

Central and peripheral *Hornungia petraea* populations: patterns and dynamics

CHRISTIAN KLUTH and HELGE BRUELHEIDE

Institute of Geobotany and Botanical Garden, Martin Luther University Halle, Am Kirchtor 1, 06108 Halle, Germany

Summary

1 More or less continuous distributions tend to become fragmented towards species' distribution limits. Peripheral or isolated populations of a species are predicted to have lower population sizes and densities than central populations, as a result of environmental and/or genetic stress. Population densities at the periphery may be reduced by decreased reproduction or higher interannual variation in reproduction. In particular, fecundity and survival are likely to be reduced by less favourable growing conditions.

2 We compared populations of the annual species *Hornungia petraea* (Brassicaceae) in two contrasting regions of the species' range and at the population scale within regions. Ten populations in Italy (central to the species range) and 10 German populations (peripheral) were monitored for three growing periods from spring 1999 to spring 2001.

3 All life-cycle stages, adult plant density, seed production and pre- and post-dispersal seed bank density were studied in a nested sampling design and variation in various demographic factors was attributed to the effects of the two countries, of populations nested within country and to temporal effects.

4 Peripheral populations had higher densities than populations in the centre of the species distribution, both as adult plants and in the seed bank.

5 Fecundity was strongly influenced by temporal effects, but only affected to a minor degree by the study region. High interannual variation in fecundity was not reflected in high interannual variation of either adult plant density in spring or of the seed bank. Significant regional differences were, however, found in seasonal seed bank dynamics, which were more pronounced in peripheral German populations than in central Italian populations.

6 We conclude that seasonal seed bank dynamics are a key factor in explaining differences in *H. petraea* density patterns, particularly in central populations, where fewer seeds are incorporated into the seed bank.

Key-words: 'abundant centre' distribution, biogeography, central-marginal model, demography, evolutionary ecology, macroecology, nested repeated measures design, population dynamics, scale, spatio-temporal variation

Journal of Ecology (2005) **93**, 584–595

doi: 10.1111/j.1365-2745.2005.00997.x

Introduction

A commonly observed biogeographical pattern is the disintegration of more or less continuous distributions of species into fragmented populations towards the species' distribution limit (e.g. Walter & Straka 1970; Brown & Lomolino 1998; Wilson *et al.* 2002). Peripheral or isolated populations of a species are predicted to have lower population sizes and densities than central populations (e.g. Hengeveld & Haeck 1982; Brown

1984) and the explanation provided by the so-called central-marginal model (Brussard 1984; Siikamäki & Lammi 1998) has both environmental and genetic components.

Lower population sizes in geographically peripheral populations may be the result of the less favourable environmental conditions experienced by individuals in populations at a species' distribution limit (Brussard 1984). Such conditions are presumed to affect population densities either directly, via lower fecundity or recruitment (e.g. Pigott & Huntley 1981; García *et al.* 2000; Dorken & Eckert 2001; Jump & Woodward

2003), or indirectly as a result of higher year-to-year variation in fecundity or recruitment, resulting in greater interannual variation in population size (Brussard 1984; Nantel & Gagnon 1999). In general, comparisons of population dynamics at broad scales are rare for plant populations, with Nantel & Gagnon (1999) being, to our knowledge, the only comparison of dynamics of central and peripheral plant populations. For two clonal species, the perennial herb *Helianthus divaricatus* and the shrub *Rhus aromatica*, Nantel & Gagnon (1999) reported a larger interannual variation of vital rates and intrinsic growth rates in two populations at the northern limit of the species' distribution range (southern Quebec) than in two more central (Ontario) populations of each species.

The genetic component of the central-marginal model assumes that populations at a species' distribution limit have lower densities, which are associated with lower genetic variance than in central populations (Wilson *et al.* 1991). The hypothesis of low marginal genetic variance has been intensively studied recently, with both supporting (e.g. Lammi *et al.* 1999; McCauley & Ballard 2002; Tyler 2002) and conflicting (e.g. Wilson *et al.* 1991; Kaya & Temerit 1994; Safriel *et al.* 1994) results; population density has, however, rarely been evaluated.

Large demographic fluctuations may reduce the effective population size, leading to population bottlenecks. These bottlenecks induce loss of genetic variance and reduce individual fitness (Hartl & Clark 1997). The presumably higher risk of extinction in peripheral populations and the potential adaptation of marginal populations to different environmental conditions have both acted to focus the attention of conservation biologists on marginal populations (e.g. Haeck & Hengeveld 1981; Hoffmann & Blows 1994; Lesica & Allendorf 1995).

The negative genetic consequences expected from large demographic fluctuations could be buffered by seed banks, which may, in turn, conserve genetic variance (Baker 1989; McCue & Holtsford 1998) and influence effective population size (Nunney 2002). In a predictable environment (as is presumed to occur at the centre of a species' distribution), seeds should germinate as soon as conditions are favourable (Rees 1994), and lower predictability (at the periphery) would be expected to favour greater allocation to the seed bank, so that seeds remain available until the next favourable season (Rees 1994). Whether banker or non-banker morphs are favoured by selection depends on life-history traits other than the fraction of seeds allocated to the seed bank, such as fecundity (Aikio *et al.* 2002). Although seed banks play an important role in population dynamics (particularly in annuals, where the long-term persistence of populations completely depends on seed banks; Baskin & Baskin 2001; Aikio *et al.* 2002) and in evolutionary theory (e.g. Silvertown & Lovett Doust 1993; Baskin & Baskin 2001; Aikio *et al.* 2002), they have, to our knowledge, never been integrated into the central-marginal model.

Irrespective of the mechanism underlying the central-marginal model, there is limited evidence for its expected biogeographical pattern (termed the 'abundant centre' distribution). There are very few studies that directly compare densities in central and peripheral populations of plants. The review by Sagarin & Gaines (2002) mentions only two empirical studies on plant species (*Lactuca serriola*, Carter & Prince 1985; Prince *et al.* 1985; *Vulpia ciliata* ssp. *ambigua*, Carey *et al.* 1995). Moreover, support (Carey *et al.* 1995) or rejection (Carter & Prince 1985; Prince *et al.* 1985) of the 'abundant centre' hypothesis was not based on statistical tests (Sagarin & Gaines 2002).

In addition to the position of a population within its geographical range, densities or life-history traits may vary, both within and between populations, in such a way that the population effects are superimposed on the range position effects.

We directly compare local populations of the annual species *Hornungia petraea* Rchb. (L.) (Brassicaceae) in two contrasting regions within the species' range, and also at the scale of populations within the two study regions. Ten populations in each study region were monitored for 3 years. We hypothesized that Italian populations (representing the centre of the species' range) would show higher densities than German populations (representing the periphery) for both adult plant and seed bank populations. We expected demographic factors, in particular fecundity of individuals, dynamics of fecundity and annual seed bank dynamics, to contribute to these patterns. A multifactorial study design with nested factors, repeated over 3 years, was set up to partition density effects into effects of country, population and time. This study employs a statistical approach by combining two hierarchical levels and repeated measurements in one single statistical model.

Methods

STUDY SPECIES

Hornungia petraea Rchb. (L.) is a winter annual of up to 15 cm in height, with the fruit generally bearing four seeds. It germinates in autumn and overwinters as a leafy rosette. Flowering occurs in early spring and seeds are released in early summer. The species has a persistent seed bank (*sensu* Thompson & Grime 1979), implying that at least some seeds in the soil were produced more than 1 year ago.

H. petraea has a sub-Mediterranean-sub-Atlantic distribution. Its distribution is more or less continuous in the Mediterranean region but becomes fragmented towards the distribution limit (Jalas & Suominen 1996). Comparing older distribution maps (Meusel *et al.* 1965; Meusel & Buhl 1968) with recent surveys (Haeupler & Schönfelder 1989; Benkert *et al.* 1996; Jalas & Suominen 1996; Korsch *et al.* 2002), the range does not appear to change in extent. The species is generally not anthropochorous, except in Oldenburg,

Northern Germany, where it occurred on railway gravel (Herrmann 1994), and seeds are usually ant-dispersed (Detrain & Pasteels 2000), with the species having no apparent adaptations to long-distance dispersal.

H. petraea habitats are open calcareous grasslands often dominated by therophytes. Sociologically, this therophyte vegetation belongs to the Alysso-Sedion (Oberdorfer 1978), which is a priority habitat type in the EU (Natura 2000 Code 6110; European Council 1992). In addition, *H. petraea* is a rare species and is considered endangered in Germany (category 2 in the German Red Data Book; Korneck *et al.* 1996). In contrast, in central Italy the species is considered common (L. Gubellini & A. Brilli-Cattarini, personal communication) and occurs in a wider variety of habitats than at its distribution limit in Germany (Kluth & Bruelheide 2004).

STUDY SITES

Italian study sites are considered representative of central populations of *H. petraea*, whereas populations in central Germany are situated within the species' largest exclave at its continental north-eastern distribution limit. Transects of approximately 100 km in length were set up along the Apennine Mountains in central Italy (Marche and Umbria regions) and in central Germany (Thuringia and Saxony-Anhalt). Each transect consisted of 10 plots, each plot comprising an entire *H. petraea* population. In Germany, the complete west-east extent of the exclave was covered, resulting in a very steep climatic gradient although the altitude of plots only ranged from 170 to 275 m a.s.l. Italian plots were selected with the aim of obtaining interplot distances comparable with those of the German plots and altitude ranged from 280 to 1560 m a.s.l. (see Kluth & Bruelheide 2004 for details).

PLOT DESIGN AND FIELD SAMPLING

A major difficulty in sampling populations is the different shape and size of the areas they cover. In order to be able to study different populations in a comparable manner, we developed a special sampling design (Kluth & Bruelheide 2004). We first arbitrarily defined the centre of each population and measured the distance from the centre to the population boundary in eight compass directions at 45° intervals. Population boundaries were defined by the absence of *H. petraea* plants for a distance of at least 5 m and were usually accompanied by a clear change in vegetation composition. The area covered by the population was calculated on the basis of the resulting octagon. A grid adapted to the specific area covered by each population was assigned such that each cell comprised 1% of the population surface area. Subplots (30 × 30 cm) were established in 10 randomly selected grid cells per population and marked permanently for sampling. There were 100 subplots in Italy but only 90 in Germany, where one plot was destroyed several times by vandalism.

Field sampling was conducted from March 1999 to May 2001, with each subplot surveyed 13 times. Only the spring census data (adult plants in their reproductive stage) are considered here, i.e. 570 field counts of density across 190 subplots. At the beginning of each growing period, i.e. autumn, 10 *H. petraea* individuals per population were selected randomly and permanently marked. If subplots contained *H. petraea* plants, individuals were chosen from the subplots, otherwise the closest individual was selected and marked. Fruits and residual septa were counted. To obtain the seed number, and thus fecundity of individuals, the maximum number of fruits and septa recorded in each growing period was multiplied by 4. As population densities were very low in spring 2000 in the Italian populations only 564 records of fecundity data were collected (one, one and four records, respectively, missing from plots I3, I9 and I10 for this year).

Seed bank samples were taken before (spring) and after (summer) seed dispersal in 1999 and 2000 with an auger of 5.5 cm diameter (corresponding to a sampled surface area of 23.8 cm²) and a depth of 4 cm. At each sampling date, one seed bank sample was taken randomly (from one of eight pre-defined positions) adjacent to but outside of each subplot. Thick snow cover at the Italian plot I4 resulted in a much-delayed phenology, and fruits still had not released seeds by the beginning of June 1999. For this plot, the June seed bank samples and count data were considered as spring data and there was therefore no post-dispersal seed bank data for this population. A total of 720 seed bank samples were collected.

SEED BANK ANALYSIS

The seed bank size was analysed by the seedling emergence method in a glasshouse (Thompson *et al.* 1997). The seed bank samples were stored dry, in the dark at room temperature until the following autumn. They were then sieved and distributed into plastic dishes on a bed of sterilized sand. The plastic dishes were arranged randomly in blocks in a glasshouse. Each block consisted of 40 plastic dishes, with one randomly chosen pre-dispersal (spring) and one post-dispersal (summer) soil seed bank sample from each of the 10 German and Italian populations; the soil was kept permanently moist. The number of *H. petraea* seedlings that emerged was counted three times at 4-week intervals. After an observation period of 3 months, the 1999 seed bank samples were dried and kept in the dark for 5 months and then watered again. As very few *H. petraea* plants germinated in this second period, seed bank sizes were recorded as the number of seeds germinated in the first assessment. Seed bank samples collected in 2000 were not watered a second time.

TEST STATISTICS

The data were analysed using a repeated measures analysis of variance for nested designs, in which the single

counts of individuals and fecundity of individuals, in subplots, or germination events in seed bank samples, were included. Census data were first tested for normality (proc univariate, Shapiro-Wilk-statistics, SAS Institute 2000a). As data were not normally distributed at $\alpha = 0.05$, even after log-transformation, we used non-parametric statistics based on rank transformation (proc rank, SAS Institute 2000a; for appropriateness of rank transformation see Brunner & Puri 2001).

Using these data, analysis of variance was performed (proc glm, SAS Institute 2000b) with subplot as the temporally repeated subject for the class variables country and population, nested within country (referred to as Population (Coun) in ANOVA tables). First, between-subjects effects were tested (part a of ANOVA tables). Secondly, a univariate test for within-subjects effects assessed the repeated factor and its interactions with country and population with, if necessary, the Greenhouse-Geisser adjustment (Littell *et al.* 1996) (part b). If interactions involving the repeated factor were significant, univariate tests of hypotheses for between-subjects effects of the repeated factor were performed separately (part c). For spring adult plant population density, and for repeated fecundity measures, additional ANOVAs were performed separately for each country (part d in ANOVA tables). In cases of multiple repetitions, i.e. more than twice, an analysis of variance was performed for each contrast between temporal repetitions. If either the population effect (in the between-subjects test) or the interaction effect of population with the repeated factor was significant, a post-hoc test (with Tukey adjustment) was performed for all single pairwise comparisons among the 19 plots. Population dynamics were analysed by means of a contrasts analysis between years for each population. Significant contrasts between years indicate high interannual variation in population density. In order to partition the explained variance between the different effects in the model, R^2 values are given in ANOVA tables both for the total model (R_t^2) and for the partial model (R_p^2).

Results

ADULT PLANT POPULATION DENSITY

Figure 1 shows spring population densities of all 19 studied populations for three successive years and Table 1 presents the results of repeated measures ANOVA on the rank transformed data. Between-subjects effects explained 58% of the variance in the total model. Both country and population had a significant influence on the density of adult *H. petraea* populations (Table 1a), with country explaining 58% of the between-subjects variance in the partial model, due to higher densities in the peripheral (German) populations than in the central populations in Italy. The median number of *H. petraea* individuals in the three successive years was 27 plants per subplot ($n = 270$) in the German populations and one individual per sub-

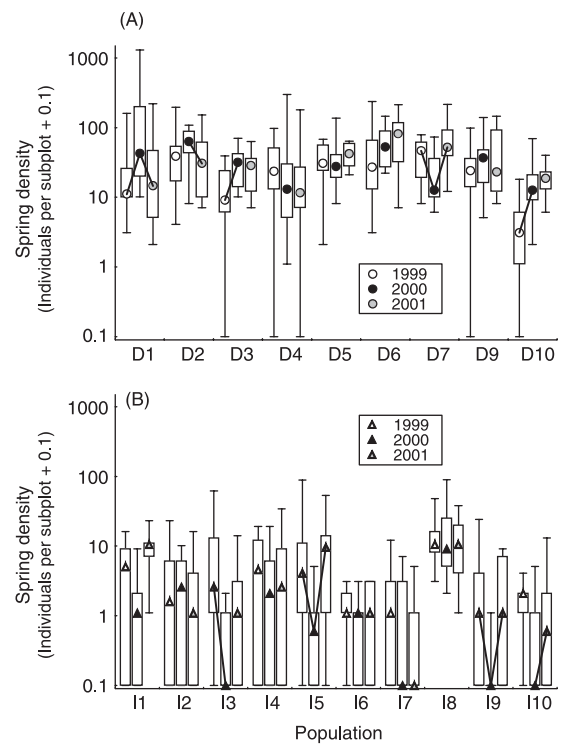


Fig. 1 Spring population density of adult *Hornungia petraea* plants in three successive years based on subplots of 30 × 30 cm. (A) Peripheral German (D) and (B) central Italian (I) populations. Box-Whisker plots with median, 25 and 75% quantiles and extremes. Lines connect median values of density if the change between successive years is significant (i.e. a significant contrast).

plot ($n = 300$) in the Italian populations. On the plot level, the median values of the mean population densities were 47 plants per m^2 ($n = 27$) and 3.4 plants per m^2 ($n = 30$) for German and Italian populations, respectively. The factor population was less important than that of country, explaining 13% of the between-subjects variance. Considering each country separately, the population effect explained most of the variance within each country (Table 1d), 15% of the variance in the total models in Germany and 23% within Italy. The variance explained by year and the interaction between population and year was similar for both countries (Table 1d). Although the univariate test for within-subjects effects revealed significant effects for all factors (Table 1b), this part of the model explained only 6% of the variance of the total model. The factor year explained only 2% of the variance in the within-subjects model, where the most important effect was the interaction between year and population, which explained 22% of the variance (Table 1b). An additional 10% of the variance in the partial model was explained by the interaction between year and country (Table 1b), resulting from the fact that the contrast between the years 1999 and 2000 was not significant, while the contrast between 2000 and 2001, with higher densities in 2001 than in 2000, was significant. For each of the contrasts the main effect of the explained variance was between the populations and, to a lesser

Table 1 Summary of repeated measures ANOVA of rank transformed spring population densities of adult *Hornungia petraea* plants (repeated subject = subplot). (a) Test of between-subjects effects. (b) Univariate test of within-subjects effects. (c) Univariate test of between-subjects effects separated by year. (d) Test of between-subjects effects and univariate test of within-subjects effects separately for each country (D, Germany; I, Italy). Country = country (representing central vs. peripheral populations); Population(Country) = population nested within country; R_t^2 = explained variation of total model; R_p^2 = explained variation of partial model

	Effect	d.f.	SS	<i>F</i>	<i>P</i>	R_t^2	R_p^2
(a)	Country	1	7211557	337.1	< 0.001	0.47	0.58
	Population(Country)	17	1666210	4.6	< 0.001	0.11	0.13
	Error	171	3658555				
(b)	Year	2	59812	5.6	< 0.001	0.00	0.02
	Year × Country	2	265924	24.7	< 0.001	0.02	0.10
	Yea × Population(Country)	34	598808	3.3	< 0.001	0.04	0.22
	Error(Year)	342	1843822				
(c)	1999	Country	1	1383229	99.5	< 0.001	0.31
		Population(Country)	17	749884	3.2	< 0.001	0.17
		Error	171	2376888			
	2000	Country	1	3627289	472.4	< 0.001	0.64
		Population(Country)	17	718576	5.5	< 0.001	0.13
		Error	171	1313004			
	2001	Country	1	2466962	232.8	< 0.001	0.49
		Population(Country)	17	796559	4.4	< 0.001	0.16
		Error	171	1812485			
	D	Population	8	242697	3.1	0.004	0.15
		Error	81	796752			
		Year	2	41635	8.0	0.001	0.03
		Yea × Population	16	135265	3.2	< 0.001	0.08
		Error(Year)	162	423284			
	I	Population	9	501376	5.2	< 0.001	0.23
		Error	90	970379			
		Year	2	96248	19.3	< 0.001	0.04
		Year × Population	18	130975	2.9	< 0.001	0.06
		Error(Year)	180	448761			

Table 2 Results of ANOVA for contrasts between the repeated spring density and fecundity of peripheral German (D) and central Italian (I) populations of *Hornungia petraea*. Direction of trends is indicated with algebraic signs for the mean and for the country effect when significant. Double signs indicate a steeper trend for the respective country

Stage	Contrast	Effect	d.f.	SS	<i>F</i>	<i>P</i>	R^2	Trend
Spring density of adults	1999/2000	Mean	1	4628	0.4	0.545	0.00	
		Country	1	530620	42.2	< 0.001	0.16	D +, I –
		Population(Country)	17	621259	2.9	< 0.001	0.19	
		Error	171	2149017				
	2000/2001	Mean	1	107384	13.2	< 0.001	0.05	+
		Country	1	111481	13.7	< 0.001	0.05	I +
		Population(Country)	17	690949	5.0	< 0.001	0.30	
		Error	171	1388231				
Fecundity	1999/2000	Mean	1	5199166	191.6	< 0.001	0.48	–
		Country	1	286581	10.6	0.001	0.03	D –, I –
		Population(Country)	17	794004	1.7	0.043	0.07	
		Error	165	4476530				
	2000/2001	Mean	1	1443538	45.9	< 0.001	0.17	+
		Country	1	894532	28.5	< 0.001	0.10	D +, I +
		Population(Country)	17	1183914	2.2	0.006	0.14	
		Error	165	5185858				

Note: as fecundity data of single subplots in the year 2000 were missing for contrast analyses a total $n = 184$ was used.

degree, between countries (Table 2). The univariate analysis for the repeated years yielded quite homogeneous results, with the main source of variance being country and, to a lower degree, population (Table 1c).

Comparing all populations for the three successive years, consistently significant differences between

populations were mainly found between the populations of the two different study regions: 47.8% of all pairwise comparisons between populations of the two different countries were significant in all three years. In Germany, no consistent differences between populations were found over the three years; in Italy only 4.4% of the

populations differed significantly and consistently. Plot I8 had significantly higher population densities than plots I6 and I7 in all three years.

POPULATION DYNAMICS

In Germany and in Italy significant contrasts between years were detected in nine out of 19 populations (Fig. 1). From 1999 to 2000 densities increased significantly in three and decreased significantly in one of the German populations. For the Italian populations, the direction of contrasts was more uniform, with significant contrasts showing only negative trends. For all populations with significant contrasts in successive transitions the directions of the trends in 1999/2000 were the reverse of those observed in 2000/2001 (D1, D7, I5, I9, Fig. 1).

SEED BANK POPULATION

Figure 2 shows the data on seed bank population densities for the four repeated monitoring dates (spring 1999, summer 1999, spring 2000, summer 2000). As the summer 1999 data for the Italian population I4 was missing, this population was omitted in the nested repeated measures ANOVA (Table 3). The density of seed bank populations differed significantly between the two countries, explaining 54% of the variance in the data set (Table 3a). The difference was significant on all four dates (Table 3c). In German seed bank samples, between 0 and 79 seeds germinated per sample (median = 5, $n = 360$). In Italy, the maximum number of germinating seeds was only 26 (median = 0, $n = 360$). In addition to the country effect, the population effect explained 12% of the between-subjects effects (Table 3a).

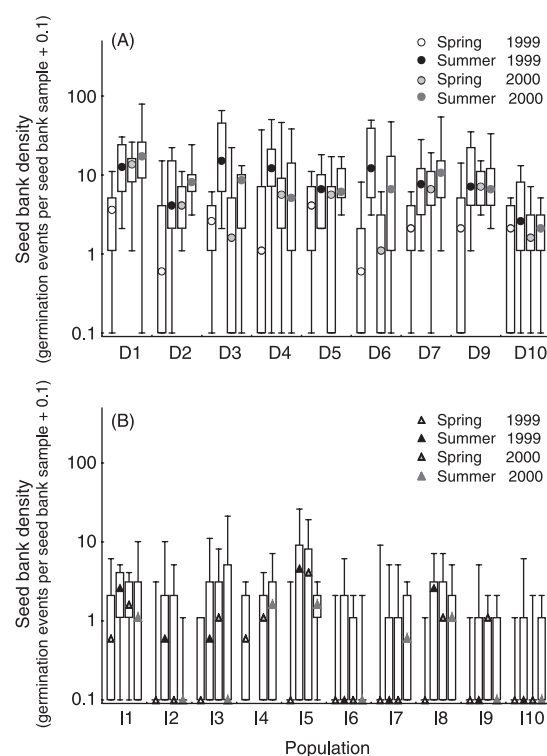


Fig. 2 Seed bank population density of *Hornungia petraea* on four repeated sample dates (spring 1999, summer 1999, spring 2000, summer 2000) based on sample surface area of 23.8 cm². (A) Peripheral German (D) and (B) central Italian (I) populations. Spring samples were taken before and summer samples after seed dispersal.

The analysis of within-subjects effects (Table 3b) resulted in a significant proportion (17%) of variance explained by the repeated factor (monitoring date). Therefore, the contrast analyses yielded significant general trends (Table 4). Except for the spring/summer

Table 3 Summary of nested repeated measures ANOVA of rank transformed seed bank population densities of *Hornungia petraea* (repeated subject = number of seedlings emerged from seed bank samples). (a) Test of between-subjects effects. (b) Univariate test of within-subjects effects. (c) Univariate test of between-subjects effects separated by monitoring date (spring 1999, 2000, summer 1999, 2000). Country = country (representing central vs. peripheral populations); Population(Country) = population nested within country; R_t^2 = explained variation of total model; R_p^2 = explained variation of partial model

	Effect	d.f.	SS	F	P	R_t^2	R_p^2
(a)	Coun	1	8961035	263.5	< 0.001	0.30	0.54
	Population(Country)	16	1995604	3.7	< 0.001	0.07	0.12
	Error	162	5509747				
(b)	Date	3	2153829	37.0	< 0.001	0.07	0.17
	Date × Country	3	319178	5.5	< 0.001	0.01	0.02
	Date × Population(Country)	48	1125998	1.2	0.168	0.04	0.09
	Error(Date)	486	9427443				
(c)	Spring 1999	Country	1	1488124	72.9	< 0.001	0.27
		Population(Country)	16	352652	1.1	0.379	0.06
		Error	162	3670899			
	Summer 1999	Country	1	2908938	112.0	< 0.001	0.35
		Population(Country)	16	701487	1.7	0.054	0.09
		Error	162	4611211			
	Spring 2000	Country	1	1481675	61.0	< 0.001	0.21
		Population(Country)	16	1232198	3.2	< 0.001	0.17
		Error	16	4343634			
	Summer 2000	Country	1	3401475	158.0	< 0.001	0.42
		Population(Country)	16	835264	2.4	0.003	0.10
		Error	162	3829496			

Table 4 Results of ANOVA for contrasts between the repeated seed bank samples of peripheral (Germany, D) and central (Italy, I) populations of *Hornungia petraea*. *P*-values for contrasts and between-subjects effects are given. Direction of trends is indicated with algebraic signs for the mean and for the country effect if significant. Double signs indicate a steeper trend

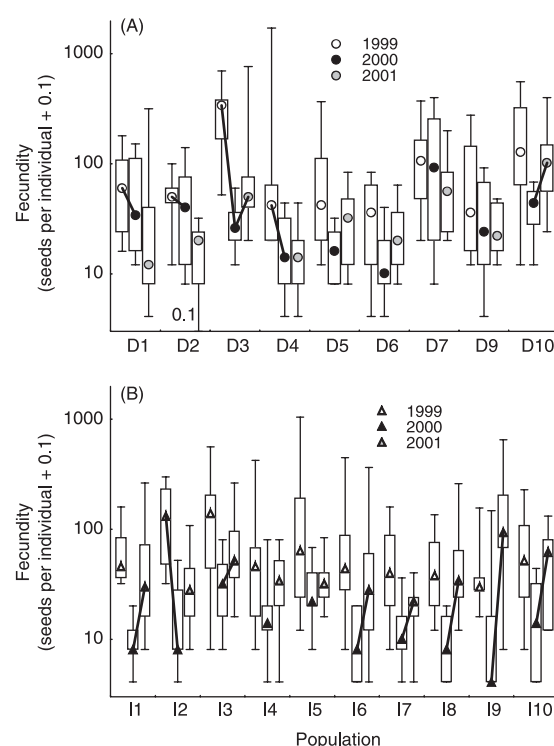
	Effect	Spring 1999		Summer 1999		Spring 2000	
		<i>P</i>	Trend	<i>P</i>	Trend	<i>P</i>	Trend
Summer 1999	Mean	< 0.001	+				
	Country	0.014	D + +, I +				
	Population(Country)	0.249					
Spring 2000	Mean	< 0.001	+	< 0.001	–		
	Country	0.989		0.017	D – –, I –		
	Population(Country)	0.085		0.100			
Summer 2000	Mean	< 0.001	+	0.019	–	0.225	
	Country	< 0.001	D + +, I +	0.498		0.003	D +, I –
	Population(Country)	0.147		0.664		0.661	

2000 contrast, trends showed, as expected, higher seed bank population densities in the summer seed bank than in the spring seed bank. The median spring seed bank population densities were 1786 and 274 seeds per m² for Germany ($n = 18$) and Italy ($n = 18$), respectively. The summer seed bank densities were 4421 and 568 seeds per m² (median values) for German and Italian plots, respectively. The interaction between the repeated monitoring date and country was significant, but it explained only 2% of the variance of the partial model (Table 3b). The interaction between the repeated factor and population was not significant. In the first study year, 1999, differences in seed bank density between populations nested within country were not significant, but in the second study year, populations explained a significant amount of the variance (Table 3c).

As expected, the contrast analysis yielded significant country effects (Table 4). Trends between two subsequent temporal repetitions were significantly different between the two countries, the trends generally less pronounced in Italy than in Germany. The contrasts between spring/summer 2000 even had different signs as more plants emerged from summer 2000 samples than from spring 2000 samples in Germany, while the opposite was found for the Italian plots.

FECUNDITY

Figure 3 shows the data on fecundity of all populations in all three study years. The corresponding statistical results are summarized in Table 5. The total statistical model explained 41% of the variance, between-subjects effects 13% of the total variance and the within-subjects effects 28% (Table 5a,b). The between-subjects effects were mainly explained by population (34%). A very small but significant amount of variance was explained by whether the individual studied was from an Italian or German population. *H. petraea* plants from Germany had more seeds (median = 32, mean = 78, $n = 270$) than those from Italy (median = 30, mean = 61, $n = 294$). The repeated factor was significant, explaining 29% of the within-subject variance (Table 5b). The interactions between the repeated factor (year) and both country

**Fig. 3** Fecundity of *Hornungia petraea* individuals in three successive years. (A) Peripheral German and (B) central Italian (I) populations. Box-Whisker plots with median, 25 and 75% quantiles and extremes. Lines connect median values of density if the change from successive years is significant (i.e. a significant contrast).

and population were also significant. This result is confirmed by the univariate analysis of between-subject effects performed separately for the three study years. In the first year, 1999, there was no significant difference in fecundity between German and Italian *H. petraea* populations (median = 56, $n = 190$), but in the following two years the differences were significant (Table 5c). In 2000, German plants had a higher fecundity (median = 20, $n = 90$) than Italian plants (median = 12, $n = 94$), whereas in 2001 the fecundity of Italian plants (median = 34, $n = 100$) exceeded the fecundity of German plants (median = 28, $n = 90$). Consequently, the post-hoc test for the pairwise comparisons of populations yielded no

Table 5 Summary of repeated measures ANOVA of rank transformed fecundity (seeds per individual) of *Hornungia petraea* (repeated subject = subplot). (a) Test of between-subjects effects. (b) Univariate test of within-subjects effects. (c) Univariate test of between-subjects effects separated by year. (d) Test of between-subjects effects and univariate test of within-subjects effects separated by country (D, Germany; I, Italy). Country = country (representing central vs. peripheral populations); Population(Country) = population nested within country; R_t^2 = explained variation of total model; R_p^2 = explained variation of partial model

	Effect	d.f.	SS	<i>F</i>	<i>P</i>	R_t^2	R_p^2
(a)	Country	1	88418	4.2	0.042	0.01	0.02
	Population(Country)	17	1812158	5.1	< 0.001	0.13	0.34
	Error	165	3461109				
(b)	Year	2	2602096	85.1	< 0.001	0.18	0.29
	Year × Country	2	449865	14.7	< 0.001	0.03	0.05
	Year × Population(Country)	34	935536	1.8	0.006	0.06	0.10
	Error(Year)	330	5046213				
(c)	1999	Country	1	16913	0.9	0.346	0.00
		Population(Country)	17	642643	2.0	0.014	0.17
		Error	165	3121545			
	2000	Country	1	442739	28.3	< 0.001	0.11
		Population(Country)	17	957512	3.6	< 0.001	0.24
		Error	165	2585261			
	2001	Country	1	78630	4.6	0.033	0.02
		Population(Country)	17	1147537	4.0	< 0.001	0.28
		Error	165	2800514			
(d)	D	Population	8	316760	7.0	< 0.001	0.19
		Error	81	456199			
		Year	2	209268	31.2	< 0.001	0.13
		Year × Population	16	109663	2.1	0.014	0.13
		Error(Year)	162	542831			
	I	Population	9	127772	3.0	0.004	0.06
		Error	84	403431			
		Year	2	591547	68.0	< 0.001	0.30
		Year × Population	18	128260	1.6	0.057	0.09
		Error(Year)	168	730267			

Note: as fecundity data of single subplots in the year 2000 were missing, the complete data set for these subplots was omitted, resulting in a total $n = 552$ for this analysis.

consistently significant differences between populations over all three years. The differences in fecundity between two successive years for both contrasts (1999/2000 and 2000/2001) were significantly influenced by the factors population and country (Table 2).

In 2000, fecundity was generally lower than in the preceding year, whilst in 2001 it was higher than in 2000. For both contrasts, trends were more pronounced in the Italian populations than in the German ones (Table 2). The factor population significantly influenced both contrasts. This means that the trends were not the same in all populations (Table 2). The separate analyses for each country assigned a high amount of explained variance in fecundity to the factor population in Germany (19%), whereas in Italy the study year explained the most (30%) and population the least (6%) (Table 5d). In contrast to Italy, the interaction between the factors year and population was significant in Germany.

Discussion

In contrast to the expected pattern of higher population densities in central than in peripheral populations, we found that population densities of *H. petraea* were significantly lower in Italy than in Germany. This applied

both to adult plant populations and to seed bank populations. Studies on population densities across the distribution range are quite rare for plant species and have yielded contradictory results. For example, in *Lactuca serriola* there was no evidence for a decline in population density towards the species' northern distribution limit in Britain (Carter & Prince 1985; Prince *et al.* 1985). In contrast, Carey *et al.* (1995) found evidence for declining population densities towards the northern distribution limit of the annual species *Vulpia ciliata* ssp. *ambigua* in Britain. Recently, Jump & Woodward (2003) confirmed the 'abundant centre' hypothesis for the northerly distributed *Cirsium heterophyllum*, whereas *Cirsium acaule*, a species from southern parts of the UK, did not confirm the hypothesis. For the two species, *V. ciliata* and *C. heterophyllum*, for which the 'abundant centre' pattern has been confirmed (Carey *et al.* 1995; Jump & Woodward 2003), lower densities were explained by reduced fecundity at the species' distribution limit (as also observed, for instance by Pigott & Huntley 1981; Eckert & Barrett 1993; García *et al.* 2000; Dorken & Eckert 2001). In contrast, the small difference in fecundity of *H. petraea* individuals between the two study regions cannot explain the differences in density. Fecundity was affected to a high degree by the year of study, which could even

invert the effect of the study region. Such a high interannual variation in seed production is especially well known in annuals (e.g. Mack & Pyke 1983; Schmidt & Levin 1985; Watkinson 1990). However, the greater interannual variation in fecundity in central Italian populations was not reflected in increased interannual variation in the adult population in spring. In contrast, in the study by Nantel & Gagnon (1999) there was a larger interannual variation in vital rates and intrinsic growth rates at the distribution limit of their study species compared with central populations. As with our results, the differences reported by Nantel & Gagnon (1999) were not reflected in population densities, as would have been predicted by the central-marginal model. In both their species there were only minor differences in the densities of the plants in the two types of populations (central vs. peripheral) (D. Gagnon, personal communication).

The fact that the large fluctuations in fecundity in *H. petraea* populations in Italy are not reflected in adult spring populations possibly means that the seed bank populations act as a buffer against environmentally driven variation in fecundity. We had expected that interannual seed bank dynamics would be more pronounced in the study region with lower population densities, whilst seasonal seed bank dynamics would be more pronounced in the study region with higher population densities. However, there was no evidence that annual seed bank dynamics differed between the two study regions, whereas seasonal seed bank dynamics were significantly influenced by country. We found more seasonal variation in seed bank densities in the denser German populations. This corresponds with the observed population densities in the two countries and with the idea that lower seasonal seed bank dynamics must be expected under less predictable conditions (Rees 1994). In particular, the transition into the seed bank (i.e. the contrast spring/summer) showed clear differences between the two countries. In the second study year, Italian *H. petraea* populations even showed a significant negative trend in seed bank density. Thus, we conclude that Italian populations may have difficulties incorporating seed into the seed bank. Seeds produced by plants in Italian populations may also have a lower germination rate than seeds originating from German populations, supported by results from glasshouse experiments (C. Kluth & H. Bruelheide, unpublished data). However, many other factors, such as carry-over effects, predation, dispersal ability, interactions with the accompanying vegetation or storage conditions in the soil, may affect the seed dormancy cycle or post-dispersal seed loss (e.g. Van Tooren 1988; Cabin *et al.* 2000; Ehrlén 2000; García *et al.* 2000; Baskin & Baskin 2001).

The importance of local dispersal processes for biogeographical patterns has recently been pointed out by Hengeveld & Hemerik (2002). For *H. petraea*, seed loss from Italian populations might be attributed to higher emigration rates associated with higher dispersal mor-

tality than in Germany. A possible cause might be a higher activity of seed feeding and seed dispersing ants, which are more abundant and have denser populations in the Mediterranean region than in central Europe. For example, the harvester ant genus *Messor* has a circum-Mediterranean distribution (C. Detrain, personal communication), with about 15 species (B. Seifert, personal communication). The only *Messor* species occurring in Germany, *Messor structor* (Latreille 1798), occurs only in a few locations and does not exist in our German study region (Seifert 1996). In contrast, in Italy *Messor structor* is a common harvester ant within the distribution range of *H. petraea* (L. Gubellini, personal communication). However, the higher seed emigration and mortality from local populations in Italy may, to some extent, be compensated for by an increased number of biotopes occupied by *H. petraea* (Kluth & Bruelheide 2004).

In addition to the effect of higher emigration rates, the greater variation in the interannual reproduction rate could lead to higher extinction risk for local populations in Italy. In combination with higher colonization rates, this increases interactions between the local populations, i.e. by metapopulation dynamics (Hanski & Gilpin 1991). Therefore, the differences in local population densities between Italian and German populations may be the result of different metapopulation structures. *H. petraea* populations are very dynamic in the Italian study region (A. Brilli-Cattarini, personal communication), where we found some extremely small populations, some consisting of only a single individual. Such 'populations' may represent colonization events. These findings are contrary to the existing theory that assumes an increasing tendency for species to persist as metapopulation towards their range boundary, where habitat is naturally more fragmented. (Hanski 1999; Wilson *et al.* 2002). So far, such patterns have only been found for relatively well-dispersed animal species, e.g. the butterflies *Aricia agestis* and *A. artaxerxes* (Wilson *et al.* 2002).

Using modelling approaches, Kirkpatrick & Barton (1997) showed that steep environmental gradients in space, combined with increased migration rates and gene flow, inhibit local adaptation and, in consequence, decrease a species' total population size. Indeed, *H. petraea* grows in a wider variety of habitats in Italy than in Germany, and the elevational range of populations in Italy is much wider than in Germany (Kluth & Bruelheide 2004). This more heterogeneous environment, in combination with higher metapopulation dynamics, could result in local maladaptation in Italian *H. petraea* populations. Such an interpretation would be in accordance with the larger proportion of variance in fecundity being explained by the population effect, and with a more population-specific response in different years in Germany than in Italy.

In general, the demography of *H. petraea* in the two studied regions conforms to the observed density patterns. However, these density patterns do not correspond with the 'abundant centre' hypothesis. This might have

various reasons. We arbitrarily chose two sample regions within the range of *H. petraea* and studied three successive vegetation periods. The 'abundant centre' pattern is expected to be the average over all range parts over a longer time span (Hengeveld & Haeck 1982; Hengeveld 1990; Hengeveld & Hemerik 2002; Holt 2003) and might therefore not be shown in our more limited data. Nevertheless, there are indications that the pattern described here might apply to the whole range of *H. petraea*. Additional central populations from other parts of the more or less continuous distribution in the Mediterranean region had low densities (Sicily, C. Kluth, personal observation; Andalusia, A. Erfmeier, personal communication; Catalonia, H.-G. Stroh, personal communication), whereas peripheral and disconnected populations consistently showed particularly high densities (Rhineland-Palatinate, Bavaria, Lower Saxony, C. Kluth, personal observation; Öland H. Bruelheide, personal observations). Geographically intermediate populations (Vienna, Trentino South Tyrol, C. Kluth, personal observations) occurred at intermediate densities. The short time span of three study years does not allow conclusions to be drawn regarding the stability of the observed density patterns. Although the literature indicates a continuous existence of the studied populations in Germany for more than a century, their densities might have undergone changes. Under global change scenarios (IPCC 2001) the peripheral German populations might be the ones most favoured by global warming and their higher densities might already be the result of such a climate change. In any case, the dense populations at the periphery would contribute most to range expansion. The general importance of dense populations in range dynamics was shown for relatively dispersible animal species, both by observations (Turin 2000 quoted in Hengeveld & Hemerik 2002) and by modelling (Hengeveld & Hemerik 2002).

The data needed to clarify these relationships between range dynamics, regional metapopulation dynamics and local population dynamics is scarce not only for *H. petraea* but for species in general. Long-term data sets of population dynamics across distribution ranges are not available, particularly for plant species. There are either long-term studies on single local populations (e.g. Watkinson 1990; Woodward 1997; Bengtsson 2000) or short-term studies on the distribution of abundance across the range (e.g. Prince *et al.* 1985; Carter & Prince 1985; Carey *et al.* 1995; Jump & Woodward 2003). Regarding the role of dispersal or metapopulation dynamics, we expect to gain more insight by including ongoing analyses of the genetic structure of the study populations of *H. petraea*. These data will allow us to test the assumption of higher gene flow in central Italian populations.

Acknowledgements

We thank Christoph Fühner, Stephanie Kluth, Holger Lieneweg, Ute Luginbühl and Gustav Schulz for help

in the field. Special thanks are due to Leonardo Gubellini and Aldo Brilli-Cattarini from the Centro Ricerche Floristiche Marche for their assistance in locating appropriate plots in Italy. We are grateful to Rob Hengeveld and an anonymous referee for their valuable constructive critique on the manuscript. Alexandra Erfmeier, Stephanie Kluth, Michael Hutchings and Lindsay Haddon contributed useful comments to previous drafts of the manuscript. This work was supported by a grant from the German Research Foundation DFG (BR 1698).

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Received 13 July 2004

revision accepted 22 November 2004

Handling Editor: Michael J. Hutchings