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Assessing vulnerability of listed Mediterranean plants based on population monitoring

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ABSTRACT

Understanding the population dynamics of rare and endangered plant species is essential to elaborate correct management plans for their conservation. Demographic monitoring of individual species provides valuable information here. However, demographic studies are limited to species for which one can follow individuals through their life history. They are also time consuming, making it difficult to make simultaneous studies of several species with different populations in order to have a more general assessment of rare species dynamics in a given region. In this paper, we illustrate how the use of an approach based on transition frequencies allows for the simultaneous study and comparison of trends in 32 populations of six species with very different life histories and growth forms in the Mediterranean region of the South of France. The results show significant effects of spring rainfall deficit on annual population dynamics but not for perennial species that show a delayed response, and illustrate population declines due to direct human impacts on populations in the study region. Our study illustrates the alarming overall vulnerability of populations and is simple and rapid to apply in a multi-population and multi-species context. It could thus be used by conservation management staff to construct assessments of population vulnerability elsewhere.

1. Introduction

Many plant species show a decline in population numbers as a result of habitat destruction and a decline in population viability due to habitat modification. There has thus been great interest in the monitoring of rare and endangered species in order to assess their status and assure their protection. There are three main approaches to monitoring that can be undertaken at different scales, each with their own particular objective (Bonnet et al., 2015; Elzinga, Salzer, & Willoughby, 1998; Palmer, 1987). First, inventories of species presence show where species are present and absent in a given territory or region and thus provide information on rarity and overall threats. Second, surveys of population characteristics allow us to have basic information on numbers of plants, flowers, sometimes seed set and also human impacts on populations and habitats. Third, detailed demographic monitoring provides information on the fates of individual plants and populations. These approaches differ markedly in their technical requirements and the time spent in the field in order to obtain informative data.

A demographic approach requires that individuals be followed through their life cycle. This allows for the estimation of population growth rates and the identification of life-cycle stages that impinge on population trends, i.e. key elements for conservation management (Schemske et al., 1994). Many studies have thus illustrated the pertinence of a demographic approach for our understanding of the population viability of rare and endangered plant populations (Andrieu et al., 2017; Fréville et al., 2004; García, 2003; Jacquemyn, Brys, Hermy, & Willems, 2007; Lehtilä, Syrjänen, Leimu, Begoña García, & Ehrlén, 2006; McCauley & Ungar, 2002; Nicolè, Brzosko, & Till-Bottraud, 2005; Schleuning & Matthies, 2008). However, it is often not possible to identify and follow individual plants due to: (i) high patch density that precludes the identification of individuals and their monitoring, (ii) the fact that plants are not visible above ground during most or part of the year, (iii) clonality and the impossibility of distinguishing genetic individuals, and (iv) problems of seedling identification at high density and when closely related species co-occur. For these reasons, and the time consuming nature of demographic monitoring, for many rare and endangered species for which management staff

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require information on their conservation status, a purely demographic approach is not possible.

In the face of these constraints, the use of frequency data based on presence / absence observations and/or classes of abundance for the yearly monitoring of plant populations provides an interesting alternative to obtain pertinent information to assess population trends (Berjano et al., 2013; Elzinga et al., 1998; Gauthier, Pons, Letourneau, Papuga, & Thompson, 2017; Joseph, Field, Wilcox, & Possingham, 2006). These authors illustrate how analyses of population transitions based on changes in frequency offer several advantages. First, frequency analyses can be applied concomitantly to compare species with different growth forms and life histories, even for clonal plants. Second, observations of presence / absence and classes of abundance in a large number of permanently marked plots can be rapidly accomplished in the field where the only decision required by the observer is to note presence / absence or a class of density. Third, such methods can be applied at different spatial scales to provide information on changes in both spatial occupation and local abundance within patches and thus identify trends at population and/or patch scale. Finally, with frequency analyses, the impact of extreme meteorological events or human-induced disturbance on population transitions can be statistically identified.

Marked variability in meteorological events is typical of Mediterranean Type Ecosystems. Here, the regular summer drought is accompanied by important irregularity in the amounts and timing of rainfall from autumn to spring. This variation in the timing and amounts of spring rainfall can cause irregular fluctuations in abundance, particularly for annual plants (Figueroa & Davy, 1991; Fox, 1995; Fox, Steele, Holl, & Fusari, 2006; Levine, McEachern, & Cowan, 2008). As these authors illustrate, annual species often germinate and grow in response to favourable water balance either in the autumn or spring while perennial species respond more to an overall yearly rainfall and temperature regime. In this respect, annual plant species can show marked variation across years with different spring rainfall regimes, whilst perennial species may show less variation in numbers, and thus may not achieve maximum numbers in highly favourable years. Theoretical models predict that fluctuations in rare annual species can positively affect their long-term persistence by reducing

competition with dominant perennial species in what are unfavourable years for above ground development (Levine & Rees, 2004). To our knowledge there have however been no long-term multiple comparisons of rare annual and perennial species to assess such variation and its implications for conservation management.

The objective of this paper is to quantify variation in population trends for rare and endangered species in Mediterranean France where populations are subject to high levels of variation in the occurrence of spring rainfall and where land-development currently impacts many populations. We show how the use of a common method to analyse transitions in occupation and abundance allows us to compile information from several populations and species to provide a general assessment of population trends and vulnerability in a range of species and in a way that is useful for conservation management.

2. Material and methods

2.1. Data collection

We apply a method based on observations of presence / absence and classes of abundance in permanently marked grids at the scale of local populations and within patches to study transitions in occupation and abundance over eight to nine years in 32 plant populations of six species with contrasting life-history strategies (Table 1). All six species are listed for protection in France (under decrees of 01/20/1982 and 08/31/1995). In the study region these species all occur at the northern limits of their Mediterranean distribution and are all rare but to different degrees. A large proportion of their populations (Fig. 1) occur in areas that have undergone rapid urbanisation and land-development for infrastructures and commercial enterprises in the last 50 years and the indirect factors that may influence population vulnerability are assessed in a separate paper (Gauthier, Bernard, & Thompson, 2019). The populations were chosen to represent a gradient of situations from populations where direct impacts were foreseeable during the nine years of our study (some were known to have part of their populations in a development programme) to secluded and low-risk zones. In each population we collected data on two spatial scales.

First, population occupation was estimated on permanent grids (marked at soil level with metal tickets and paint marks on rocks) laid

Table 1

For the six study species: Years of monitoring, number of populations, biological and habitat characteristics, and inscription to National (N) or Regional (R) conservation lists in France.

Species	Monitoring years										Life history	Peak flowering	Number of populations	Broad habitat	Conservation List
	2009	2010	2011	2012	2013	2014	2015	2016	2017						
<i>Stipellula capensis</i> (Thunb.) Röser & Hamasha	x	x	x	x	x	x	x	x	x	x	Annual	May	8	Thermophilous grassland, garrigues	R
<i>Ononis mitissima</i> L.		x	x	x	x	x	x	x	x	x	Annual	June	6	Garrigues, pastures, old fields	R
<i>Convolvulus lineatus</i> L.	x	x	x	x	x					x	Clonal perennial	June	5	Garrigues, rocky pastures, old fields	R
<i>Helianthemum marifolium</i> Mill.		x	x	x	x	x				x	Woody perennial	June	6	Garrigues, path edges	N
<i>Allium chamaemoly</i> L.		x	x	x	x	x	x	x	x	x	Geophyte	January	4	Garrigues, rocky pastures	N
<i>Astragalus glaucus</i> L.		x	x	x	x	x	x	x	x	x	Herbaceous perennial	May	3	Garrigues, rocky pastures, old fields	R

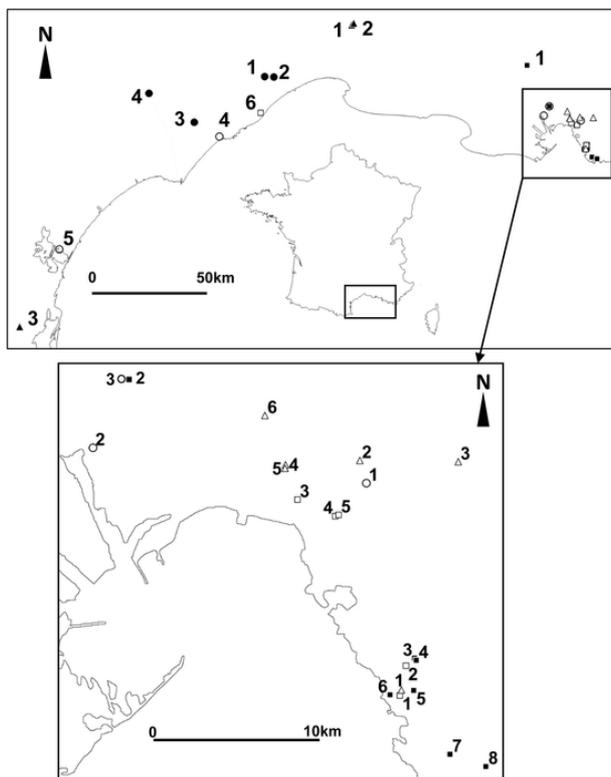


Fig. 1. The location of the 32 monitored populations in Mediterranean France: *Stipellula capensis* (black squares), *Ononis mitissima* (white squares), *Convolvulus lineatus* (white circles), *Allium chamaemoly* (black circles), *Helianthemum marifolium* (white triangles) and *Astragalus glaux* (black triangles).

out across a representative part of the population (i.e. a major patch of the population) where presence / absence of the species was noted across the whole area for perennial plants or in transects that covered areas where the species was both present or absent for annual plants. All grid cells were 0.25 m². The spatial extent of the whole grid depended on the spatial extent of the population. This estimation of occupation at the population level was conducted annually for the annual species and at three occasions in perennial populations, i.e. in the first year of the study (2009 or 2010), again in 2013 or 2014 (the first part of the study) and in the final year (2017: the second part of the study). The number of grid cells (in each population) in which we quantified presence / absence at this scale is shown in Table 2. In setting out the grid, the objective was to have a large numbers of cells in which the species is present and also absent within the zone of occupation.

Second, we quantified abundance in quadrats in which the species were present at a scale adapted to the biology of each species. The size and number of individual quadrats for annual estimates of changes in abundance differed among species and populations because of differences in population spatial extent and patchiness of populations and individual plants that sometimes induced constraints on access to quadrats (to avoid damage to the population). Although quadrats differed in size and number they consistently produced the same type of data. For perennial species, changes in abundance were estimated using presence / absence data within six to 16 quadrats (1 m² or 0.25 m²) divided into 100 cells (of 10 × 10 cm or 5 × 5 cm) in which presence / absence was quantified annually (Table 2) at the time of peak flowering. The quadrats were placed in a stratified random sample in order to encompass the range of local density observed in each population. There were thus quadrats at low density, intermediate density and high density for each population of each species.

For annual species we adopted a different approach because we could not place a grid to quantify presence / absence for many small

Table 2

Population locations for the six studied species and surface areas used to study population occupation and abundance in quadrats: longitude (LO), latitude (LA), area mapped (AM), number of 0.25 m² grid cells used to assess spatial occupation across the population (NO) and number of quadrats used to estimate abundance (NA).

Population	GPS coordinates		AM (m ²)	NO	NA
	LO	LA			
<i>Stipella capensis</i>					
1	4.80244	43.59179	56	224	224
2	4.88583	43.48026	56	224	224
3	5.02908	43.37705	56	224	224
4	5.02996	43.37622	56	224	224
5	5.02863	43.36522	56	224	224
6	5.0165	43.36353	56	224	224
7	5.04693	43.34162	56	224	224
8	5.06527	43.33712	56	224	224
<i>Ononis mitissima</i>					
1	5.02164	43.36333	64	256	256
2	5.02459	43.37423	58	232	232
3	4.96961	43.43553	25	100	100
4	4.9888	43.42948	56	224	224
5	4.99048	43.42989	56	224	224
6	3.80534	43.46237	80	320	320
<i>Convolvulus lineatus</i>					
1	5.00456	43.44158	215	860	6 (0.25)
2	4.86594	43.45459	180	720	6 (0.25)
3	4.88583	43.48026	145	580	6 (0.25)
4	3.6504	43.39775	330	1320	6 (0.25)
5	3.05139	43.08993	280	1120	6 (0.25)
<i>Helianthemum marifolium</i>					
1	5.02245	43.36537	104	416	12 (1)
2	5.00116	43.44993	116	464	13 (1)
3	5.05113	43.44942	142.5	570	12 (1)
4	4.96365	43.44839	79.25	317	12 (1)
5	4.96326	43.44699	109.75	439	12 (1)
6	4.95317	43.46648	165.25	661	13 (1)
<i>Allium chamaemoly</i>					
1	3.82068	43.56105	217.5	870	14 (1)
2	3.85524	43.55924	208.5	834	12 (1)
3	3.55718	43.43622	208.5	834	14 (1)
4	3.38753	43.51483	180.25	721	14 (1)
<i>Astragalus glaux</i>					
1	4.14572	43.70132	34	136	16 (1)
2	4.15323	43.70623	144	576	8 (1)
3	2.90211	42.87829	130	520	14 (1)

plots without causing major damage to the plants. We thus quantified abundance (in the same quadrats used for presence /absence) based on classes that can also be analysed by frequency analyses. As *S. capensis* can have extremely high individual plant densities with >1000 individuals per m², changes in abundance were assessed with four classes (class 1: 1–20 plants, class 2: 21–125 plants, class 3: 126–500 plants and class 4: >500 plants) using all the cells of 0.25 m² in which the species was present in a given year. For *O. mitissima* abundance was quantified as the number of individual plants counted annually in each cell of 0.25 m² where the species was present. Again, four classes were constructed (class 1: 1 plant, class 2: 2–3 plants, class 3: 4–8 plants, class 4: >8 plants). The maximum number of plants in a grid cell was 29 in population 2 in 2011.

Direct impacts and alterations in population habitats were assessed in the 32 monitored populations each year at the time of monitoring (January / February for *A. chamaemoly*, April - June for the other species). Some of these impacts were considered as “expected” because

they were planned to occur in development and industrial projects for which we had knowledge. Other impacts occurred in populations that were “not expected” to experience disturbance. Each year we assessed the spatial extent and the number of quadrats impacted by disturbance in each population.

To test for a relationship between changes in population occupation and spring rainfall we collected data for the study period and calculated a mean spring rainfall value for the 28 year period from 1990 to 2017 from the national weather data-base for the weather station at Marignane in the study area (<http://publitheque.meteo.fr>).

2.2. Data analysis

To analyse population changes, we performed McNemar (1947) chi-squared tests with an excel spread sheet. This method is adapted to binomial frequency data that are in matched (i.e. non-independent - the same quadrats are monitored each year) pairs in a 2×2 contingency table and assesses the heterogeneity of row and column marginal frequencies using data on transition rates based on the number of gains and losses of presence in grid cells in two successive samples. Because we studied permanent quadrats, data from one year to another are not independent. To overcome this lack of independence we were constrained to using and comparing only data that involve a gain or loss in presence, hence grid cells that show stability (i.e. either presence or absence on two successive dates) are not used in the analysis, as recommended by McNemar (1947).

We used McNemar (1947) chi-squared tests to test (1) for changes in overall population grid occupation each year in annual species and in each part of the study and across the entire study for perennial plants and (2) for changes in abundance within quadrats between each pair of successive years over the entire study in all species except *C. lineatus* and *H. marifolium* for whom this was done only in the first part of the study. For perennial species this was based on presence / absence data in small plots in each quadrat, and for annual species, we tested for abundance variation based on the number of abundance classes that increased or decreased in two successive years. Transitions to or from a class of zero were not taken into account because they contribute to variation in occupation. If a population was totally destroyed it was removed from the analysis. Based on these analyses we determined for each transition the proportion of declining, stable or growing populations.

3. Results

Three of the 32 populations went extinct in the nine years of this study. Table 3 and Supplementary Table 1 provide the data on significant variation in occupation and abundance in the two parts of the study and across the entire study period.

3.1. *Stipellula capensis* (Fig. 2)

There was no global trend in inter-annual variation in spatial occupation for the eight studied populations. Populations 4 and 8 were relatively stable across the overall study period with several significant year-to-year transitions in gains or losses but no trend across all years. Populations 3, 6 and 7 showed an overall decline in occupation and populations 1, 2 and 5 showed important year to year variations but no overall trend. In 2011, 2012 and 2014 a significant decrease in occupation was observed in all populations except population 3 in 2011, populations 2 and 8 in 2012, and populations 3 and 4 in 2014. 2013 and 2015 were globally favourable years. The other years of study showed much annual variability with no general trend. The comparison of occupation in 2009 and 2017 shows that five populations decreased (3, 5, 6, 7, 8) two remained stable (2 and 4) and one increased (1).

A significant decline in abundance was observed in seven populations in 2010, six populations in 2011 and six populations in 2016, while a significant increase in abundance was observed in five populations in 2013 and 2015. Populations 3 and 6 never showed a significant increase in abundance during the study.

3.2. *Ononis mitissima* (Fig. 3)

In *O. mitissima*, populations 2, 3, 4 and 6 showed significant year-to-year variation with a significant overall decline. In these four populations, a significant increase in occupation was observed in 2013 and in 2017. For the remaining two populations, population 1 went extinct in 2014 and population 5 declined to a single plant in 2016.

We only observed five significant changes in abundance among the 36 analysed year-to-year combinations primarily the result of the loss of high density in most populations and increased abundance in some years and populations.

3.3. *Convolvulus lineatus* (Fig. 4)

Three types of variation in population occupation were observed. First, populations 3 and 5, showed a significant gradual decrease in occupation over the study period. Visits to population 3 in 2015, 2016, and 2017 revealed that this population went extinct in 2015. Second, populations 1 and 4 showed a significant increase in occupation in the first part of the study and a significant decrease in the second part of the study. The pattern was different in these two populations because of a very small decline in population 4, which significantly increased over the whole study. Third, population 2 showed a significant increase in the first part of the study followed by a non-significant increase in the second part of the study, hence a significant increase in occupation over the study period.

The populations showed contrasting patterns of annual variation in abundance during the five first years of annual monitoring albeit with a repeated significant increase in abundance in 2012 (populations 1, 2 and 4) and a subsequent decline in abundance in most populations in 2013. A further decline in abundance was observed in the second part of the study (except population 2). All populations showed a decrease in abundance through the whole study period.

3.4. *Helianthemum marifolium* (Fig. 5)

In the first part of the study, five populations (1, 3, 4, 5 and 6) showed a significant increase in occupation while in population 2 the increase was non-significant. Populations 3, 5 and 6 showed a significant decline in occupation in the second part of the study, hence they remained stable over the overall study period and population 2 showed a significant increase in occupation. As a result no populations showed a significant decline.

Although all populations showed significant or non-significant increases in abundance during the first part of this study, all populations decreased in abundance in the second part of the study. As a result over the overall study period, abundance was stable in populations 1, 2, 4 and 6, population 5 had a significant increase and population 3 a significant decrease.

3.5. *Allium chamaemoly* (Fig. 6)

Overall occupation showed very different significant changes over the study period in the different populations. Three populations (2, 3 and 4) showed a significant decline in occupation during the second half of the study.

In contrast, populations showed several common significant year-to-year changes in abundance, with a generally significant increase in

Table 3

Values of McNemar Chi-squared tests for transitions in occupation and abundance in part 1 (i.e. between 2009 and 2013 or 2010 and 2014), part 2 (i.e. between 2013 and 2017 or 2014 and 2017) and the entire study (2009 and 2017 or 2010 and 2017). Left column contains population code numbers. An upward arrow is a significant positive transition and a downward arrow is a significant negative transition.

	Population Occupation						Abundance							
	Part 1		Part 2		Entire study		Part 1		Part2		Entire study			
<i>Stipella capensis</i>														
1	31.1	*** ↑	2.9	ns	39.4	*** ↑	8.0	** ↓	5.4	* ↓	48.3	*** ↓		
2	9.3	** ↓	20.0	*** ↑	2.0	ns	3.8	ns	26.7	*** ↑	6.4	* ↑		
3	54.1	*** ↓	0.2	ns	45.8	*** ↓	9.1	** ↓	0.0	ns	10.1	*** ↓		
4	0.5	ns	7.6	** ↓	3.4	ns	54.2	*** ↓	8.2	** ↓	26.4	*** ↓		
5	31.6	*** ↓	0.1	ns	24.5	*** ↓	46.2	*** ↓	1.0	ns	47.4	*** ↓		
6	37.0	*** ↓	119.0	*** ↓	158.0	*** ↓	118.0	*** ↓	0.0	ns	E	0.0	ns	E
7	7.8	** ↓	57.1	*** ↓	82.1	*** ↓	62.0	*** ↓	6.1	* ↓	28.0	*** ↓		
8	1.6	ns	31.2	*** ↓	22.3	*** ↓	90.1	*** ↓	4.0	* ↓	95.0	*** ↓		
<i>Ononis mitissima</i>														
1	15.1	*** ↓	0.0	ns	15.1	*** ↓	0.0	ns	E	0.0	ns	E		
2	163.4	*** ↓	88.3	*** ↑	48.7	*** ↓	0.8	ns	7.1	** ↑	1.7	ns		
3	6.6	* ↓	1.6	ns	14.2	*** ↓	4.8	* ↓	1.1	ns	3.5	ns		
4	81.6	*** ↓	3.9	* ↑	57.6	*** ↓	0.5	ns	0.0	ns	0.5	ns		
5	78.7	*** ↓	27.7	*** ↓	130.1	*** ↓	2.5	ns	0.0	ns	0.0	ns		
6	147.8	*** ↓	60.9	*** ↑	37.8	*** ↓	7.8	** ↓	2.1	ns	9.4	** ↓		
<i>Convolvulus lineatus</i>														
1	6.1	* ↑	8.8	** ↓	0.1	ns	22.5	*** ↓	72.0	*** ↓	133.0	*** ↓		
2	80.4	*** ↑	2.4	ns	72.6	*** ↑	34.1	*** ↓	0.0	ns	26.0	*** ↓		
3	22.2	*** ↓	82.0	*** ↓	121.0	*** ↓	55.9	*** ↓	162.0	*** ↓	281.0	*** E		
4	115.6	*** ↑	11.3	*** ↓	32.6	*** ↑	6.8	** ↑	35.0	*** ↓	52.0	*** ↓		
5	9.3	** ↓	54.0	*** ↓	78.9	*** ↓	26.1	*** ↓	45.0	*** ↓	99.0	*** ↓		
<i>Helianthemum marifolium</i>														
1	49.3	*** ↑	2.1	ns	23.8	*** ↑	6.5	* ↑	19.8	*** ↓	2.9	ns		
2	0.1	ns	6.9	** ↑	7.1	** ↑	11.8	*** ↑	18.1	*** ↓	0.2	ns		
3	18.5	*** ↑	4.1	* ↓	3.5	ns	0.0	ns	38.8	*** ↓	31.0	*** ↓		
4	9.2	** ↑	0.3	ns	6.0	* ↑	22.2	*** ↑	36.7	*** ↓	1.7	ns		
5	18.2	*** ↑	12.0	*** ↓	0.0	ns	27.3	*** ↑	5.6	* ↓	5.5	* ↑		
6	35.2	*** ↑	18.5	*** ↓	1.3	ns	16.3	*** ↑	30.8	*** ↓	3.8	ns		
<i>Allium chamaemoly</i>														
1	35.7	*** ↓	12.2	*** ↑	7.9	** ↓	7.9	** ↓	4.9	* ↓	17.1	*** ↓		
2	3.8	ns	52.0	*** ↓	63.6	*** ↓	2.7	ns	25.3	*** ↓	5.6	* ↓		
3	50.3	*** ↑	5.5	* ↓	21.0	*** ↑	9.8	** ↑	2.1	ns	2.6	ns		
4	0.0	ns	8.7	** ↓	6.6	* ↓	1.6	ns	9.2	** ↓	0.6	ns		
<i>Astragalus glaux</i>														
1	12.2	*** ↑	20.0	*** ↓	2.3	ns	35.1	*** ↑	52.8	*** ↓	1.8	ns		
2	22.7	*** ↓	0.8	ns	27.4	*** ↓	0.0	ns	5.9	* ↓	5.2	* ↓		
3	1.3	ns	0.0	ns	1.5	ns	13.1	*** ↑	14.0	*** ↑	40.3	*** ↑		

(df = 1: *p < 0.05, **p < 0.01, ***p < 0.001).

2011 followed by decreases in abundance in most populations in 2013 and 2017. In the second part of the study, three populations decreased in abundance (1, 2 and 4) and the last population (3) remained stable. For the entire study, populations 1 and 2 showed a significant decrease while the other two populations were stable.

3.6. *Astragalus glaux* (Fig. 7)

The three studied populations showed contrasting patterns of overall occupation. Population 1 increased significantly in the first part of the study then decreased significantly with thus an overall stability, population 2 decreased significantly then remained stable and population 3 remained stable during the eight-year monitoring period.

After a generally significant increase in 2011, no general pattern of change was observed for abundance. Abundance in population 1 oscillated during the eight years of monitoring but remained unchanged over the whole study period. In population 2, abundance significantly

decreased after 2011 and again in 2015 and as a result declined significantly across the whole study. In population 3, abundance increased significantly in three years of the study, and was thus significantly higher at the end of the study.

3.7. Comparative trends

The three populations that disappeared in our study involved one population of the perennial *C. lineatus*, one population of *S. capensis* and one population of *O. mitissima*. None reappeared at the end of the study so it would appear that they are extinct. A further visit in several years may be necessary to confirm this.

In the first part of the study, almost 50% of populations (15 out of 32) showed a significant decrease in overall occupation (Fig. 8). Whereas 11 of the 14 annual species populations declined, 10 out of 18 perennial species populations showed an increase. In the second part of the study, 50% of the 32 studied populations showed a significant de-

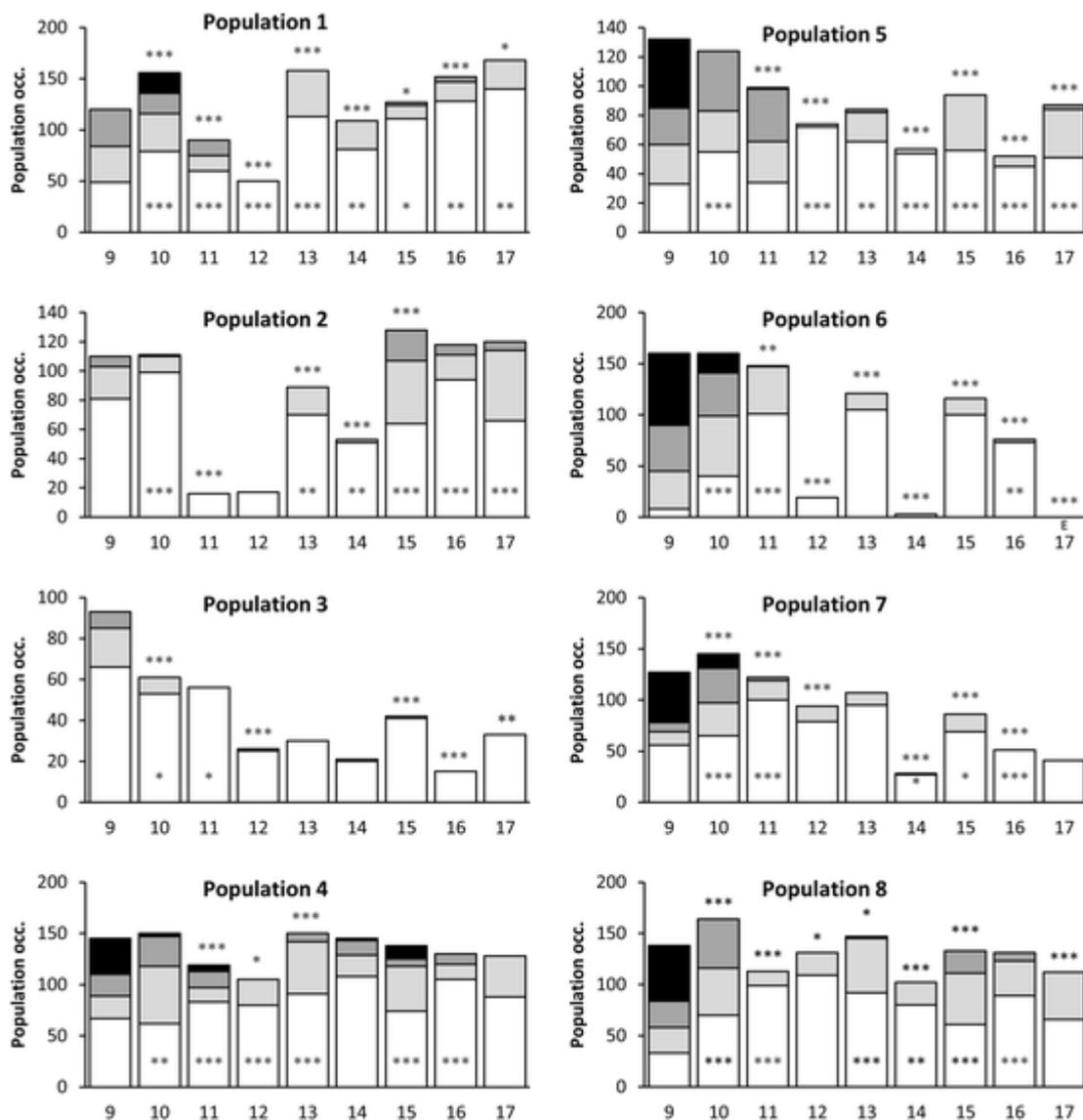


Fig. 2. Change in overall population occupation and abundance during nine years of monitoring in eight populations of *Stipellula capensis*. Abundance (number of plants per 0,25m²) was estimated in four classes: (1) 1–20 plants (white), (2) 20–125 plants (light grey), (3) 125–500 plants (dark grey), (4) > 500 plants (black). For each population the significance of changes in occupation and abundance using the McNemar χ^2 test ($df = 1$: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) between years is indicated above the bars for occupation and inside the bars for abundance (or when the bars are too small under the axis). “E” represents an extinct population.

crease in overall occupation, due to a decline in 11 of the 18 populations of perennial species. Over the whole study, a decline in overall occupation was primarily associated with a decline in occupation for annual species (11 of their 14 populations). However given their annual fluctuations this result (based on a comparison of the first and last year) should be interpreted with caution.

Abundance within quadrats declined during the first part of the study due to decline in nine of the 13 populations of the annual species primarily in 2011 and 2012 (Fig. 8). During the second part of the study, a marked decline in abundance in quadrats was observed for populations of perennial plants (15 out of 18 populations). During the overall study period of this study, 64% of the populations of the two annual species (7 out of 11 populations) and 50% of the populations of the four perennial species showed a significant decrease in quadrat abundance.

Multiple significant transitions (declines) in occupation and abundance of the two annual species in these years are correlated with a deficit of spring rainfall; 2011 and 2012 are the only spring periods when rainfall was well below the mean for the last 28 year period (Fig.

9). While perennial species show no trends in occupation and abundance related to rainfall deficit in these years, the two annual species show a large number of significant negative transitions in occupation and abundance in these years (compare Table 3 & Fig. 9).

In 2011, seven of the eight *S. capensis* populations showed a significant decline in occupation and six of the eight populations showed a significant decline in abundance. In 2012, for seven of the eight populations there was either no subsequent increase or a significant decline in occupation and in abundance. In association with increased rainfall in 2013, five populations showed a significant increase in occupation and five populations a significant increase in abundance. With the decline in rainfall in 2014, six populations showed a significant decline in occupation and five populations showed a decline in abundance. With increased rainfall in 2017, three populations showed a significant increase in occupation and three a significant increase in abundance.

Four of the *O. mitissima* populations showed a significant decline in occupation and one population for abundance in 2011. In 2012 four populations showed a significant decline in occupation, one population remained stable after a major decline in 2011 and occupation increased

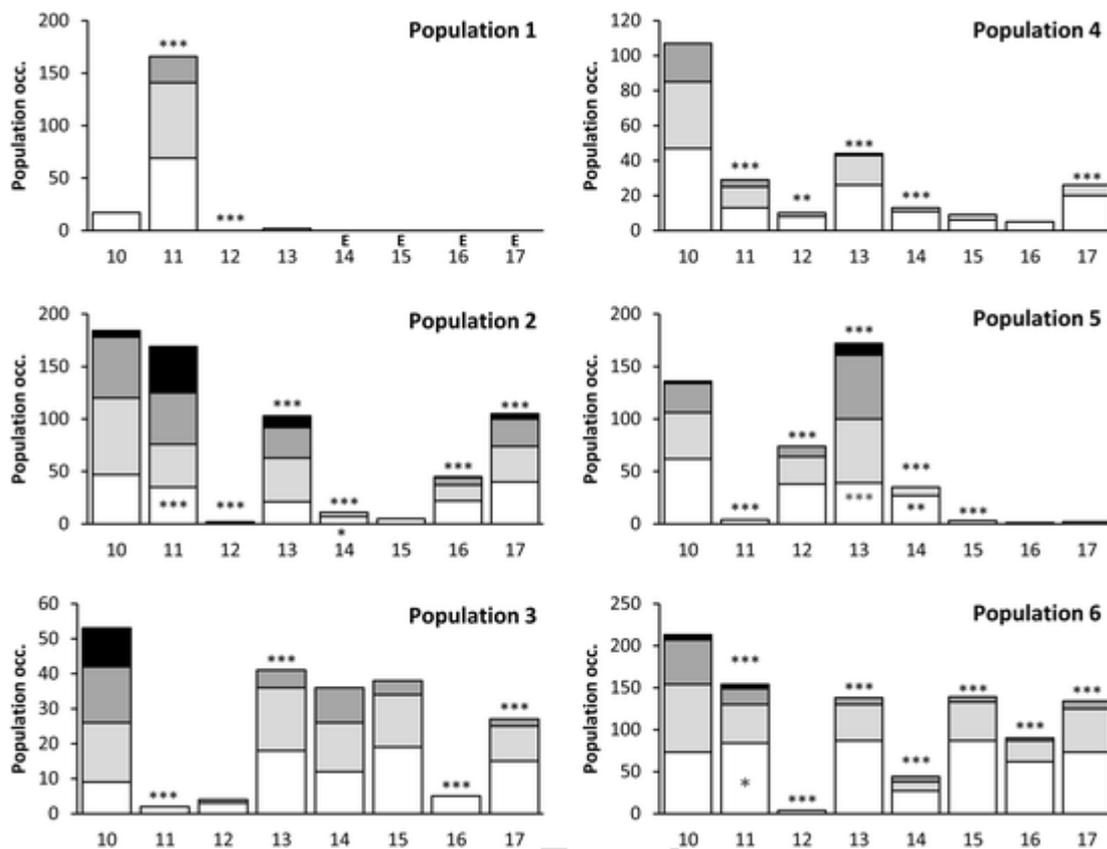


Fig. 3. Change in overall population occupation and abundance during eight years of monitoring in six populations of *Ononis mitissima*. Abundance (number of plants per 0,25m²) was estimated in four classes: (1) 1 plant (white), (2) 2–3 plants (light grey), (3) 4–8 plants (dark grey), (4) > 8 plants (black). For each population, the significance of changes in occupation and abundance using the McNemar χ^2 test ($df = 1$: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) between years is indicated above the bars for occupation and inside the bars for abundance (or when the bars are too small under the axis). “E” represents an extinct population.

in one population. With the increased spring rainfall in 2013, five of the six populations showed a significant positive transition in occupation, and one of these showed an increase in abundance. Four populations showed significant declines from 2013 to 2014 that are not related to changes in rainfall. From 2016 to 2017, four of the five remaining populations showed a significant increase in occupation that is correlated with an increase in rainfall from a previously dry spring.

Eight populations were subject to “expected” impacts prior to or during the first two years of the study. As a result, population 3 of *S. capensis*, population 1 of *O. mitissima* and population 3 of *C. lineatus* showed a significant decrease in both occupation and abundance, and the two latter populations disappeared. In contrast, population 2 of *S. capensis*, and populations 4 and 6 of *H. marifolium* recolonized after the impact.

A total of 13 other populations incurred some form of partial destruction (i.e. in some quadrats) due to human activities (including grazing), wild boar or competition with other species. For *S. capensis*, populations 5 and 6 (not within the perimeters of known development projects) incurred either total or partial destruction, with a significant decline in both occupation and abundance. Population 1 was grazed occasionally at flowering time and showed a decline in abundance (Fig. 2). Population 6 of *O. mitissima* was impacted by grazing and showed a significant decline in occupation and abundance (Fig. 3). Populations 2 and 5 of *C. lineatus* were partially impacted by wild boars with significant declines in abundance for the first one and both occupation and abundance for the second one (Fig. 4). Populations 3 and 4 of *H. marifolium* were partially impacted by woody plant clearance with a decline in abundance (Fig. 5). Vegetation succession as a result of human activity occurred in ten populations (populations 2 and 3 in *S. capensis*,

populations 1 and 4 of *O. mitissima*, population 2 in *H. marifolium*, populations 1, 2 and 4 of *A. chamaemoly* and populations 1 and 3 of *A. glaux*). As a result, only 11 of the 32 populations showed no signs of any impact.

4. Discussion

4.1. Irregularity of rainfall and population transitions

Studies of annual plants in desert and Mediterranean type ecosystems have shown marked variability among species in response to annual fluctuations in rainfall that have important consequences for the long-term persistence of rare annual plants (Angert, Huxman, Barron-Gafford, Gerst, & Venable, 2007; Figueroa & Davy, 1991; Fox, 1995; Fox et al., 2006; Gutierrez & Meserve, 2003; Levine et al., 2008; Venable, Pake, & Caprio, 1993).

Levine et al. (2008) illustrate how rare annual species in the Californian Mediterranean Type Ecosystem display large between-year variation in plant density in relation to rainfall and discuss the importance of two other associated factors. First, germination cueing can be of fundamental importance to annual fluctuations in population dynamics. Second, annual variation in rainfall may benefit the persistence of rare annual plants by causing reduced competition from species that do not respond to unfavourable conditions (Levine & Rees, 2004). Their response to environmental variability gives rare annual species the opportunity to avoid unfavourable years that gradually impact perennial species while the annual species remain dormant in the seed bank. Hence, in subsequent more favourable years annual species may benefit from reduced competition and higher abundance. That reduced abundance in drought years may be essential for rare annual species persis-

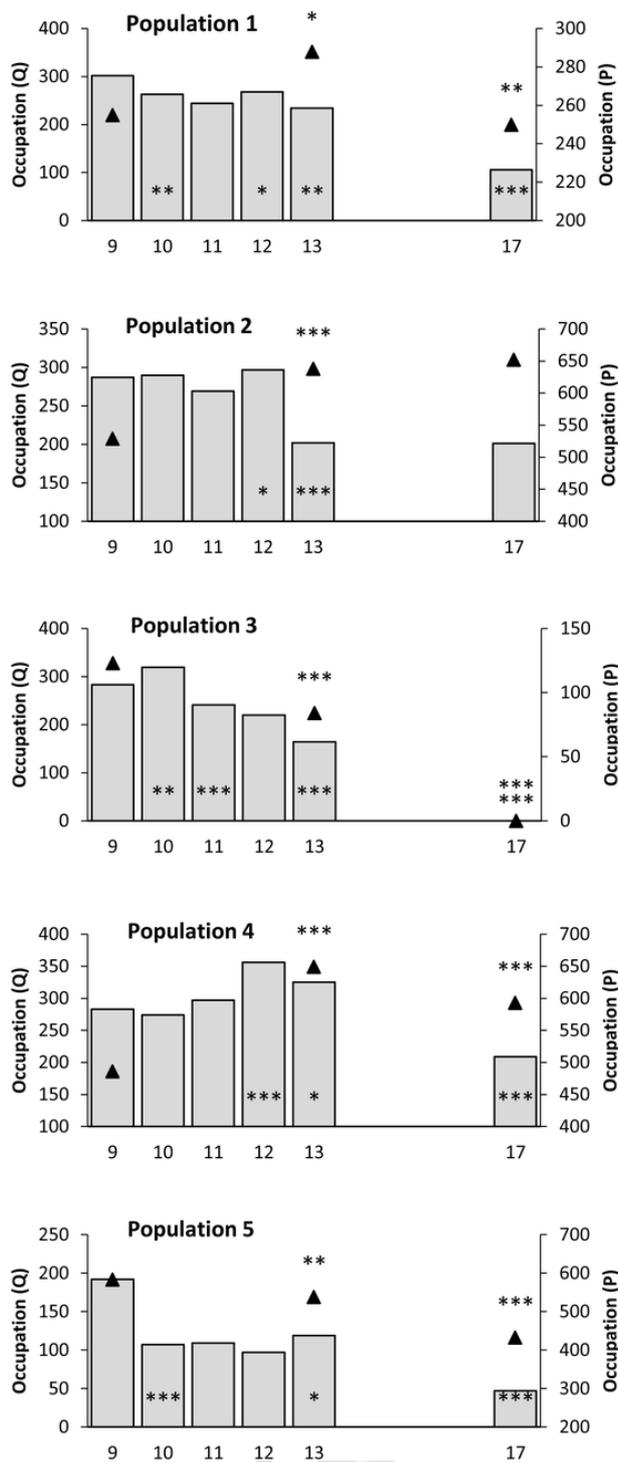


Fig. 4. Change in the overall population occupation over a four to five year interval (black triangles) and changes in permanent quadrat occupation (bars), i.e. local abundance, over five consecutive years and in a latter year (2017) in five populations of *Convolvulus lineatus*. For each population, the significance of changes in occupation between the two parts of the study is indicated above the triangles and the significance of changes in abundance between years is indicated inside the bars using the McNemar χ^2 test ($df = 1$: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

tence represents an idea that has not been fully appreciated in management plans.

The two annual species we studied here, *O. mitissima* and *S. capensis*, both showed significant declines in spatial occupation and abundance in association with extremely low spring rainfall below the mean

for the last 28-year period. Both species showed a capacity to respond to rainfall by enhanced germination and flowering in a high rainfall year after one or two years of rainfall deficit, indicative of a persistent seed bank in the soil that responds to rainfall-linked germination cues. This drought-avoidance strategy in annual plants enables them to track major changes in their germination environment and illustrates the importance of maintaining a persistent seed bank through unfavourable years in a Mediterranean Type Ecosystem (Fox et al., 2006). In other annual plant populations in the Mediterranean, rainfall variability is significantly correlated with emergence (Baumel et al., 2009; Vilellas, Berjano, Terrab, & García, 2014). In *Plantago coronopus* L. populations of annual plants have higher seedling emergence and survival than perennial populations (that have to survive the summer drought to become adults) in high-rainfall years and dramatically reduced emergence in dry years thus spreading recruitment over time in an annually variable precipitation regime (Braza & García, 2011; Vilellas et al., 2014).

Declines in population occupation and quadrat abundance of annual species were mostly observed in the first part of the study whereas populations of perennial species did not show a decline in the first part of our study and no significant annual fluctuation in relation to spring rainfall deficits in 2011 and 2012, remaining stable across the driest years of our study. This difference between annual and perennial species was reversed in the second part of this study, when declines in population occupation and local abundance were observed in populations of perennial but not annual species (other than a decline in the dry year of 2016). This clear temporal separation between declines in annual and perennial species' populations may positively affect the long-term presence of annual species. The typical strategy of endemic, perennial Mediterranean plants in dry, rocky habitats such as those studied here, is indeed, after an initial bottleneck of high seedling mortality in their first summer, one of persistence and adult longevity (Thompson, 2005). It appears from our work that perennial species may however show a decline on a longer-term basis as a result of two consecutive previous years of severe drought stress. Hence, although our study species do not co-occur in the same sites (other than in one site), the pattern of annual variation in annual species' populations followed by a longer term but later decline in perennial species populations' fits the models described above for a drought-avoidance strategy in annuals relative to a drought-tolerance strategy of perennial species. In annual plants it is important to avoid and not buffer unfavourable years, and critical to maximise fitness in favourable years.

4.2. Population disturbance and conservation

Land use change and modifications of human practices are a major threat to rare species populations in the Mediterranean region (Amat, Vargas, & Gómez, 2013; Andrieu, Thompson, & Debussche, 2007; Domínguez Lozano, Moreno Saiz, & Sainz Ollero, 2003; Gauthier et al., 2017; Hardion et al., 2015; Minuto, Casazza, & Profumo, 2004; Pouget, Baumel, Diadema, & Médail, 2016; Salanon, Gandioli, Kulesza, & Pintaud, 1994). Initially, eight populations were "expected" to have some form of impact and indeed one population of each of *S. capensis*, *O. mitissima* and *C. lineatus* showed a significant decrease in both occupation and abundance, and the latter two populations disappeared before the end of the study. An important point here is that for the population of *C. lineatus* administrative measures were taken to avoid an impact by prevention of access to this population that, in fact, became isolated from other natural vegetation and enclosed between hangars. These measures were totally ineffective, the population went extinct in <10 years after its enclosure. In contrast, one population of *S. capensis*, and two populations of *H. marifolium* recolonized parts of a population destroyed by the installation of an underground pipeline.

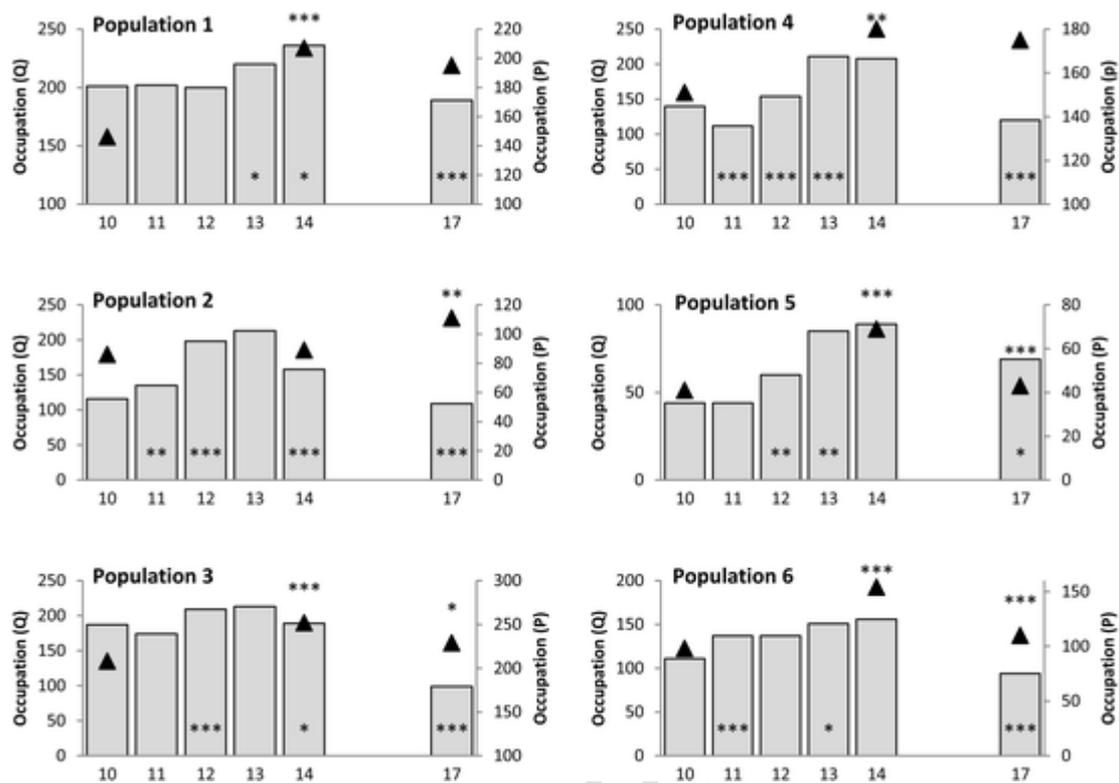


Fig. 5. Change in the overall population occupation over a four to five year interval (black triangles) and changes in permanent quadrat occupation (bars), i.e. local abundance, for five consecutive years and a supplementary year (2017) in six populations of *Helianthemum marifolium*. For each population, the significance of changes in occupation between the two parts of the study is indicated above the triangles and the significance of changes in abundance between years is indicated inside the bars using the McNemar χ^2 test ($df = 1$: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Thirteen populations also incurred direct destruction due to human activities (including grazing), wild boar or competition with other species following human disturbance that had significant effects on population transitions. As a result, 16 (50%) populations showed a decline due to human disturbance and three populations disappeared in the 10 years that we visited sites. Although all species are listed for protection, the viability of their populations is compromised by human impacts. In a subsequent study (Gauthier et al., 2019) this vulnerability is analysed at the scale of their surrounding landscape and risk of further impacts.

4.3. Pertinence of the method

The generalised impact of human activities on the population dynamics of the six species we studied illustrates the critical need for monitoring studies of protected plant species. Such monitoring should identify impacts on populations that affect their dynamics and make comparisons among populations and species in a given region to assess the overall effects of such impacts in relation to general environmental change, as the IUCN red list recommends. This requires the simultaneous study of a large number of sites and the examination of species with very different life forms and life histories. In the species we studied here, some species are clonal, some populations have extremely high patch density whilst others have individuals that are so close together that it is not possible to discriminate them in a multi-year study. The method we used in this study based on transitions in frequency (due to either changes in occupation or classes of local abundance) with a single type of analysis, allowed us to detect significant modifications in population size and abundance in a range of annual and perennial species for which a classic demographic study would simply not be possible. The field method and data analyses we present are easy to apply and the results simple to interpret; we have thus been able to present

our work to conservation management staff as a practical tool for monitoring rare species. This does not mean that, during such work, the importance of variability within and among populations or the search for new or vulnerable populations be neglected.

The main limit to this study is that we cannot identify the life history stages most impacted by environmental variation or disturbance. Studying presence / absence or classes of abundance only at the moment of peak flowering means that we cannot differentiate between seed to juvenile regeneration and adult survival as causes of significant transitions among years. The regeneration of young plants is well known to be of vital importance for the viability of annual and perennial plant populations in diverse situations, as the references cited above and others (Budroni et al., 2014; Colling & Matthies, 2006) including the Mediterranean region (Matias, Zamora, & Castro, 2012; Thompson, 2005) illustrate. In addition, in typical arid Mediterranean habitats where most endemic species occur, adult survival is critical for long-term population persistence (García & Zamora, 2003; Thompson, 2005). Our method should thus be used as a basis for general studies of population dynamics across a landscape to guide choices for more detailed population and life-history level studies.

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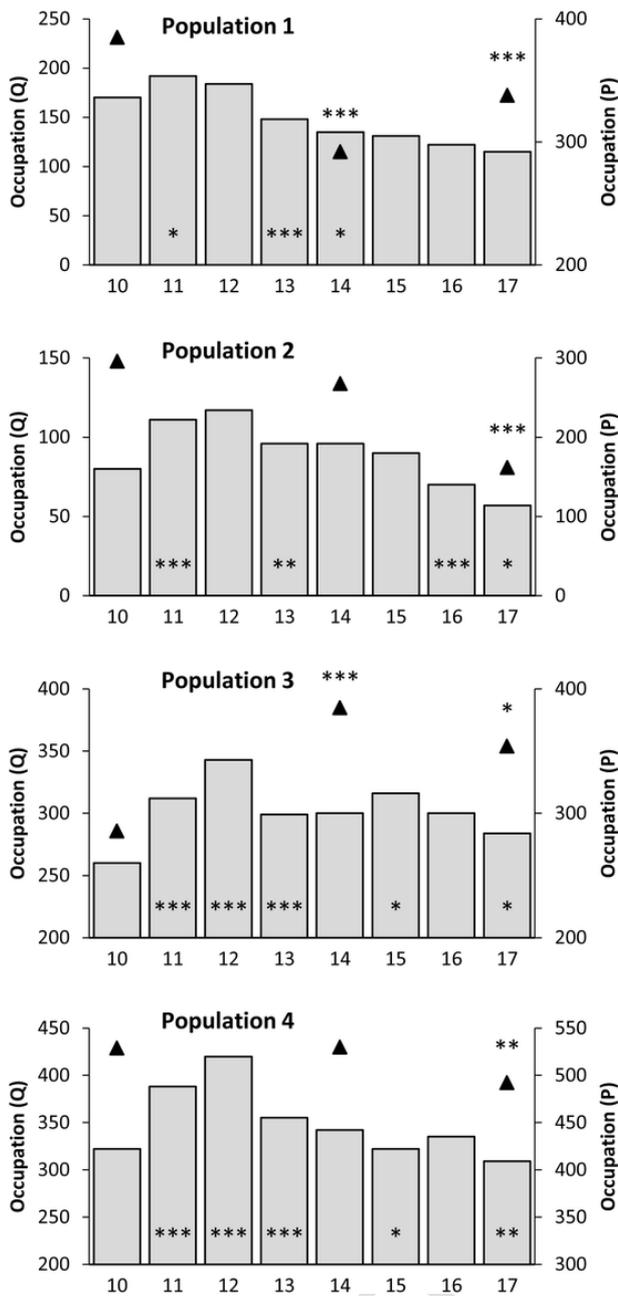


Fig. 6. Change in the overall population occupation over a five or four year interval (black triangles) and annual changes in permanent quadrats occupation (bars) in four populations of *Allium chamaemoly*. For each population, the significance of changes in occupation between the two parts of the study is indicated above the triangles and the significance of changes in abundance between years is indicated inside the bars using the McNemar χ^2 test ($df = 1$: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

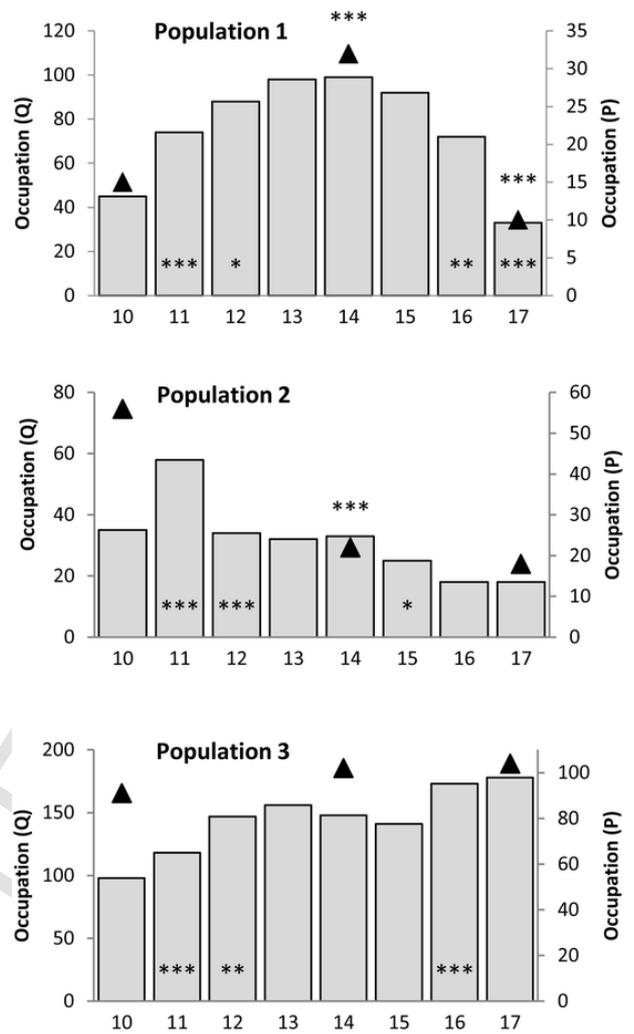


Fig. 7. Change in the overall population occupation over a five or four year interval (black triangles) and annual changes in permanent quadrats occupation (bars) in three populations of *Astragalus glaux*. For each population, the significance of changes in occupation between the two parts of the study is indicated above the triangles and the significance of changes in abundance between years is indicated inside the bars using the McNemar χ^2 test ($df = 1$: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

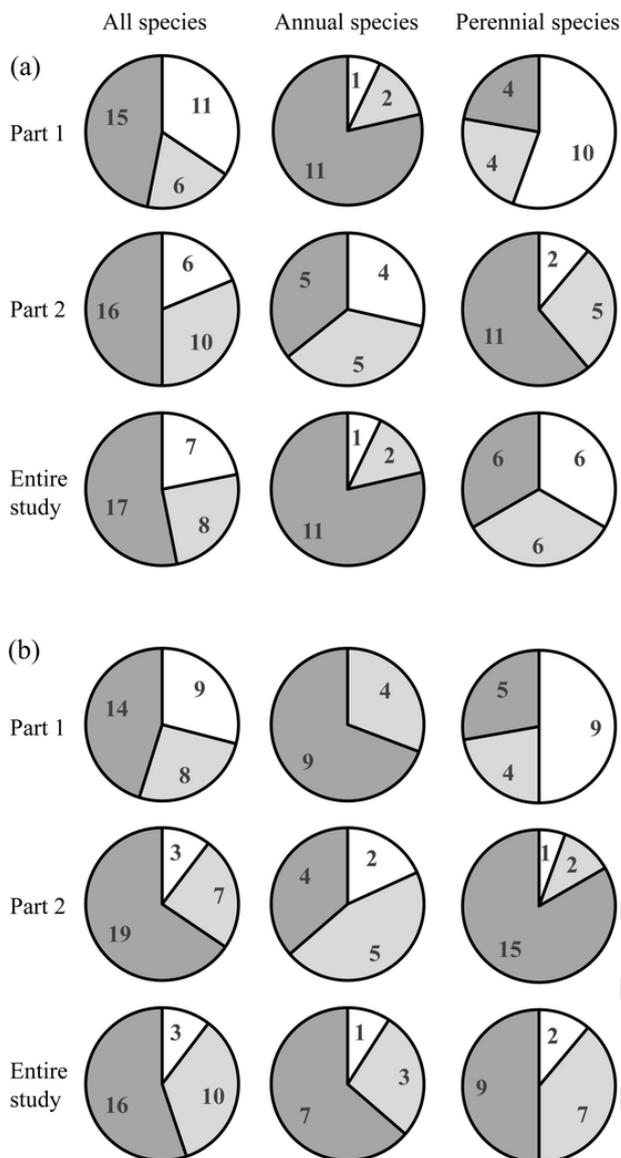


Fig. 8. Proportion of populations that show a significant increase (white), decrease (dark grey) or no significant change indicative of stability (pale grey) for (a) overall population occupation and (b) abundance within quadrats. The left-hand column is for all 32 populations, the middle column is for the 14 annual species populations and the right-hand column is for the 18 perennial species populations. Each row is a period of the study (see text). Annual populations that went extinct were deleted from subsequent analyses.

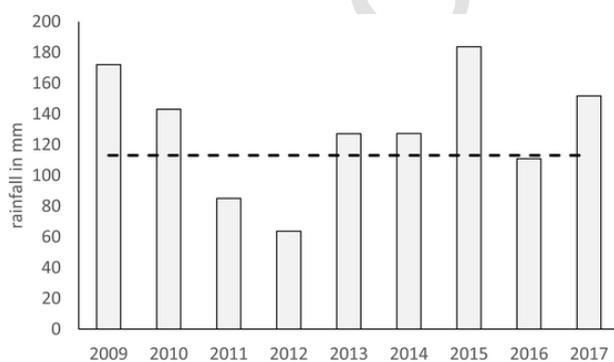


Fig. 9. Total rainfall recorded during the spring growing season (February–April) in each year of the study period at nearby meteorological station.

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