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ORIGINAL ARTICLE

Environmental and human factors influencing rare plant local occurrence, extinction and persistence: a 115-year study in the Mediterranean region

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ABSTRACT

Aim Assessing whether environmental and human factors influenced the spatial distribution and the dynamics of regionally rare plant species since the late nineteenth century, and whether these spatial and temporal patterns of rare species occurrences differ according to their chorology (level of endemism and biogeographic affinity).

Location An area extending over 6250 km^2 in the French Mediterranean Region.

Methods We used two botanical surveys achieved in 1886 and in 2001, and considered species rare if occurring in only one or two sites in the study area. Each rare species was assigned to a group of endemism level (restricted endemic, non-endemic), and of biogeographic affinity (Mediterranean, South/Central European, Mountain, Eurosiberian). A 1 × 1 km grid was applied to the study zone. Generalized linear models were developed to study the spatial distribution and the fate of rare species occurrences (local extinction vs. local persistence between 1886 and 2001), as a function of environmental and human variables. Multivariate analyses were used to test whether the spatial distribution and the fate of rare species occurrences differed according to their chorology.

Results In 2001, rare species as a whole tended to occur at higher altitude, in zones dominated by semi-natural open habitats, and where cultivated area had decreased in the last 30 years. Between 1886 and 2001, rare species were the most prone to local extinction in zones where human population density, cultivated area and livestock density had increased the most. Between 1886 and 2001, rare species had a higher probability of local persistence in zones of high altitude and steep slope, on basic bedrocks and with low cultivated area. Rare species with Mountain and Eurosiberian affinities occurred in marginal habitats in the study region, i.e. on gneiss-micaschist bedrocks and at high altitudes, whereas Mediterranean and South/Central European rare species occupied more varied environmental conditions. Between 1886 and 2001, Eurosiberian rare species showed high rates of local extinction whereas Mediterranean rare species had a significantly higher probability of local persistence. Restricted endemic species mostly occurred in zones of high slope, low human population density, and where cultivated area had decreased in the last 30 years. Occurrences of restricted endemics remained significantly stable between 1886 and 2001.

Main conclusions Environmental and land-use changes that occurred over the twentieth century in the Mediterranean Basin had significant impacts on the spatial distribution and on the long-term dynamics of rare species occurrences. Urbanization and recent agriculture intensification, occurring mainly in coastal plains and littoral zones, caused most local extinctions of rare species from 1886 to 2001. Local populations of Eurosiberian species, which reach their range limits in marginal zones of the Mediterranean, also appear to be highly vulnerable.

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Conversely, most restricted endemic species occur in habitats with harsh topography and low human disturbance and have a higher potential of local persistence.

Keywords

Chorology, endemism, generalized linear models, land-use change, local extinction, Mediterranean Basin, outlying mean index, rarity.

INTRODUCTION

Human activities currently cause dramatic losses of species from local to global scale (Pimm, 2002). These extinctions result from a variety of causes, including habitat modification and destruction, biological invasions and climate change (Pimm, 1996; Vitousek *et al.*, 1997; Parmesan & Yohe, 2003). Identifying the geographical patterns of distribution of rare or endangered species is thus crucial for understanding how human activities threaten biodiversity, and ultimately for prioritizing sites or species to preserve (Prendergast *et al.*, 1993a). Hotspots of biodiversity and rarity have been accurately matched at global or continental scale (Myers *et al.*, 2000; Dobson *et al.*, 2001). However, in order to understand the mechanisms by which human activities and land-use changes can affect rare species persistence or extinction, more spatial studies must be conducted at intermediate scales, i.e. within small biogeographic region or provinces (Heikkinen, 1998; Luoto, 2000).

Land use and environmental changes pose a serious threat to biodiversity in the Mediterranean Basin (Sala *et al.*, 2000). The Mediterranean flora consists of *c.* 25,000 vascular plant species, of which *c.* 59% are restricted endemics (Greuter, 1991). Mediterranean regional assemblages of plant species result from complex interactions between geological history and climatic influences: many Eurosiberian taxa reach their range limits in the Mediterranean Region where they co-occur with Mediterranean taxa, South or Central European taxa, and mountain taxa (Quézel, 1985). Since 8500 yr BP, Mediterranean ecosystems have been continuously influenced by human activities such as extensive agriculture and animal breeding (Pons & Quézel, 1985). Indeed, the intense land-use changes that have occurred during the twentieth century have had profound consequences on most Mediterranean landscapes (Lepart & Debussche, 1992). Hinterlands have been subject to dramatic rural depopulation, resulting in the spread of woodlands, and in the decrease of many semi-natural open habitats, whereas rapid urbanization and intensification of agriculture have occurred in lowlands and coastal areas, reducing wetland habitats to small fragments (Pons & Quézel, 1985; Debussche *et al.*, 1999).

A critical task in the Mediterranean Basin is thus to identify the land use and environmental changes that most threaten rare species populations. However, rare species do not constitute an ecologically and biologically consistent assemblage, making it difficult to provide generalized guidelines for their conservation (Fiedler, 1986; Gitzendanner & Soltis, 2000). First, all species which are rare in a given region and on a given date may have experienced contrasting histories of population dynamics: some may have persisted as rare species over a long period of time, while other rare species may result from more recent and abrupt rarefaction (Lawton, 1995). It is thus important to discriminate environmental conditions that support historically stable rare species from those that support currently declining rare species. Second, at regional scale, plant species response to environmental factors can differ according to their chorology, i.e. their biogeographical affinities (Thuiller *et al.*, 2003) or their geographical range size (Anderson, 1994; McGlone *et al.*, 2001). Mediterranean regional floras are very complex; therefore, it would be valuable to determine which components of the Mediterranean rare flora experience the most serious risks of regression under the current scenarios of environmental and land-use changes.

In this study, we compared 115-year-old and contemporary records of rare plant species distribution in a French Mediterranean region, to assess the effects of environmental factors, human activities and land-use changes on the spatial distribution and the dynamics of regionally rare plant species since the late nineteenth century. Rare species were defined as species present in one or two occurrences in the Hérault département, an administrative subdivision which covers 6250 km^2 in southern France. We addressed the following questions: (i) How did environmental and human factors affect the spatial distribution and the fate (local persistence vs. local extinction) of rare species occurrences from 1886 to 2001? (ii) Do these spatial and temporal patterns differ for rare species with different distribution patterns in Europe (i.e. according to their level of endemism and their biogeographic affinities)?

MATERIALS AND METHODS

Study area

Hérault is an administrative subdivision covering 6250 km^2 in southern France, from the Mediterranean seashore to the southern mountain ranges of the Massif Central (Fig. 1). Its vascular flora is composed of *c.* 2200 native species of phanerogams and ferns, i.e. 55% of the flora of France in only 1.1% of the French territory. The climate is mainly

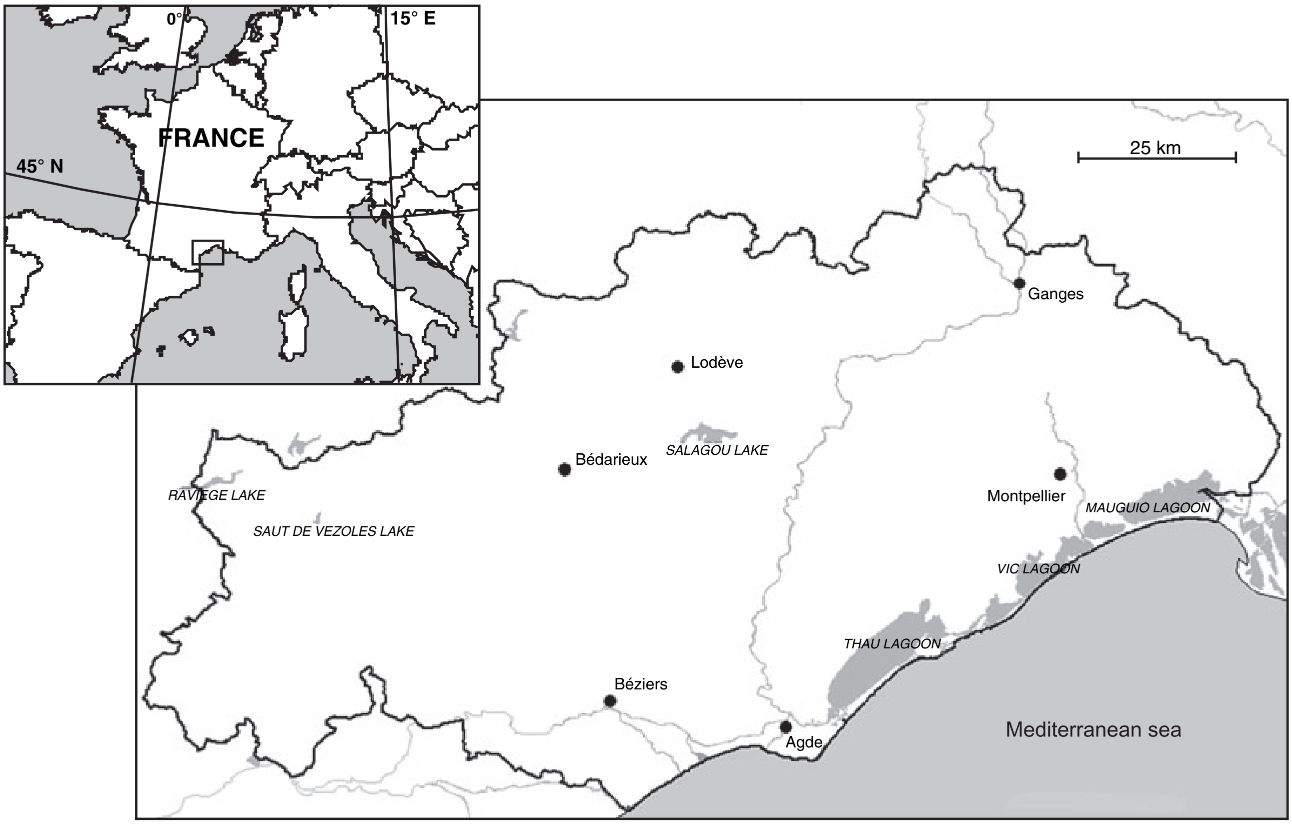

Figure 1 Geographical location of the study area. Names of main cities, lake and lagoons are given.

Mediterranean, with a dry and hot summer and precipitations mostly occurring, sometimes in large amounts, in autumn and in spring. However, the north-western part of Hérault experiences oceanic influences, with a moister (and cooler) summer period. Frost occurs each year, even near the coast. Important gradients of rainfall and temperature are observed with distance from the sea and towards higher elevation (i.e. up to 1205 m a.s.l.). Bedrocks have diverse origins: sedimentary bedrocks (limestone, dolomite and marl) occur at low altitude and on the north-eastern part of Hérault, whereas metamorphic (schist) and intrusive (granite) bedrocks mainly occur on the north-western and highest part (Dugrand, 1971). Basalt outcrops can occur very locally: these zones generally harbour particular habitats (e.g. temporary ponds) of special importance for several rare plants.

The landscape of Hérault is highly representative of most Mediterranean landscapes in Europe, because it results from long-lasting interactions between human activities and ecological factors, and has experienced dramatic changes during the twentieth century (Lepart & Debussche, 1992). During the nineteenth century, landscapes were still shaped by traditional human activities, mainly sheep breeding, extensive farming, and forest clearing. The landscapes were thus composed of a mosaic of open shrublands, grasslands and extensive crops, with rare dense woodlands occurring in hardly accessible areas. Over the twentieth century, because of a decrease in traditional activities and dramatic rural depopulation, hinterlands have experienced important forest spread by secondary succession and by re-afforestation of non-native tree species (Debussche *et al.*, 1999). Conversely, in the second part of the twentieth century, rapid urbanization has occurred at the periphery of main towns, while agriculture and tourism have strongly intensified in lower and coastal areas.

Species data sets

The surveys carried out by Loret & Barrandon (hereafter L&B, 1886) and by the National Botanical Conservatory in the Mediterranean (hereafter CBNMP, 2001) respectively recorded the presence of 2038 and 2162 native plant species in Hérault. Our study focused on the rarest species recorded in Hérault in 1886 and/or 2001, defined as species with one or two occurrences. This threshold of two occurrences was not chosen arbitrarily. The geographical location of species occurrences in 1886 were precisely reported by L&B only for species present in one and two sites. The same criterion was thus applied in the 2001 survey to delimitate the actual sample of rare species. Only species unambiguously validated by the nomenclature of *Flora Europaea* were considered (Tutin *et al.*, 1964–1993). Taxonomic synonymy between the two surveys was checked using the *Synonymy Index of the French Flora* (Kerguélen, 1993) and *Flora Europaea* (Tutin *et al.*, 1964–1993). The exsiccates of the herbarium of L&B (deposited in the Botanical Institute of Montpellier, MPU, France) were examined when necessary.

We thus retained 237 rare species (for 332 occurrences) from the survey of L&B and 214 rare species (for 312 occurrences) from the survey of the CBNMP, with 84 rare species common to the two dates.

Rare species occurrences in 1886 and in 2001 were georeferenced under ARCVIEW GIS 3.2a (ESRI Inc., Redlands, CA, USA), using digitized maps of 1/25,000 scale (National Geographic Institute, IGN, Paris, France). The comparison of the 1886 and 2001 layers allowed us to identify: (a) which rare species occurrences known in 1886 still existed in 2001 (local persistence); (b) which rare species occurrences known in 1886 were extinct in 2001 (local extinction); and (c) which rare species occurrences known in 2001 did not exist in 1886 (local appearance).

Within the pool of rare species, we separately examined restricted endemic species, defined as species occurring in no more than two countries bordering southern France. Each rare species was also assigned to a group of biogeographic affinity according to Coste (1900–1906), Greuter *et al.* (1984–1989), and Tutin *et al.* (1964–1993), as follows:

(1) Mediterranean/sub-Mediterranean species, which occur in Mediterranean Europe and often in North Africa, and rarely extend beyond. For some of these species, Hérault constitutes their northern limit of distribution.

(2) South/Central European species, which occur in Southern and Central Europe, and often in North Africa and Western Asia.

(3) Mountain species, which occur in mountain chains of Europe and possibly in Boreal Europe.

(4) Eurosiberian species, which are largely distributed throughout Europe and are often present in Asia, but rarely occur in the Mediterranean Region.

Sampling bias

Spatial variation in sampling effort can introduce important biases in the study of species distribution (Prendergast *et al.*, 1993b). As it was unlikely that L&B uniformly prospected the study area, Denelle *et al.* (1995) have quantified L&B prospecting effort throughout Hérault (Table 1). We georeferenced Denelle *et al.*'s (1995) data of prospecting effort and included it as an explanatory variable in the models of rare species distribution (see numerical analyses). Since the CBNMP survey was carried out in collaboration with a large network of experienced field botanists, we considered that the prospecting effort was homogeneous for the 2001 survey. Moreover, 1886 rare species occurrences had all been checked on the field at the occasion of the 2001 survey so that pseudo-extinctions are highly unlikely in our data set.

Physical, human and land use variables

Many physical variables can influence plant species distributions. We selected bedrock, altitude and slope (Table 1) because these three variables are known to broadly influence plant species distribution on a mesoscale (White & Miller, 1988; Heikkinen, 1998) and to be highly correlated with many other environmental variables (e.g. altitude is correlated with mean annual temperature or rainfall in the study region). We digitized the geological map of Hérault (adapted from Dugrand, 1971), with the nine following bedrock types: (a) alluvial/colluvial deposits, (b) limestone, (c) dolomite/chert limestone, (d) marl/marly limestone, (e) sandstone, (f) shale/quartzite, (g) gneiss/mica-schist, (h) granite and (i) basalt. It was necessary to use such separate bedrock categories since geology largely contributes to environmental heterogeneity in Mediterranean regions and since unusual bedrocks often support rare or endemic plants. Altitude and mean slope were derived from a digital elevation model (50-m resolution, provided by SIG Languedoc-Roussillon, MTD, Montpellier, France). We did not use any variable of environmental heterogeneity such as altitude range or slope variance since preliminary analyses showed that such variables were strongly correlated with mean slope. Thus, the use of mean slope as an explanatory variable allowed to capture the topographic heterogeneity of landscapes.

To quantify the spatial distribution of human population and the temporal changes in this distribution, we digitized data of human population in the 343 communes (smallest French administrative subdivision, ranging from 1.5 to 12 km^2) of Hérault, using the National Demographic Censuses of 1881, 1954 and 1999 (National Institute of Statistics and Economical Studies, INSEE, Montpellier, France). Under ARCVIEW GIS, boundaries of communes were used in vector format to calculate human population density in each commune of Hérault in 1881, 1954 and 1999, and to calculate the change in human population density in each commune from 1881 to 1999 and from 1954 to 1999 (Table 1).

Since the nomenclature of Agricultural National Censuses (provided by Agreste, Paris, France) has changed, comparable agriculture data was only available from 1970 to 2000. For each date, we selected three synthetic variables to describe agricultural practices in each of the 343 communes of Hérault: (i) area covered by permanent grassland and heathland (i.e. open semi-natural habitats devoted to feed livestock), (ii) total cultivated area, and (iii) size of total livestock (ovine, caprine and bovine head number). Under ARCVIEW GIS, these variables were normalized by the commune area (Table 1) and we also quantified the strength of change in these variables between 1970 and 2000 (Table 1). In the Mediterranean, most trends in agricultural practices were detectable in the 1950s and accelerated afterwards. The 1970–2000 period was the most intense in terms of agricultural changes and was thus adequate to characterize most agricultural changes that occurred since the World War II in the study region.

Numerical analyses

The study of spatial pattern of rare species richness was performed using a grid of 1 × 1 km cells. In each grid square, we calculated the mean value of each quantitative explicative variable (listed in Table 1) and the dominant bedrock type

Table 1 Description of explanatory variables used to model rare species richness in Hérault. See text for further explanations on the variables

Variables	Code	Derivation/calculation	Source
Sampling			
Prospecting effort for 1886 survey (%)	Prop_Intens	Percentage of prospected communes*	Denelle *et al.* (1995)
Physical			
Bedrock	Bedrock	Nine classes (see text)	Adapted from Dugrand (1971)
Mean slope angle (°)	Slope_mean	Derived with ARCVIEW 3D analyst	Digital elevation model (50 × 50 m)
Altitude (m)	Alti_Mean	Derived with ARCVIEW 3D analyst	Digital elevation model (50 × 50 m)
Human population			
Population density in 1881 (hab nb km^{-2})	PopDens1881	Inhabitants number per commune/commune area	1881 National census
Population density in 1954 (hab nb km^{-2})	PopDens1954	Inhabitants number per commune/commune area	1954 National census
Population density in 1999 (hab nb km^{-2})	PopDens1999	Inhabitants number per commune/commune area	1999 National census
Population density variation from 1954 to 1999 (%)	VarPop1954	100* (PopDens1999 – PopDens1954)/PopDens1954	1954 and 1999 National censuses
Population density variation from 1881 to 1999 (%)	VarPop1881	100* (PopDens1999 – PopDens1881)/PopDens1881	1881 and 1999 National censuses
Land use			
Area of permanent grassland and heathland (%)	PctSth2000	100* Grassland and heathland area/commune area	2000 Agricultural census
Total cultivated area (%)	PctSau2000	100* Total cultivated area/commune area	2000 Agricultural census
Total livestock density (head number km^{-2})	DnsChp2000	Ovine + caprine + bovine livestock/commune area	2000 Agricultural census
Grassland/heathland area variation from 1970 to 2000 (%)	VarSth1970	100* (PctSth2000 – PctSth1970)/PctSth1970	1970 and 2000 Agricultural censuses
Total cultivated area variation from 1970 to 2000 (%)	VarSau1970	100* (PctSau2000 – PctSau1970)/PctSau1970	1970 and 2000 Agricultural censuses
Livestock density variation from 1970 to 2000 (%)	VarChp1970	100* (DnsChp2000 – DnsChp1970)/DnsChp1970	1970 and 2000 Agricultural censuses

*Communes are the smallest French administrative subdivision.

under ARCVIEW GIS 3.2a (Spatial Analyst 2.0a and personal scripts routines).

Each study species had no more than one occurrence per 1 × 1 km grid cell. We computed the following response variables: (a) number of rare species occurrences in 1886 (local rare species richness in 1886 hereafter), (b) number of rare species occurrences in 2001 (local rare species richness in 2001 hereafter), (c) number of occurrences of restricted endemic species in 2001 (local endemic species richness in 2001 hereafter), (d) number of local extinction of rare species from 1886 to 2001, (e) number of local persistence of rare species from 1886 to 2001, and (f) number of local appearance of rare species from 1886 to 2001. All these response variables followed Poisson distributions, but their distributions were highly skewed toward 0 (many cells with no rare species occurrences). The response variables were then analysed with General Linear Models (GLM hereafter) with a negative binomial error (Venables & Ripley, 2002), using Splus software (Anonymous, 1999). We fitted two types of GLM: GLM with linear terms only (GLMs hereafter), and GLM with linear and second order polynomial terms (GLMp hereafter). The advantage of GLMp is that polynomial terms allow skewed or bimodal responses. Since potential explanatory variables were numerous and potentially interrelated, we used a stepwise selection procedure (using the Akaike Information Criterion) to determine the physical, human and land use variables that best explained the spatial patterns of the above response variables. After the stepwise selection procedure, GLMs and GLMp were compared by performing a sequential likelihood ratio test for Negative Binomial Generalized Linear Models (Venables & Ripley, 2002). The best model retained explained the greatest amount of deviance. Finally, to characterize the spatial structure in our data and check for spatial autocorrelation, we computed semi-variance (γ statistic) of model residuals between different 1 × 1 km cells. Then, we performed semi-variograms for each response variable by plotting semi-variance of residuals as a function of spatial distance between grid cells.

In each 1 × 1 km grid cell, the number of rare species occurrences was also computed for each of the four groups of biogeographic affinity (i.e. Mediterranean, South/Central European, Mountain, and Eurosiberian species, see above). Next, we performed an Outlying Mean Index (OMI; Dolédec *et al.*, 2000) analysis on the four biogeographic groups. OMI is a multivariate analysis especially designed to separate ecological niche across group of occurrences in a multidimensional space defined by environmental variables. Here, we used the OMI to approximate the 'niche' occupied by each biogeographic group of rare species. We thus tested if the four different biogeographic groups of rare species had different responses to physical, human and land use variables (Table 1). Using a two-step procedure, the OMI analysis estimated the mean environmental conditions used by each biogeographic group with respect to the mean conditions of the study area (Choler & Michalet, 2002; Thuiller *et al.*, 2004). First, a normalized PCA analysis was performed on the environmental variables to determine the major environmental gradients of the study area (called OMI axis hereafter). Each OMI axis is thus a linear combination of environmental variables. Second, the mean habitat condition of each biogeographic group of rare species was projected in this environmental hyperspace. The OMI analysis was performed with 'R' Software (Ihaca & Gentleman, 1996), implementing into the ADE4 library (Thioulouse *et al.*, 1997).

We also performed contingency analyses using PROC FREQ in SAS (1999) to test whether rare species had different probabilities of local extinction, local persistence or local appearance between 1886 and 2001 according to their biogeographic affinities (Mediterranean, South/Central European, Mountain, and Eurosiberian species), and to their level of endemism (restricted endemic vs. non-endemic species).

RESULTS

Spatial pattern of local rare species richness in 1886 and 2001

For the analysis of spatial patterns of rare species occurrences, stepwise selection procedures always retained two or more explanatory variables in the final GLM (Table 2). Here, we present the four most explicative variables, which explained from 62% to 75% of the total deviance. GLMp were always better than GLMs except to model the number of rare species local extinctions (Table 2). Semi-variograms of model residuals showed no evidence of spatial structure. For all response variables, residuals semi-variance did not vary with spatial distance, and did not drop to zero for low distances (Fig. 2a–f), indicating that spatial autocorrelation in our data was very low, even at fine spatial scale.

In 1886, local rare species richness increased along with altitude (Fig. 3a): almost no rare species in 1886 occurred under 400 m a.s.l. Highest local rare species richness values were reached on basalt, shale/quartzite, gneiss/mica-schist and limestone bedrocks (Fig. 4a), and in zones of intermediate human population density in 1881 (Fig. 3b). Prospecting effort of L&B also explained a substantial part of the spatial pattern of rare species richness in 1886: rare species were more numerous in the most prospected areas (Fig. 3c).

In 2001, local rare species richness had a slightly different relation with altitude (Fig. 3d): rare species mostly occurred above 700 m, but some rare species were also observed under 200 m (Fig. 3d). Rare species in 2001 were most numerous on basalt, dolomite/chert limestone, shale/quartzite, limestone,

Table 2 Results of stepwise selection in GLM of local rare species richness in 2001, local rare species richness in 1886, local richness in rare endemic species in 2001, number of rare species local appearance from 1886 to 2001, number of rare species local persistence from 1886 to 2001, and number of rare species local extinction from 1886 to 2001. The four best explanatory variables are given, and listed in order of decreasing explained deviance

	GLMp	GLMs	χ^2_{df}
Local rare sp. richness in 1886	**pol(Alti_mean)**, **pol(PopDens1881)**, **Prosp_Intens**, **Bedrock**	Bedrock, Prosp_Intens, PopDens1881, Alti_mean	21.9_4***
Local rare sp. richness in 2001	**pol(Alti_mean)**, **Bedrock**, **pol(PctSth2000)**, **VarSau1970**	Bedrock, Alti_mean, VarSau1970, VarChp1970	78.5_5***
Local endemic sp. richness in 2001	**Slope_Mean**, **pol(PctSth2000)**, **VarSau1970**, **PopDens1999**	Slope_Mean, VarSau1970, VarChp1970	17.9_4**
Nb of rare sp. local appearance 1886–2001	**Prosp_Intens**, **PctSau2000**	Prosp_Intens	2.22_6^{ns}
Nb of rare sp. local persistence 1886–2001	**pol(PctSau2000)**, **pol(Alti_Mean)**, **pol(Slope_Mean)**, **Bedrock**	Bedrock, Slope_Mean, Alti_Mean, PctSth2000	14.2_3**
Nb of rare sp. local extinction 1886–2001	pol(VarPop1881), VarChp1970, pol(VarPop1954), VarSau1970	**VarPop1881**, **VarChp1970**, **VarSau1970**, **Bedrock**	4.03_5^{ns}

Results are presented for GLMp and GLMs. GLMp are GLM allowing for second order polynomial terms, e.g. pol(Slope_Mean) being a second order polynome for Slope_Mean effect, and GLMs are GLM with linear terms only. The last column gives the χ^2 statistic and its associated degrees of freedom (in subscript) for the log-likelihood ratio test, which compares the two GLM, with ^{ns}not significant, $^{**}P < 0.01$, $^{***}P < 0.001$. The best model (with higher deviance) is written in boldface.

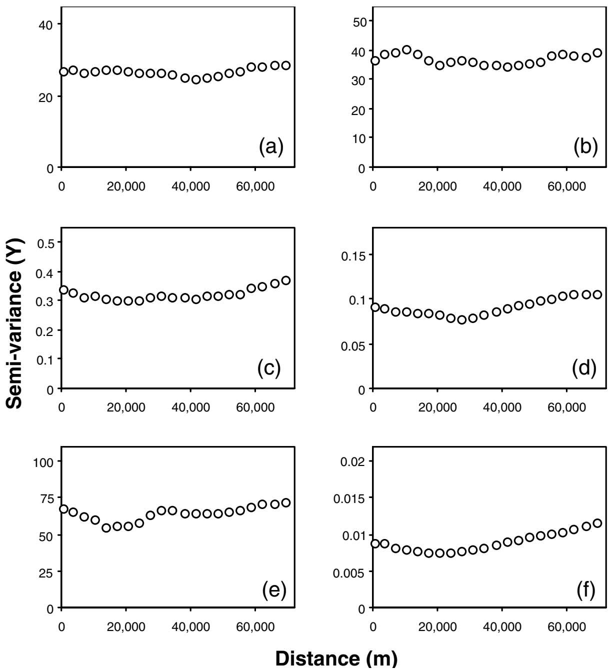

Figure 2 Semi-variograms (γ statistic as a function of distance) of rare species richness in 1886 (a), rare species richness in 2001 (b), endemic species richness in 2001 (c), number of rare species local appearance from 1886 to 2001 (d), number of rare species local persistence from 1886 to 2001 (e), and number of rare species local extinction from 1886 to 2001 (f).

and alluvial/colluvial deposits (Fig. 4b). Local rare species richness in 2001 also increased with permanent grassland and heathland area (Fig. 3e). The changes in percentage of cultivated area which have occurred from 1970 to 2000 had a significant impact on patterns of local rare species richness in 2001: fewer rare species were found in areas where cultivated area increased the most (Fig. 3f).

Local appearance, persistence, and extinction of rare species from 1886 to 2001

Spatial patterns in the local appearances of rare species between 1886 and 2001 were primarily explained by L&B prospecting effort, and to a lesser extent by the percentage of cultivated area (Table 2). Most rare species occurrences that appeared between 1886 and 2001 were thus present in zones of low prospecting effort in the 1886 survey. The spatial analysis of local appearance of rare species in relation with ecological, human and land use variables is thus inappropriate.

Table 2 also lists the physical and human variables which best explained spatial patterns of local extinction and local persistence of rare species. The number of local extinctions of rare species from 1886 to 2001 increased with the rise of human population density during the 1881–2001 period (Fig. 5a), of livestock density during the 1970–2000 period (Fig. 5b), and of cultivated area during the 1970–2000 period (Fig. 5c). Local extinctions of rare species mainly occurred on basalt, gneiss/mica-schist, basalt, limestone and alluvial/colluvial deposits (Fig. 4c).

During the 1886–2001 period, rare species occurrences were more likely to remain stable when present in zones with a low percentage of cultivated area (Fig. 5d), in zones of higher slope and higher altitude (Fig. 5e,f). Local persistence of rare species also mainly occurred on basalt, limestone, and marl/marly limestone (Fig. 4d).

Distribution and fate of occurrences in relation to species chorology

The first two axes of the OMI analysis captured 95.6% of variation in rare species niches. Ordination diagrams on the two first axes of the OMI describe the environmental gradients which best discriminated the occurrences of the four different biogeographic groups of rare species (Fig. 6). The first OMI axis separated zones of high elevation with acid bedrocks

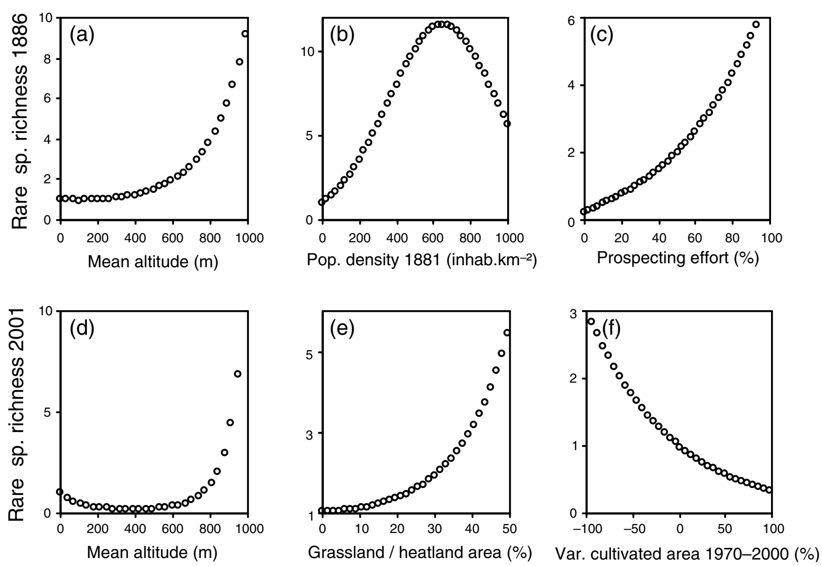

Figure 3 Fitted values of rare species richness in 1886 as a function of altitude (a), population density in 1881 (b), L&B prospecting effort (c). Fitted values of rare species richness in 2001 as a function of altitude (d), percentage area of permanent grassland and heathland (e), and variation of cultivated area from 1970 to 2000 (f). Fitted values were calculated by exponential transformation of estimates generated by GLM.

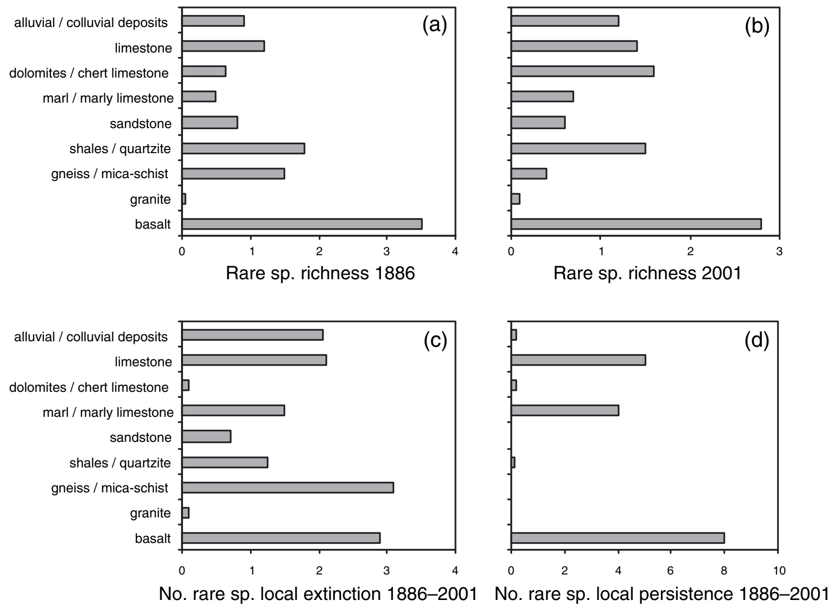

Figure 4 Fitted values of rare species richness in 1886 (a), rare species richness in 2001 (b), number of rare species local extinction from 1886 to 2001 (c), and number of rare species local persistence from 1886 to 2001 (d), as a function of bedrock classes. Fitted values were calculated by exponential transformation of estimates generated by GLM.

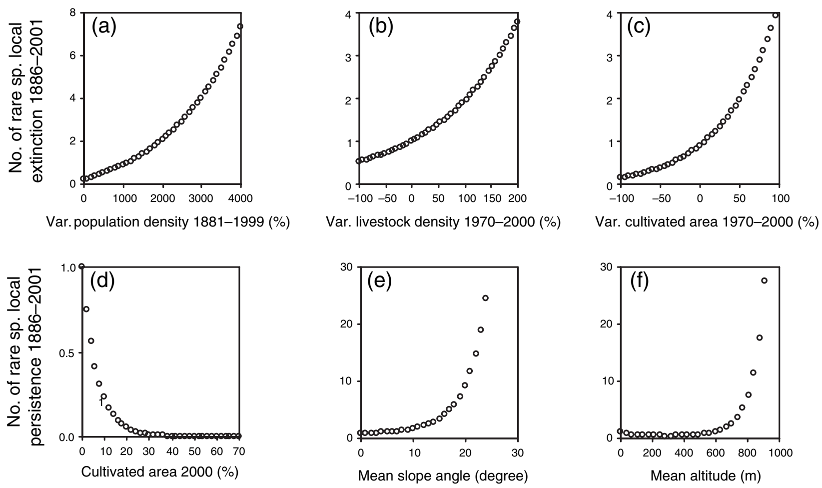

Figure 5 Fitted values of number of rare species local extinctions between 1886 and 2001 as a function of variation of population density from 1881 to 1999 (a), variation of livestock density between 1970 and 2000 (b), variation of cultivated area between 1970 and 2000 (c). Fitted values for number of rare species local persistence between 1886 and 2001 as a function of percentage of cultivated area in 2000 (d), mean slope angle (e), and altitude (f). Fitted values were calculated by exponential transformation of estimates generated by GLM.

(gneiss/mica-schist) from lowland zones with bedrocks of sedimentary origin (alluvial/colluvial deposits, sandstone, marl/marly limestone), high percentage of cultivated area and high human population density (Fig. 6a). The second OMI axis was only related to the occurrence of basalt bedrocks, which showed no correlation with any other variables (Fig. 6a).

In 2001, these two ecological gradients did not have the same impact on the spatial distribution of rare species occurrences according to their biogeographic group. Mediterranean and South/Central European rare species tended to occur in a variety of habitats in the study area: the envelope of their occurrences is close to and includes the centre of the first OMI plane (Fig. 6b,c). Conversely, the positions of Mountain and Eurosiberian rare species were marginal on the first OMI axis. These two groups of rare species both tended to occur in the most elevated zones of Hérault and on gneiss/mica-schist bedrocks (Fig. 6d,e).

In 2001, local richness in endemic species was strongly correlated with physical, human and land use variables (Table 2). The probability of restricted endemic species occurrence increased with mean slope angle (Fig. 7a), and was found to be low in zones where area of permanent grassland and heathland was intermediate (Fig. 7b), where percentage of cultivated area had increased the most from 1970 to 2000 (Fig. 7c) and where human population density was the highest in 1999 (Fig. 7d).

During 1886–2001, rare species showed different probabilities of local extinction, local persistence and local appearance according to their chorology. Occurrences of rare species were significantly more likely to become extinct during 1886–2001 for species with a Eurosiberian distribution (Fig. 8a), and were significantly more stable for Mediterranean/sub-Mediterranean species (Fig. 8a) and for restricted endemic species (Fig. 8b). Occurrences of Mountain and South/Central

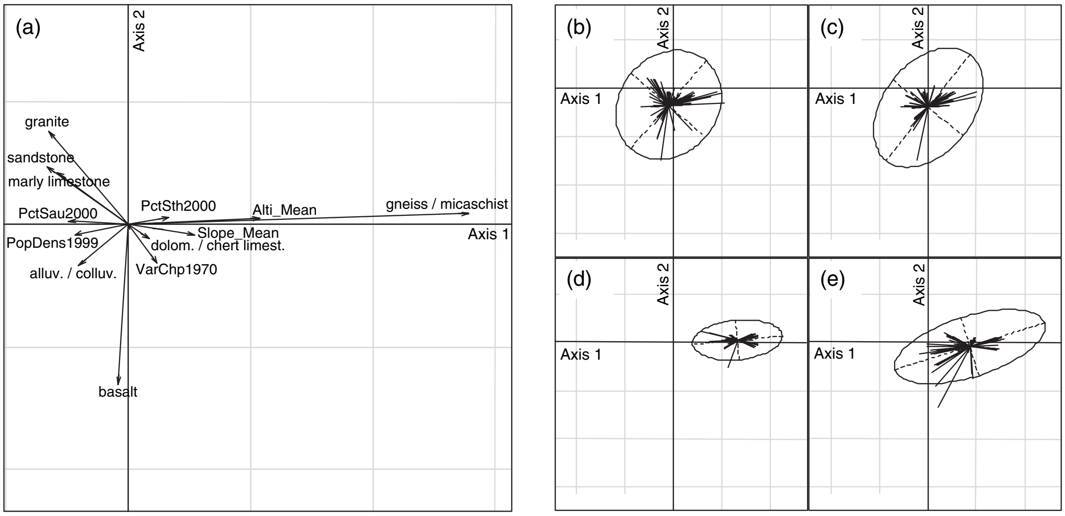

Figure 6 Contribution of environmental, human and land use variables to the first axes produced by the OMI analysis for the 2001 rare species (a). The ecological position of the four biogeographic groups of rare species are represented on the first OMI plane with Mediterranean/sub-Mediterranean rare species (b), South/Central European rare species (c), Mountain rare species (d), Eurosiberian rare species (e). Variables codes in Table 1 and dolom./chert limest. (dolomite/chert limestone), alluv./colluv. (alluvial/colluvial deposits).

European rare species showed no significant trend during the 1886–2001 period (Fig. 8a).

DISCUSSION

The compilation of archival data is plagued by the problem of spatial heterogeneity of sampling effort (Prendergast *et al.*, 1993b). In our study, the prospecting effort of L&B was spatially heterogeneous because of limited handling in the late nineteenth century. This partly influenced the observed distribution of rare species occurrences in Hérault in 1886. Hence, our result that 1886 rare species tend to occur in areas of intermediate human population density probably reflects the fact that L&B prospections mainly occurred in areas surrounding main towns. We have shown that this spatial heterogeneity in sampling effort also strongly biased the analysis of rare species local appearance between 1886 and

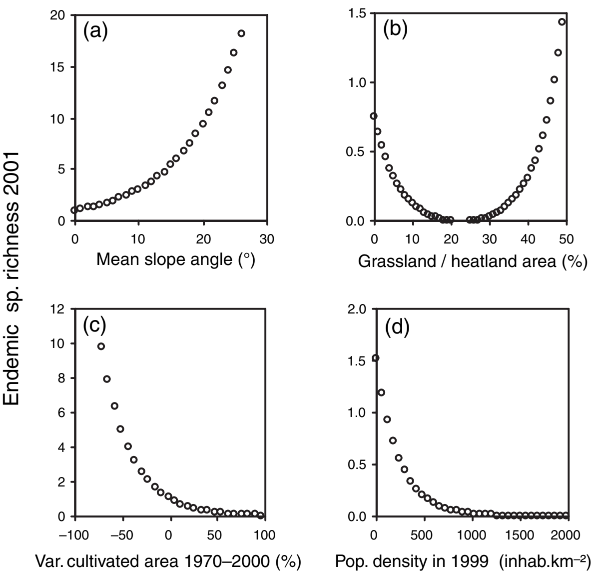

Figure 7 Fitted values of endemic species richness in 2001 as a function of mean slope angle (a), area of permanent grassland and heathland (b), variation of cultivated area from 1970 to 2000 (c), and human population density in 1999 (d). Fitted values of endemic species richness were calculated by exponential transformation of estimates generated by GLM.

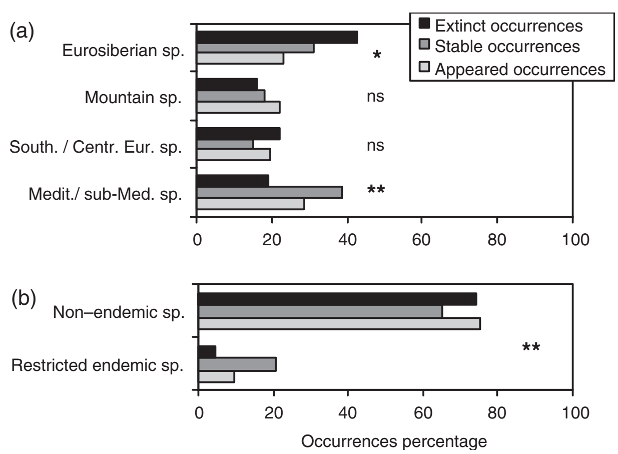

Figure 8 Percentage of extinct, stable and appeared occurrences within rare species groups of different biogeographic affinities (a) and level of endemism (b). Fisher tests have been computed to test the heterogeneity of each group, i.e. Eurosiberian, Mountain, South/Central European (South./Centr. Eur.), Mediterranean/sub-Mediterranean (Medit./sub-Medit.) and restricted endemics. *P*-values are given with $^*P < 0.05$; $^{**}P < 0.01$; and ^{ns}non-significant.

2001. However, the analyses of the spatial patterns of rare species richness in 2001 and of local extinction and persistence of rare species from 1886 to 2001 were unbiased with respect to the prospecting effort. Our study thus emphasizes that, despite some imprecision, historical recordings of plant distribution and abundance can provide valuable data to study long-term plant species population trends and biodiversity loss in relation to human activities and landscape changes.

At this scale of study (*c.* 6250 km^2), the 1-km resolution chosen for the spatial analysis seemed to be appropriate. In the Mediterranean, physical variables often exhibit a spatial heterogeneity at so fine scales that a coarser resolution would have increased their variability within grid cells, and thus decreased their predictive power. Conversely, semi-variograms performed on model residuals showed absolutely no evidence of spatial structure in the data, suggesting that a finer spatial resolution would have increased spatial autocorrelation in our study. Of course, several rare species can occur within one 1-km cell, but this reflects the importance of very localized biotopes for rare species occurrence. The aim of this study was to characterize such biotopes and to determine their effect on rare species persistence over the last century.

The regional distribution of rare species occurrences is influenced by a combination of physical and human factors. In our study, the spatial distribution of rare species in 1886 and 2001 were primarily explained by topography and bedrock, as documented in other regions (White & Miller, 1988; Heikkinen, 1998; Wiser *et al.*, 1998). At both dates, rare species richness was higher in elevated zones and on particular bedrocks such as shales/quartzites and basalt. Because shales/quartzites are distributed at medium and high altitudes in the study area, the significance of this bedrock type might be partly confounded with the significance of altitude. However, as shown by the OMI analysis, basalt bedrocks occur independently from any other physical gradient. This bedrock generally harbours very peculiar and rare habitats (e.g. temporary ponds) with ecologically specialized plant species (e.g. *Damasonium alisma* Mill., *Isoetes duriei* Bory, *Ranunculus lateriflorus* DC.); these species are thus rare in the study region. In 2001, the regional distribution of rare species occurrences was also strongly influenced by human activities and their recent changes. Most rare species were present in areas where permanent grasslands and heathlands, i.e. open semi-natural habitats, dominate the landscape, and occurred less in zones of recent agriculture intensification. In Europe, this pattern has been already observed in human-shaped landscapes (Fischer & Stöcklin, 1997; Olsson *et al.*, 2000; Luoto *et al.*, 2002).

Despite a general spatial pattern of rare species richness, the fate of rare species occurrences varied in relation to local environmental conditions. During the 1886–2001 period, rare species occurrences went extinct where human pressure and agriculture have been greatly intensified. Rare species local extinctions were not significantly related to the loss of semi-natural open habitats (measured by the decrease in permanent grasslands and heathlands) because of forest progression. Our findings illustrate that urbanization, tourism development and agriculture intensification are the land-use changes that have the most deleterious impacts on rare species persistence in the Mediterranean region. Although often assumed, this has seldom been demonstrated (e.g. Thompson & Jones, 1999), despite several calls for such data (Pimm, 2002). Increased urbanization, tourism development and agricultural intensification have greatly modified the landscape and the habitats of Mediterranean lowlands, particularly in littoral zones (Corre, 1991). As illustrated by the increase in rare species richness at low altitude and on alluvial/colluvial deposits between the 1886 and 2001 surveys, many natural habitats of the Mediterranean coast have been destroyed and fragmented by tourism development and wetland drainage since the 1960s. This resulted in the rarefaction of many plant species occurring in these habitats (e.g. *Limonium* sp. pl., *Otanthus maritimus* (L.) Hoffmanns. & Link, *Triglochin maritima* L.). These rare coastal species thus currently experience a very high risk of extinction in Hérault and probably in most Western Mediterranean regions.

However, local persistence of rare species during the 1886–2001 period was enhanced in zones of high elevation, on steep slopes and on basic bedrocks (basalt, limestone), and in areas with low agricultural impact. Rare species occurrences thus had high rates of local persistence in zones where human activities may have been continuously limited by harsh topography and stony and shallow soils. This explains the findings of several studies documenting higher local rare species richness in heterogeneous and inaccessible zones of natural (Heikkinen, 1998) and semi-natural landscapes (White & Miller, 1988; Luoto, 2000).

In our study area, rare species with Mountain and Eurosiberian affinities tended to occur in marginal ecological conditions, i.e. in zones of high elevation and on metamorphic substrates. Some of these rare species are widely distributed and common throughout non-Mediterranean Europe, but rare in the Mediterranean region from which they are excluded mostly by climatic constraints. First, rare species classified in this study as Mountain species are generally present in most European mountains, and occur in their lower altitudinal range in Hérault (e.g. *Allium victoriale* L., *Arabis alpina* L., *Carex frigida* All.). Second, Eurosiberian rare species are widely distributed onto Northern Europe but some of them can reach their range limits in the Mediterranean regions (e.g. *Actaea spicata* L., *Euphorbia palustris* L., *Equisetum fluviatile* L.). Thus, in our study, Eurosiberian rare species experienced high rates of local extinction between 1886 and 2001, but no general trend was observed for the occurrences of Mountain rare species. Conversely, Mediterranean and sub-Mediterranean rare species, which were found in a larger array of ecological conditions in Hérault, showed a significant higher probability of local persistence between 1886 and 2001 (e.g. *Cistus ladanifer* L., *Iberis ciliata* All., *Iris xiphium* L.). As a whole, these results indicate that Mediterranean peripheral populations of plant species with large Eurosiberian distributions are currently experiencing more important threats than

Mediterranean rare species, possibly in relation to current climate change. The conservation of populations in the range margins of widespread species would be highly valuable, given their functional and genetic peculiarity, and their potential for future differentiation and even speciation (Lesica & Allendorf, 1995; Nantel & Gagnon, 1999).

Finally, we found that restricted endemic species frequently occurred in areas of heterogeneous topography such as cliffs and rocky outcrops and had a very high potential of local persistence (e.g. *Aquilegia viscosa* Gouan, *Saxifraga cebennensis* Rouy & Camus). Many ecological features of their habitats, such as reduced competition for space and light (Baskin & Baskin, 1988; Lavergne *et al.*, 2003, 2004), may allow restricted endemic species to persist locally for long periods of time. Our results also show that restricted endemic species richness was higher in zones that strongly suffered from rural depopulation, i.e. where human density and cultivated areas have decreased. Thus, the high local persistence of endemic species populations observed between 1886 and 2001 despite the surrounding land abandonment suggests that this group of rare species is less likely to be threatened by land-use changes than other rare species.

To develop efficient conservation guidelines, conservation scientists need to predict which rare species are most likely to be threatened in the future. Conservation efforts traditionally tend to concentrate on narrow endemic species (Olivier *et al.*, 1995). Here, we have found that restricted endemic rare species had a high probability of local persistence over the twentieth century because they occur in habitats where they are less likely to suffer from land-use changes. Conversely, rare species occurring in coastal habitats and in zones of current urbanization and agricultural intensification currently face the strongest threat of extinction in the Mediterranean. Eurosiberian species that are rare in the Mediterranean where they occur at their range margins are also dangerously declining. This could cause the loss of Mediterranean ecotypes of these widespread species and thus the loss of important evolutionary potential. Together, our results may provide a scientific basis for the redistribution of conservation efforts between biogeographic groups of rare species in the Mediterranean Region.

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