and Eckert (2009) for another coastal plant (but see Tremblay et al. 2002, Castro et al. 2004). Recruitment was estimated in our study as the presence of new seedlings in a given year relative to the number of reproductive individuals in the previous year. Hence, this measure includes three fitness components, i.e. fecundity, germination and early survival, which estimate overall reproductive success better than seed production alone. It is thus noteworthy that although fecundity was higher in central populations, overall reproductive success was higher in the periphery. Similarly, diverging patterns in seed production and germination rates have been found between central and peripheral populations of other annual and perennial species (Kluth and Bruelheide 2005a, Yakimowski and Eckert 2007). Altogether, these results highlight the necessity to consider different vital rates when analyzing population performance, and particularly warn against assessing reproductive success from fecundity data alone. The lower recruitment in central populations of _P. coronopus_ might respond to their occurrence in sand dunes, a harsh habitat with unstable soils where seedling establishment is extremely hazardous (Crawford 2008). In contrast, the higher and less variable precipitation in the coastal meadows of northern locations offers more favourable conditions for recruitment in terms of water availability (Castro et al. 2004).

Survival and growth rates did not differ between central and peripheral populations of _P. coronopus_. However, there was a marginal tendency in central populations to present higher growth, which seems to be correlated to a lower intraspecific competition in their locations. The few studies carried out on survival and individual growth across other plant species' ranges are also inconclusive: some reported reduced survival rates in peripheral populations (Carey et al. 1995), while others did not find a consistent pattern (Angert 2009, Gerst et al. 2011). Regarding growth, Jump et al. (2006) reported lower values in marginal populations in _Fagus sylvatica_, whereas Purves (2009) found diverging results between northern and southern edges in an ample survey of trees in US, although spatial scales were not comparable in both studies.

Our study showed thus important differences in vital rates between central and peripheral populations of _P. coronopus_. However, beyond the central-peripheral comparison, significant differences among populations were also detected within regions for all vital rates (Fig. 2), which highlights the interest of analyzing demographic patterns of widespread species at different geographical scales. Some patterns found in vital rates across the species' range were linked to precipitation or intraspecific competition. Local environmental conditions, therefore, may have a crucial role in population performance, not only when comparing different parts of the distribution area, but also at lower scales. Indeed, large variation in local conditions has been found within central and peripheral regions of _P. coronopus_, e.g. in precipitation regime (Table 1).

**Temporal variability in vital rates**

Peripheral populations of _P. coronopus_ showed a higher average temporal variability in recruitment and survival than central ones, but fecundity and growth were on average more variable in central locations, and more importantly, none of these differences were significant. Although the analyses of single vital rates were not completely reliable due to low sample sizes (six populations), the opposite tendencies in fecundity and growth with respect to recruitment and survival revealed no clear patterns in temporal variability between range positions, in contrast with classical predictions. This was confirmed by the overall analysis of variability, which did not show significant differences between range positions either.

The lack of pattern in _P. coronopus_ is not surprising, considering the discrepancy among the few related studies carried out with other plant species. On the one hand, fecundity and survival were more variable in peripheral than in central populations in several annual taxa (Gerst et al. 2011), and higher fluctuations were also reported in mortality for peripheral populations of two perennial species (Nantel and Gagnon 1999). In contrast, survival was more variable in marginal populations in the perennial _Mimulus lewisii_ but not in its congener _M. cardinalis_ (Angert 2009), fecundity and survival showed higher variability in the range centre of the annual _Hornungia petraea_ (Kluth and Bruelheide 2005a), and there were no differences between range positions in variation of population growth rates in the annual _Hordeum spontaneum_ (Volis et al. 2004). Thus, besides the relative scarcity of studies, there seems to be a mismatch between classical predictions and the heterogeneous conclusions provided by empirical research, which hinders the establishment of general patterns in plant performance across species' distributions.

**Density in central and peripheral populations**

Our study of _P. coronopus_ does not support the abundant-centre model, as northern peripheral populations showed higher densities than central populations. The higher average values of resource area in central locations indicated a sparser distribution of plants in these populations, and...
confirmed the differences found in density. The widely accepted idea that species are more abundant in the centre than in the edge of their range has been indeed questioned by recent comprehensive reviews (Sagarin and Gaines 2002, Gaston 2003, Sagarin et al. 2006), and our results confirm that the abundant-centre model can no longer be assumed without previous testing. Differences in vital rates between central and peripheral populations are expected to affect density (Kluth and Bruelheide 2005b), and recruitment seems to be the most determinant factor in the case of *P. coronopus*, attending to its positive relationship with density. The higher establishment of seedlings in peripheral populations, due to higher germination and/or early survival rates, would maintain the higher density of older individuals, compensating the lower fecundity and growth in these locations. Our result highlights the importance of the early life stages of plants for population performance in *P. coronopus*, as corresponds for a short-lived species (Silvertown et al. 1996, Picó et al. 2003).

Geographical periphery vs ecological marginality

Peripheral populations are assumed to occur at the extremes of species’ niches, where less favourable conditions are expected. *Plantago coronopus*, e.g. occurs in different habitats in the central part of its range while it is rather restricted to coastal meadows in the northern periphery, indicating that some environmental factors are limiting its spreading northwards. However, the distinction between geographical periphery and ecological marginality is crucial, as these concepts not always overlap in real populations (Soulé 1973, Grant and Antonovics 1978, Herrera and Bazzaga 2008). The higher fecundity and growth in central populations of *P. coronopus* suggest more favourable conditions for the development of established plants in dunes, in part due to a positive effect of resource area. This seems to be true for at least three of the five central populations (T, CA, F), which present as well larger plants than most peripheral populations (Table 1). However, northern peripheral locations appear to be more suitable for seedling recruitment, due to higher precipitation. Additionally, northern populations show higher densities of established plants than central populations and similar temporal variability in vital rates, which contrasts with some characteristics ascribed to ecologically marginal populations (Soulé 1973). *Plantago coronopus* is indeed successfully competing with other plant species of similar life histories and resource requirements in the northern coastal meadows, while it behaves as a poor competitor in sand dunes of central areas. Thus, despite a restriction of northern populations of *P. coronopus* to coastal environments, our study shows that habitats may be more favourable at the range periphery, at least for some vital rates (Sexton et al. 2009), and highlights the importance of carefully distinguishing between geographical periphery and ecological marginality when forecasting population performance (but see Gerst et al. 2011).

Final remarks

Theoretical studies often simplify comparisons between central and peripheral populations. However, variation in population performance across species’ ranges may be complex, and the best way to understand such intraspecific variation is to carry out large-scale studies of different life cycle components (Sexton et al. 2009, Gerst et al. 2011). The life cycle might actually be regarded as a plastic phenotypic trait (Caswell 1983) that characterizes species in a particular combination of environmental variables, and which may change across ranges. In our study, the contrasting patterns of recruitment, fecundity and growth suggest compensatory changes in vital rates across the range of *P. coronopus*, to adjust the life cycle of populations to their local conditions (Suryan et al. 2009, Doak and Morris 2010). Such variation in the arrangement of vital rates would have allowed this plant to successfully adapt to contrasting environments over large distribution areas.

It is difficult to evaluate to what extent the patterns shown by *P. coronopus* are common among other widespread taxa, but our results contribute to understand that 1) simplistic considerations, such as positive vs negative diagnosis of the status of populations based only on their geographical position, may fail because peripheral populations might not be located in ecologically marginal conditions; 2) assessments of population performance including the full set of vital rates are much more reliable, since low values in some rates can be counterbalanced by high values in others; and 3) the reliability of niche-models predicting future species’ distributions under global warming could be greatly improved by considering intraspecific variation in population performance. The management of peripheral populations will significantly gain from studies that show the importance and arrangement of different fitness components in species, and their variability over time and across ranges.

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References


Tremblay, M. F. et al. 2002. The potential effects of sexual repro-duction and seedling recruitment on the maintenance of red
maple (Acer rubrum L.) populations at the northern limit of the species range. – J. Biogeogr. 29: 365–373.


