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Fingerprints of environmental change on the rare mediterranean flora: a 115-year study

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Abstract

We empirically assessed the long-term changes in the rare species assemblage of a Mediterranean flora, in terms of species life history traits, niche and biogeographic features, and taxonomic groups. We used a 115-year historical record of ca. 2100 plant species occurrences in a 6250 km^2 region in Mediterranean France. Species were assigned to two classes of regional abundance for the years 1886 and 2001 (rare species, i.e. exhibiting one or two occurrences vs. nonrare species), and to three classes of abundance changes during 1886–2001 (decreasing/extinct, stable, increasing/immigrant). Then, we tested whether species regional abundance and species abundance change were related to their morphological and life-history traits (life form, perenniality, height, dispersal agent, pollination mode), niche and biogeographic features (habitat specialization, level of endemism, biogeographic origin) and taxonomic group. The regional assemblage of rare species was not biologically random and significantly changed between 1886 and 2001. Species classified as rare in 1886 had a significantly higher rate of extinction in the study region during 1886–2001. The highest rate of regression/extinction was found among hydrophyte and/or water-dispersed rare species, and among annual rare species. However, herbaceous perennial, tree and wind-dispersed rare species significantly increased in abundance during 1886–2001. Rare species with Eurosiberian distributions, occurring at the southern margin of their range in the study region, dramatically declined or went extinct in the region during 1886–2001; whereas rare species with Mediterranean affinities remained significantly stable. We also found strong evidence for taxonomic patterns in species abundance and abundance changes from 1886 to 2001. The long-term biological changes documented here in the rare species assemblage of a Mediterranean flora are consistent with the predicted consequences of climate and land use changes currently occurring in the Mediterranean Basin. With the potential decline or even extinction of entire taxa and the loss of southern ecotypes of widespread Eurosiberian species, both evolutionary history and speciation potential of the Mediterranean Region could be strongly altered in future decades.

Key words: biodiversity conservation, endemism, environmental change, extinction, life-history traits, mediterranean region, niche features, rarity, vascular plants

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Introduction

In order to contain the biodiversity erosion caused by the current global changes, scientists need to develop predictive tools to determine plant species groups that need urgent conservation efforts (Mace *et al*., 2003; Lughadha *et al*., 2005). As rare species are theoretically the most prone to extinction (Gaston, 1994, 2003), a plethora of studies have attempted to determine recurrent ecological and biological features among rare plant species in particular regions (Hodgson, 1986; Hedge & Ellstrand, 1999; Cadotte & Lovett-Doust, 2002; Pilgrim *et al*., 2004). Although such studies documented significant patterns among rare species, rare species

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assemblages were never completely consistent in terms of ecological and biological features. Different sets of niche characteristics and life history traits may translate into different responses to habitat quality and spatial configuration (Harrison, 1999; Dupré & Ehrlén, 2002), and then into different dynamics when facing habitat fragmentation and environmental change. Thus, in a given region, different rare species may not incur equal risks of extinction owing to different niche characteristics and life history traits. Some rare species result from a recent and rapid decline and totter on the brink of extinction whereas other rare species are able to persist in small or isolated populations for long periods of time (Lawton, 1995; Mace & Kershaw, 1997).

Population viability analyses using demographic data have been repeatedly used to assess the extinction risk vs. the persistence potential of many rare plant species (Menges, 1990; Maschinski *et al*., 1997; Fréville *et al*., 2004; Menges & Quintana-Ascencio, 2004), but there are still insufficient demographic data to build reliable models for most threatened species (Coulson *et al*., 2001). As a result, there is growing interest in documenting how ecological and biological features of plant species relate to their rate of local extinction, persistence, and colonization. This can be achieved by using temporal data on species occurrence or abundance, although such data sets are very scarce (e.g. Drayton & Primack, 1996; McCollin *et al*., 2000). At regional scale, rare species dynamics and extinction risk may be related to their population size and spatial isolation (Ouborg, 1993; Matthies *et al*., 2004), and to a number of ecological and life-history traits (Quintana-Ascencio & Menges, 1996; Fischer & Stöcklin, 1997; Duncan & Young, 2000).

Plant species distribution and abundance also vary significantly between taxonomic groups (Edwards, 1998; Edwards & Westoby, 2000; Lozano & Schwartz, 2005b), owing to some degree of phylogenetic conservatism of life-history traits and ecological niche (Prinzing *et al*., 2001; Qian & Ricklefs, 2004). As features that influence species response to environmental and human factors are partially inherited from their ancestors, we may expect rare species dynamics and extinction risk to be taxonomically nonrandom. This has been clearly demonstrated for bird and mammal taxa (Bennett & Owens, 1997; Purvis *et al*., 2000), but rarely for plant taxa (e.g. Gustafsson, 1994).

Attempts to assess the long-term consequences of global changes on the rare flora of the Mediterranean Basin have been very scarce (Verlaque *et al*., 2001; Lavergne *et al*., 2005), although more than 10% of the world flora is present in this region (Myers *et al*., 2000). The Mediterranean flora exhibits a very high taxonomic diversity, consisting of ca. 25 000 vascular plant species, of which about 59% are endemic to small biogeographic regions (Greuter, 1991). The rest of the Mediterranean flora consists of more widespread taxa from varied biogeographic origins: many Eurosiberian taxa reach their southern range limit in the Mediterranean Region where they co-occur with South-Central Europe and Boreo-alpine taxa (Quézel, 1985). Unfortunately, this high taxonomic diversity is currently threatened by abrupt climate and land use changes (Sala *et al*., 2000; Thuiller *et al*., 2005a). Hence, understanding the response of Mediterranean rare plants to global changes is a critical task that may provide a hierarchy of biological criteria for the conservation of the Mediterranean botanic diversity.

In a previous study dealing with the historical biogeography of rare plant species in the French Mediterranean region (Lavergne *et al*., 2005), we showed that environmental and land use changes have significantly impacted the spatial distribution and long-term dynamics of rare plant occurrences since the late 19th century. In the present study, we analyzed a 115-year historical record of ca. 2100 vascular plant species in the same study region to assess the long-term effects of global change on Mediterranean rare plants. Species were assigned to two classes of regional abundance for the dates 1886 and 2001 ('rare species' vs. 'nonrare species'), and to classes of abundance changes during 1886–2001 ('decreasing/extinct', 'stable', 'increasing/immigrant'). We tested whether species regional abundance in 1886 and 2001 and species abundance change during 1886–2001 were related to their morphological and life-history traits, their niche and biogeographic features and their taxonomic group.

The study region and its current environmental changes

The study region is the Hérault Département, an administrative subdivision extending on 6250 km^2 in southern France, from the Mediterranean seashore to the southern mountain ranges of the Massif Central (Fig. 1). Hérault exhibits a highly rich flora, composed of ca. 2100 native phanerogam and fern species. This constitutes 43% of the French flora on only 1.1% of the national territory.

Hérault has a Mediterranean climate with a dry and hot summer, a cold winter, and peaks of precipitations during the fall and the spring. The region exhibits highly heterogeneous landscapes, mainly due to a high diversity of sedimentary, metamorphic and intrusive bedrocks (Dugrand, 1971). Landscapes of Hérault are representative of the Mediterranean Basin, as they result from long-lasting interactions between human activities and ecological factors and are currently

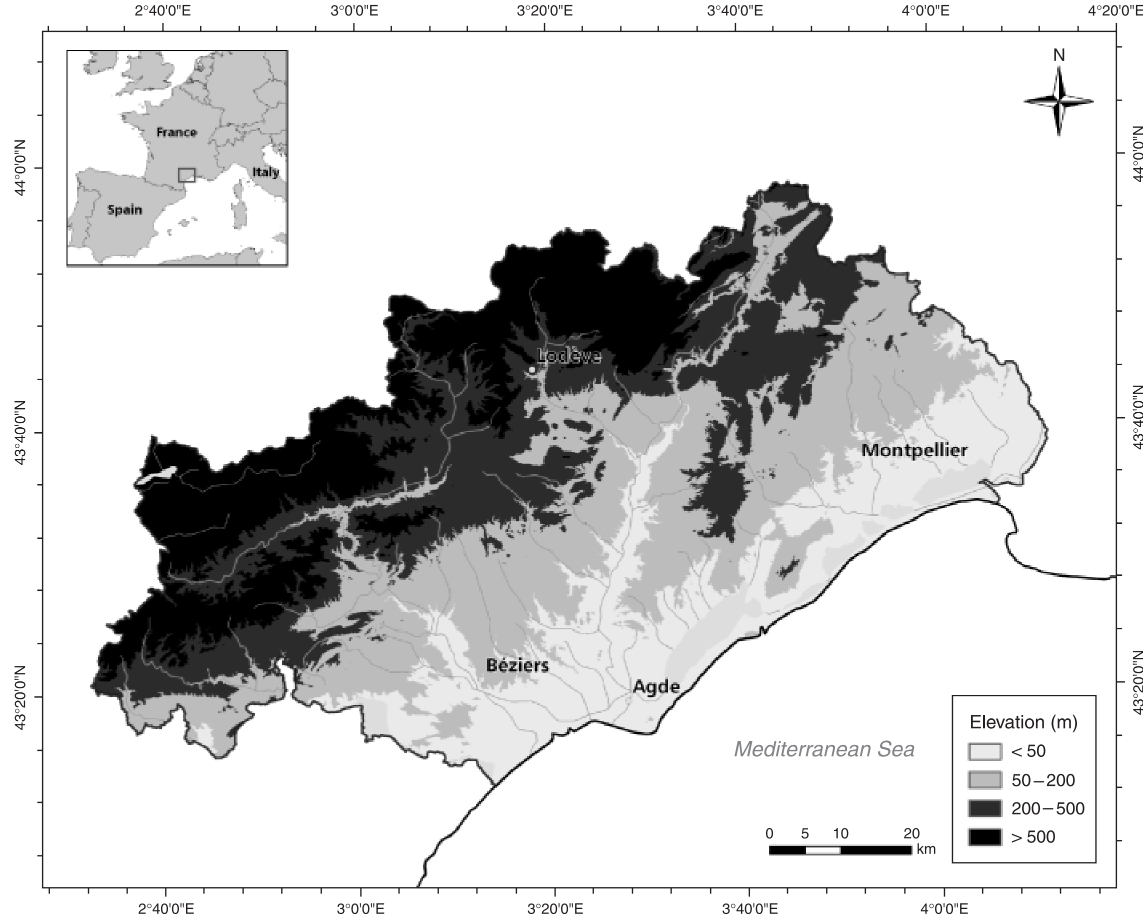

Fig. 1 Location, physical map and main cities of the study region.

experiencing dramatic modifications due to global changes.

As in most Mediterranean Region, Hérault hinterland has experienced a strong decline in traditional agriculture along with a severe depopulation of rural areas, which began at the end of World War I and intensified during the 1960s (Lepart & Debussche, 1992). This lead to forest spread by secondary succession and reafforestation (Debussche *et al*., 1999), and to large decrease in open habitats such as semi-natural grasslands and heathlands (Lavergne *et al*., 2005). Meanwhile, rapid urbanization occurred at the periphery of main towns (see Fig. 1), and agriculture and tourism strongly intensified in low lying and coastal areas (Pons & Quézel, 1985). In the lowlands of Hérault, human population density has exploded over the 20th century, and the percentage of cultivated area have doubled since 1970s in some places (Lavergne *et al*., 2005). Finally, an increase in temperature and atmospheric CO_2 has been detected over the 20th century in the Mediterranean Region (Osborne *et al*., 2000; Gordo & Sanz, 2005), with a clear warmth intensification occurring since the 1950s, especially for mean spring temperatures ($>2.5\,^{\circ}$C increase in 60 years). Precipitation changes over the last century did not show any clear temporal trend.

Materials and methods

Species data set and abundance criteria in 1886 and 2001

The plant species occurring in Hérault were first listed by Loret & Barrandon (hereafter L&B) in 1886 (Loret & Barrandon, 1886). The National Mediterranean Botanical Conservatory (hereafter CBNMP) conducted the same survey in 2001, in collaboration with a large network of experienced field botanists. Using these two surveys, we built two data sets, listing the 2038 and 2162 native plant species occurring in Hérault in 1886 and 2001, respectively.

In each survey, species were assigned to one class of regional abundance. We defined 'rare' species as species with one or two occurrences recorded in the study area, and remaining species were assigned to the 'nonrare' class. This threshold of two occurrences was not chosen arbitrarily. The geographical locations of species occurrences in 1886 were precisely reported by L&B for species present in one or two different sites, so that at the occasion of the 2001 survey, revisitation of all 1886 rare species locations allowed us to document the local extinctions of 1886 rare species. The same criterion of rarity was thus applied for the 2001 survey. Only species following the nomenclature of Flora Europaea were considered (Tutin *et al*., 1964–1993). To avoid any taxonomic artifact in patterns of species abundance and abundance changes, taxonomic synonymy between the two lists of species was checked using the Synonymy Index of the French Flora (Kerguélen, 1993) and Flora Europaea (Tutin *et al*., 1964–1993). We finally retained 237 rare species in the 1886 survey, and 214 rare species in the 2001 survey.

Abundance changes during 1886–2001

We constructed a third data set depicting the abundance change of plant species between 1886 and 2001. Given the available information on species abundance at both dates, we were able to assign species to the following classes of abundance change during 1886–2001:

- *Increasing/immigrant species*: species 'appeared' in the study region during 1886–2001, species classified as 'rare' in 1886 and as 'nonrare' in 2001, rare species with one occurrence in 1886 and two occurrences in 2001;
- *Stable species*: rare species with the same number of occurrences in 1886 and in 2001;
- *Decreasing/extinct species*: species extinct in the study region during 1886–2001, species classified as 'nonrare' in 1886 and as 'rare' in 2001, rare species with two occurrences in 1886 and with one occurrence in 2001.

With this method, we documented the abundance changes of 417 species during 1886–2001. This species sample consists of all species present in the study region with the exception of species classified as 'nonrare' in both 1886 and 2001 surveys. Thus, this data set describes the regional dynamics of the rarest fifth of the study flora rather than the dynamics of the entire flora.

Taxonomic, morphological and life-history information

For every species present in our three data sets, we determined its:

- *taxonomic family*, using Flora Europaea (Tutin *et al*., 1964–1993), and recent systematic actualizations of angiosperms phylogeny (Soltis *et al*., 2000);
- *life-form* following Bolos *et al*. (1993) and Gachet *et al*. (2005), with: hydrophyte, therophyte, geophyte, hemicryptophyte, chamaephytes and phanerophyte;
- *perenniality* following Bolos *et al*. (1993) and Gachet *et al*. (2005), with: annual, herbaceous perennial and woody perennial;
- *height class*, using Tutin *et al*. (1964–1993) and Gachet *et al*. (2005), with: 0–0.1, 0.1–0.3, 0.3–0.5, 0.5–1, 1–2 and >2 m;
- *dispersal agent*, following Molinier & Müller (1938), van der Pijl (1972) and Gachet *et al*. (2005), with: ants (including myrmecochory and diszoochory), vertebrates (including endozoochory and epizoochory), mecanic (i.e. autochory), wind (i.e. anemochory), water (hydrochory) and none (no dispersal specialization);
- *pollination mode*, from Gachet *et al*. (2005) and morphological descriptions in Tutin *et al*. (1964–1993), with: anemogamous (wind pollination), entomogamous (insect pollination), hydrogamous (water pollination) and mixed (wind and insect pollination).

Niche and biogeographic information

For the 417 species included in the abundance change data set, we documented three additional features: degree of habitat specialization, level of endemism and biogeographic affinity. We used Coste (1900–1906) to distinguish habitat specialist species (species always occurring in one single habitat type, e.g. peat-bog, rocky outcrops) from habitat generalist (species found in varying habitats, with evidence of wider ecological tolerance). For species level of endemism, we distinguished restricted endemic species (restricted to Mediterranean France and no more than two countries bordering Mediterranean France) from nonendemic species. Finally, rare species were assigned to groups of biogeographic affinity according to Coste (1900–1906), Greuter *et al*. (1984–1989) and Tutin *et al*. (1964–1993), as follows:

- 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.
- South/Central European species, which occur in Southern and Central Europe, and often in North Africa and Western Asia.
- Mountain species, which occur in mountain ranges of Europe and possibly in Boreal Europe.
- Eurosiberian species, which are largely distributed throughout Europe and are often present in Asia, but rarely occur in the Mediterranean Region.

Variation in sampling effort

Spatial variation in sampling effort can strongly bias the documented changes in species distribution. It has been shown that L&B (1886) did not uniformly prospect the study region (Denelle *et al*., 1995), and that this biased the observed spatial patterns of local colonization of rare species during the 1886–2001 period (Lavergne *et al*., 2005). The 2001 survey was conducted more uniformly than in 1886, and most rare species populations described in 1886 have been repeatedly visited since then. Hence, species pseudo-extinctions are very unlikely in our data set of species abundance change (Shaw, 2005).

To take into account the biases of pseudo-colonization and interspecific variation in census effort, we determined the species for which some populations have been potentially overlooked in 1886 or 2001, thus leading to incorrectly estimate their abundance changes. These species were determined using the available data on spatial variation in 1886 L&B sampling effort (Denelle *et al*., 1995), and the critical evaluation of the CBNMP sampling effort during the 2001 survey. Among the 417 species present in the abundance change data set, 176 species were determined to occur in sites that had been potentially overlooked in 1886 or 2001. Both the full data set (417 species) and the truncated data set (241 species unlikely to have been overlooked) were used in statistical analyses in order to determine the sensitivity of our results to the variation in sampling effort.

Statistical analyses

As required in the case of binary or ordered categorical variables, the distribution of species between abundance classes in 1886 and 2001 (rare, nonrare species), and classes of abundance change during 1886–2001 (decreasing/extinct, stable, increasing/immigrant species) were analyzed by fitting logistic models (PROC LOGISTIC, SAS, 1999). Models of species abundance in 1886 and 2001 were binomial models with a complementary log–log link function. The model fitted for species abundance changes during 1886–2001 was a proportional odds ratio model with a cumulative logit link function.

As explanatory variables were potentially interrelated, we performed a stepwise selection to determine the minimum set of explanatory variables which explain most of the interspecific variation in abundance and abundance change. Perenniality and life form are highly confounded variables but both were used in model selection because of their different number of parameters. To take into account the potential biases in the analysis of abundance changes during 1886–2001, we fitted a second set of odds ratio model using the 241 species that were unlikely overlooked in 1886 or 2001.

To determine the classes of each explanatory variable which contributed the most to data heterogeneity, we performed contingency tests between abundance classes (or abundance change classes) and separate classes of each explanatory variable, using a generalized algorithm of Fisher exact test for $r \times c$ contingency tables (PROC FREQ, SAS, 1999). When needed to understand structure in the data, the relation between different explanatory variables was also analyzed by performing χ^2 contingency tests.

To study taxonomic patterns in species abundance and abundance changes, we tested whether each family deviated significantly from the rest of the flora in terms of proportion of 1886 rare species, 2001 rare species, decreasing/extinct species during 1886–2001 and increasing/immigrant species during 1886–2001. To do so, we separately performed Fisher's exact tests for 2×2 tables (PROC FREQ, SAS, 1999) between each of the 128 vascular plant families and the rest of the flora.

Results

After stepwise selection, the best model explaining species abundance retained species pollination mode and height class in 1886 and 2001 (Table 1a, b), as well as life form in 1886, and perenniality in 2001 (Table 1a, b). Dispersal agent alone had a significant effect on species abundance in 1886, but was not selected in the final model (Table 1a, Fig. 3d). This was due to some recurrent associations between some dispersal agents and life forms (life form vs. dispersal agent, $\chi^2_{(\mathrm{df}=25)} = 1321.9$ $P < 0.001$).

Species extinction risk during 1886–2001 was highly related to species abundance in 1886 ($\chi^2_{(\mathrm{df}=1)} = 121.3$ $P < 0.001$), with 1886 rare species being disproportionately overrepresented in extinct species during 1886–2001 (Fig. 2). Of the 104 species that went extinct in Hérault during the study period, 72 species were rare in the 1886 survey. Odds ratio models showed that life-history traits and biogeographic features also had important effects on species abundance changes during 1886–2001 (Table 1c). After stepwise selection, the best model explaining species abundance changes during 1886–2001 consisted of species biogeographic affinity, life-form, height class and dispersal agent (Table 1c).

Patterns of morphological and life-history traits

Patterns of species abundance and pollination mode showed almost no change between 1886 and 2001 (Fig. 3e). Both in 1886 and 2001, hydrogamous species

Table 1 Results of logistic models of species abundance in 1886 and 2001 and odds ratio models of species abundance change during 1886–2001

(a) Abundance in 1886		(b) Abundance in 2001		(c) Abundance change (1886–2001)	
Variables alone		*Variables alone*		*Variables alone*	
Life form	$\chi^2_{(\mathrm{df}=5)} = 27.5$***	Life form	$\chi^2_{(\mathrm{df}=5)} = 27.8$***	Life form	$\chi^2_{(\mathrm{df}=5)} = 26.7$***
Perenniality	$\chi^2_{(\mathrm{df}=2)} = 21.1$***	Perenniality	$\chi^2_{(\mathrm{df}=2)} = 12.4$**	Perenniality	$\chi^2_{(\mathrm{df}=2)} = 17.2$***
Height	$\chi^2_{(\mathrm{df}=5)} = 18.6$**	Height	$\chi^2_{(\mathrm{df}=5)} = 31.6$***	Height	$\chi^2_{(\mathrm{df}=5)} = 12.9$*
Dispersal agent	$\chi^2_{(\mathrm{df}=5)} = 16.1$**	Dispersal agent	$\chi^2_{(\mathrm{df}=5)} = 6.21$, ns	Dispersal agent	$\chi^2_{(\mathrm{df}=5)} = 18.4$**
Pollination mode	$\chi^2_{(\mathrm{df}=3)} = 12.5$**	Pollination mode	$\chi^2_{(\mathrm{df}=3)} = 32.8$***	Pollination mode	$\chi^2_{(\mathrm{df}=2)} = 1.66$, ns
				Habitat specific	$\chi^2_{(\mathrm{df}=1)} = 0.99$, ns
				Geographical affinity	$\chi^2_{(\mathrm{df}=3)} = 28.6$***
				Endemism	$\chi^2_{(\mathrm{df}=1)} = 4.02$*
Stepwise selection		*Stepwise selection*		*Stepwise selection*	
Life form	$\chi^2_{(\mathrm{df}=5)} = 28.1$***	Pollination mode	$\chi^2_{(\mathrm{df}=3)} = 36.9$***	Geographical affinity	$\chi^2_{(\mathrm{df}=3)} = 22.6$***
Height	$\chi^2_{(\mathrm{df}=5)} = 16.4$**	Height	$\chi^2_{(\mathrm{df}=5)} = 22.9$***	Life form	$\chi^2_{(\mathrm{df}=5)} = 21.6$***
Pollination mode	$\chi^2_{(\mathrm{df}=3)} = 9.2$*	Perenniality	$\chi^2_{(\mathrm{df}=2)} = 18.7$***	Height	$\chi^2_{(\mathrm{df}=5)} = 18.2$**
				Dispersal agent	$\chi^2_{(\mathrm{df}=5)} = 12.1$*

ns, nonsignificant, *$P < 0.05$. **$P < 0.01$. ***$P < 0.001$.

Change in model deviance associated with each explanatory variable is tested with a $\chi 2$ test using the appropriate degrees of freedom. Effects of variables alone (single variable models) and along the steps of stepwise selection procedure (Type I tests) are given.

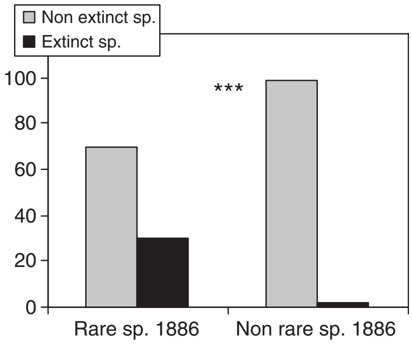

Fig. 2 Percentages of nonextinct and extinct species during 1886–2001 among rare and nonrare species of the 1886 survey. The *P*-value was obtained from a Fisher exact test, with: ***$P < 0.001$.

had a significantly high proportion of rare species, and anemogamous species a significantly low proportion of rare species (Fig. 3e). Entomogamous species exhibited more rare species than nonrare species at both dates but this was significant only in 1886 (Fig. 3e). Thus, pollination mode was not related to species abundance changes during 1886–2001 (Table 1c, Fig. 3e).

For species abundance changes during 1886–2001, life form had a stronger effect than perenniality and was selected in the final model (Table 1c). The most striking pattern was the dramatic decline of hydrophyte species in the study region during 1886–2001. Hydrophytes were disproportionately overrepresented among decreasing/extinct species (Fig. 2a) relative to other classes of abundance changes. As a result, the proportion of hydrophytes among rare species was increased in 2001 relative to 1886, but this change was not significant (Fig. 3a).

Among herbaceous species, annual and perennial species showed contrasting patterns of abundance and abundance changes. Annuals (i.e. therophytes) were significantly more represented among nonrare species than among rare species, both in 1886 and 2001 (Fig. 3b). During 1886–2001, annuals exhibited a significantly higher proportion of decreasing/extinct species relative to stable species, suggesting very transient spatial dynamics and a tendency to local extinction (Fig. 3b). On the contrary, herbaceous perennials (i.e. geophytes and hemicryptophytes) exhibited more rare species than nonrare species in 1886 (Fig. 3b). Herbaceous perennials tended to increase in the study region during 1886–2001, and, as a result, were no longer significantly overrepresented among rare species in 2001 (Fig. 3b). This increasing trend was clearly stronger for geophytes than for hemicryptophytes (Fig. 3a).

Among woody species, chamaephytes and phanerophytes also exhibit contrasting patterns. Phanerophytes were significantly under-represented among rare species in 1886 and 2001, and overrepresented among increasing/immigrant species during 1886–2001 (Fig. 3a). Chamaephytes exhibited no significant patterns of abundance in 1886 and abundance changes during 1886–2001, but presented more rare species than nonrare species in 2001 (Fig. 3a).

Species height was also a significant predictor of species abundance and abundance changes during

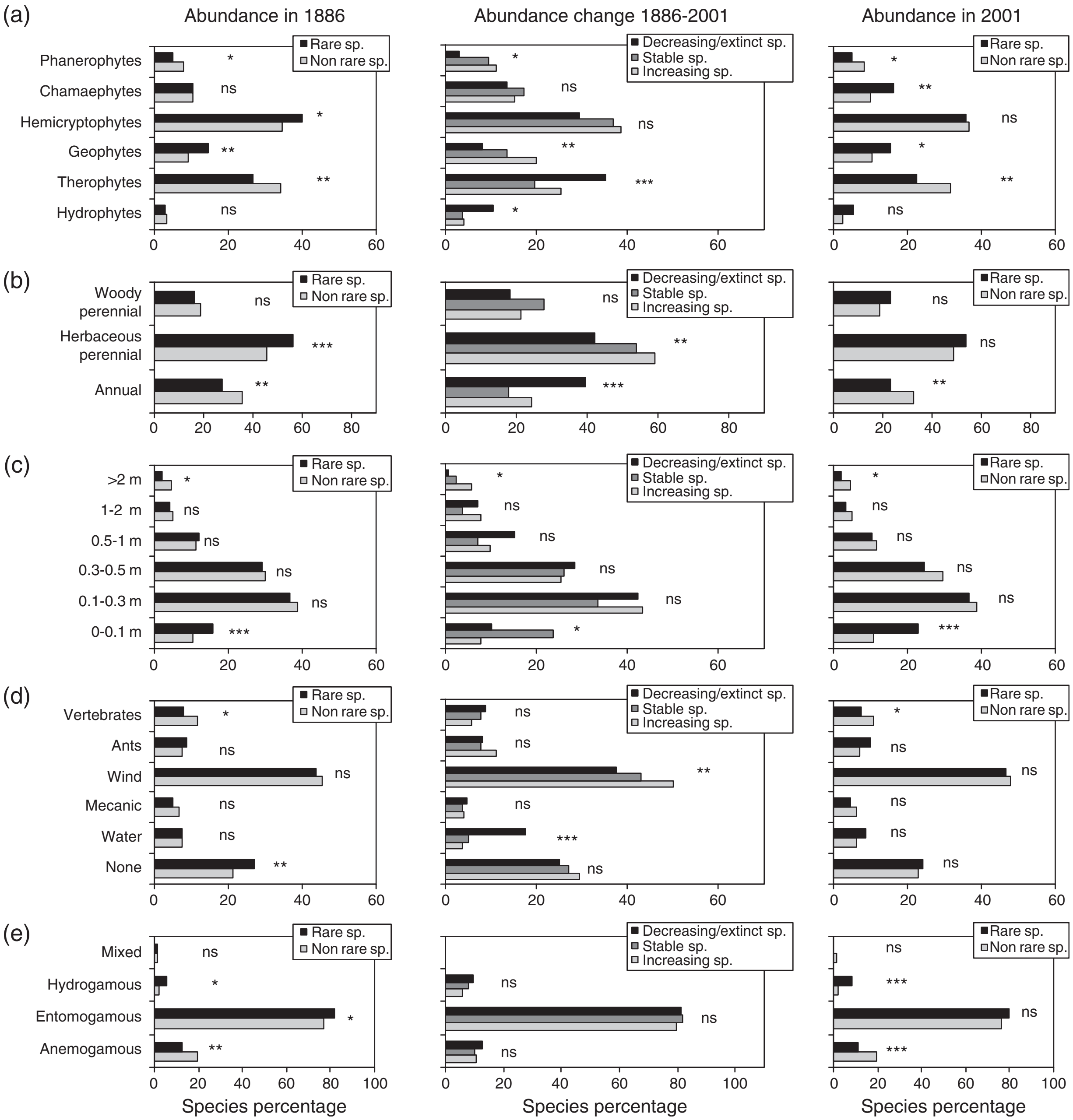

Fig. 3 Results of contingency analyses between abundance classes in 1886 and 2001, abundance changes from 1886 to 2001 and classes of life forms (a), perenniality (b), height (c), dispersal agents (d) and pollination modes (e). *P*-values result from Fisher exact tests, with: ns, nonsignificant; *$P<0.05$, **$P<0.01$, ***$P<0.001$.

1886–2001, independently of species life form or perenniality (Table 1a–c). Height had a significant effect on species abundance across different perenniality classes (Fig. 4). In 1886 and 2001, the shortest species (0–0.1 m tall) were more represented among rare species than nonrare species (Fig. 3c); this was significant for both annual and perennial life forms (Fig. 4a–f). Within woody species, species shorter than 0.3 m (i.e. lower chamaephytes) were overrepresented among 2001 rare species (Fig. 4f) whereas species taller than 1 m (i.e. higher chamaephytes and phanerophytes) were underrepresented among 2001 rare species (Fig. 4f). During 1886–2001, the shortest species (0–0.1 m height class) exhibited disproportionately more stable species (Fig. 3c). The tallest species (>2 m class) were significantly overrepresented among increasing/immigrant

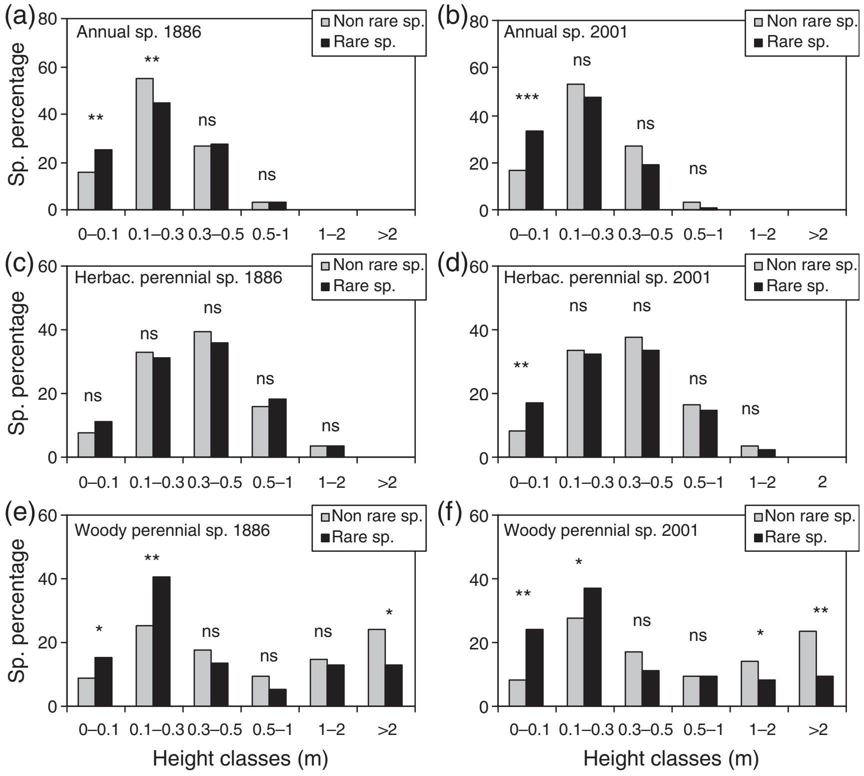

Fig. 4 Percentage of rare species and nonrare species across different height classes, within annual species in 1886 and 2001 (a, b), herbaceous perennials in 1886 and 2001 (c, d), woody species in 1886 and 2001 (e, f). *P*-values result from Fisher's exact tests, with: ns, nonsignificant; $^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$.

species during 1886–2001 (Fig. 3c). This pattern was clearly related to the increasing trend observed for phanerophytes.

In 1886 and 2001, dispersal agent was not selected in the final models of species abundance (Table 1a, b), as the effect of some dispersal agents was recurrently confounded with those of life forms. However, dispersal agent alone had a significant effect on species abundance changes during 1886–2001 and was selected in the final model (Table 1c). Wind-dispersed species showed an increasing trend in the study region whereas water-dispersed species showed a strong trend to regression/extinction during 1886–2001 (Fig. 3d).

Patterns of niche and biogeographic features

Habitat specificity was not related to species abundance changes, whereas level of endemism was significantly related to species abundance changes during 1886–2001 (Table 1c). This latter effect was confounded by the effect of species biogeographic affinity, as narrow endemic species were almost exclusively categorized as Mediterranean species (level of endemism vs. biogeographic affinity, $\chi^2_{(\mathrm{df}=3)} = 34.5$ $P<0.001$). As a result, biogeographic affinity was the only biogeographic feature selected in the final model of abundance changes (Table 1c). Mediterranean and Mountain species showed a tendency to stability during 1886–2001, whereas Eurosiberian species strongly decreased during 1886–2001 (Fig. 5).

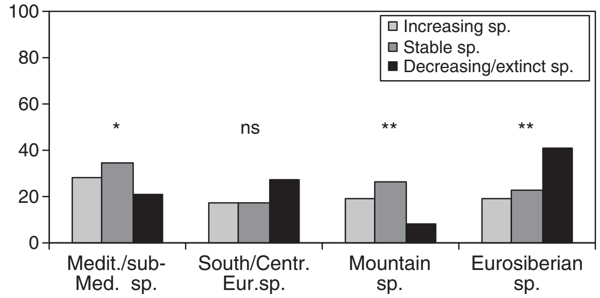

Fig. 5 Percentages of increasing, stable and decreasing/extinct rare species during 1886–2001 across different groups of biogeographic affinities. *P*-values result from Fisher's exact tests, with: ns, nonsignificant; $^{*}P<0.05$, $^{**}P<0.01$.

Effects of variation in sampling effort

We fitted a second odds ratio model of abundance changes using the reduced data set of 241 species that were unlikely to have been overlooked in 1886 or 2001. Results of single variable models were qualitatively unchanged because variables with significant effects were life form ($\chi^2_{(\mathrm{df}=5)} = 17.5$ $P < 0.01$), perenniality ($\chi^2_{(\mathrm{df}=2)} = 9.5$ $P < 0.01$), dispersal agent ($\chi^2_{(\mathrm{df}=5)} = 12.5$ $P < 0.05$), geographic affinity ($\chi^2_{(\mathrm{df}=3)} = 21.5$ $P < 0.001$), and level of endemism ($\chi^2_{(\mathrm{df}=1)} = 4.5$ $P < 0.05$). The effect of species height, previously significant with the full data set, became marginally nonsignificant ($\chi^2_{(\mathrm{df}=5)} = 10.7$ $P = 0.058$). After stepwise selection, the final model was invalid because the assumption of parallel regression between different classes of each variable did not hold (see SAS, 1999, score test of proportional odds assumption $\chi^2_{(\mathrm{df}=8)} = 41.4$ $P < 0.001$). Thus, this model was not interpretable due to the low number of observations relative to the number of fitted parameters. However, the results obtained with the single variables odds ratio models indicate that the observed biological patterns of species abundance changes are quite robust to the spatial heterogeneity in sampling effort.

Taxonomic patterns

Species abundance and abundance changes during 1886–2001 significantly varied between taxonomic groups. The study flora consists of 128 families, among which only 15 include more than 40 species, and 73 include 1–5 species. Appendix A presents the list of families that showed a significantly low or high proportion of rare species in 1886 and 2001, of decreasing/extinct species during 1886–2001, and of increasing/immigrant species during 1886–2001.

Fabaceae and Poaceae had less rare species than expected by chance in 1886 and 2001, as well as Euphorbiaceae in 1886 and Asteraceae and Chenopodiaceae in 2001. Conversely, Cyperaceae, Gentianaceae, Liliaceae and Saxifragaceae exhibited a significantly high proportion of rare species in 1886 and 2001. Apiaceae, Brassicaceae, Crassulaceae, Iridaceae, Naïadaceae, Rosaceae and Scrophulariaceae exhibited significantly many rare species in 1886 but not in 2001. Equisetaceae, Lentibulariaceae, Lycopodiaceae, Marsileaceae, Ophioglossaceae, Papaveraceae, Plumbaginaceae, Polypodiaceae, Primulaceae, Pyrolaceae and Ranunculaceae exhibited significantly many rare species in 2001 only.

Some families showed significant regression/extinction trends during 1886–2001: Brassicaceae, Gentianaceae, Orobanchaceae, Papaveraceae and Poaceae had significantly more decreasing/extinct and/or less increasing/immigrant species than expected by chance. However, Cyperaceae, Fabaceae, Liliaceae, Orchidaceae and Rubiaceae had significantly fewer decreasing/extinct species and/or more numerous increasing/immigrant species.

Discussion

Botanic diversity is currently threatened in many regions of the world, including Tropical and Mediterranean regions (Pitman *et al*., 2002; Thomas *et al*., 2004). Here, we document the changes that occurred in the rare species assemblage of a Mediterranean flora over the course of the 20th century, in terms of species life history traits, niche and biogeographic features and taxonomic groups. Few assessments have been achieved on such a large timescale (e.g. Duncan & Young, 2000), although they can provide highly valuable data for future conservation planning. The main challenge of studies using archival data is probably that they must assess the robustness of their results to the spatio-temporal heterogeneity in sampling effort. Based on previous spatial analyses conducted in the same study region (Denelle *et al*., 1995; Lavergne *et al*., 2005), we showed that species pseudo-extinctions are highly unlikely in our data set, and that biological patterns of species colonization are quite robust to pseudo-colonization events. Hence, our study highlights several robust patterns about the relationship between species biological and ecological features and their long-term response to environmental changes in the Western Mediterranean Basin.

A primary result of our study is that long-term rate of rare species extinction is largely predicted by their initial abundance, as species with the smallest number of occurrences in the study region in 1886 were the most prone to regional extinction by 2001. We also showed that in the Mediterranean Basin, regional assemblages of rare species may be biologically nonrandom and significantly changing over time, as rates of rare species local extinction, persistence and colonization were related to their life-history traits, niche characteristics, and taxonomic group. During the 20th century, the Mediterranean Region experienced intense land use and climate changes that appear to have differently affected individual rare plant species. Our results allow separating groups of rare plant species undergoing high risk of extinction from those not affected or even favored by current global changes.

Some life-history traits predict the species abundance changes over the 20th century, as they influence their population biology and their response to environmental change. First, the observed higher abundance and colonization rate of taller woody species (above 1 m) relative to shorter woody species (under 0.3 m) may be primarily associated with land abandonment and decrease in livestock grazing that occurred in most Mediterranean backcountries, but also with the increase in atmospheric CO_2 that can favor woodland progression under Mediterranean climates (Bond *et al*., 2003). However, fire is unlikely to have generated this pattern in our study region. Second, the regional abundance and dynamics of herbaceous species were strongly related to their life span. Annual species exhibited highly transient dynamics from 1886 to 2001, with a high rate of decline or regional extinction while perennial species showed a higher potential of local persistence, and even significantly increased in abundance over the study period. This pattern may be due to: (i) the higher sensitivity of short-lived plant species to environmental and demographic stochasticity, as found in other floras (Fischer & Stöcklin, 1997), (ii) the decrease of early successionnal habitats that were traditionally maintained by grazing, managed fire and the use of fallow lands and, (iii) the intensification of agriculture which may have negatively affected many annual opportunistic species. Third, traits controlling seed and pollen flow had little effect on rare species dynamics and extinction rate during 1886–2001. Only wind-dispersed rare species have clearly increased in the study area during 1886–2001, indicating that in fragmented landscapes, wind dispersal may confer a higher chance of colonization. Pollination modes were however not related to rare species dynamics, as both insect and water pollination remained overrepresented among rare species from 1886 to 2001. This is consistent with previous studies where pollination and breeding systems poorly predicted species response to habitat fragmentation (Aizen *et al*., 2002; Jacquemyn *et al*., 2005).

Another striking change in the flora of Hérault is the high rate of local and regional extinction of species associated with wet habitats, such as hydrophytes and water-pollinated or water-dispersed species. Such species were overrepresented among decreasing/extinct species during 1886–2001 and/or among rare species in 2001. Accordingly, families usually associated with wet habitats, such as Equisetaceae, Lentibulariaceae, Marsileaceae, Ophioglossaceae, have become significantly rare in 2001. These results point out the dramatic rate of destruction and alteration of wet habitats that occurred in Mediterranean lowlands and coastal zones over the last century (Pons & Quézel, 1985; Lavergne *et al*., 2005), causing a strong decline of wetland species in Mediterranean floras. The same dramatic decline of hydrophyte species had already been documented in other local floras of the Western Mediterranean Basin (Verlaque *et al*., 2001). Entire taxa associated with wet habitats may thus be highly threatened and deserve a high conservation priority in the Mediterranean Region.

Rare species regional dynamics during 1886–2001 were also strongly related to their biogeographic origin. First, Mediterranean rare species, including a large proportion of narrow endemic species, remained stable in the study region during 1886–2001. This result is consistent with: (i) the known tendency of narrow Mediterranean endemic species to occur in habitats with low interspecific competition and low human disturbances (Lavergne *et al*., 2003, 2004) and (ii) recent bioclimatic projections that predict a low effect of climate changes on species occurring at the warmer and drier end of European climatic gradients (Thuiller *et al*., 2005a, b). Second, mountain rare species also tended to be stable during 1886–2001. This pattern is surprising given that mountain rare species occur in marginal habitats in the study area and have thus been thought to be threatened by climate changes (Dirnbock *et al*., 2003; Lavergne *et al*., 2005). Third, rare species with Eurosiberian distributions showed a dramatically high rate of regression and extinction in Hérault during 1886–2001. Most of these species are widely distributed and abundant throughout Europe but reach their range limits in the Mediterranean Region where they can be rare at regional scales. Our results thus suggest that southern peripheral populations of Eurosiberian species are currently prone to extinction. This is consistent with the predicted loss of favorable habitat at the southern margin of their range as a result of global warming (Thuiller *et al*., 2005b), and with the previously observed biological consequences of climate change on plant species, including northwards shifts in their geographic range (Parmesan & Yohe, 2003; Root *et al*., 2003). The loss of southern ecotypes of widespread Eurosiberian species may impoverish their future evolutionary potential (Hampe & Petit, 2005), and ultimately endanger future biodiversity (Rosenzweig, 2001).

We also found evidence for strong taxonomic patterns in species abundance and abundance changes from 1886 to 2001. Eleven and fifteen families were significantly rare species-rich in 1886 and 2001, respectively (see Appendix A). But the taxonomic patterns of species abundance strongly differed between the two survey dates, as only four families consistently exhibited an excess of rare species in 1886 and 2001 (see Appendix A). Brassicaceae, Gentianaceae, Orobanchaceae, Papaveraceae and Poaceae showed a significantly high proportion of decreasing or extinct rare species during 1886–2001 and constitute the most threatened taxonomic groups of rare species in the study region, while Cyperaceae, Fabaceae, Liliaceae, Orchidaceae and Rubiaceae significantly exhibited an increasing trend. Thus, the taxonomic patterns of rarity vary over time in the Mediterranean Basin and differ from other regions with a similar Mediterranean climate (Cowling *et al*., 1994; Lozano & Schwartz, 2005a). Species rarity and declining rate in the Mediterranean Flora are not taxonomically random, which may lead to a substantial loss of evolutionary history relative to a taxonomically random extinction process (Nee & May, 1997). Hence, the taxonomic patterns of plant species rarity and extinction threat observed in the Mediterranean Region should be further investigated as a function of taxa size or evolutionary age (Schwartz, 1993; Lozano & Schwartz, 2005b).

Conservation implications for the Western Mediterranean flora

Recent assessment show that less than 5% of the worldwide plant species have received a formal assessment of their global conservation status using IUCN criteria (Lughadha *et al*., 2005), and that the reliability of Red Lists still needs to be improved (Burgman, 2002; Possingham *et al*., 2002). Empirical modeling of species extinction rate as a function of their life-history traits, niche characteristics and taxonomic group can be used to determine species groups that are not yet declining steeply but whose features make them very susceptible to global change. This type of study also allows to assess the projections of species response to global change obtained from bioclimatic envelope models (e.g. Thuiller *et al*., 2005b).

Species with Eurosiberian distributions but rare in the Mediterranean zone are strongly declining in the Mediterranean, while Mediterranean-rare species, including many narrow endemics, are generally very stable. The most threatened rare Mediterranean plant species are also annual and hydrophyte rare species, as well as entire hydrophyte taxa such as Equisetaceae, Lentibulariaceae, Marsileaceae and Ophioglossaceae. Rare species of Brassicaceae, Gentianaceae, Orobanchaceae, Papaveraceae and Poaceae also seem threatened. With the potential decline or even extinction of entire taxa in Mediterranean regions and the loss of southern ecotypes of widespread Eurosiberian species, both evolutionary history and speciation potential are currently threatened in the Mediterranean Region. This emphasizes the need for more biogeographic and phylogenetic information in future conservation planning in the Mediterranean Region and other Biodiversity Hotspots.

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References

Aizen MA, Ashworth L, Galetto L (2002) Reproductive success in fragmented habitats: do compatibility systems and pollination specialization matter? *Journal of Vegetation Science*, **13**, 885–892.

Bennett PM, Owens IPF (1997) Variation in extinction risk among birds: chance or evolutionary predisposition? *Proceedings of Royal Society of London Series B*, **264**, 401–408.

Bolos OD, Vigo J, Masalles RM *et al*. (1993) *Flora manual dels Països Catalans*. Editorial Portic s.a, Barcelona.

Bond WJ, Midgley GF, Woodward FI (2003) The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. *Global Change Biology*, **9**, 973–982.

Burgman MA (2002) Are listed threatened plant species actually at risk? *Australian Journal of Botany*, **50**, 1–13.

Cadotte MW, Lovett-Doust J (2002) Ecological and taxonomic differences between rare and common plants of southwestern Ontario. *Ecoscience*, **9**, 397–406.

Coste H (1900–1906) *lore descriptive et illustrée de la France et de la Corse et des contrées limitrophes*. Librairie scientifique et technique, Paris.

Coulson T, Mace GM, Hudson E *et al*. (2001) The use and abuse of population viability analysis. *Trends in Ecology and Evolution*, **16**, 219–221.

Cowling RM, Witkowski ETF, Milewski AV *et al*. (1994) Taxonomic, edaphic and biological aspects of narrow plant endemism on matched sites in mediterranean South Africa and Australia. *Journal of Biogeography*, **21**, 651–664.

Debussche M, Lepart J, Dervieux A (1999) Mediterranean landscape changes: evidence from old postcards. *Global Ecology and Biogeography*, **8**, 3–15.

Denelle N, Bertrand L, Granel de Solignac L *et al*. (1995) Connaissance et exploration floristiques en Languedoc-Roussillon (France): cartographie des points d'herborisation et répartition des Malvaceae pour l'Hérault. *Acta Botanica Gallica*, **142**, 37–53.

Dirnbock T, Dullinger S, Grabherr G (2003) A regional impact assessment of climate and land use change on alpine vegetation. *Journal of Biogeography*, **30**, 401–417.

Drayton B, Primack RB (1996) Plant species lost in an isolated conservation area in metropolitan Boston from 1894 to 1993. *Conservation Biology*, **10**, 30–39.

Dugrand R (1971) *Atlas Régional du Languedoc-Roussillon*. Berger-Levrault, Paris.

Duncan RP, Young JR (2000) Determinants of plant extinction and rarity 145 years after European settlement of Auckland, New Zealand. *Ecology*, **81**, 3048–3061.

Dupré C, Ehrlén J (2002) Habitat configuration, species traits and plant distributions. *Journal of Ecology*, **90**, 796–805.

Edwards W (1998) Rarity with taxonomic lineages and the use of taxa above the level of species. *Ecography*, **21**, 625–629.

Edwards W, Westoby M (2000) Families with highest proportions of rare species are not consistent between floras. *Journal of Biogeography*, **27**, 733–740.

Fischer M, Stöcklin J (1997) Local extinctions of plants in remnants of extensively used calcareous grasslands 1950–1985. *Conservation Biology*, **11**, 727–737.

Fréville H, Colas B, Riba M *et al*. (2004) Spatial and temporal demographic variability in the endemic plant species *Centaurea corymbosa* (Asteraceae). *Ecology*, **85**, 694–703.

Gachet S, Véla E, Tatoni T (2005) BASECO: a floristic and ecological database of Mediterranean French flora. *Biodiversity and Conservation*, **14**, 1023–1034.

Gaston KJ (1994) *Rarity*. Chapman & Hall, London.

Gaston KJ (2003) *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, Oxford.

Gordo O, Sanz JJ (2005) Phenology and climate change: a long term study in a Mediterranean locality. *Oecologia*, **146**, 484–495.

Greuter W (1991) Botanical diversity, endemism, rarity, and extinction in the Mediterranean area: an analysis based on the published volumes of Med-Checklist. *Botanika Chronika*, **10**, 63–79.

Greuter W, Burdet HM, Long G (1984–1989) *Med-Checklist*. Conservatoire et Jardin botaniques de Genève, Genève.

Gustafsson L (1994) A comparison of biological characteristics and distribution between Swedish threatened and non-threatened forest vascular plants. *Ecography*, **17**, 39–49.

Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, **8**, 461–467.

Harrison S (1999) Local and regional diversity in a patchy landscape: native, alien, and endemic herbs on serpentine. *Ecology*, **80**, 70–80.

Hedge SG, Ellstrand NC (1999) Life history differences between rare and common flowering plant species of California and the British Isles. *International Journal of Plant Science*, **160**, 1083–1091.

Hodgson JG (1986) Commonness and rarity in plants with special reference to the Sheffield Flora. *Biological Conservation*, **36**, 199–314.

Jacquemyn H, Brys R, Hermy M *et al*. (2005) Does nectar reward affect rarity and extinction probabilities of orchid species? An assessment using historical records from Belgium and Netherlands. *Biological Conservation*, **121**, 257–263.

Kerguélen M (1993) *Index synonymique de la flore de France*. Musém National d'Histoire Naturelle, Paris.

Lavergne S, Garnier E, Debussche M (2003) Do rock endemic and widespread plant species differ under the leaf-height-seed plant ecology strategy scheme? *Ecology Letters*, **6**, 398–404.

Lavergne S, Thompson JD, Garnier E *et al*. (2004) The biology of endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. *Oikos*, **107**, 505–518.

Lavergne S, Thuiller W, Molina J *et al*. (2005) Environmental and human factors influencing rare plant local occurrence, extinction and persistence: a 115 year study in the Mediterranean region. *Journal of Biogeography*, **32**, 799–811.

Lawton JH (1995) Population dynamics principles. In: *Extinction Rates* (eds Lawton JH, May RM), pp. 147–163. Oxford University Press, Oxford, UK.

Lepart J, Debussche M (1992) Human impact on landscape patterning: mediterranean examples. In: *Landscape Boundaries. Consequences for Biotic Diversity and Ecological Flows* (eds Hansen AJ, Di Castri F), pp. 76–106. Springer-Verlag, New York.

Loret H, Barrandon A (1886) *Flore de Montpellier ou analyse descriptive des plantes vasculaires de l'Hérault*, 2ème Edn. Montpellier.

Lozano FD, Schwartz MW (2005a) Comparative taxonomic structure of the floras of two Mediterranean-climate regions: Iberia and California. *Diversity and Distributions*, **11**, 399–408.

Lozano FD, Schwartz MW (2005b) Patterns of rarity and taxonomic group size in plants. *Biological Conservation*, **126**, 146–154.

Lughadha EN, Baillie J, Barthlott W *et al*. (2005) Measuring the fate of plant diversity: towards a foundation for future monitoring and opportunities for urgent action. *Philosophical Transactions of Royal Society of London Series B*, **360**, 359–372.

Mace GM, Gittleman JL, Purvis A (2003) Preserving the Tree of life. *Science*, **300**, 1707–1709.

Mace GM, Kershaw M (1997) Extinction and rarity on an ecological timescale. In: *The Biology of Rarity: Causes and Consequences of Rare-Common Differences* (eds Kunin WE, Gaston KJ), pp. 130–149. Chapman & Hall, London.

Maschinski J, Frye R, Rutman S (1997) Demography and population viability of an endangered plant species before and after protection from trampling. *Conservation Biology*, **11**, 990–999.

Matthies D, Bräuer I, Maibom W *et al*. (2004) Population size and the risk of local extinction: empirical evidence from rare plants. *Oikos*, **105**, 481–488.

McCollin D, Moore L, Sparks T (2000) The flora of a cultural landscape: environmental determinants of change revealed using archival sources. *Biological Conservation*, **92**, 249–263.

Menges ES (1990) Population viability analysis for an endangered plant. *Conservation Biology*, **4**, 52–62.

Menges ES, Quintana-Ascencio PF (2004) Population viability with fire in *Eryngium cuneifolium*: deciphering a decade of demographic data. *Ecological Monographs*, **74**, 79–99.

Molinier R, Müller P (1938) *La dissémination des espèces végétales*. Imprimerie André Lesot, Paris, 169 pp.

Myers N, Mittermeier RA, Mittermeier CG *et al*. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Nee S, May RM (1997) Extinction and the loss of evolutionary history. *Science*, **288**, 328–330.

Osborne CP, Mitchell PL, Sheehy JE *et al*. (2000) Modelling the recent historical impacts of atmospheric CO_2 and climate change on mediterranean vegetation. *Global Change Biology*, **2000**, 445–458.

Ouborg NJ (1993) Isolation, population size and extinction: the classical and metapopulation approaches applied to vascular plants along the Dune Rhine-system. *Oikos*, **66**, 298–308.

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Pilgrim ES, Crawley MJ, Dolphin K (2004) Patterns of rarity in the native British flora. *Biological Conservation*, **120**, 165–174.

Pitman NC, Jorgensen PM, Williams RSR *et al*. (2002) Extinction-rate estimates for a modern neotopical flora. *Conservation Biology*, **16**, 1427–1431.

Pons A, Quézel P (1985) The history of the flora and vegetation and past and present human disturbance in the mediterranean region. In: *Plant Conservation in the Mediterranean Area*, Vol. 7 (ed. Gomez-Campo C), pp. 9–24. Geobotany, Dordrecht, the Netherlands.

Possingham HP, Andelman SJ, Burgman MA *et al*. (2002) Limits to the use of threatened species lists. *Trends in Ecology and Evolution*, **17**, 503–507.

Prinzing A, Durka W, Klotz S *et al*. (2001) The niche of higher plants: evidence for phylogenetic conservatism. *Proceedings of the Royal Society of London Series B*, **268**, 1–7.

Purvis A, Agapow P, Gittleman JL *et al*. (2000) Nonrandom extinction and loss of evolutionary history. *Science*, **288**, 328–330.

Qian H, Ricklefs RE (2004) Geographical distribution and ecological conservatism of disjunct genera of vascular plants in eastern Asia and eastern North America. *Journal of Ecology*, **92**, 253–265.

Quintana-Ascencio PF, Menges ES (1996) Inferring metapopulation dynamics from patch-level incidence of florida scrub plants. *Conservation Biology*, **10**, 1210–1219.

Quézel P (1985) Definition of the Mediterranean region and the origin of its flora. In: *Plant Conservation in the Mediterranean Area*, Vol. 7 (ed. Gomez-Campo C), pp. 9–24. Geobotany, Dordrecht, the Netherlands.

Root TL, Price JT, Hall KR *et al*. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

Rosenzweig C (2001) Loss of speciation rate will impoverish future diversity. *Proceedings of National Academy of Sciences of USA*, **98**, 5404–5410.

Sala OE, Chapin FSI, Armesto JJ *et al*. (2000) Global biodiversity scenarios for the year 2000. *Science*, **287**, 1770–1774.

SAS (1999) *SAS/STAT user's guide*. SAS, Cary, NC.

Schwartz MW (1993) The search for pattern among rare plants: are primitive species more likely to be rare? *Biological Conservation*, **64**, 121–127.

Shaw P (2005) Estimating local extinction rates over successive time-frames. *Biological Conservation*, **121**, 281–287.

Soltis DE, Soltis PS, Chase MW *et al*. (2000) Angiosperm phylogeny inferred from 18S rDNA, *rbcL*, and *atpB* sequences. *Botanical Journal of the Linnean Society*, **133**, 381–461.

Thomas JA, Telfer MG, Roy DB *et al*. (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science*, **303**, 1879–1881.

Thuiller W, Lavorel S, Araujo M *et al*. (2005a) Climate change threats to plant diversity in Europe. *Proceedings of National Academy of Sciences USA*, **102**, 8245–8250.

Thuiller W, Lavorel S, Araújo MB (2005b) Niche properties and geographic extent as predictors of species sensitivity to climate change. *Global Ecology and Biogeography*, **14**, 347–357.

Tutin TG, Burges NA, Chater AO *et al*. (1964–1993) *Flora Europaea*. Cambridge University Press, Cambridge.

van der Pijl L (1972) *Principles of Dispersal in Higher Plants*. Springer, Berlin.

Verlaque R, Médail F, Aboucaya A (2001) Valeur prédictive des types biologiques pour la conservation de la flore méditerranéenne. *C.R. Acad. Sci. Paris, Sciences de la vie/Life Sciences*, **324**, 1157–1165.

Appendix A

Table A1

Table A1 List of families that showed a significantly low or high proportion of rare species in 1886 and 2001, of decreasing/extinct species from 1886 to 2001, and of increasing/immigrant species from 1886 to 2001

Rare sp. 1886		Rare sp. 2001		Decreasing/extinct sp. 1886–2001		Increasing/immigrant sp. 1886–2001	
Family	Fisher's test	Family	Fisher's test	Family	Fisher's test	Family	Fisher's test
Less than expected							
Euphorbiaceae	0.022	Asteraceae*	0.018	Liliaceae*	0.011	Brassicaceae*	0.042
Fabaceae*	0.001	Chenopodiaceae*	0.017	Orchidaceae*	0.005	Gentianaceae	0.033
Poaceae*	0.001	Fabaceae*	0.021			Papaveraceae	0.044
		Poaceae*	<0.001			Poaceae*	0.020
More than expected							
Apiaceae*	0.022	Cyperaceae*	0.031	Orobanchaceae	0.046	Cyperaceae*	0.035
Brassicaceae*	0.024	Equisetaceae	0.031	Brassicaceae*	0.047	Fabaceae*	0.040
Crassulaceae	0.001	Gentianaceae	0.003	Poaceae*	0.009	Liliaceae*	0.037
Cyperaceae*	0.040	Lentibulariaceae	0.002			Orchidaceae*	0.005
Gentianaceae	0.004	Liliaceae*	0.018			Rubiaceae	0.037
Iridaceae	0.041	Lycopodiaceae	0.002				
Liliaceae*	0.002	Marsileaceae	0.018				
Naïadaceae	0.034	Ophioglossiaceae	0.046				
Rosaceae*	0.039	Papaveraceae	0.028				
Saxifragaceae	0.041	Plumbaginaceae	0.012				
Scrophulariaceae*	0.011	Polypodiaceae	0.004				
		Primulaceae	0.011				
		Pyrolaceae	0.018				
		Ranunculaceae*	0.018				
		Saxifragaceae	0.012				

*Families that were among the 15 largest families in the study flora are marked with.

Each *P*-value results from a Fisher's exact test between each family vs. the rest of the flora for the proportion of rare, decreasing or increasing species.