INTER-ANNUAL VARIABILITY IN FLOWERING OF ORCHIDS: LESSONS LEARNED FROM 8 YEARS OF MONITORING IN A MEDITERRANEAN REGION OF FRANCE

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ABSTRACT

It is important to evaluate the loss of biodiversity caused by global changes. In the case of orchids, it is still unclear how long the monitoring duration should be chosen in order to achieve a good compromise between the reliability of the orchid dynamics recorded and sampling duration (e.g. years of monitoring). This study aims to propose a method of monitoring orchids. Using a large database, we investigated the inter-annual variability in flowering of orchids in a French Mediterranean region. The database includes an 8-year-long study (2006–2013) of 47 species at 26 locations in three different types of habitats. The number of individual plants that flowered per species varied significantly between years, but not the number of species. Depending on habitat, two to four years were needed to observe the total number of species per location. Therefore, in Mediterranean regions a one-year-study seems to be insufficient to produce reliable results.

Keywords: orchid community, diachronic studies, orchid monitoring, similarity index, conservation

Introduction

In the era of global change that deeply affects organisms on our planet (Parmesan 2006), there is an increasing urgency to evaluate the loss in biodiversity (Barnosky et al. 2011; Thuiller et al. 2011). In order to propose appropriate conservation strategies, it is essential for conservation biologists to precisely evaluate shifts in communities. Limiting our topic in orchids, it has been well acknowledged that orchids are ideal models to evaluate the impact of global change on biodiversity. First of all, they show clear and fast responses to environmental changes, including a current and well documented decline in occurrence or population size (Whigham and Willems 2003; Schatz et al. 2013). Then, many orchids are emblematic species (Cribb et al. 2003) and there is an increasing need to study them with the aim of conservation. Thirdly, they show well-documented patterns of endemism and rarity (Bournérias and Prat 2005; Dusak and Prat 2010).

The availability of long-run data or diachronic studies on the distribution of orchids provides opportunities to document temporal variation in communities (Jacquemyn et al. 2005; Kull and Hutchings 2006). These studies enable us to predict response of organisms to future environmental changes. However, there is a lack of standardized methods of recording and analyzing the data (Kati et al. 2004; Archaux et al. 2009). As a result, it is necessary to document the natural variability in the life-history traits of species (e.g. frequency of flowering) and to develop of sampling methods suitable to monitor orchids.

At the species scale, several studies have shown that the number of flowering individuals varied from year to year in response to climatic fluctuations (Tamm 1991; Sieg and King 1995; Wells et al. 1998; Tali 2002; Oien and Moen 2002; Brzosko 2003; Kindlmann 2003; Hrivnak et al. 2006; Jacquemyn et al. 2007). This inter-annual variability is recorded in several different species of orchids, such as *Anacamptis morio* (Wells et al. 1998), *Dactylorhiza majalis* (Hrivnak et al. 2006), *D. lapponica* (Oien and Moen 2002), *D. sambucina* (Tamm 1991), *D. incarnata* (Tamm 1991), *Gymnadenia conopsea* (Oien and Moen 2002), *Neotinea ustulata* (Tali 2002), *Neottia ovata* (Tamm 1991), *Orchis mascula* (Tamm 1991), *Platanthera praeclara* (Sieg and King 1995), *P. bifolia* (Brzosko 2003) and *Spiranthes spiralis* (Jacquemyn et al. 2007). A common characteristic of these studies is that they are all located in northern Europe. Yet, little is known about such variation in Mediterranean species (but see Sirami et al. 2010; Schatz and Geniez 2011). In Mediterranean regions, a high variability in the incidence of flowering of orchids is expected due to the high intra- and inter- annual variation in climate. In the future, longer and more severe drought periods (IPCC 2007; Giorgi and Lionello 2008) may disturb the phenology of orchids. Moreover, the region hosts different types of habitats, e.g. grassland, shrubland and woodland, which may affect flowering patterns of orchids differently.

We investigated the temporal dynamics of orchid assemblages, at both the species and community level (47 species of orchids) in a Mediterranean region of France (Languedoc-Roussillon). This study aims to address the following questions:

(1) How does the fluctuating Mediterranean climate affect flowering patterns of orchids?

(2) Are there differences in inter-annual flowering of orchids between habitat types?

We documented the inter-annual variations in flowering patterns (e.g. number in flowering individuals and probability of presence) of orchids in order to provide a framework for future monitoring in this region.

Materials and Methods

Study sites

Study sites are situated in the North of the Languedoc-Roussillon region in southern France (43°17′31″N–44°17′31″N, 3°05′27″E–3°50′41″E). At these sites, the climate is of Mediterranean type with annual precipitation ranging from 950 mm to 1350 mm (Debussche and Escarré 1983). Air temperature varies from 0 °C in winter to 28 °C in summer (Sirami et al. 2010). We sampled at 26 locations, where many species with patchy distributions co-occurred. Three types of habitat were distinguished, corresponding to three stages of succession, hereafter called "grassland" (n = 10), "shrubland" (n = 8) and "woodland" (n = 8). We excluded locations that experienced high levels of disturbance, e.g. intensive tree cutting and grazing. The sampled locations differed in area, ranging from 500 m² to 2000 m². In each location, yearly orchid inventory was always carried out in the same area so that outcomes between inventories can be compared.

The study was conducted for eight consecutive years, from 2006 to 2013. In each year, all the flowering individuals were recorded at each location during the same period (between March and July). In total, 47 species of orchids were included in this study. A full list of the species studied is given in Table S1.

Species traits

Species traits were not measured in the field, but based on the information available in the literature (Bournérias and Prat 2005). The traits included:

1. Number of species of pollinators and mycorrhizal symbionts. They were classified as either a specialist (1 species), an intermediate (2–5 species) or a generalist (more than 5 species).
2. Flower morphology. We considered the number of flowers, the size of the inflorescence (mean in cm) and plant height (mean in cm).
3. Phenology. We considered the duration of flowering (mean in months) and the flowering period (mean in terms of particular months).

Data analysis

We used Wilcoxon or Kruskal-Wallis tests, i.e. two non-parametric tests, to investigate the effect of year sampled on the variability in the presence and number of flowering individuals. For each median, we calculated the confidence interval (IC), as $[1.57 \times (Q_3 - Q_1)] / n^{0.5}$, where, Q_1 and Q_3 are the 25th and 75th percentile of the data, respectively; and n is the number of observations (Chambers et al. 1983).

We averaged the number of species per location and the number of flowering individuals per species and location. Concerning the inter-annual variability between species, we calculated the probability of presence for each species, as the ratio of the number of years when the species was recorded divided by the total number of years monitored, i.e. eight years. We considered that an absence of a record in one or several years did not mean death of an individual, but flowering dormancy. We used Jaccard's similarity index (Jaccard 1901) to determine how similar the species composition was between pairs of consecutive years. The similarity index was calculated as $c/(a + b - c)$, where a is the total number of species in one year; b is the total number of species recorded in the following year; and c is the number of species in common found in both of years (Jaccard 1901). In regard to the number of records, we applied the same similarity index. In this case, the similarity index was equal to the minimum recorded number of flowering individuals divided to the maximum recorded number of flowering individuals between two consecutive years. To compare the similarity index between species, we only considered species that occurred at least at five locations in order to augment the spatial representativeness of the study site.

We used a principal component analysis in order to investigate the relationship between inter-annual variability of flowering (index of similarity and probability of presence) and traits of species. We investigated the species-time relationships using an accumulation curve of species recorded at the site level. We calculated the ratio of the cumulated number of species recorded and the maximum number of species recorded at the same location between 2006 and 2013. This process was repeated for each pair of successive years (e.g. 2007 and 2008, i.e. seven possibilities) and each location.

All analyses were performed using R software (R development core team, version 2.15.0). For the principal component analyses, we used the package FactoMineR (Husson et al. 2007).

Results

Inter-annual variability in flowering at community level

The number of species recorded per location did not differ significantly between years (Kruskal-Wallis test, $K = 3.64$, $p > 0.05$), with the median varying slightly, from 5 ± 1.23 (Median ± IC, idem for all the following cases) in 2011 to 6.5 ± 1.85 in 2010 (Wilcoxon test, $W = 417$, $p > 0.05$, Fig. 1A). The median of Jaccard-similarity index between consecutive years was 0.94 ± 0.02 for all locations, meaning that the species composition differed

Table 1 Median ± confidence interval of Jaccard-similarity index for pairs of consecutive years for all locations and three habitats. Based on Wilcoxon non-parametric test, different letters indicate a significant difference in the Jaccard similarity index between different pairs of consecutive years for a particular habitat. N is the number of locations.

	All locations			**Grassland**			**Shrubland**			**Woodland**		
N	26			10			8			8		
2006 *vs* 2007	0.77	± 0.11	a	0.77	± 0.10	a	0.92	± 0.27	ab	0.69	± 0.18	a
2007 *vs* 2008	0.97	± 0.05	bd	1.00	± 0.03	bc	0.83	± 0.14	a	0.97	± 0.25	abc
2008 *vs* 2009	1.00	± 0.05	bc	1.00	± 0.00	b	1.00	± 0.02	b	0.8	± 0.12	ab
2009 *vs* 2010	1.00	± 0.00	c	1.00	± 0.00	bc	1.00	± 0.02	b	1.00	± 0.00	c
2010 *vs* 2011	0.77	± 0.07	ad	0.85	± 0.10	a	0.69	± 0.11	a	0.75	± 0.11	ab
2011 *vs* 2012	0.88	± 0.07	b	0.87	± 0.11	ac	0.94	± 0.09	ab	0.87	± 0.12	abc
2012 *vs* 2013	0.97	± 0.05	b	1.00	± 0.00	b	0.81	± 0.12	a	0.92	± 0.08	bc
Total	0.94	± 0.02		1.00	± 0.03		0.87	± 0.06		0.88	± 0.06	

by 6% between consecutive years (Table 1). The Jaccard-similarity index differed significantly between habitats ($p < 0.05$*) and the medians were 1 ± 0.03, 0.87 ± 0.06 and 0.88 ± 0.06 for grassland, shrubland and woodland, respectively (Table 1).

For the 47 species of orchids studied the average number of flowering individuals per species and location differed between years (Kruskal-Wallis test, $K = 24.75$, $p < 0.001$***), with the median varying significantly from 5.2 ± 3.4 individuals in 2011 to 28 ± 10.7 individuals in 2010 (Wilcoxon test, $W = 1619.5$, $p < 0.001$***, Fig. 1B). The similarity index of the number of flowering individuals between two consecutive years did not differ between habitats ($p > 0.05$).

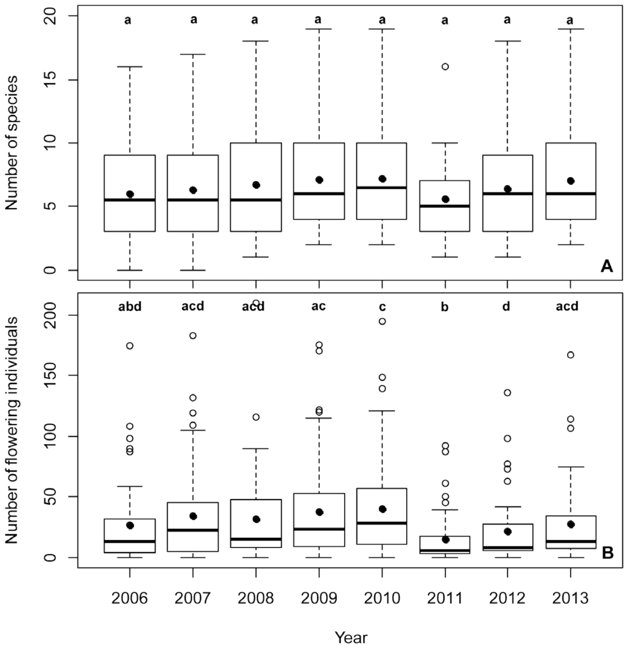

Fig. 1 Boxplots of (A) the average number of species per location and (B) the average number of flowering individuals per species and location recorded per year. Black points correspond to (A) the mean of the number of species per location or (B) the number of flowering individuals per species. Different letters indicate a significant difference based on Wilcoxon non-parametric test. Significant codes: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Inter-annual variability in flowering at species level

In the eight years of inventory, probability of being present differed significantly between species (Kruskal-Wallis test, $K = 69.7$, $p < 0.05$*, Fig. 2A, Table S2). The median of theaverage probability of presence was 0.82 ± 0.06 and 0.87 ± 0.05 for the 17 species and all the species studied, respectively (Fig. 2B). The probability of presence varied from 0.52 (for *Platanthera chlorantha*) to 0.98 (for *Anacamptis pyramidalis*) (Fig. 2A).

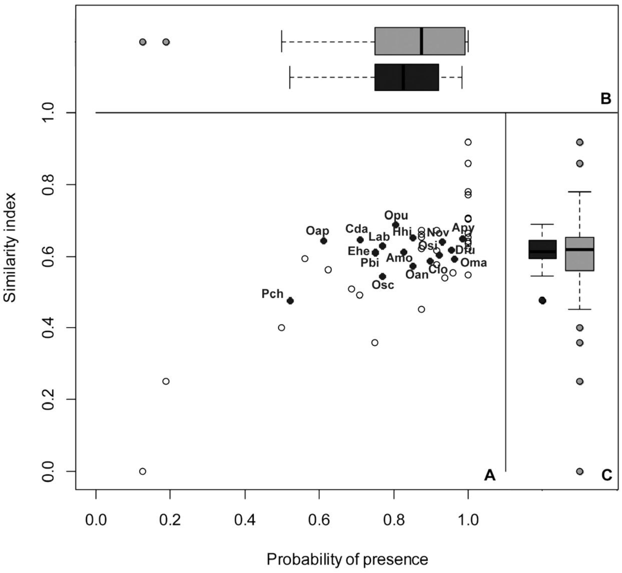

Fig. 2 Plot of the probability of presence and the similarity index of the number of flowering individuals between two consecutive years per year (A). Each point represents the mean probability of presence and similarity index of the orchid species studied that occurred in ≥ 5 locations (dark-grey points) and < 5 locations (hollow points). Boxplots of (B) the probability of presence and (C) inter-annual similarity index are depicted for all the species (in light-grey) and for the 17 species that occurred in ≥ 5 locations (in dark-grey). Abbreviations of species: Amo = *Anacamptis morio*, Apy = *Anacamptis pyramidalis*, Cda = *Cephalanthera damasonium*, Clo = *Cephalanthera longifolia*, Dfu = *Dactylorhiza fuchsii*, Ehe = *Epipactis helleborine*, Hhi = *Himantoglossum hircinum*, Lab = *Limodorum abortivum*, Nov = *Neottia ovata*, Oap = *Ophrys apifera*, Osc = *Ophrys scolopax*, Oan = *Orchis anthropophora*, Oma = *Orchis mascula,* Opu = *Orchis purpurea*, Osi = *Orchis simia*, Pbi = *Platanthera bifolia*, Pch = *Platanthera chlorantha*.

In regard to inter-annual similarity of flowering individuals, there were significant differences between six pairs of species: *P. chlorantha* versus *A. pyramidalis* (Wilcoxon test, $W = 74$; $p < 0.05$*), *P. chlorantha* versus *H. hircinum* (Wilcoxon test, $W = 35$, $p < 0.05$*), *P. chlorantha* versus *O. purpurea* (Wilcoxon test, $W = 26$, $p < 0.05$*), *O. scolopax* versus *H. hircinum* (Wilcoxon test, $W = 49.5$, $p < 0.05$*), *O. purpurea* versus *O. anthropophora* (Wilcoxon test, $W = 59$, $p < 0.05$*) and *O. purpurea* versus *O. scolopax* (Wilcoxon test, $W = 37$, $p < 0.05$*) (Fig. 2, Table S2). Medians of the averaged similarity index were 0.61 ± 0.02 and 0.62 ± 0.02 for the 17 species and all of the species studied, respectively (Fig. 2C). The similarity index varied from 0.48 (for *Platanthera chlorantha*) to 0.70 (for *Orchis purpurea*) (Fig. 2A).

According to the principal component analysis, the first two factorial axes accounted for 34.89% (axis 1) and 20.93% (axis 2) of the total variability, respectively (Fig. S1). The similarity index was negatively related with the duration of flowering. The other traits, e.g. height and number in pollinator species, were neither related to the similarity index, nor to the probability of presence (Fig. S1).

Accumulation in the number of species recorded over time

The increased percentage in the number of the recorded species that accumulated with time differed between habitats (Fig. 3). One year of sampling captured 87.5% of the species in grassland, 88.9% of those in shrubland and 80% of those in woodland. Significant difference was found between shrubland and woodland (Wilcoxon test, $W = 1620.5$, $p < 0.05$*), but was absent between grassland and shrubland or between grassland and woodland ($p > 0.05$). The total number of species (median-value of 100%) was observed after the 2nd year of sampling for shrubland, the 3rd year for woodland and the 4th year for grassland (Fig. 3).

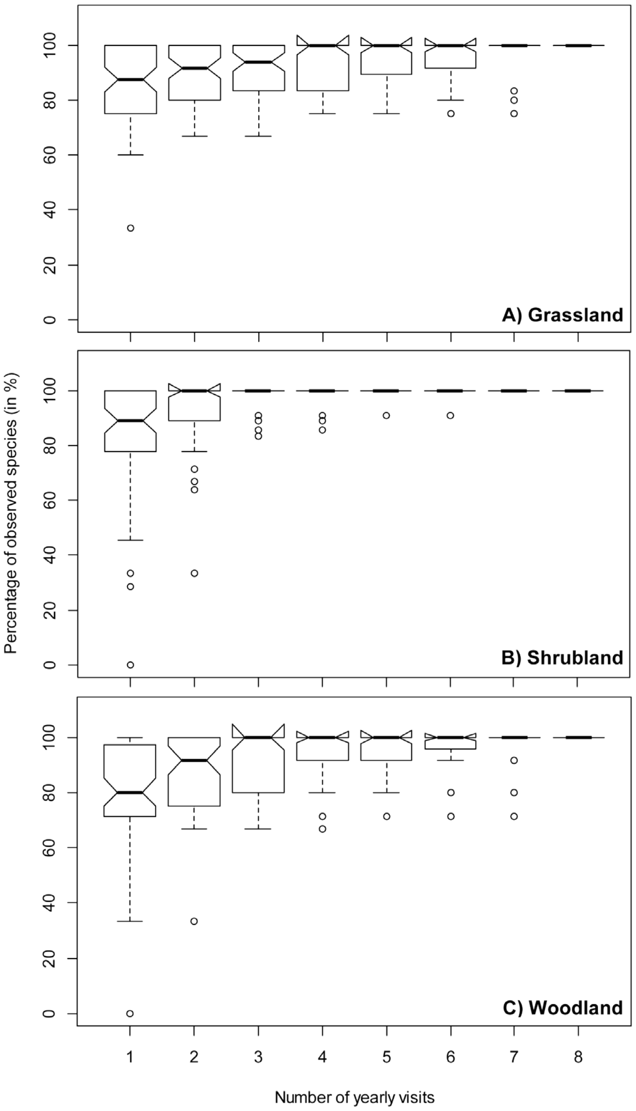

Fig. 3 Boxplot of the cumulative percentage of species recorded in successive yearly inventory, for (A) grassland, (B) shrubland and (C) woodland. A non-overlapping of the notches of two plots denotes a significant difference between the two medians as proposed by Chambers *et al.* (1983).

Discussion

Inter-annual variability in flowering at community level

We showed that the number of orchid flowering individuals varied conspicuously between years in the Mediterranean region (Fig. 1B). These results are in accordance with the previous findings on the variability in the inter-annual records of orchid numbers in northern Europe (Tamm 1991; Kindlmann and Balounova 1999; Oien and Moen 2002; Tali 2002; Brzosko 2003). Inter-annual fluctuations in orchid abundance are mainly induced by variations in climate, in particular temperature and rainfall (Wells et al. 1998; Pfeifer et al. 2006, 2011). 2006 and 2011 were the driest during the sampling period and the lowest number of individuals per species was recorded in 2011 at most of the study sites. This result indicates that orchids may respond to drought by reducing the number of flowering individuals, as observed by Hutch-ings (2010) in the case of *Ophrys sphegodes.* We suppose that the high inter-annual variability in flowering of orchids is due to dormancy induced by unfavourable weather conditions. Summer drought can cause premature senescence and death of leaves, which results in insufficient reserves of nutrients for the orchids to flower the subsequent year (Wells et al. 1998).

At community scale, no evidence was detected regarding the significance of the number of species between years (Fig. 1A). In addition, species composition differed only by 6% between consecutive years (Table 1). We suppose that rare species vary less in terms of the incidence of flowering than abundant species, and thus can be maintained between years. As a result, we can distinguish two different strategies, i.e. high numbers of individuals combined with a high incidence of inter-annual fluctuations (abundant species) and few individuals combined with a low incidence of inter-annual fluctuations (rare species). Similarly, Lavergne et al. (2004) evidenced that narrow endemic plants were locally persistent, despite the fact that they produced fewer flowers than their widespread congeners. The persistence of rare species could be related to a better success in reproduction or establishment (Simon and Hay 2003; Byers and Meagher 1996).

Inter-annual variability in flowering at species level

We evidenced that species responded differently in terms of orchid presence and similarity index (Fig. 2). We attributed this to the disparity of traits between species. The results indicated that the similarity index seems to be negatively related to the duration of flowering. Increasing the flowering duration can lead to an increase in the probability of pollination, and thus to an increase of the reproductive success (fruit production). However, according to Primack and Stacy (1998), a cost of fruit production leads to a reduction in flowering probability in subsequent years (in case of *Cypripedium acaule*). Further analyses need to be carried out, in order to relate reproductive success to traits, as suggested for the nectar presence (Neiland and Wilcock 1998). In particular, our principal component analysis was based on the mean of traits. Traits should be measured locally in order to consider the variability in a trait in individuals and between habitats.

Orchid species can be detected more or less easily. This is probably due to their particular life-state (dormant or flowering state) and species biological traits, e.g. color of the flower and plant height. Our study evidenced a weak probability of presence for *Platanthera chlorantha*, in contrast to *Anacamptis pyramidalis*. This can be due to different levels of difficulty in terms of species detection. *Platanthera chlorantha* has white-greenish flowers, which is more difficult to be detected compared to *Anacamptis pyramidalis* that has purple flowers. In order to take into account the imperfect detection, we suggest using the capture-recapture model proposed by Kery and Gregg (2004) in future orchid inventories. Such model can be used to calculate the extent to which orchid records are underestimated due to imperfect detection of orchids. However, inventories of at least three years are needed in order to estimate and correct for imperfect detection.

Inter-annual variability in flowering in different habitats

Our study revealed that, in Mediterranean regions, a one-year-study is insufficient for monitoring orchids. This may be due to the fact that most of orchid species can stay in dormancy during in which flowering does not occur for one to three years (Shefferson et al. 2001; Brzosko 2003; Kery and Gregg 2004; Coates et al. 2006). Regarding the number of years needed to observe 100% of the species (Fig. 3), we found: shrubland (2 years) < woodland (3 years) < grassland (4 years). We attribute this result to the disparity of microclimate and light availability between habitats. Higher light availability can increase probability of flowering (Diez et al. 2007; Jacquemyn et al. 2010). Stable microclimatic conditions, e.g. a warm winter or fresh summer, can favour population performance and avoid dormancy of flowering (Pfeifer et al. 2006). The two factors antagonistically act in the case of grassland and woodland toward probability in flowering. In grassland, there is high light availability, but the microclimatic condition tends to be unstable. On the contrary, in woodland, light availability is low, but the microclimate is more regulated than in open habitat. For example, because of the tree canopy closure, the seasonal variation of air and soil temperature tend to be less contrasted under tree clusters than in open areas (Morecroft et al. 1998; Mao et al. 2013). Therefore, a trade-off effect between microclimate and light availability may exist in both grassland and woodland, thus resulting in higher numbers of years needed to observe 100% of the species (≥ 3 years). Compared to grassland and woodland, an intermediate condition of light availability and microclimate exists in shrubland, resulting in a lower number of years needed to observe all of the species.

Conclusion and perspectives

This study showed that in Mediterranean context, climate affects the inter-annual variability of orchid flowering. We evidenced a species-based response in regard to orchid presence. The number of years needed to observe 100% of species diverged between habitats and last from two to four years. As a result, we suggest that further studies use data collected over periods of a minimum of two years. Species and habitat should be considered equally important when interpreting results.

In the future, relationships between species-specific traits of orchids (e.g. strategies of rare species versus abundant species) and inter-annual variability of flowering need to be better understood in order to enhance the conservation of orchids. Capture-recapture models of orchids, which can take into account imperfect detection, will be a promising tool when characterizing the temporal dynamics of orchid communities.

Acknowledgements

This study was funded by the Languedoc-Roussillon region, France and a CIFRE convention (No. 187/2011) between the French National Association for Research and Technology (ANRT) and Biotope. We are grateful to the people who helped during fieldwork, including F. Corbion, P. Dabin, F. Dabonneville, G. Delvare, B. Delprat, J. Demarque, T. Disca, P. Escudié, P. Feldmann, F. Geniez, M. Geniez, D. Gruffat, J.-Y. Guillosson, L. Guillosson, T. Guillosson, J.-P. Hervy, M. Imbert, T. Lafranchis, P. Martin, F. Melki, T. Menut, M. Nicole, J. Pommet, S. Roux-Viljoen, G. Soupart, J.-C. Stahl, G. Toreilles and M. Zimmermann.

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SUPPLEMENTARY MATERIALS

Table S1 List of the orchid species studied with the abbreviated names (Abb) and the number of locations where the species was recorded for each habitat (Grassland, Shrubland, Woodland).

Species	Abb	Grassland	Shrubland	Woodland	Total
Anacamptis fragrans	Afr	2	0	1	3
Anacamptis laxiflora	Ala	1	0	0	1
Anacamptis morio	Amo	5	0	0	5
Anacamptis pyramidalis	Apy	10	7	5	22
Cephalanthera damasonium	Cda	1	2	3	6
Cephalanthera longifolia	Clo	1	2	3	6
Cephalanthera rubra	Cru	0	1	1	2
Coeloglossum viride	Cvi	1	0	0	1
Cypripedium calceolus	Cca	0	0	1	1
Dactylorhiza elata	Del	0	0	1	1
Dactylorhiza fuchsii	Dfu	1	3	4	8
Dactylorhiza occitanica	Doc	1	0	0	1
Dactylorhiza sambucina	Dsa	1	0	1	2
Epipactis atrorubens	Eat	0	0	2	2
Epipactis helleborine	Ehe	0	1	4	5
Epipactis microphylla	Emi	0	0	1	1
Goodyera repens	Gre	0	0	1	1
Gymnadenia conopsea	Gco	3	0	1	4
Himantoglossum hircinum	Hhi	4	4	2	10
Himantoglossum robertianum	Hro	1	1	1	3
Limodorum abortivum	Lab	1	3	3	7
Neotinea ustulata	Nus	3	0	1	4
Neottia nidus-avis	Nni	0	0	2	2
Neottia ovata	Nov	2	1	4	7
Ophrys apifera	Oap	4	1	3	8
Ophrys araneola	Oar	1	0	1	2
Ophrys aveyronensis	Oav	1	0	0	1
Ophrys aymonini	Oay	1	0	1	2
Ophrys bilunulata	Obi	0	1	0	1
Ophrys insectifera	Oin	1	1	1	3
Ophrys lupercalis	Olu	0	2	0	2

Species	Abb	Grassland	Shrubland	Woodland	Total
Ophrys lutea	Olut	2	1	0	3
Ophrys massiliensis	Omas	0	1	0	1
Ophrys occidentalis	Ooc	1	1	1	3
Ophrys passionis	Opa	3	0	0	3
Ophrys scolopax	Osc	2	4	1	7
Ophrys sulcata	Osu	1	0	0	1
Ophrys virescens	Ovi	1	0	1	2
Orchis anthropophora	Oan	3	3	4	10
Orchis mascula	Oma	4	3	3	10
Orchis militaris	Omi	2	0	2	4
Orchis provincialis	Opr	0	0	1	1
Orchis purpurea	Opu	4	2	1	7
Orchis simia	Osi	2	4	2	8
Platanthera bifolia	Pbi	4	3	2	9
Platanthera chlorantha	Pch	1	2	3	6
Spiranthes spiralis	Ssp	1	1	1	3

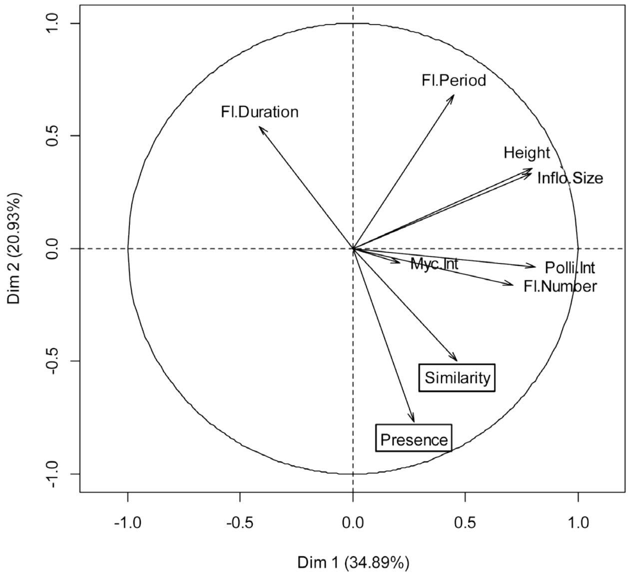

Fig. S1 Principal component analysis of the similarity index, probability of presence and species traits. Similarity = Similarity index, Presence = probability of presence, Polli.Int = number of species of pollinators, Myc.Int = number of mycorrhizal symbionts, Height = plant height, Inflo.Size = inflorescence size, Fl.Number = number of flowers, Fl.Duration = duration of the flowering period, Fl.Period = flowering duration.

Table S2 Results of Wilcoxon test of the comparison of the similarity-index of the recorded numbers (upper right) and probability of presence (bottom left) of species (a $p < 0.05$ is considered as significant). Abbreviations of species: Amo = *Anacamptis morio*, Apy = *Anacamptis pyramidalis*, Cda = *Cephalanthera damasonium*, Clo = *Cephalanthera longifolia*, Dfu = *Dactylorhiza fuchsii*, Ehe = *Epipactis helleborine*, Hhi = *Himantoglossum hircinum*, Lab = *Limodorum abortivum*, Nov = *Neottia ovata*, Oan = *Orchis anthropophora*, Oap = *Ophrys apifera*, Oma = *Orchis mascula*, Opu = *Orchis purpurea*, Osc = *Ophrys scolopax*, Osi = *Orchis simia*, Pbi = *Platanthera bifolia*, Pch = *Platanthera chlorantha*.

	Amo	**Apy**	**Cda**	**Clo**	**Dfu**	**Ehe**	**Hhi**	**Lab**	**Nov**	**Oan**	**Oap**	**Oma**	**Opu**	**Osc**	**Osi**	**Pbi**	**Pch**
Amo		0.7065	0.7619	0.91	1	0.73	0.84	0.79	0.79	0.63	0.93	0.63	0.31	0.48	0.93	0.93	0.34
Apy	0.24		1	0.26	0.56	0.61	0.80	0.67	0.78	0.11	0.67	0.19	0.47	0.05	0.32	0.53	**0.03***
Cda	0.21	**5.85e-05*** **		0.40	0.95	0.66	1	0.89	0.94	0.28	0.72	0.49	0.83	0.26	0.44	0.56	0.11
Clo	0.91	0.05	0.13		0.95	0.54	0.43	0.57	0.44	0.74	0.62	0.87	0.07	0.39	0.75	0.75	0.35
Dfu	0.73	0.48	**0.02***	0.42		0.62	0.57	0.96	0.69	0.51	1	0.70	0.15	0.18	0.88	0.64	0.15
Ehe	0.48	**0.002****	0.78	0.37	0.09		0.71	0.57	0.87	0.22	0.93	0.44	0.29	0.33	0.62	1	0.14
Hhi	0.53	**0.003****	0.19	0.63	0.14	0.52		0.81	1	0.17	0.66	0.14	0.20	**0.04***	0.46	0.37	**0.04***
Lab	0.70	**0.01***	0.55	0.57	0.18	0.86	0.79		0.80	0.30	1	0.36	0.08	0.15	0.46	0.64	0.07
Nov	0.70	**0.02***	0.09	0.93	0.33	0.38	0.56	0.57		0.31	0.80	0.42	0.32	0.14	0.61	0.54	0.07
Oan	0.94	**0.04***	0.14	1	0.33	0.33	0.76	0.53	1		0.49	0.85	**0.02***	0.45	0.76	0.72	0.26
Oap	0.07	**1.56e-06*** **	0.51	**0.02***	**0.003****	0.34	**0.04***	0.24	**0.008****	**0.03***		0.74	0.34	0.39	0.87	0.77	0.16
Oma	0.93	0.21	**0.01***	0.57	0.84	0.11	0.14	0.20	0.40	0.45	**9.15e-05*** **		0.09	0.31	0.70	0.97	0.19
Opu	0.47	**0.002****	0.46	0.43	0.10	0.80	0.68	1	0.37	0.50	0.14	0.10		**0.02***	0.15	0.28	**0.02***
Osc	0.63	**0.01***	0.46	0.62	0.21	0.86	0.96	1	0.78	0.53	0.14	0.27	0.94		0.23	0.30	0.48
Osi	0.79	**0.03***	0.07	1	0.37	0.30	0.49	0.51	0.95	0.91	**0.007****	0.46	0.31	0.65		0.96	0.11
Pbi	0.42	**0.002****	0.59	0.37	0.10	1	0.70	0.82	0.36	0.39	0.17	0.09	0.96	0.73	0.32		0.21
Pch	0.27	**0.00043*** **	0.52	0.14	**0.03***	0.40	0.15	0.23	0.11	0.10	0.80	**0.03***	0.27	0.33	0.10	0.33	