



Ecology and biogeography of plant communities associated with the post Plio-Pleistocene relict *Rhododendron ponticum* subsp. *baeticum* in southern Spain

José A. Mejías^{1*}, Juan Arroyo¹ and Teodoro Marañón²

¹Departamento de Biología Vegetal y Ecología, Universidad de Sevilla, Apdo. 1095, E-41080 Sevilla, Spain and ²IRNA, CSIC, PO Box 1052, E-41080 Sevilla, Spain

ABSTRACT

Aims *Rhododendron ponticum* L. is reputed to be a post Plio-Pleistocene relict plant species with a disjunct distribution that comprises the Iberian Peninsula to the west and the Euxinian region plus some restricted Mediterranean areas to the east. We analysed the ecological range (of subsp. *baeticum*) in the western area (Aljibe Mountains, north of the Strait of Gibraltar) to understand the factors determining the present area limitation.

Location Sierra del Aljibe, north of the Strait of Gibraltar (Iberian Peninsula).

Methods We selected 20 riparian sites where *R. ponticum* is common, and compiled data on the ecological diversity of associated woody species and ferns. We established a 500-m main transect in each site, along the stream or river course, in which we placed five 20-m-long plots at regular intervals. We recorded physiographic habitat features, woody plants and fern abundance, and the number of *R. ponticum* individuals.

Results *Rhododendron ponticum* in southern Spain is restricted to riparian forests in acidic soils (pH 4.0–6.4), and is mainly found on the banks of inclined and enclosed streams. In our inventory we recorded 59 woody taxa and 12 ferns, with *R. ponticum* being the dominant species of the understorey (mean abundance 78.6%). The communities are characterized by a high incidence of the humid warm temperate element, both in number of species (18.8 ± 3.7 per site) and abundance; meanwhile, the presence of the modern Mediterranean element (mean number of species 3.4 ± 3.8 per site) appears to be favoured by disturbance. These ecological–historical groups of taxa also show distinct patterns of typological habit, frequency of endemism, infrageneric diversity and geographical range. Populations of *R. ponticum* are characterized by a very variable density of seedlings in many sites, and the virtual lack of juveniles.

Main conclusions Riparian forests of the Aljibe Mountains constitute a refuge for *R. ponticum* where the species persists, but populations appear to be in decline. The narrow ecological range of *R. ponticum* in the area strongly contrasts with its wide amplitude in the eastern natural area, mainly the Euxinian region, where *R. ponticum* probably finds better conditions due to the environmental heterogeneity of the region, and the lack of a hot dry season.

Keywords

Canonical correspondence analysis, ecological amplitude, growth rings, Neogene vegetation, plant demography, *Rhododendron ponticum*, riparian forest, spatial heterogeneity, species decline, Strait of Gibraltar.

*Correspondence: José A. Mejías, Departamento de Biología Vegetal y Ecología, Universidad de Sevilla, Apdo. 1095, E-41080 Sevilla, Spain. E-mail: jmejias@us.es

INTRODUCTION

Paratropical summer-wet evergreen and deciduous forests were predominant vegetation types during the Early Cainozoic (65 to c. 40 Ma; Mai, 1989; Willis & McElwain, 2002) in western Eurasia. Subsequently, the progressive increase of seasonality and cooling of the climate led to the gradual loss of the exotic element and to the disruption of previously homogeneous biota (Palamarev, 1989; Mai, 1995). Nevertheless, humid warm temperate forests with a substantial evergreen component persisted at least until the Pliocene (c. 5–1.8 Ma). Only then, and during the following Pleistocene cold phases, have most of the evergreen and many deciduous elements (*Cinnamomum*-type leaves, *Magnolia*, *Rhododendron*, *Sassafras*, *Taxodium*, *Ginkgo*, etc.) disappeared from Europe and western Asia. Indications in fossil floras (both macrofloras and pollen data) of a Mediterranean sclerophyllous vegetation prior to the Pleistocene are absent from Europe, except for the southern Mediterranean area (Gregor, 1990; Fauquette *et al.*, 1999). Some taxa with affinities to Late Cainozoic (Miocene to Pliocene/Pleistocene) forests have persisted in southern Europe and western Asia, and today are elements of the Mediterranean and Euxinian forests (south of the Black Sea, Transcaucasia). These taxa are defined by Denk *et al.* (2001) as Tertiary relict taxa, usually attested by a disjunct geographical range (Raven & Axelrod, 1974). Nevertheless, some of them, such as *Rhododendron ponticum* L., are considered to have had a continuous distribution in the Pleistocene (Tralau, 1963; Milne, 2004) but are disjunct today. As such, they should be more accurately called Plio-Pleistocene relict taxa (C. Humphries, personal communication).

Persistence of western Eurasia Tertiary or Plio-Pleistocene relicts occurs in refuges where the effects of cooling during Pleistocene glaciations were not so marked (Hewitt, 2000); where seasonal drought is absent or alleviated; and where severe winter frosts are absent. Often these taxa show disjunct distributions between the western (mainly Iberian Peninsula) and eastern parts of the Mediterranean Basin plus the Euxinian area. The eastern refuges have been assessed thoroughly (Denk *et al.*, 2001), but not the western range.

During the past decade, several authors have postulated refugia of relict species using a phylogeographical approach, or used integrated genetic analyses to better explain past species movements or present plant ranges (Demesure *et al.*, 1996; Arroyo-García *et al.*, 2001; Hampe *et al.*, 2003). In contrast, the analysis of ecological limitations for the expansion of relict species in refugia and the implications of regional-scale heterogeneity in their persistence have commonly been neglected (Hampe & Petit, 2005). In general, the few studies designed to assess ecological constraints and matching between the plant's life and regional climate are related to the decline of relict populations by current climate warming (Hamburg & Cogbill, 1988; Hódar *et al.*, 2003; Peñuelas & Boada, 2003). Many plant species have been shown to be relatively conservative in their ecological and climatic requirements (Davis & Shaw, 2001; Svenning, 2003). Thus the interpretation of Late Neogene

vegetation in western Eurasia and its evolution would be improved by the analysis of plant communities, including humid warm temperate and modern Mediterranean elements, the ecological factors determining contemporary plant abundance and the population dynamics of the relictual elements.

In the Iberian Peninsula, the mountain ranges of the south (Aljibe Mountains) have been considered an important refuge of Tertiary relicts (after Rivas-Goday, 1968; Hampe *et al.*, 2000; Arroyo *et al.*, 2001). These relict species are well represented among contrasted life-forms: trees, shrubs and ferns. Among the former, *R. ponticum* is one of the best known and most significant relicts in the area, being a characteristic representative of certain riparian communities. This species was distributed more widely throughout Europe during the Neogene as a component of broadleaved deciduous and evergreen forest (Tralau, 1963; Mai, 1995), but at present shows a disjunct distribution (Fig. 1) between the Iberian Peninsula to the west and the Black Sea coast and Lebanon to the east (Cross, 1975; Chamberlain, 1982). Standard floras (Tutin *et al.*, 1964–80; Stevens, 1978; Valdés *et al.*, 1987; Castroviejo *et al.*, 1986–2001) distinguish two disjunct taxa as subspecies: *R. ponticum* L. subsp. *ponticum* for eastern plants, and *R. ponticum* subsp. *baeticum* (Boissier & Reuter) Handel-Mazzetti for western (Iberian) plants.

The biogeographical significance of *R. ponticum* as a relict species is well recognized, but despite its dramatic incidence as an invasive plant in some areas of Atlantic Western Europe, its habitat range and ecological constraints have not been adequately studied (Cross, 1981; Mitchell *et al.*, 1998). Previous studies have shown that Iberian relict populations persist under a Mediterranean climate regime by means of non-specialized vegetative multiplication, with the scarcity of safe microsites for germination being the main threat to the species in the area (Mejías *et al.*, 2002).

Here we analyse the ecological range of *R. ponticum* at community and population levels in southern Spain, in order to understand factors determining present area boundaries and ecological constraints restricting the expansion, and even the persistence, of *R. ponticum* in its native range. Further, we evaluate the significance of the Aljibe Mountains as a refuge for this relict plant. Three particular topics we investigate are: (1) environmental gradients and trends of floristic variation at the community level, (2) the biogeographical origin of community components, and (3) the population structure of *R. ponticum* in the area. We have considered only woody and fern species in these communities. Finally, we compare the features of the ecological niche of *R. ponticum* in the western Mediterranean populations (results of our study) with those for the eastern (Euxinian) populations (based on published studies).

MATERIALS AND METHODS

Study area

The distribution of *R. ponticum* in the western Mediterranean is concentrated in southern Spain (mainly on the Aljibe

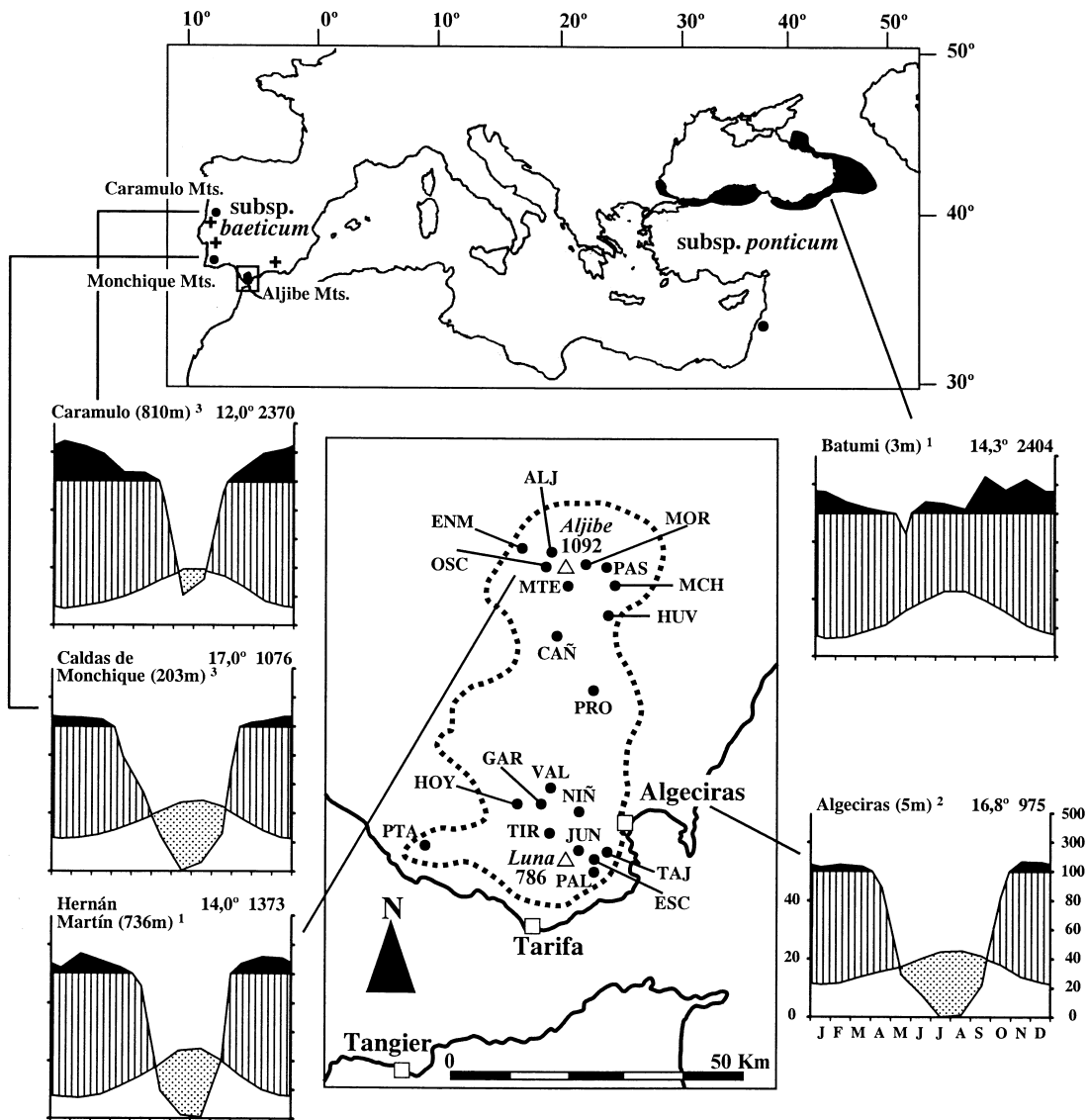


Figure 1 Map of the Mediterranean Basin with the present natural distribution of *Rhododendron ponticum* and location of the 20 communities studied within the range of the species (broken line) in southern Spain. (1) Adapted from Walter & Lieth (1960–67); (2) climatic data from Montero & González (1983); (3) climatic data from INMG (1990–91); (+) Fossil pollen record.

Mountains) and southern and western Portugal (Fig. 1). The Aljibe Mountains, where this species is most abundant in the Iberian Peninsula, was chosen as the study area. It is located at the southern tip of the Iberian Peninsula, and occupies the northern side of the Strait of Gibraltar (Fig. 1). The rough topography of the landscape is due to Oligo-Miocene sandstone, with a highest elevation of 1092 m a.s.l. The soils are acidic, siliceous and nutrient-poor. Sparse limestone outcrops are also found in the area, resulting in basic, compact, fertile soils. In its entirety, this area can be considered as an edaphic island surrounded by fertile, basic, loamy soils in lowlands, and limestone-derived soils on calcareous mountains (CSIC, 1968; Ojeda *et al.*, 1995).

The climate in the Aljibe Mountains is meso-Mediterranean with warm, dry summers and mild, humid winters. Mean

annual temperature ranges from 14.6 to 18.4°C ($16.96 \pm 1.18^\circ\text{C}$, $n = 8$ weather stations), with a monthly maximum mean of 36.4°C in July and a monthly minimum mean of 1.6°C in January. Absolute maximum summer and minimum winter temperatures reach 41.6 and -5.0°C , respectively. Mean annual rainfall ranges from 700.8 to 1330.8 mm (1056.4 ± 182.9 mm, $n = 15$ weather stations). The mean number of frost days ranges from 10–20 days per year at the highest altitude, to 1 day per year in the vicinity of the coast (SINAMBA, 1997).

Of the five main types of woody vegetation in this area (Ojeda *et al.*, 1995), *R. ponticum* is found almost exclusively in riparian forests (locally named ‘canutos’), which have the highest diversity of trees and arborescent shrubs. Data-logger records, obtained over a 32-month period from 17 December

2000 to 19 August 2003, showed that inside the riparian forest the air was moister during the day (c. 26% higher values of minimum relative humidity), and cooler (c. 8.5% lower values of maximum temperature) than in the adjacent oak forest. The abundance of relict tree species in the riparian forests of the region has been assessed by staff at Los Alcornocales Natural Park (unpublished data). The presence of *R. ponticum* was recorded in 97 (63%) of the 154 sites examined. Other species were the relicts *Laurus nobilis* (85 sites) and *Frangula alnus* subsp. *baetica* (75 sites), and the widespread *Alnus glutinosa* (103 sites).

Sampling and community analysis

Based on the preliminary survey of *Rhododendron* communities, we selected 20 sampling sites: 19 are riparian communities whereas one exceptional community represents the understorey of a 'cloud' forest near the coast (Table 1; Fig. 1). Clouds and fog are very frequent at this site due to the persistence of humid easterly and westerly winds along the Strait of Gibraltar.

Vegetation sampling was conducted in 1997 (July–October). In each riparian community, a 500-m main transect was established along a stream or river course. Five plots were arranged regularly (separated 100 m from each other) along the transect. Plots were 20 m long and had a variable width (3–35 m, depending on the stream width; exceptionally a 49-m-wide plot was used in the anastomosing springs of site MCH). When streams were too short to hold five plots, a smaller number was used, i.e. four plots in site MOR; three in PAL; and two in ESC. In cases of non-linear catchment area (as

in TAJ) or in the understorey of cloud forests (site JUN), the five plots were established in parallel transects. In each plot, the total number of *R. ponticum* adults and juveniles was counted.

Additionally, within each plot (20 m length × streamside width) five sub-transects (1 m width) were set perpendicularly to the stream (and separated from each other by 5 m). Woody plants, ferns and seedlings of *R. ponticum* were inventoried along these sub-transects.

Plant abundance for every single taxon (of woody plants and ferns) was estimated at different scales: (1) at the landscape scale, as the number of sites where a particular taxon was recorded (frequency), (2) at the community scale, as the percentage of sub-transects where it was registered in a particular site (local abundance), and (3) as the calculated mean value of local abundance ($n = 20$), considering a nil value for sites where it was absent (average abundance). The nomenclature for all taxa included in this study follows Valdés *et al.* (1987). Taxa recorded in the communities studied, including abundance and ecological group (see below) for each taxa, are shown in Supplementary Material (Appendix S1).

For each sampling site we recorded mean altitude (ALTITUDE), mean river bank angle (BANKS ENCLOSURE) and slope (SLOPE). Tree and arborescent shrub cover (FOREST COVER) and width of stream channels (CHANNEL WIDTH) were calculated as the mean value of the measured values in the five plots of each site; for the exceptional 'cloud' forest understorey site (JUN) we assigned the mean value of channel width from the remaining sites to make it 'passive' in the analysis. Geographical exposure (ASPECT) of transects was indicated by a semi-quantitative scale, from highest shaded 5

Table 1 Study sites of plant communities associated with *Rhododendron ponticum* from southern Spain (see Fig. 1 for geographical location)

Study site	Acronym	Geographical location		Habitat	Conservation status
		Latitude (N)	Longitude (W)		
Garganta de Enmedio	ENM	36°32'26"	5°38'03"	Permanent stream gorge	Preserved
Garganta del Aljibe	ALJ	36°32'13"	5°37'26"	Permanent stream gorge	Preserved
Garganta de Puerto Oscuro	OSC	36°31'10"	5°37'05"	Permanent stream gorge	Preserved
Puerto del Moral	MOR	36°31'43"	5°35'50"	Permanent source area	Preserved
Garganta de Pasadallana	PAS	36°31'04"	5°35'40"	Permanent stream gorge	Preserved
Affluent of Canuto del Montero	MTE	36°30'02"	5°36'03"	Temporary stream gorge	Highly preserved
Garganta de los Caños	CAÑ	36°26'17"	5°35'10"	Permanent stream gorge	Preserved
Garganta de la Moracha	MCH	36°30'06"	5°34'53"	Permanent source area	Preserved
Garganta del Parroso	PRO	36°21'02"	5°35'01"	Permanent stream gorge	Highly preserved
Garganta del Huevo	HUV	36°27'50"	5°33'27"	Permanent stream gorge	Highly preserved
Arroyo de los Garlitos	GAR	36°12'18"	5°37'52"	Permanent stream gorge	Preserved
Arroyo de Valdeinferno	VAL	36°13'43"	5°36'37"	Permanent stream gorge	Partially browsed
Garganta de la Hoya	HOY	36°12'18"	5°38'09"	Permanent stream gorge	Preserved
Affluent of Garganta del Niño	NIÑ	36°11'25"	5°35'55"	Permanent stream gorge	Medium preserved
Stream in Sierra de la Plata	PTA	36°07'26"	5°46'25"	Temporary stream gorge	Deforested, highly browsed
Garganta del Tiradero	TIR	36°09'55"	5°35'58"	Permanent stream gorge	Highly preserved
Tajo del Espino	TAJ	36°06'45"	5°31'44"	Catchment area gorges	Medium preserved
El Palancar Spring	PAL	36°05'01"	5°32'32"	Permanent source gorge	Shepherd area
Tajo de las Escobas	ESC	36°05'52"	5°31'50"	Temporary stream gorge	Preserved
Llanos del Juncal	JUN	36°06'24"	5°32'17"	Deciduous forest understorey	Preserved

(north exposure), to 4 (north-west or north-east), 3 (west or east), 2 (south-west or south-east), and to highest sun-exposed 1 (south exposure). Water flow (WATER FLOW) in the stream or river was evaluated on a 0–5 scale based on visual observations of the effects of rains during several winters.

Two samples of the top soil (0–20 cm) were taken at each transect, mixed into one single sample and analysed in the laboratory. Samples were oven-dried (40°C for at least 2 days) and crushed to pass a 2-mm sieve. Size-particle distribution was measured using a Boyoucos hydrometer. Acidity (pH) was determined potentiometrically in a 1:2.5 soil–water suspension. Organic matter was determined using a modified Walkley and Black method. Available phosphorus was extracted using ammonium fluoride and hydrochloric acid, and measured by spectrophotometry. Available calcium, magnesium and potassium were extracted using ammonium acetate; K was measured by flame photometry, and Ca and Mg were determined by atomic absorption spectroscopy (for methodological details see Page *et al.*, 1982). Concentrations of the elements are given on a dry weight basis.

Analysis of diversity patterns

Three parameters were calculated to assess plant diversity: (1) species richness, as the number of taxa registered in each site, (2) endemism level, as the number of species with their geographical range restricted to the south Iberian–Tingitanian region or narrower ranges in each site, and (3) taxonomic singularity, as the inverse of infra-generic diversity in each community analysed (see methods in Ojeda *et al.*, 1995). Two geographical levels were considered for establishing co-generic taxa: Western Andalusia (region of south-western Spain that includes the study area) and the Mediterranean Basin. The levels were selected to show the taxonomic particularities of *R. ponticum* communities in the region and in the Mediterranean as a whole. The number of species per genus in western Andalusia was taken from the standard flora (Valdés *et al.*, 1987). The number of species per genus in the Mediterranean Basin was taken from the regional checklist (Greuter *et al.*, 1984–89), and for those genera not included there, from the comprehensive *Flora Europaea* (Tutin *et al.*, 1960–84) and *Index Kewensis* (Royal Botanic Gardens Kew, 1997).

In addition, the Shannon–Wiener index of diversity was calculated, combining the values of species richness and abundance. We used the species frequency in a standardized 100 (± 5)-m transect, randomly selected at each site, as the surrogate for species abundance.

Biogeographical analysis

Woody plant taxa were arranged into two ecological and partly historical groups: (1) humid warm temperate (HWT) element, of which many are known from the Late Neogene fossil record; and (2) modern Mediterranean (MM) taxa that typically occur in drier habitats and are absent from the pre-Pleistocene fossil record (Appendix S1). Such a division is basically in accord-

ance with the historical classification of woody plants from western Andalusia by Herrera (1992), with the exception of the genus *Erica* (following the criterion of Raven & Axelrod, 1974) and *Frangula* (according to Hampe *et al.*, 2003), which were both considered as HWT taxa. Despite their combined historical and ecological nature, these groups are referred to here as ‘historicals’, for simplicity and given the strong evidence supplied by fossils in their differentiation (for details see Herrera, 1992).

Woody plant and fern taxa were arranged in nine chorological types: (1) Cosmopolitan (C), (2) Mediterranean-Eurosiberian-Macaronesian (MEM), (3) Mediterranean-Eurosiberian (ME), (4) Mediterranean-Macaronesian (MMC), (5) Circum-Mediterranean (CM), (6) Western Mediterranean (WM), (7) Ibero-North African (INA), (8) Southwestern Iberian-Tingitanian (SIT), and (9) Gibraltarian (G). These areas roughly correspond with floristic units as used in phytogeography (Ojeda *et al.*, 1995). Information about distribution of taxa was taken from Castroviejo *et al.* (1986–2001) and Valdés *et al.* (1987). Two chorological spectra were calculated, based on: (1) number of taxa inventoried for each chorological type; and (2) weighted taxon number by abundance of each chorological type.

To investigate the relative proportion of ‘old’ (humid warm temperate, HWT) and ‘recent’ (modern Mediterranean, MM) elements in the riparian forests, in comparison with other shrub and forest communities in the same region, we used the data set compiled by Garrido & Hidalgo (1998).

Population structure of *Rhododendron ponticum*

In each of the 20 plots, four age classes for *R. ponticum* individuals were distinguished: (1) small seedlings with all leaves < 20 mm long, (2) large seedlings with at least one leaf ≥ 20 mm, (3) juveniles – individuals < 0.5 m high and showing a woody stalk and adult-sized leaves, and (4) adults.

In addition, we selected seven populations, within the 20 sampled sites, which represented most of the ecological diversity among them: ENM, MOR, MTE, GAR, VAL, PAL and JUN (Table 1). In each we selected a random point and chose the nearest 30 adult *Rhododendron* plants. For each of these plants, we counted or measured number of basal stems, averaged perimeter and maximum stem perimeter, and height, number of branches and number of annual growth rings (from wood cores taken *c.* 20 cm above-ground) of the largest stem. These rings are indicative only of stem age, not plant age. In fact, *R. ponticum* lignotubers have a strong resprouting ability after damage or even complete collapse of stems; a main cause of stem death is drought, probably by embolism (Mejías *et al.*, 2002). Rarely, it suffers cutting or slashing for fuel. It is also rarely subject to herbivory due to presence of andromedotoxine (Cross, 1975).

Statistical analyses

A detrended correspondence analysis (DCA) was carried out to examine the gradients in floristic composition among

communities. Then a canonical correspondence analysis (CCA) was carried out to study the relationships between the floristic variation and the environmental gradients. The program PC-ORD (McCune & Mefford, 1999) was used for the multivariate analyses.

Differences among frequency and average abundance of historical groups were analysed by Kruskal–Wallis tests. Frequency pair comparisons between groups were performed using χ^2 tests. For this, five classes of frequency were distinguished: 1–4; 5–8; 9–12; 13–16; 17–20, and the number of taxa in each frequency class was obtained for the humid warm temperate, modern Mediterranean and fern groups. Subsequently, the frequency pattern in each group was compared with the expected frequency calculated according to the pattern detected in the other groups. Mann–Whitney tests were performed to compare average abundance between groups.

Species richness and cumulative frequency comparisons between humid warm temperate and modern Mediterranean woody taxa per site were performed by mean tests. One-way ANOVA and Tukey tests for unequal sample sizes were used to detect differences among taxonomic singularities corresponding to groups of taxa in the communities, as well as to compare the composition of taxa with other woody vegetation types in the area. Differences of infra-generic diversity patterns between groups in the whole inventory were analysed by χ^2 tests as above. In this case, three classes were established: high diversified (four or more taxa per genus); medium diversified class (three or two taxa); and low diversified class (one taxon).

In order to depict the possible ontogenetic change in niche relationships between adult plants and seedlings of *Rhododendron*, two analyses were performed. First, single Pearson correlation between abundance of adults and seedlings was estimated, at both population level (averaged data from plots in each population, $n = 20$) and plot level (all plots from 20 populations, $n = 94$). Second, multiple regression analyses were performed independently on the abundance of adults or seedlings and physiographic and edaphic variables (James & McCulloch, 1990). For this, population mean values were used. This statistical procedure has been considered appropriate for depicting relationships between the density of plants of several stages and environmental variables (Colling *et al.*, 2002). Different sets of these variables have frequently been analysed separately if they are assumed to have different biological meaning (Escudero *et al.*, 1999; Garrido *et al.*, 2003).

In seven selected populations (ENM, MOR, MTE, GAR, VAL, PAL, JUN), architecture–size–age features of plants were analysed by means of correlation and regression analyses. This was made on a population basis (30 plants per population) and compared across populations. Missing data (2.4%) were substituted by population means. Single Pearson correlation coefficients were estimated for all variable pairs within each population. When the number of annual growth rings showed a significant correlation with any size-related variable, the slope (b) of the linear regression was estimated.

Unless indicated, the null hypothesis was rejected at a significance level of at least 0.05. When necessary, data were log-transformed for mean tests and ANOVA. Means \pm SD are indicated in the text.

RESULTS

Environmental range of *Rhododendron ponticum* habitats

Southern Spanish forests with *R. ponticum* in the understorey showed a relatively narrow range of environmental characteristics (Table 2). Most forests were at a mid-range elevation (mean altitude 464 m a.s.l.), ranging from 140 to 730 m. They usually occupied the banks of narrow (mean width 14.9 m), inclined (mean slope 17%) and confined (mean bank angle 125°) streams. The overstorey canopy was almost closed (mean cover 84%), giving rise to a shaded condition; this feature was rather general, with a CV of only 20.7%. In contrast, reduced tree cover (e.g. 32% in PTA) was related to community disturbance.

Soil had a coarse texture (mean proportion of gravel 66.1%) across all sites; it was acidic (mean pH 5.1), derived mostly from sandstone material, rich in organic matter (mean 3.9%), and poor in the mineral nutrients P (mean 6.0 mg kg⁻¹) and K (mean 133 mg kg⁻¹).

Woody plant communities

Species richness and plant abundance

A total pool of 59 woody species (22 trees or arborescent shrubs, 30 medium or small shrubs, seven lianas) was recorded

Table 2 Environmental range and mean values for physiographic and edaphic variables of the *Rhododendron ponticum* communities studied in southern Spain ($n = 20$)

Variable	Mean	Min–max	CV (%)
Altitude (m)	464	140–730	41.3
Slope (%)	17	1–30	47.7
Aspect	3	1–5	37.5
Channel width (m)	14.9	5.4–40	46.3
Banks enclosure (°)	125	92–180	19.9
Water flow	2.8	0–4	47.0
Forest cover (%)	84.1	31.8–100	20.7
Soil features			
Gravel (%)	66.1	41.8–83.3	18.3
Sand (%)	5.5	1.7–10.3	47.8
Silt (%)	13.5	5.2–24.6	36.6
Clay (%)	14.9	4.4–32.0	45.6
pH	5.1	4.0–6.4	11.6
Organic matter (%)	3.9	1.0–11.6	62.6
P (mg kg ⁻¹)	6.0	2.0–18.3	69.1
Ca (mg kg ⁻¹)	1839	353–4437	65.2
Mg (mg kg ⁻¹)	254	109–370	24.5
K (mg kg ⁻¹)	133	44–337	65.3

in the 20 communities sampled. The number of taxa per site ranged from 41 in VAL to 13 in ESC (mean 22.2 ± 6.4).

Rhododendron ponticum subsp. *baeticum* had an average abundance of 78.6%. In addition, four lianas (*Hedera helix*, *Lonicera periclymenum* subsp. *hispanica*, *Rubus ulmifolius*, *Smilax aspera*) were also present in all 20 sites; they had average abundance values higher than 50%, with the exception of *L. periclymenum* subsp. *hispanica* (16.5%). Six more taxa were recorded in 19 or 18 samples, showing average abundance values that ranged from 67.4% to 29.3%. They were the following trees or arborescent shrubs (in order of mean average abundance): *Quercus canariensis*, *Erica arborea*, *Frangula alnus* subsp. *baetica*, *Viburnum tinus*, *Quercus suber*, and the small shrub *Ruscus aculeatus*. Nine more taxa were recorded in 15–10 communities, with an average abundance ranging from 39.2–6.9%. They were the following trees or arborescent shrubs: *Phillyrea latifolia*, *Arbutus unedo*, *Crataegus monogyna* subsp. *brevispina*, *Laurus nobilis*, *Salix pedicellata*, *Ilex aquifolium*, and the shrubs *Ruscus hypophyllum* and *Erica scoparia* subsp. *scoparia*. The remaining 39 woody species occurred in < 10 (50%) sites (Appendix S1).

The Shannon–Wiener index (log_e basis) ranged from 2.26 to 3.25 (mean 2.59 ± 0.25). It was positive and significantly correlated with the species richness at each site ($r = 0.86$, $P < 0.05$).

Floristic and environmental gradients

Because the results of the ordination of the 20 riparian communities by their floristic composition (DCA) were similar to the results of the ordination constrained by the environmental variables (CCA), here we discuss only the CCA results. The CCA analysis combining the floristic matrix (59 species and 20 sites) and the environmental matrix (17 variables and 20 sites) resulted in a total variance (inertia) of

Table 3 Results of CCA analyses (only environmental variables with significant correlation values are indicated)

	CCA total (20 sites)		CCA preserved (18 sites)	
	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalue	0.241	0.178	0.200	0.135
Variance (%)	21.9	16.1	22.4	15.1
Correlation with environmental variables				
Overstorey cover	0.888	-0.092	0.220	-0.230
Altitude	0.523	0.658	-0.680	-0.235
Water flow	-0.013	-0.667	0.604	0.249
Soil pH	-0.427	-0.212	0.037	-0.230
Soil organic matter	-0.016	0.559	-0.510	-0.066
Gravel	-0.107	-0.530	0.490	0.044
Silt	0.036	0.441	-0.428	0.102
Potassium	-0.066	0.438	-0.420	-0.114
Calcium	-0.226	0.284	-0.314	-0.134
Phosphorus	0.109	0.431	0.369	0.335

1.10 (Table 3). The first CCA axis (22% of variance) was significantly correlated with the overstorey cover ($r = 0.89$). The axis separated out two sites at the left (negative) end of the axis: PTA and VAL. These two sites are degraded riparian forests, with low overstorey cover (32% in PTA; 68% in VAL) and have been colonized by a group of 10 woody species (not found in the other 18 sites) that are light-demanding and typical of drier shrublands, such as *Lavandula stoechas* subsp. *stoechas*, *Cistus crispus*, *Daphne gnidium*, *Phlomis purpurea* and *Calicotome villosa*. Because of the particular floristic composition of these two communities, they are considered as outliers in the analysis (following Sorensen's criterion for PTA and Euclidean distance for VAL; McCune & Mefford, 1999). Therefore we decided to carry out a new CCA analysis omitting these two sites and the 10 associated species.

The new CCA analysis of the undisturbed communities (49 species and 18 sites) resulted in a total variance (inertia) of 0.89 (Table 3). The first CCA axis (22% of variance) separates a group of five sites at the left (negative) end (PAL, MOR, ESC, PAS, JUN), and a group of four sites at the right (positive) end (HUV, PRO, GAR, ENM), the remaining nine sites having intermediate scores (Fig. 2). This first axis had a higher negative correlation with altitude (-0.68), organic matter (-0.51) and silt (-0.43), while the correlation was positive with water flow (0.60) and gravel (0.49). At one end of the gradient we found riparian communities in the upper course of rivers and streams, with a mean elevation of 658 m (the total average being 464 m): two of these (MOR and JUN) had the highest elevation (730 m), with low water flow (mean 1.4) and soils of fine texture and richer in organic matter (mean 10%) and available potassium (mean 204 mg kg⁻¹) compared with mean values for all 20 sites (Table 2). The woody species

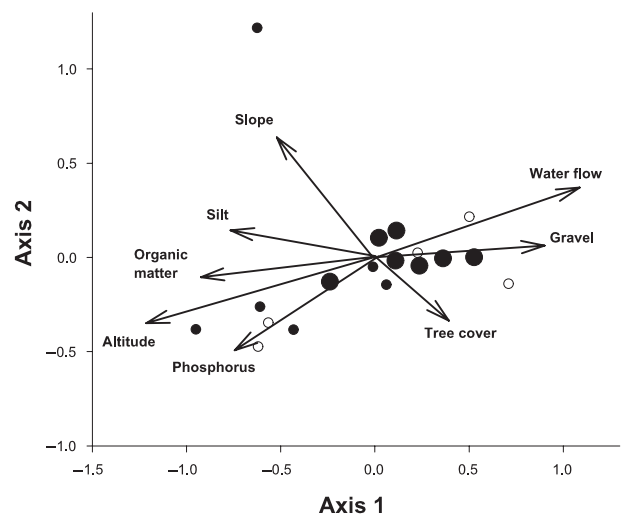


Figure 2 Results of the CCA analysis of 18 riparian communities with *Rhododendron ponticum* (excluding two deforested sites). Symbols represent the density of seedlings per site: 0–5 (○); 5–50 (●); 50–268 (●). Vectors indicate correlations (biplot scores) of environmental variables; for clarity values have been multiplied by four, only those with higher scores are represented.

associated (having highest negative scores) with this group of higher-altitude riparian communities are typical of moist forests, such as the trees *Ilex aquifolium*, *Salix pedicellata* and *Crataegus monogyna*, and the climbers *Lonicera periclymenum* and *Rubus ulmifolius*. The abundance of *R. ponticum* is very high in these sites (mean 93%) and thus has a relatively high negative score (14th among 49 species) for axis 1, despite being the common species for all 20 sites.

At the opposite end of the gradient, we found the riparian communities in the lower course of the rivers at a relatively lower altitude (mean 310 m a.s.l.), with a higher water flow (mean index 3.8), with soils of coarser texture (mean 67.5% gravel), and in general poorer in organic matter (mean 5.8%) and lower availability of potassium (mean 135 mg kg⁻¹; some low values, e.g. 53 mg kg⁻¹ in GAR). Associated with these sites were species (with higher positive scores) such as the climbers *Clematis flammula* and *Vitis vinifera*, the shrubs *Pistacia lentiscus* and *Myrtus communis*, and the riparian species *Nerium oleander*.

Ecological, historical and biogeographical patterns

From the whole pool of 59 woody taxa recorded in the 20 sites, 36 (61%) were assigned to the humid warm temperate (HWT) element, many of which were components of a widespread Neogene European vegetation: these are 20 trees or arborescent shrubs, 10 medium-small shrubs and six climbers (Appendix S1). At the community level, a mean of 18.8 HWT species were found, ranging from 25 (VAL) to 12 (PAL). The remaining 23 taxa (39%) were assigned to modern Mediterranean taxa (MM) origin, being two trees or arborescent shrubs, 20 medium-small shrubs and one climber (Appendix S1). The mean number of MM taxa in each community was 3.4, ranging from 14 (VAL) to none (MTE, ESC and JUN).

The HWT origin had higher importance than MM origin at the community level, according to the mean number of taxa per community sample ($t = 11.63$, $P < 0.001$), the cumulative local abundance ($t = 22.06$, $P < 0.001$), the frequency pattern ($\chi^2_{(4)} = 47.74$, $P < 0.001$) and the mean local abundance ($U_{36,23} = 137.5$, $P < 0.001$) (Table 4). The most frequent taxa

(those recorded in at least 50% of sites) in this set of riparian communities were of HWT origin, with the exception of *Salix pedicellata*. With regard to life form, 56% of the HWT taxa were trees and arborescent shrubs, while 87% of the MM taxa were medium and small shrubs. Almost all the climbers (86%) were of HWT origin.

The riparian communities studied had a high diversity of chorological types (Fig. 3). The widest distributions – Circum-Mediterranean (CM) with 13 taxa and Macaronesian-Mediterranean (MMC) with 12 taxa – were the most highly represented in the total species pool. Regional endemic taxa, with south Iberian-Tingitanian (SIT) or narrower distribution, were also well represented (eight taxa).

Separating by historical origin, HWT taxa had, in general, a wider distribution range than MM taxa; for example, 50% of HWT taxa display a range extending beyond the Mediterranean area (C + MEM + MMC + ME), but only 4% of MM taxa display that wide distribution. On the other hand, 39% of MM taxa are restricted to the western Mediterranean (INA + SIT + G), compared with 14% of HWT taxa having the same limited range. The cumulative proportion of the abundance of different chorological types was also different between historical HWT and MM origins (Fig. 3). HWT taxa of wider ranges (C + MEM + MMC + ME) made up to 48% of the total abundance within the average community sample, while western Mediterranean MM taxa of narrower range (INA + SIT + G) made up just 2%.

The distribution spectra of plant abundance at the community level (global; Fig. 3) is almost identical to the HWT taxa spectra, confirming the significance of the taxa with this origin in the riparian communities with which *R. ponticum* (a HWT taxon) is associated.

Endemism pattern

A total pool of eight woody endemic taxa was recorded in the 20 communities sampled, with a mean of 3.70 per site, and range from six to two. There were three endemic taxa of HWT origin (at subspecies level): *Frangula alnus* subsp. *baetica*, *Lonicera periclymenum* subsp. *hispanica*, and *R. pont-*

Table 4 Comparisons among plant abundance and plant diversity patterns of historical groups of angiosperm woody taxa and ferns in 20 *Rhododendron ponticum* communities from southern Spain

Taxon group	Plant abundance			Endemism abundance			Infra-generic diversity	
	<i>N</i>	Frequency (<i>n</i> = 20)	Average abundance (%)	<i>N</i>	Frequency (<i>n</i> = 20)	Average abundance (%)	Western Andalusia	Mediterranean region
Humid warm temperate angiosperms (HWT)	36	10.50 ± 6.87 ^a	19.75 ± 23.60 ^a	3	19.67 ± 0.58 ^a	47.27 ± 31.05 ^a	3.30 ± 3.82 ^a	16.9 ± 21.12 ^a
Modern Mediterranean angiosperms (MM)	23	2.87 ± 2.58 ^b	1.86 ± 1.78 ^b	5	3.00 ± 1.22 ^b	2.60 ± 1.33 ^b	6.43 ± 3.74 ^b	36.17 ± 40.78 ^b
Ferns	12	9.58 ± 6.63 ^a	14.06 ± 15.05 ^a	0	–	–	2.83 ± 3.43 ^a	10.50 ± 15.52 ^c

N, whole number of taxa recorded throughout the sampling; Frequency, mean number of sites where taxa were recorded; Average abundance, mean local abundance; Infra-generic diversity, mean number of species and subspecies for genera represented in groups at the geographical range indicated. Mean ± SD for the groups. Different letters indicate significant differences within columns.

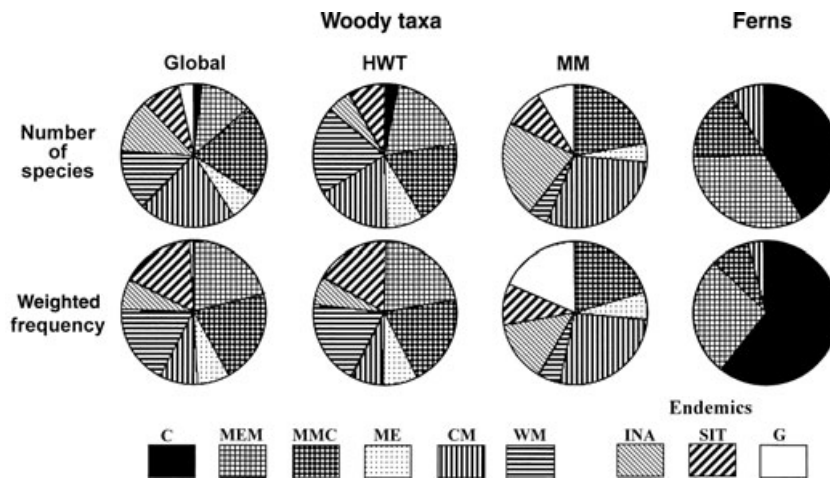


Figure 3 Chorological spectra of taxon groups in *Rhododendron ponticum* communities from southern Spain (see Materials and methods for full names of chorological types), calculated based on number of species (upper row) and weighted taxa number and abundance (lower row). Columns correspond to spectra of the woody plant community (Global), separated by groups of angiosperms according to historical origin (HWT, humid warm temperate; MM, modern Mediterranean); ferns in right-hand column.

icum subsp. *baeticum*; while five endemics had an MM origin: *Cytisus baeticus*, *C. striatus*, *C. tribracteolatus*, *Stauracanthus boivinii* and *Ulex borgiae*; within this MM group, two taxa – *C. tribracteolatus* and *U. borgiae* – had the narrowest, Gibraltarian endemic range.

Most riparian communities (17 from 20 sites) had three HWT endemic taxa (mean 2.9 ± 0.2) in their composition, while MM endemic taxa were rare (mean 0.7 ± 1.0 , being absent from 10 sites). The abundance of HWT endemic taxa (including *R. ponticum*) in the riparian communities was relatively high (mean $42.3 \pm 31.0\%$), compared with MM endemic taxa (mean $2.6 \pm 1.3\%$) (Table 4).

Taxonomic singularity

The mean taxonomic singularity of the 20 woody plant communities was 0.59, ranging from 0.48 (PTA) to 0.74 (JUN), at the western Andalusia level. When considering this index (inverse of number of species per genus) at a wider, Mediterranean region level the mean was 0.19, ranging from 0.13 (ESC) to 0.25 (MTE). The index of taxonomic singularity for each community was significantly correlated with the percentage of HWT taxa in the site ($r = 0.69$, $P < 0.001$), if considered at the western Andalusia level, but not at the larger Mediterranean region level ($r = 0.03$, $P \leq 0.9$).

One-way ANOVA showed significant differences in taxonomic singularity between HWT and MM historical groups of woody plants at both geographical levels ($F_{2,54} = 173.05$, $P < 0.001$ for the western Andalusia range; and $F_{2,54} = 105.22$, $P < 0.001$ for the Mediterranean region).

Fern components

A total of 12 species of ferns were recorded in the 20 sites (Appendix S1). The mean fern richness was 5.8 species per site. The most common fern species was *Pteridium aquilinum*, present in 19 plots with an average abundance of 50.3%. Other common ferns were *Asplenium onopteris*, *Osmunda regalis*, *Athyrium filix-femina* and *Asplenium billotii*. Ferns, as a whole,

were similar to HWT woody plants (Table 4) in terms of frequency pattern over the 20 sites ($\chi^2_{(4)} = 4.55$, $P = 0.34$) and average abundance per site ($U_{36,12} = 205.00$, $P = 0.79$).

Most of the fern species (nine out of 12) showed a wide distribution range, with none showing an endemic distribution range (Fig. 3). They show a low infra-generic diversity and similar taxonomic singularity pattern to that of the HWT woody taxa group at the western Andalusia level (Table 4).

Rhododendron ponticum population structure

Niche relationships between adults and seedlings

Seedling density (mean 24.0 ± 37.8 seedlings 100 m^{-2} ; 22.9 ± 36.1 small seedlings plus 1.1 ± 1.9 large seedlings 100 m^{-2}) was not correlated with adult density (mean 12.3 ± 10.1 individuals 100 m^{-2}) at the same sites (small seedling class: $r = 0.036$, $P = 0.881$, $n = 20$; large seedling class: $r = 0.099$, $P = 0.678$, $n = 20$). However, small and large seedling densities were highly and positively correlated between them ($r = 0.870$, $P < 0.001$, $n = 20$). The number of saplings (juveniles) was so small (only two juveniles were authenticated in the 20 populations sampled against 2487 adults in the census; Mejías *et al.*, 2002), and restricted to only two sites, that no reliable correlation analysis was possible.

Multiple regression analyses on adult and seedling density, with physiographic and edaphic variables, revealed contrasting patterns (Table 5). Adult density was significantly predicted by elevation (positively) and, marginally, by tree cover (negatively) and exposure (positively). Edaphic variables within the range and variability covered by the populations sampled did not significantly explain adult density in the whole model. However, some variables showed marginally significant partial correlations: pH, organic matter and available calcium. Total seedling density (summing up small and large seedling classes) was not explained by any of the physiographic or edaphic variables.

Seedling abundance was associated with particular habitats, which were not characterized by their abiotic features but were

Table 5 Results of multiple regression analyses of physiographic and edaphic variables on adult and seedling density of 20 *Rhododendron ponticum* populations from southern Spain

	Adult density	Total seedling density
Physiographic dependent variables		
Intercept	-6.573	-127.520
Channel width	0.113	3.347
Forest cover	-0.256 ($r = -0.499$, $P = 0.069$)	0.155
Aspect	3.807 ($r = 0.472$, $P = 0.088$)	1.553
Water flow	-0.411	11.738
Slope	-0.439	1.180
Altitude	0.049 ($r = 0.740$, $P = 0.002$)	-0.015
Bank enclosure	0.105	0.341
$F_{7,12}$	4.320	0.705
Adjusted R^2	0.550	0.291
P	0.013	0.669
Edaphic dependent variables		
Intercept	-367.538	331.155
pH	16.216 ($r = 0.561$, $P = 0.073$)	45.736
MO	2.242 ($r = 0.563$, $P = 0.071$)	0.253
P	0.784	-3.439
K	0.089	0.091
Ca	-0.014 ($r = -0.537$, $P = 0.088$)	-0.046
Mg	-0.036	0.087
Gravel	2.932	-5.802
Sand	2.981	-0.661
Silt	2.181	-1.011
Clay	3.960	-6.503
$F_{10,9}$	2.220	0.745
Adjusted R^2	0.391	-0.155
P	0.123	0.675

Adult density range 0.9–38 individuals 100 m⁻²; total seedling density range 0–134.4 seedlings 100 m⁻² (nil value in five sites). Significant ($P < 0.05$) or marginally significant values ($P < 0.1$) in bold type.

clearly indicated by the presence of other plants. In particular, a continuous carpet of mosses, liverworts, or a mixture of these harboured most of the seedlings found, being also the most frequent habitats among the populations sampled (Table 6). Occasionally seedlings were found on the spongy, thick basal stems of *Osmunda regalis* ferns. Although this microhabitat contained many seedlings, representing a 'safe site' (*sensu* Harper, 1977) for *R. ponticum* seedling emergence and survival,

Table 6 Frequency and density of seedlings of *Rhododendron ponticum* (mean \pm SD) in different microhabitats of 20 riparian forest sites from southern Spain

Microhabitat	Frequency ($n = 20$)	Density (n seedlings 100 m ⁻²)
Bare soil	5	1.12 \pm 0.58
Moss community	14	10.62 \pm 4.11
Liverwort community	7	8.51 \pm 5.06
Moss + liverwort community	3	2.79 \pm 2.08
Fern (<i>Osmunda regalis</i>) clump	1	0.32 \pm 0.32

orship, it was very scarce and thus the available regeneration area was very limited.

Plant architecture and size classes in selected populations

Populations were significantly different in terms of the mean values of all variables measured, both when taken together (MANOVA: Wilks' lambda = 0.34, $P < 0.001$) or independently (the effect was significant in all variables, $0.002 < P < 0.001$). The number of basal stems per plant was highly variable within populations: plants were either multi- or single-stemmed (tree-like), independently of the maximum age of the thickest stem.

The relationship between number of growth rings and size-related variables indicated that plant growth showed some variability among populations. In most populations the slope (b) of the regression was similar (b values for maximum and mean stem perimeter ranged from 0.225–0.486; for stem height 3.455–6.061). The main exception was the population GAR, which did not show any significant relationship between number of growth rings and size of plants; and population JUN, which showed a gently rising, yet statistically significant slope, highlighting a slower growth rate in terms of maximum and mean stem perimeter (b : 0.063 and 0.166).

The frequency distribution of size/age classes was also variable among populations. Thus populations at the northern range of the region (ENM, MOR and especially MTE) showed the most even distribution (Fig. 4), reaching a maximum value of 120 growth rings in the latter, whereas other populations (especially GAR) showed a highly concentrated distribution to lower size/age classes.

DISCUSSION

Ecology of Iberian *Rhododendron ponticum*

The habitat of *R. ponticum* subsp. *baeticum* in southern Spain is mainly restricted to azonal riparian forests on acidic soils (pH range 4.0–6.4), originating from Oligo-Miocene sandstones; this preference for acidic soils is common in the genus *Rhododendron* (Williams *et al.*, 1990). The riparian communities associated with *R. ponticum* are established preferentially on the relatively steep (mean slope 17%) upper or middle reaches of permanent and temporary mountain streams forming narrow gorges (mean bank angle 125°), at a mid-range altitude (mean 464 m). Portuguese populations of *Rhododendron* (western and south-western Iberian Peninsula) show a similar habitat (Dias & Nogueira, 1973–74; Sales, 1995). Exceptionally, extensive populations can be established in the understorey of *Quercus canariensis* forests, favoured by the high incidence of coastal orographical fogs (Rivas-Goday, 1968; Jurado, 2002).

Forest overstorey cover was a main factor determining the variation in species composition within the 20 sites studied. In general, riparian understorey species, and in particular *R. ponticum* (at least under Mediterranean climate conditions), are highly dependent on moist and shaded forest conditions.

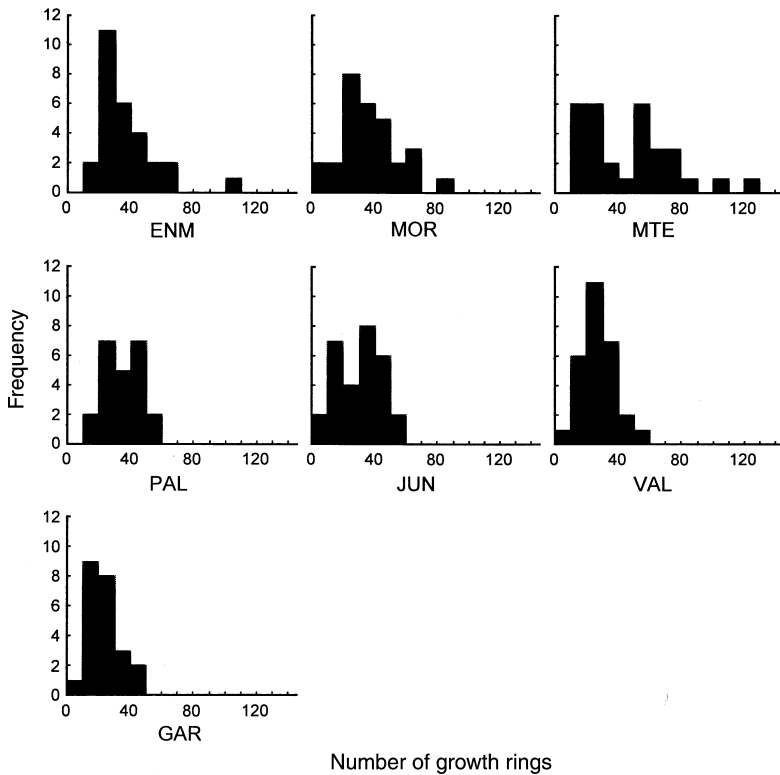


Figure 4 Frequency distribution of growth rings in seven populations of *Rhododendron ponticum*.

After disturbance of riparian habitats, in particular of the tree overstorey, shrub species from neighbouring drier and light-exposed habitats colonize and replace most of the typical riparian species, as shown in two of the sites studied.

In riparian habitats, *R. ponticum* meets its ecological optimum in the area, often being the dominant species of the forest understorey (it had the highest abundance in 15 of the 20 sites studied). This dominance and singularity probably inspired phytosociologists to name this plant community *Frangulo-Rhododendro baetici* (Díez Garretas *et al.*, 1986). This type of community occupies *c.* 800 ha in the Aljibe Mountains region (with *c.* 170,000 ha) (B. Cabezudo, personal communication). Local dominance of *Rhododendron* in the understorey has also been reported for Portuguese riparian forests (Dias & Nogueira, 1973–74).

The earliest well documented records of *R. ponticum*-like taxa date from the Miocene of Transcaucasia (Mai, 1995; C. Humphries, personal communication), but the wider distribution of the species prior to the present disjunction appears to be a Pleistocene phenomenon (Tralau, 1963). *Rhododendron ponticum* probably also had a considerably larger distribution range in the Iberian Peninsula during recent geological times, as *Rhododendron*-type pollen has been recorded in some Pleistocene deposits. Romariz (1950) indicated the presence of fossil pollen grains in deposits from coast-facing areas of central and south-western Portugal (although these observations have been questioned; Sales, 1995). Pons & Reille (1988) also found this pollen type in peat bog deposits from Padul in south-eastern Spain (37° N 3°40' W; Fig. 1), dating the record to the Middle Würm (*c.* 40,000–45,000 yr ago) and previous

Pleistocene periods. Most probably these pollen records correspond to *R. ponticum*, as closer populations of the remaining Iberian rhododendron species (*R. ferrugineum*) grow in the Pyrenean Range (northern Spain) at present, quite far from the deposit sites (J.S. Carrión, personal communication). Pollen of these two species can be distinguished by the size of the tetrads and pollen morphology (Díez & Fernández, 1989).

In the West Mediterranean Basin, *R. ponticum* has not been found in the mountains of northern Morocco, despite being very close to the dense populations of southern Spain (separated by the Strait of Gibraltar by 14 km), and having high affinities in climate, geology and flora (Didon *et al.*, 1973; Deil, 1990; Valdés, 1991; Ojeda *et al.*, 1996; Marañón *et al.*, 1999; Ajbilou *et al.*, 2006). Few palaeopollenological studies have been carried out in the region (but cf. Reille, 1977), and it is difficult to establish hypotheses concerning the origin and antiquity of this absence of *R. ponticum* from the mountains of northern Morocco.

The narrow habitat range of *R. ponticum* in the Iberian Peninsula strongly contrasts with the wide ecological amplitude reported for the eastern Mediterranean and Euxinian areas. The vicariant *R. ponticum* subsp. *ponticum*, usually associated with *Fagus* forests (Stevens, 1978), but exceptionally with *Pinus* forests (Lebanon; Browicz, 1983), has been extensively inventoried in lowland hardwood forests, montane deciduous evergreen forests, high montane mixed forests up to 2100 m a.s.l. (Denk *et al.*, 2001), and grass-rich *Sphagnum* marshes (GGC, 1996) in the Colchic region (Transcaucasia). These differences in the amplitude of habitats between western

and eastern populations of *R. ponticum* could be explained, in part, by their different ecological behaviour (Erfmeier & Bruehlheide, 2005), and more likely because the present ecological (mainly climatic) conditions (Fig. 1) are more favourable for this plant in the Euxinian and in the eastern Mediterranean areas (Mejías *et al.*, 2002).

In general, ecological factors such as continued moisture availability and varied topography appear to provide long-term stable habitats buffering Quaternary climatic variability where older species can survive (Fjeldså & Lovett, 1997; Hewitt, 2000; Tzedakis *et al.*, 2002). In this context, the Black Sea area appears to provide suitable habitats for a number of humid warm temperate relicts, and in particular for *R. ponticum*, which is reflected in its wide ecological amplitude there. In contrast, Iberian populations are virtually restricted to riparian forest habitats. These azonal vegetation habitats have been sometimes claimed as refuges from Quaternary oscillations (Udra & Khokhryakov, 1995; Aide & Rivera, 1998), benefiting from their comparatively favourable microclimate.

Paradoxically, *R. ponticum* is currently an invasive species in western Europe, causing ecological and conservation problems. Introduced plants from southern Spain (Milne & Abbott, 2000) have become aggressive invaders, threatening biodiversity in woodlands, heathlands and peatlands (Cross, 1981; Mitchell *et al.*, 1998). The contrast between the lack of regeneration in the southern Iberian native habitats (where they persist as relicts) and the aggressive colonizing ability in the moister new areas supports the hypothesis that *R. ponticum* is currently limited by unfavourable conditions, probably by seasonal drought, and not by biological or genetic degradation.

Biogeographical and historical patterns

Rhododendron ponticum communities in southern Spain show a relatively high species diversity compared with the understorey of temperate European forests (Grubb, 1987). At the landscape level, riparian communities are not as species-rich as the shrub understorey of *Q. suber* forests in middle slopes, nor as endemic species-rich as the open heathlands on mountain ridges, but they harbour a diverse group of woody taxa of high taxonomic singularity (Ojeda *et al.*, 1996, 2000). From a biogeographical point of view, the most remarkable feature of *R. ponticum* communities is the high proportion of HWT taxa. Almost all the 19 most common taxa (present in at least 50% of communities sampled) showed HWT origin, with the exception of *S. pedicellata* (which, according to Thiébaud (2002), should be considered an old origin taxa). In addition, the scarce presence of MM taxa appears to be positively associated with disturbance.

Most of the communities sampled ought to be evaluated not exclusively from the perspective of relict taxa areas, but also as possible representatives of Late Neogene plant communities. In general, HWT taxa are not rare in Mediterranean riparian communities, with several of the HWT taxa inventoried in this study being common as riparian components (*Hedera helix*, *Myrtus communis*, *Nerium oleander*, *Ruscus aculeatus*, *Rubus*

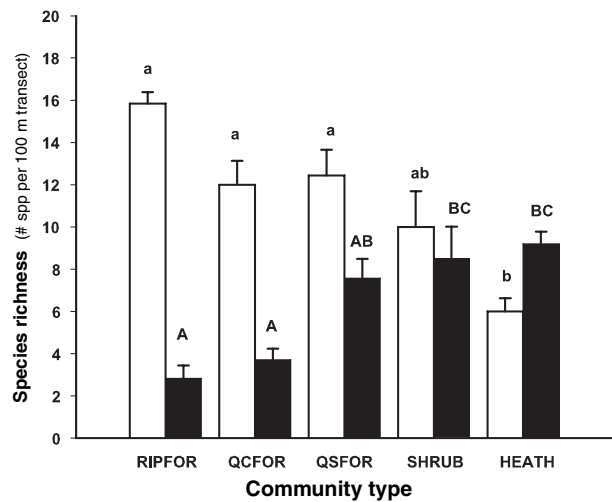


Figure 5 Comparative abundance of the two groups of woody angiosperms of different origin (white bars, humid warm temperate; black bars, modern Mediterranean) in five main vegetation types of the Aljibe Mountains (RIPFOR, riparian forest; QCFOR, *Quercus canariensis* forest; QSFOR, *Quercus suber* forest; SHRUB, limestone shrubland; HEATH, heathland; data from Garrido & Hidalgo, 1998). Different letters represent significant differences between vegetation types according to ANOVA.

ulmifolius, *Smilax aspera*, *Viburnum tinus*, *Vitis vinifera*, etc.). Compared with other vegetation units in the area, the highest diversity of the HWT historical group was concentrated in riparian communities (Fig. 5; Appendix S2). The unusual and extensive *Rhododendron* community from Los Llanos del Juncal (JUN), not associated with any water source, is very rare in the western Mediterranean area. In its composition of deciduous and evergreen trees and shrubs, and the high diversity of lianas, it resembles physiognomically forest types that were common in large parts of Europe in the Late Neogene. Its rarity and biogeographical significance are worthy of a focused conservation strategy for the whole area.

Apart from the high contrast in species richness and plant abundance, historical groups of woody taxa also show differences of general pattern in the remaining parameters assessing plant diversity for the communities recorded. First, the frequency of endemism, endemism narrowness, and taxonomic category level of endemics are higher in the MM taxa group (HWT endemics mainly show differentiation at a subspecies level as a result of vicariance); second, infra-generic diversification is usually lower for the HWT element (17 of 29 HWT genera are monospecific at the western Andalusia level, whereas only one of 16 genera were in the MM group). In addition, contrasted typological habit scopes are found in the groups (Appendix S1). This reflects differences in evolutionary histories that reinforce the hypothesis of conservatism in climatic requirements of relict taxa (Huntley *et al.*, 1989; Prentice *et al.*, 1991; Chuine & Beaubien, 2001; Davis & Shaw, 2001; Svenning, 2003). Fern and HWT taxa groups showed remarkable similarities in vegetation components and diversity patterns, indicating some parallelism in evolutionary histories.

In fact, species diversity of fern communities is also favoured in mid-altitude wet mountains with low soil fertility (Barrington, 1993; Richard *et al.*, 2000).

Demographic decline of *Rhododendron ponticum* in native areas

Adults of *R. ponticum* in southern Spain are long-lived, with a large lignotuber allowing vigorous resprouting (James, 1984) and single stems more than a century old. The contrasted pattern between microhabitats of seedlings and adults can be explained by two independent factors. First, the regeneration niche of the species may have changed over time, which could possibly be due to the longevity of the plants. Second, there may be a difference between habitat requirements for different age classes (see example of changing light-requirements in tropical species, Poorter *et al.*, 2005), so that only a few seedlings germinate and grow under conditions suitable for survival and establishment.

A remarkable issue of population structure concerns the lack of juveniles. Most small individuals encountered were, in fact, resprouted ramets, which are relatively old. The lack of middle age classes also precluded a proper demographic analysis through the transition probabilities between demographic stages (Caswell, 2001). The possible decline of populations due to a lack of juveniles could be compensated by the long-lived adults and very sporadic recruitment episodes. During a recent survey of 240 marked adult plants, c. 10% actually died (after 8 years) due to a mixture of senescence and drought episodes during that period. An additional number of plants appeared to have died but resprouted after heavy rains (J.A.M. and J.A., unpublished data). As no apparent recruitment of adults from saplings was observed in the survey, we can extrapolate a decline, at least for this short period, in concordance with a U-shaped demographic structure. Our results are consistent with those found previously in a single population, where we marked up to 800 emerged seedlings and documented complete mortality in four years (Mejías *et al.*, 2002). These findings are also in agreement with data reported from the relict (Iberia, Caucasus) and the invasive (British Isles) ranges. In native areas, populations were older and seedling recruitment very scarce, whereas in Ireland, seedlings and even saplings were quite common (Erfmeier & Bruelheide, 2004). These authors also reported differences in the frequency of vegetative reproduction and clonality (see also Esen & Zedaker, 2004), with the Iberian populations showing the comparatively lowest clonality values. However, the importance of clonality in the study area has been demonstrated recently by DNA microsatellite-based screening, with individuals (ramets) sampled as far as 20 m apart (J.A. and co-workers, unpublished data).

Our survey also revealed a very restricted habitat for seedlings, with most found on carpets of mosses and/or liverworts. Although we do not have data on the abiotic features of these microsites, it seems plausible to suggest that continuous water availability was the key factor, as some

watering experiments have demonstrated (J.A.M. and co-workers, unpublished data). In the study area, these microsites retain water for longer than the remaining surfaces. In some sense they could represent a particular case of positive interaction (facilitation) among plants (Callaway, 1995), although the final fate of most seedlings is death, caused either by summer drought when mosses and liverworts wither, or by flooding from strong winter rains. At present, this type of substrate is too scarce in the area to offer opportunities for real recruitment of new individuals.

Many relict species frequently show narrow actual niches due to loss of appropriate environmental conditions. However, the variety of growth patterns shown by adult plants of *R. ponticum* among and within native populations contrasts with the more homogeneous structure reported in invasive populations (Erfmeier & Bruelheide, 2004). Probably this native heterogeneity depends on unequal responses to limiting environmental conditions, but also on differences in site (and microsite) limitations. Independently of the genetic basis of this plastic response to differences in habitat conditions, it should confer on the adults a deal of resilience from environmental changes that might, in part, explain their persistence. In extreme cases this resilience is achieved by resprouting after severe drought. The lack of coupling between seedling and adult stages is possibly due to the longevity of plants, lasting over several centuries, and witnessing past climatic changes and more favourable conditions for recruitment. Therefore *R. ponticum* in its relict western range represents a paradigmatic case of the persistence pathway by both longevity and resprouting (*sensu* García & Zamora, 2003) for avoiding extinction under strong abiotic stress.

The Aljibe Mountains as a *Rhododendron ponticum* refuge

If we compare the narrow habitat range of *R. ponticum* in the southern Iberian Peninsula and its remarkable ubiquity in other regions (Cross, 1975, 1981; Mitchell *et al.*, 1998; Denk *et al.*, 2001), we can conclude that the ecological requirements of the species do not fit the conditions currently found in the Aljibe Mountains. Seasonal water stress of a Mediterranean-type climate appears to be the main restrictive factor, determining a precarious recruitment of juveniles. In contrast, adults do well in undisturbed riparian forests. The maintenance of community structure, basically a mixture of trees, arborescent shrubs and climbers of old origin, appears to be essential for the persistence of *R. ponticum* and other relict components in the area. From an applied perspective, results from this study will contribute to the design of conservation strategies in *R. ponticum*'s native region, and to the planning of invasiveness control programmes for *R. ponticum* in the affected Atlantic areas of Europe.

The communities studied must be considered as refuges for *R. ponticum*, where seasonality endurance is possible but expansion is strictly prevented. The future of the remnant

Rhododendron populations depends on forthcoming climate scenarios. Current predictions of increasing aridity and temperatures in the Mediterranean area (IPCC, 2001) are expected to affect *R. ponticum* regeneration negatively, with the decline of extant populations becoming more acute. In a long-term perspective, if the species persists in the area, supposed forthcoming periods of humid and temperate climate in the next glacial cycle will be a determinant of better ecological fit, and probably of expansion processes during these favourable periods (Hewitt, 1996, 2000). In contrast, eastern populations appear to have a more promising outlook, given the absence of dry hot seasons and the higher environmental heterogeneity in the area.

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SUPPLEMENTARY MATERIAL

The following material is available for this article:

Appendix S1 Taxa recorded in the plant communities associated with *Rhododendron ponticum* sampling in southern Spain.

Appendix S2 Mean cover and frequency of taxa assumed to belong to the humid warm temperate element in the vegetation units of river Hozgarganta basin (Los Alcornocales Natural Park).

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BIOSKETCHES

José A. Mejías is a lecturer in the Department of Plant Biology and Ecology at the University of Seville. His research interests include biosystematics and the reproductive biology of angiosperms. In recent years he has focused on the analysis of factors determining area restriction and extinction in endangered Mediterranean plants.

Juan Arroyo is also a lecturer in the Department of Plant Biology and Ecology at the University of Seville. His research focuses on plant reproductive ecology and biogeography in the Mediterranean area.

Teodoro Marañón is a plant ecologist in the Department of Geoecology, IRNA, CSIC in Seville, Spain. His current work focuses on ecological factors determining forest biodiversity patterns, and on the ecology of regeneration processes.

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