Floristic Analyses of the Corsican Flora: Biogeographical Origin and Endemism

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Floristic analyses of the Corsican flora: biogeographical origin and endemism

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Abstract

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This article discusses various aspects of the biogeographical origin and endemism of the Corsican flora based on data retrieved from "Flora Corsica" project. It focuses on species richness, taxonomy, life forms, taxa abundance, distribution in vegetation belts, habitats and substrate types. The results are compared to other geographic regions, particularly Mediterranean ones. These data show that in Corsica the species of Mediterranean origin are slightly more numerous than those of Holarctic origin. It is surprising that the Holarctic elements start to dominate at low altitude in the supramediterranean belt. The endemic flora (12.7%) shows distribution patterns often distinct from those of the non-endemic native flora, particularly regarding taxonomy, biological types and altitudinal distributions. The rates of hemicryptophytes and chamaephytes are for instance higher for the former compared to the latter while it is the reverse for therophytes. These rates are quite similar to those recorded in Sardinia, but rather different from those of other Mediterranean islands. More unexpected is the abundance pattern of endemic species which is quite similar to that of non-endemic ones. However, strictly endemic Corsican species are generally rarer than subendemics. The number of endemic species increases from the coast to the montane belt and then decreases in the upper belts. The percentage of endemic species, meanwhile, regularly increases from the thermomediterranean belt to the alpine one where it reachs a maximum of 43.1%. The endemic flora also shows a wider altitudinal spectrum than other native species. The distribution of endemic species in the different Corsican habitats is slightly different from the one recorded for the indigeneous taxa. Endemics are however preferentially found in rocky habitats, but without any preference for a particular substrate. In the endemic flora, the Mediterranean origin is predominant but this trend is more marked in subendemics. The strict Corsican endemics have a mostly Holarctic origin and are more often found at high altitudes. These results shed light on the specificity of the Corsican endemic flora and should help the management of endemic species.

Résumé

JEANMONOD, D., Y. NACIRI, A. SCHLÜSSEL & J. GAMISANS (2015). Analyses floristiques de la flore corse: origine biogéographique et endémisme. *Candollea* 70: 21-41. En anglais, résumés anglais et français. DOI: http://dx.doi.org/10.15553/c2015v701a3

Cet article analyse divers aspects de l'origine biogéographique et de l'endémisme de la flore de la Corse sur la base des résultats publiés du projet «Flora Corsica». L'analyse traite de la richesse floristique, de la taxonomie, des formes biologiques, de l'abondance des taxons, de la distribution dans les étages de végétation, des habitats et des types de substrats. Les résultats sont comparés à ceux d'autres régions géographiques, en particulier méditerranéennes. Ces données montrent qu'en Corse les espèces d'origine méditerranéenne sont à peine plus nombreuses que celles d'origine holarctique. Il est surprenant de constater que le cortège holarctique domine déjà à partir de l'étage supraméditerranéen. La flore endémique (12,7%) montre des patrons de distribution souvent distincts de ceux de la flore indigène non endémique, notamment en ce qui concerne la taxonomie, les types biologiques et la distribution altitudinale. Les taux d'hémicryptophytes et de chamaephytes sont par

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exemple plus élevés alors que celui des thérophytes est plus bas. Ce patron se retrouve en Sardaigne mais pas dans les autres îles méditerranéennes. Par ailleurs, de façon inattendue, le patron d'abondance des endémiques est proche de celui des non endémiques. Toutefois les endémiques strictement corses sont globalement plus rares que les subendémiques. Le nombre d'endémiques croît depuis le littoral jusqu'à l'étage montagnard puis décroît dans les étages supérieurs. Le pourcentage d'endémiques, quant à lui, croît régulièrement depuis le thermoméditerranéen jusqu'à l'alpin où il atteint un maximum de 43,1%. Les endémiques montrent par ailleurs un plus large spectre altitudinal que les autres espèces indigènes. La présence des endémiques dans les habitats est légèrement distincte de celle des non endémiques, avec une préférence pour les habitats rocheux, mais sans préférence particulière pour un substrat donné. L'origine biogéographique méditerranéenne des endémiques est globalement prédominante, mais surtout chez les subendémiques. Les endémiques strictes ont, quant à elles, une origine holarctique prédominante et poussent de préférence dans les étages d'altitude. Ces résultats permettent de mieux appréhender les spécificités des endémiques corses et de servir à la gestion de la flore corse.

Keywords

Corsica – Diversity – Ecology – Endemism – Floristics – Life forms – Mediterranean – Mountains – Vegetation belts

Introduction

Following the publication of *Flora Corsica* (Jeanmonod & Gamisans, 2007), several analyses of the Corsican flora using taxon characteristics were undertaken. After Jeanmonod et al. (2011a) dealing with species richness, taxonomic distribution, abundance, life forms and phenology, Jeanmonod et al. (2011b) focused on the island alien flora and Schlüssel et al. (2014) dealt with the flora distribution in the island vegetation belts, habitats, and substrates. In the present paper, the biogeographical origin of the Corsican flora is analysed, with special attention to its endemic fraction. The purpose is to highlight the differences that exist between Corsica and other geographic regions such as Sardinia, Italy or the Balearic Islands. A subsidiary objective is to allow better target actions for the protection of the Corsican endemic flora, which meets a particularly important population concern.

A first biogeographic analysis of the Corsican flora has been performed by Gamisans et al. (1985), and its endemism has already been the subject of several publications (Levier, 1885; Contandriopoulos, 1962a, 1962b, 1964, 1981, 1990; Gamisans, 1981; Verlaque et al., 1995; Gamisans & Marzocchi, 1996), that sometimes included comparisons with a few other regions (Cardona & Contandriopoulos, 1977; Verlaque et al., 1991; Médail & Verlaque, 1997; Verlaque, 1999). Most of these studies have already highlighted the importance of endemism in Corsica, but they mainly focused on its distribution within the different biogeographic elements or within cytotaxonomic levels. The present study is based on a comprehensive and homogeneous dataset across the entire island, using recent records (which allows assessing the evolution of the flora when compared to previous studies), and includes information that was not available before, such as the biogeographic type, the abundance level, or the type of substrate for instance.

In this study we therefore aim at answering the following questions:

- what are the relative weights of the various floristic elements on Corsica?
- what are the most important floristic elements in each vegetation belt? More specifically, are the Mediterranean elements dominant in the Mediterranean belts, and are the Holarctic elements dominant in the Eurosiberian belts?
- what is the proportion of the endemic flora compared to the whole indigenous flora?
- what is the biogeographical origin of the endemic flora?
- what are the patterns (in terms of taxonomy, life forms, abundance, altitudinal distribution, habitats and substrates) of the endemic flora, and are they similar to that of the whole native flora?

Material and methods

Analysed taxa

All analyses use the data extracted from Jeanmonod & Gamisans (2007). Information from more recent publications (Jeanmonod & Schlüssel, 2008, 2010, 2012) has not been included to ensure consistency among all analyses (Jeanmonod et al., 2011a, 2011b; Schlüssel et al., 2014). For the reasons discussed in Jeanmonod et al. (2011a), the taxonomic level includes only species and subspecies, but not varieties and forms, for a total of 2680 taxa. This number comprises both native and introduced taxa (but not cultivated ones). Unless specified, our analysis however focuses on the indigenous component of the flora, which includes 2237 taxa.

The plant family concept is classical, mainly based on Cronquist (1981), as it is the most commonly used in published floras of the surrounding geographical areas. Thus, some families such as *Liliaceae* and *Scrophulariaceae* are treated in the broad sense (for more details see Jeanmonod & Gamisans, 2007).

Biogeographical origin

The biogeographical types are given and fully explained in Jeanmonod & Gamisans, (2007), Gamisans (1985) and Gamisans & Jeanmonod (1993). These types have been attributed to twelve chorological elements (see Table 1) that were subsequently grouped into five main clusters:

a) endemic and subendemic element;
b) Mediterranean element that includes the widely distributed taxa in the Mediterranean territory (Eurymediterranean taxa), the taxa limited to the coastal areas of the Mediterranean region (Stenomediterranean taxa), and the taxa limited to the Mediterranean mountains (Mediterranean-montane taxa);
c) Holarctic non Mediterranean element that includes the Eurasian taxa, the taxa distributed along the European Atlantic coast (Atlantic taxa), the taxa limited to the European mountains (orophytes), and the taxa limited to the cold and temperate climates of the Northern Hemisphere (circumboreal taxa);
d) other native plants (taxa from the deserts of North Africa to India, the Mediterranean-Touranian taxa, the tropical and subtropical taxa, and the cosmopolitan taxa).
e) neophytes (alien taxa).

Endemism

In order to avoid any ambiguity, different types of endemism were defined according to the endemic taxa distribution. Those restricted to the Corsican Island (as politically delimited) are designated as strictly endemic to Corsica (end. Co). All the other ones are grouped among the subendemic taxa, and are divided in four categories: a) the taxa limited to Corsica and Sardinia (end. Co-Sa); b) the taxa limited to Corsica and the Tuscan Archipelago (end. Co-AT); c) the taxa limited to Corsica and the Balearic Islands (end. Co-Bl) and d) the taxa limited to Corsica and some very particular and more remote areas such as Calabria (e.g. *Alnus cordata* (Loisel.) Duby) or Crete (e.g. *Lepidium hirtum* subsp. *oxyotum* (DC.) Thell.). Although focused on Corsica, the former classification is similar to the one used by Arrigoni & Di Tommaso (1991) and Bacchetta & Pontecorvo (2005) who defined the following categories: "Sardo-Corsican endemics" (ESC), "Thyrrenian insular endemics" (ETI) and "W-Mediterranean insular endemics" (EMOI).

Vegetation belts, abundance classes, life forms, habitats and substrates

The categories used to classify the taxa are extensively explained in Jeanmonod et al. (2011a, 2011b) and Schlüssel et al. (2014). As a reminder, the vegetation belts are the following (ordered by altitude): the littoral zone (LI), the thermomediterranean belt (TM), the mesomediterranean belt (ME), the supramediterranean belt (SM), the montane belt (MO), the cryo-oromediterranean belt (OR), the subalpine belt (SA), and the alpine belt (AL).

The taxa were clustered into seven abundance classes (Gamisans & Jeanmonod, 1993) as follows (ordered by rarity): CC = very common; C = common; PF = infrequent or disseminated; LOC = localised (only in small areas, where it can however be abundant); R = rare with only 6 to 10 known localities; RR = very rare with only 1 to 5 known localities; D? = presumably extinct in Corsica. The life forms are those defined by Raunkier (1934). The longevity forms are the classical ones: annual, biennial and perennial.

Comparisons with other geographical territories

Whenever possible, the results were compared with other geographical regions, especially regions with a Mediterranean climate such as different regions of southern France like

Table 1. – Number of taxa and proportion of the biogeographical elements in the Corsican flora, with percentages calculated on the whole flora (2680 taxa) and on the native flora (2237 taxa).

		Mediterranean				Holarctic-eurosiberian				Others		
	Endemic	Stenomed.	Eurymed.	Med-Mont.	Med-Touranian	Eurasiatic	Atlantic	Orophytic	Circumboreal	Tropical	Cosmopolitan	Introduced
Taxa number	284	497	346	35	58	489	137	53	175	42	121	443
Whole flora [%]	10.6	18.5	12.9	1.3	2.2	18.2	5.1	2.0	6.5	1.6	4.5	16.5
Group [%]	**10.6**	**34.9**				**31.9**				**6.1**		**16.5**
Native flora [%]	12.7	22.2	15.5	1.6	2.6	21.9	6.1	2.3	7.8	1.9	5.4	–
Group [%]	**12.7**	**41.8**				**38.2**				**7.3**		**–**

Table 2. – Proportions (%) of the biogeographical elements in the flora of various countries and probabilities associated with percentage comparisons of the Corsican Flora with other floras.
[*** = significant χ^2values at $\alpha = 0.001$; $ = χ^2 was calculated although one cell has less than 5 records, but only the value was used for comparative purposes]

Country	Endemic	Mediterranean	Holarctic-eurosiberian	Others	χ^2	References
Corsica	12.7	41.8	38.2	7.3	-	
Sardinia	7.1	49.1	27.7	14.3	129***	Pignatti, 1994
Sicily	7.6	49.6	18.0	15.9	284***	Pignatti, 1994
Balearic islands	11.0	52.0	5.5	30.7	778***	Larrucea & Coll, 2006
Cyprus	11.3	50.3	19.9	18.5	210***	Alziar, 1995
Crete	10.5	76.3	10.7	2.5	534***	Jahn & Schönfelder, 1995
Gard	2.8	31.8	54.2	11.2	252***	Aubin, 1999
Bouches-du-Rhône	-	54.6	29.6	15.8	300$	Molinier, 1980
Vaucluse	2.1	35.4	52.7	9.8	196***	Girerd, 1978
Alpes-Hte-Provence	6.5	24.0	68.3	1.2	480***	Boucher, 1998
Tuscany	3.9	34.7	46.9	13.4	206***	Pignatti, 1994
Italy	13.5	31.5	43.0	12.0	94***	Pignatti, 1994
Alps	12.6	19.8	65.5	2.1	542***	Aeschimann et al., 2011b

the Gard (Aubin, 1999), the Vaucluse (Girerd, 1978), the Alpes de Haute-Provence (Boucher, 1998), the Bouches-du-Rhône (Molinier, 1980), The Alpes-Maritimes (Casazza et al., 2005), different regions of Italy (Pignatti, 1994; Conti et al., 2005; Peruzzi et al., 2014), and especially Sardinia (Bacchetta et al., 2005; Conti et al., 2005), big Mediterranean islands such as the Balearic Islands (Vilà & Muñoz, 1999; Larrucea & Coll, 2006), Crete (Greece) (Jahn & Schönfelder, 1900; Jahn, 2003) and Cyprus (Alziar, 1995), the southern Iberian Peninsula (Melendo et al., 2003; Giménez et al., 2004) and Greece (Georghiou & Delipetrou, 2010). We additionally compared our data with the Alps (Austria, France, Germany, Italy, Lichtenstein, Slovenia, Switzerland; Aeschimann et al., 2011a, 2011b, 2012a, 2012b), because it is the only territory for which a comparable dataset was published, keeping in mind that this territory is however much greater than Corsica.

For some regions, the recent published data are quite different from older datasets. This is the case for Italy and some of its provinces, especially Sardinia. Current authors are indeed prone to splitting species, more than previous authors used to do, including us. Consequently, the number (and percentage) of Italian endemics increased from 754 (13%) according to Pignatti (1994), to 1024 (13.4%) following Conti et al. (2005), then to 1371 (18.9%) for Peruzzi et al. (2014). Depending on which type of data was analysed for Corsica, comparable datasets had to be used that were sometimes different from the most recent ones. This is why differing percentages are sometimes given, depending on which question was addressed (e.g. 7.2% of Sardinian endemics in Table 2 according to Pignatti (1994) but 10.5 to 11.5% in Table 3 following Conti et al. (2005), whereas Bacchetta et al. (2005, 2012b) report 14.4% of endemics for the island, including varieties and hybrides, but without the figures that could have been appropriately included in Table 2 and 3).

Statistical analyses

The size of the different vegetation belts was taken into account in all comparisons. The species-area relationship was performed using a logarithmic scale (Arrhenius, 1921), as well as regression lines and coefficients of determination *(r^2)* between pairs of variables (Zar, 1996). Independent proportions were compared by pairs using the z-ratio (Sokal & Rohlf, 1995), and associated significance obtained (see http://vassarstats.net/). When percentage calculation relied on counts lower than 5, 95% confidence intervals were computed for each percentage and the two percentages were considered as significantly different at $\alpha = 5\%$ when intervals did not overlap. χ^2 tests were used to compare contingency tables (see http://www.quantpsy.org) (Preacher, 2001). When at least one cell displayed a count lower than 5, a Yate's correction was applied.

Results and discussion

1. Biogeographical types

The proportions of the various biogeographical elements are shown in Table 1. Given the large amount of non-native plants, the values change depending on the considered flora: all taxa (2680) or only the native ones (2237). From here onward we will only consider the native flora.

Table 3. – Comparison of the number of taxa and of the percentage of endemics calculated on the whole flora and on the native flora of different countries ordered as increasing surface-area.
[$ = only species are numbered; in bold = The z-ratio compares the percentage of endemics/native flora for each region vs. Corsica and significant ratios are indicated; nt = not tested due to too low counts (<5)]

Country	Whole flora	Native flora	Endemic flora	Endemic [%] / whole flora	Endemic [%] / native flora	P (z-ratio)	References
Vaucluse	1775	1730	35	2.0	2.0	**<0.001**	Girerd, 1978
Balearic islands	1853	1729	173	9.3	10.0	**0.009**	Larrucea & Coll, 2006; Vilà & Muñoz, 1999
Palermo	2433	?	232	9.5	?	?	Raimondo et al., 2003
Bouches-du-Rhône	2898	1887	0	0	0	nt	Molinier, 1980
Liguria	3131	2915	54	1.7	1.9	**<0.001**	Conti et al., 1995
Gard$	2325	2253	64	2.8	2.8	**<0.001**	Aubin, 1999
Alpes-Hte-Provence	2600	?	169	6.5	?	?	Boucher, 1998
Crete	2001	1839	174	8.7	9.5	**0.001**	Jahn, 2003
Corsica	**2680**	**2237**	**284**	**10.6**	**12.7**	**-**	**Present study**
Alpes maritimes	3605	?	115	3.2	?	?	Casazza et al., 2005
Cyprus$	1576	1514	171	10.9	11.3	0.197	Alziar, 1995
Tuscany	3435	3117	155	4.5	5.0	**<0.001**	Conti et al., 1995
Sardinia	2407	2199	253	10.5	11.5	0.224	Conti et al., 1995
Piémont	3510	3138	40	1.1	1.3	**<0.001**	Conti et al., 1995
Sicily	3010	2718	322	10.7	11.8	0.364	Conti et al., 1995
Switzerland	3051	2584	2	0.1	0.1	nt	Aeschimann & Heitz, 2005
Greece$	?	5855	913	?	15.6	**0.001**	Georghiou & Delipetrou, 2010
Italy	7634	6852	1024	13.4	15.0	**0.009**	Conti et al., 1995
Alps	4452	3950	501	11.2	12.7	0.989	Aeschimann et al., 2011a

Our results (Table 1) show that the Mediterranean element in the native flora (41.8%) is significantly higher than the Holarctic non-Mediterranean element (38.2%) (z-ratio = 2.502, $P = 0.006$). These results are similar to those obtained by Gamisans et al. (1985), who included the varieties and forms in their study (42.5% for the Mediterranean and Touranian elements vs. 38.1% for the Holarctic ones). Moreover, if the origin of the endemic taxa (see chapter 2, "Endemic flora") is taken into account, the proportion of the Mediterranean element increases to 48.9% (vs. 43.7% for the Holarctic non Mediterranean element, z-ratio = 3.478, $P < 0.001$).

Comparisons with other geographical territories

The comparison of our data with those of other regions shows that Corsica has a lower proportion of Mediterranean taxa than other Mediterranean islands or than the Bouches-du-Rhône (Table 2). This result seems to relate to the importance of the mountaneous areas in the Corsican Island. Corsica shows the greatest similarity (lowest χ^2 value) with the whole Italian territory (including the islands, $\chi^2 = 94$, df = 3, $P < 0.001$) then with Sardinia ($\chi^2 = 129$, df = 3, $P < 0.001$). The more northern regions such as the Gard, the Vaucluse and the Alpes-de-Haute-Provence are less similar and have a lower proportion of Mediterranean taxa; Tuscany, the Vaucluse and the Gard show a much lower importance of the endemic element, whereas the Alps have a high proportion of Holarctic taxa. Overall, these comparisons show that Corsica has stronger affinities with the other Mediterranean areas (excepting the Balearic Islands, $\chi^2 = 778$, df = 3, $P < 0.001$) than with the Alpine region ($\chi^2 = 542$, df = 3, $P < 0.001$) despite Corsica and the Alps being both montaneous areas.

Vegetation belts

The distribution of the biogeographical elements within the vegetation belts of Corsica, excluding endemic and alien taxa, is shown in Figure 1. There is a marqued decrease of the Mediterranean elements with higher altitudes (Fig. 1A) counterbalanced by an increase of the Holarctic elements (Fig. 1B): 65.4% of Mediterranean taxa in the littoral zone and 68.8% in the thermomediterranean belt vs. 86.1% of Holarctic taxa in the subalpine belt and 89.7% in the alpine belt. The Mediterranean elements are already relatively low (48.9%) in the mesomediterranean belt, whereas the Holarctic elements become dominant in the supramediterranean belt (54.9% vs. 34.1% for the Mediterranean elements). These results corroborate and refine data of Gamisans et al. (1985) who found

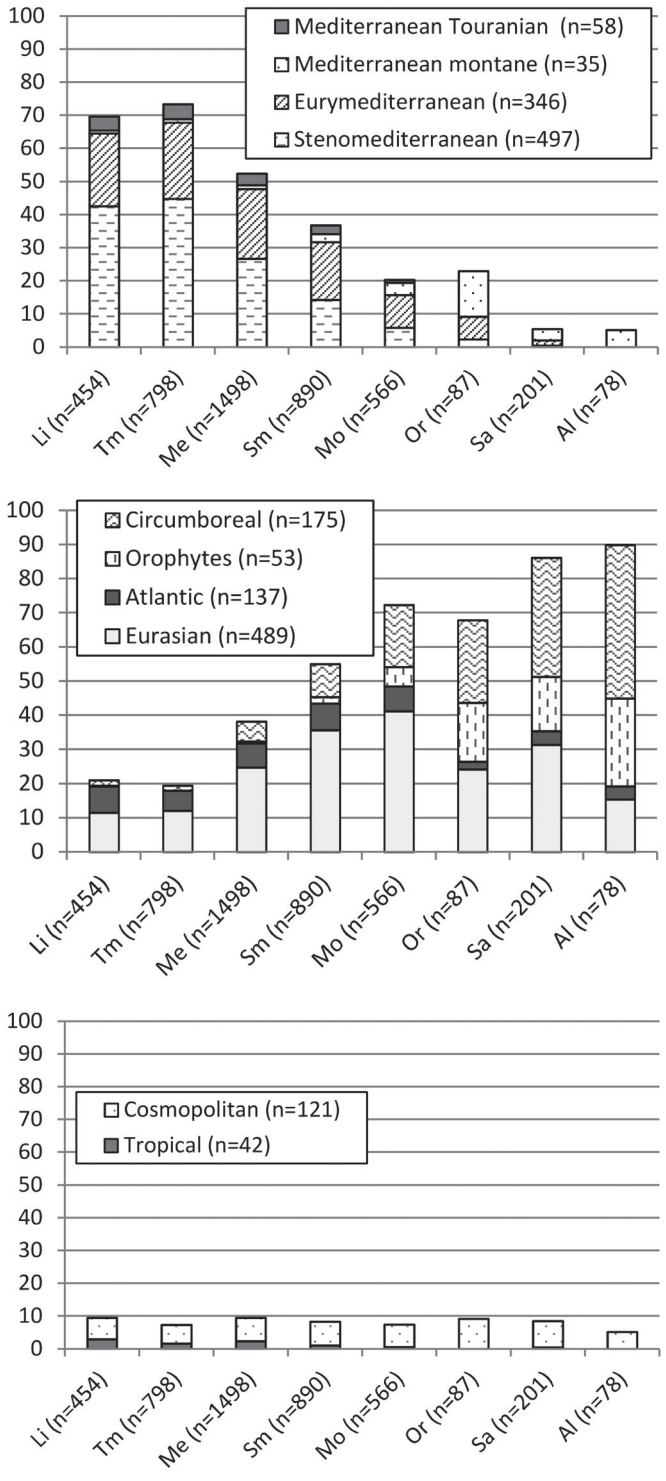

Fig. 1. – Biogeographical origin of the native non-endemic flora in each vegetation belt. [n = total in each category; A: Mediterranean elements; B: Holarctic elements; C: Others elements; Li: coastal zone; Tm: thermomediterranean; Me: mesomediterranean; Sm: supramediterranean; Mo: montane; Or: cryo-oromediterranean; Sa: subalpine; Al: alpine]

6.2% for the Mediterranean elements, 53.7% for the holarctic ones, 35.7% for the endemics and 4.4% for others in the higher vegetation belts (Or, Sa and Al), with a total of 339 taxa (vs. 6%, 52.2%, 56.4% and 5.4%, respectively, on 579 taxa in our study, $\chi^2 = 1.787$, df = 3, $P = 0.617$). In the Alps (Aeschimann et al., 2011b), the Mediterranean elements account for 16.2% of the total flora in the montane belt (20.3% on Corsica, $\chi^2 = 5.929$, df = 1, $P = 0.018$), 7.4% in the subalpine belt (5.5% on Corsica, $\chi^2 = 1.04$, df = 1, $P = 0.308$) and 1.4% in the alpine belt (5.1% on Corsica, Yate's $\chi^2 = 4.341$, $P = 0.037$). Thus, both the montane and the alpine belts are significantly different between the two regions. On Corsica, it seems that the Mediterranean taxa have been able to adapt to higher altitudes due to the lack of many Holarctic taxa on the island. When the endemic elements of Corsica are added to the Mediterranean elements, as did Aeschimann et al. (2011b), the latter reach 30.6% in the montane belt, 18.4% in the subalpine belt and 29.5% in the alpine belt. This result suggests an adaptation of the Mediterranean flora to the upper vegetation belts, a phenomenon that might have induced speciation events and favoured the establishment of endemic taxa at high altitudes (see chapter 2, "Endemic flora").

Abundance classes

The above mentionned results do not take into account taxa abundance. Figure 2 shows the biogeographic elements distribution in the various abundance classes. This distribution is quite homogenous. However, the Mediterranean elements contain more common taxa (C+CC = 51.3% and R+RR = 39.9%) compared to the Holarctic elements that have more taxa with restricted ranges (C+CC = 40% and R+RR = 50.9%, z-ratio = 4.817, $P < 0.001$ and z-ratio = 3.295, $P = 0.001$, respectively). This reveals that the Mediterranean elements are the most important overall, in terms of taxon number and abundance.

When applied to the most common taxa of the non-endemic indigeneous flora (CC+C+PF, i.e. 1342 taxa), the analysis of the biogeographical elements proportion shows almost identical results, which therefore confirms the analysis of Fig. 1. When focusing on the supramediterranean and the cryo-oromediterranean belts, that suprisingly comprise more taxa of Holarctic origin than taxa of Mediterranean origin, it appears that more frequent taxa (CC+C) are found in the Mediterranean element (57.8% of all supramediterranean taxa and 75% of all cryo-oromediterranean taxa) than in the Holarctic element (40.3% and 54.2%, respectively). A former analysis from Gamisans (1978) established the phytogeographic spectrum according to the different belts using the floristic composition of the phytosociological associations found in these belts. In the supramediterranean and the montane belts, only the dwarf bushy/shrubby habitats are dominated by the Mediterranean element (55-58%), the other associations (forests, meadows) being dominated by Holarctic elements. For the

cryo-oromediterranean, the meadows and the dwarf bushy/shrubby habitats (the only associations covering most of the surface) are dominated by the Mediterranean elements (54%). These results seem to contradict the ones obtained here (only 23% of Mediterranean taxa). To our opinion, this is due to the fact that in the flora of Corsica, Holarctic species have been recorded in the cryo-oromediterranean belt, even when they were rare or very rare, when they played no role in the vegetation structuration, and when they were consequently absent from phytosociological relevés. This comment meets the taxon abundance analysis within each element and downweights the observed predominance of the Holarctic element in the former belts (and more specifically in the cryo-oromediterranean one).

Correlation with the main families

Jeanmonod et al. (2011a) have showed that the distribution of the 13 most important families of the native Corsican flora stands in between those of temperate and Mediterranean regions, due to the Corsican altitudinal amplitude and to the numerous vegetation belts found in the island. The analysis of these 13 families within the Mediterranean and Holarctic elements reveals differing distribution patterns with *Fabaceae*, *Apiaceae* and *Lamiaceae* exhibiting a clear dominance of Mediterranean elements (77.8%, 60.8% and 59.3%, respectively), whereas other families are characterized by a dominance of Holarctic elements such as *Rosaceae* (63.8%), *Cyperaceae* (60.9%) and *Scrophulariaceae* (60.9%). Within the Mediterranean elements, the family ranking is then the following: *Fabaceae, Asteraceae, Poaceae, Apiaceae, Caryophyllaceae* etc, close to the ones recorded in Crete or the Balearic Islands (Jeanmonod et al., 2011a). Conversely, the ranking within the Holarctic element starts with *Asteraceae, Poaceae, Cyperaceae, Fabaceae, Rosaceae* etc., and is therefore closer to the one observed in the Alpine Arc (Aeschimann et al., 2011a).

2. Endemic flora

Level of endemism

Jeanmonod & Gamisans (2007) has identified 316 endemic taxa s.l. (strict endemic + subendemic), which corresponds to 13.6% of the indigeneous flora or 11.4% of the total flora, including varieties. These taxa are found in 49 families (over 156, i.e. 31%) and 152 genera (over 846, i.e. 18%). When excluding varieties, the number of endemic taxa decreases to 284, which corresponds to 12.7% of the native flora or 10.6% of the total flora (Table 3). The following analysis are based on 284 endemic taxa.

The percentage of endemics varies a lot according to regions and more specifically to islands (Table 3). It should be however noticed that for a given territory, the published figures may vary from one author to the other due to their species concept or to their data. For instance Conti et al. (2005) give 253 endemic taxa for Sardinia, but Bacchetta

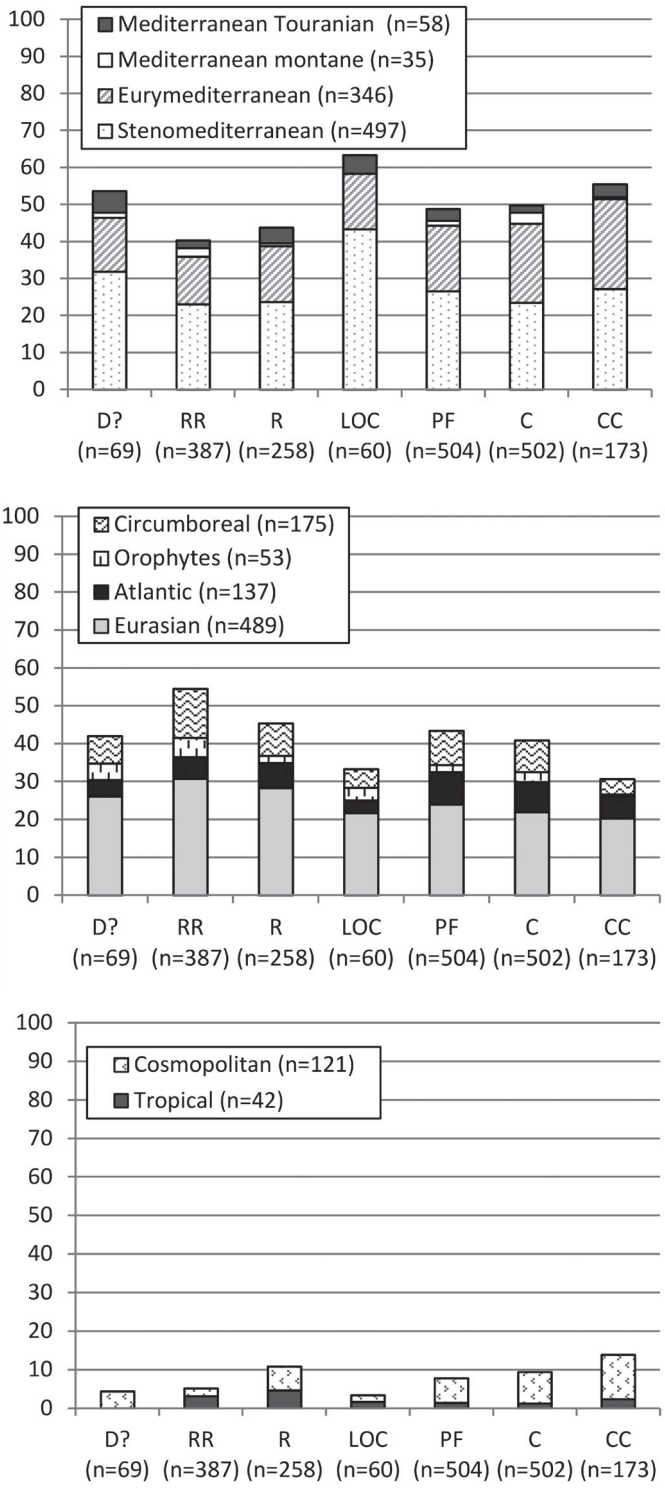

Fig. 2. – Biogeographical origin of the native non-endemic flora for each abundance class. [n = total in each category; D? = probably extinct; RR = very rare; R = rare; PF = infrequent or disseminated; LOC = localised; C = common; CC = very common]

et al. (2005), who used another species concept, report a total number of 347 endemics (including 331 species and subspecies, and 16 varieties and hybrids). According to Table 3, Corsica is the Mediterranean island that exhibits the highest rate of endemism when calculated on the native flora. When compared to other continental areas, Corsica exhibits again a higher rate than the surrounding Mediterranean regions, excluding Greece and Italy. Four regions, the Alps, Sicily, Sardinia and Cyprus, exhibit rates of endemism that are not significantly different from that of Corsica (Table 3). The high rate of endemism observed in Corsica is mainly due to the conjunction of two factors: a mountaneous lanscape and a long-standing isolation.

Endemism typology

The figures given for Corsica are the result of a broad view of endemism. Endemics can be divided into strict Corsican ones (122 taxa, i.e. 5.5% of the native flora) and subendemics (162 taxa i.e. 7.2% of the native flora). A finer analysis of the latter taxa (Table 4) highlights the paleogeographic relationships that exist between Corsica and the surrounding territories, as already underlined by Contandriopoulos (1990) among others. In Sardinia for instance, Bacchetta et al. (2005) counted 45.8% of strictly Sardinian endemics and 26.4% of Cyrno-Sardinian ones (Table 4).

Table 4. – Analysis of the different elements of the Corsican endemism, with the number of taxa in each category, and percentages on the whole endemic taxa and on the whole native flora.
[Co: strictly in Corsica; Co-Sa: Corsica and Sardinia; Co-AT: Corsica and Tuscan Archipelago; Co-Bl: Corsica and Balearic Islands]

Endemics category	Number of taxa	Endemic taxa [%]	Native taxa [%]
Co	122	43.0	5.5
Co-Sa	75	26.4	3.4
Co-AT	17	6.0	0.8
Co-Bl	7	2.5	0.3
Corsica and nearest France-Italy	13	4.6	0.6
Corsica and central Italy	3	1.1	0.1
Corsica and south Italy	20	7.0	0.9
Corsica and Alps	7	2.5	0.3
Corsica and Italy	7	2.5	0.3
Corsica and others	13	4.6	0.6

The 75 taxa shared among Corsica and Sardinia are an illustration of the tight link that exists between the two islands, distant by only 12 km, with a land bridge that appeared during the last glaciations. Moreover, among the 87 other subendemic taxa (for instance common to Corsica and the Baleares), 62 are also found in Sardinia. Therefore the number of endemics common to Corsica and Sardinia increases to 137 (84% of all subendemics). Subendemics of Corsica that are absent from Sardinia are also worth noticing, notably those of the Tuscany Archipelago that did not reach Sardinia such as *Trisetum flavescens* subsp. *corsicum* (Rouy) Cif. & Giacom. and *Galium caprarium* Natali.

The link between Corsica and the Balearic Islands is weaker, with only seven shared taxa (or 13 if enlarged to other subendemics). This reflects the past existence of a common flora for the block constituted by Corsica, Sardinia and the Baleares before it splitted into different islands that drifted during the Miocene to their present location (between 25 and 18 MYA). Among the other remarkable Corsican subendemics, 13 are shared with Sardinia, Calabria and Sicily, and might have survived the separation of the Sicilo-Calabrian block from the Cyrno-Sardinian one 15 MYA. Another 13 are shared with the Alps and the Provence region, nine with Tuscany and/or Liguria and other surrounding areas, three with south Spain (*Bunium alpinum* subsp. *corydalinum* (DC.) Nyman, *Scleranthus burnatii* Briq., *Armeria pungens* (Link) Hoffmanns. & Link) and two with the Pyrenees (*Galium cometherhizon* Lapeyr. and *Gagea soleirolii* Mutel). These taxa are either evidence of ancient connexions with the Pyrenees, south France and the Alps (30 MYA) or footprint of the ancient block constituted by the Betic chain, the Baleares, Cyrno-Sardinia, Calabria and Sicily (30 MYA). They might also be witnesses of the terrestrial contacts that existed between Tuscany, North Italy and Corsica during the Messinian Salinity Crisis (5.2 MYA). Conversely, some subendemic taxa might have been wind or bird-dispersed into Corsica during the former periods or lately after the Quaternary glaciations, when the present vegetation settled. Finally human introduction cannot be excluded for some taxa. The palynologic analyses of Reille et al. (1996) in Lake Creno indeed showed that *Pinus nigra* subsp. *laricio* Maire (a Corsican-Calabrian-Sicilian endemic) appeared in Corsica during the latest glacial period and might have been introduced by Humans. Therefore, the presence of this species in Corsica is not a footprint of the Corsican-Sardinian-Sicilian block, as initially envisionned.

Taxonomy

The ten families with the highest number of endemic taxa are the following: *Asteraceae* (67 taxa from which 45 are strictly endemic to Corsica), *Caryophyllaceae* (19/4), *Plumbaginaceae* (17/12), *Orchidaceae* (16/2), *Scrophulariaceae* (14/7), *Ranunculaceae* (13/8), *Poaceae* (13/5), *Apiaceae* (12/6), *Liliaceae* (12/3) and *Lamiaceae* (11/5). Seven of these families, but not in the same order except for *Asteraceae*, belong to the main families of the native Corsican flora. A comparison with the endemic flora of other areas such as Sardinia (Bacchetta et al., 2005), the Balearic Islands (Vilà & Muñoz, 1999; Larrucea & Coll, 2006), the south of the Iberian Peninsula (Melendo et al., 2003), Greece (Georghiou & Delipetrou, 2010) or the

Alps (Aeschimann et al., 2011a), shows disparities in family sequences as well as in families themselves. In Corsica, excluding families with less than 10 taxa (for instance *Berberidaceae* with one endemic taxon (100%) or *Paeoniaceae*, with three taxa among which two are endemics (66.7%), the five families with the highest percentages of endemics are *Plumbaginaceae* (51.5%), *Iridaceae* (33.3%), *Scrophulariaceae* (23.3%), *Orchidaceae* (22.9%) and *Ranunculaceae* (22.8%). This is totally different from what has been found in the Alps (Aeschimann et al., 2011a) with *Campanulaceae, Saxifragaceae, Dipsacaceae, Primulaceae* and *Thymelaeaceae* similarly ordered. This shows that endemism does not follow any particular taxonomic pattern and that it is only partially linked to the diversity displayed within families. *Hieracium* L. (28), *Limonium* Mill. (13), *Taraxacum* F. H. Wigg. and *Ophrys* L. (12), *Ranunculus* L. (6), then *Silene* L., *Galium* L. and *Euphorbia* L. (5) are the genera displaying the highest number of endemic taxa. Again this is very different from what is seen in the Alps where only *Ranunculus* and *Galium* are found in the list of the eight genera with the highest number of endemics. It comes however closer to the sequence reported for Greece (Georghiou & Delipetrou, 2010) with *Taraxacum, Silene, Galium* and *Limonium* among the eight genera with the highest number of endemics.

Longevity and life forms

Endemics s.l. do not show the same pattern than the native flora (Jeanmonod et al., 2011a), with 11.3% of annuals against 36.3% for the total native flora (Table 5). It can be seen however that this pattern is relatively variable within the various groups of endemics. Corsican endemics s.str. display a very high percentage of perennials (91%), as do the Balearic subendemics (100%). This might be due to Corsican endemics s.str. being more bound to the highest altitudinal belts that are conversely poor in therophytes (Jeanmonod et al., 2011a) as it will be discussed later. Furthermore, the "Co-AT" subendemics display a comparatively high percentage of annuals and biennials because therophytes are more numerous at low altitudes.

The range of life forms (Table 6) reflects this situation but describes more precisely some characteristics of perennial plants. Compared to the indigenous flora, endemics s.l. display a significantly higher number of hemicryptophytes and chamaephytes (and conversely a significantly lower number of therophytes and hydrophytes). Figure 3 shows that this trend is even stronger when restricted on the Corsican endemics s.str. for which the proportion of both hemicryptophytes and chamaephytes reaches 82.7%. This analysis highlights the very low proportion of geophytes (7.1%) in the strict Corsican endemics (Co) compared to the others subcategories (Co-Sa, Co-AT and Co-Bl; 26.2%; z-ratio = -3.985, $P < 0.001$).

Table 5. – Number and proportion (between brackets) on the whole flora in each category of longevity form. For each category, the sum of the percentage of the longevity form may exceed 100% because some taxa display several longevity forms. Significant differences are indicated in bold. [Co: strictly in Corsica; Co-Sa: Corsica and Sardinia; Co-AT: Corsica and Tuscan Archipelago; Co-Bl: Corsica and Balearic Islands]

Endemics category	Annual	Biennial	Perennial
Co (n = 122)	11 (9.0%)	3 (2.5%)	111 (91.0%)
Co-Sa (n = 75)	9 (12.0%)	4 (5.3%)	66 (88.0%)
Co-AT (n = 17)	3 (17.6%)	3 (17.6%)	15 (88.2%)
Co-Bl (n = 7)	0 (0%)	0 (0%)	7 (100%)
Others (n = 63)	9 (14.3%)	6 (9.5%)	53 (84.1%)
Whole endemics (n = 284)	32 (11.3%)	16 (5.6%)	252 (88.7%)
Whole native (n = 2237)	813 (36.3%)	150 (6.7%)	1419 (63.4%)
***P*(z-ratio)**	**< 0.001**	0.493	**< 0.001**

Table 6. – Numbers of the endemic life forms and proportions on the whole endemic flora, compared with the proportion of native flora in the same life forms. The sum of the life forms percentages may exceed 100% because some taxa may display several life forms. Significant differences are indicated in bold. [Hydr. = hydrophytes; Ther. = therophytes; Geo. = geophytes; Cham. = chamaephytes; Phan. = phanerophytes]

	Hydr.	Ther.	Geo.	Hemi.	Cham.	Phan.
Number of endemics	1	32	47	160	49	13
Endemic flora [%]	0.4	11.3	16.5	56.3	17.3	4.6
Native flora [%][1]	4.0	35.7	13.8	40.3	7.7	7.3
***P*(z-ratio)**	**< 0.05**[2]	**< 0.001**	0.212	**< 0.001**	**< 0.001**	0.087

[1] According to Jeanmonod et al. (2011b) on 2237 taxa.
[2] Because the number of endemics was too low (<5) we only calculated the 95% confidence interval for the percentage of hydrophytes taxa on the native flora: 3.2% ≤ 4% ≤ 4.8%.

Table 7 shows that life form pattern in Corsica is significantly different from that of all other regions analysed. The closest pattern is found in Greece ($\chi^2 = 30$, df = 4, $P < 0.001$; Georghiou & Delipetrou, 2010), followed by Sardinia ($\chi^2 = 34$, df = 4, $P < 0.001$; Bacchetta et al., 2005) with the same four and three dominating types, respectively. The percentage of hemicryptophytes is however clearly lower in the two latter regions compared to Corsica. Phanerophytes (including nanophanerophytes) are however more important in Sardinia. The pattern in the Balearic Islands (Vilà & Munoz, 1999) is very different from that of Corsica with the dominating type being the chamaephytes (37.7%), followed by the hemicryptophytes (30.8%) and the phanerophytes (14.6%). Cyprus and the south of the Iberian Peninsula show the same tendencies with some differences however. The higher altitude range of the Corsican mountains (when the Sierra Nevada is excluded) likely explains the differences between Corsica and the other studied areas. Indeed, higher altitudes might favour a high percentage of hemicryptophytes as shown by Jeanmonod et al. (2011a). Accordingly the endemic flora of

Table 7. – Proportion (%), in decreasing order for Corsica, of life forms of endemic taxa in various countries. The χ^2 values were calculated excluding hydrophytes for all comparisons. [*** indicates significant χ^2 values at $\alpha = 0.001$]

	Corsica	Sardinia	Balearic islands	Cyprus	South Spain	Greece	Alps
	Present study	Baccheta et al., 2005	Larrucea et al., 2006	Alziar, 1995	Melendo et al., 2003	Georghiou & Delipetrou, 2010	Aeschimann et al., 2012a
Hemicryptophytes	56.3	34.3	30.8	22.9	33	44	70.7
Chamaephytes	17.3	30.0	37.7	29.8	45	27	24.2
Geophytes	16.5	17.3	10.8	20.6	5	17	6.6
Therophytes	11.3	8.3	6.2	15.3	11	11	4.2
Phanerophytes	4.6	9.8	14.6	14.0	6	1	1.8
Hydrophytes	0.4	0.3	0	0	0	0	4.8
χ^2	-	34***	45***	41***	92***	30***	46***

the Alps displays a still higher percentage of hemicryptophytes (70.7%) followed by 24.2% of chamaephytes (Aeschimann et al., 2012a). These percentages are close to the ones calculated on the Corsican endemics s.str. (65.4% and 17.3%, respectively; Fig. 3). It is then noticable, that endemics do not follow the life form pattern recorded for the whole Corsican flora, nor the one observed on the other Mediterranean Islands. This quite original pattern is closer to the one observed in Greece, which might be explained by the mountaneous landscape (presence of higher altitudinal belts) in these areas.

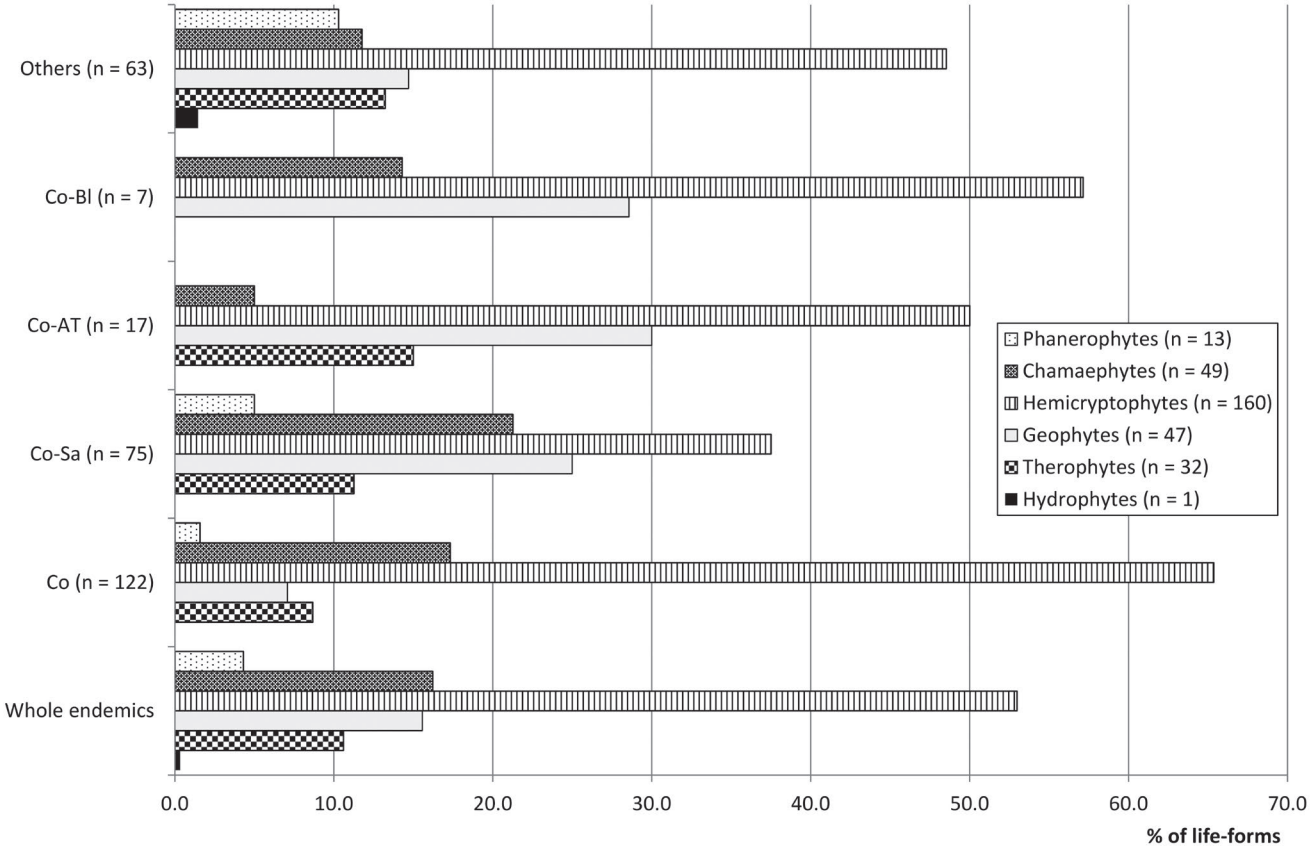

Fig. 3. – Relative proportion of life forms in each endemic element. [n = number of taxa in each category]

Abundance

The abundance pattern for endemic species s.l. (Table 8) is very close to the one of native plants, except for localised species (LOC). For these species the difference between the two percentages was found significant (z-ratio = 3.888, $P < 0.001$, Table 8). The percentage of the D+RR+R+LOC taxa is 42.6% (40% for the native flora, z-ratio = 0.84, $P = 0.401$) and the one of the C+CC is 32% (34.2%, z-ratio = -0.737, $P = 0.461$). This shows that unlike observations made on the continent (see Médail & Verlaque, 1997), Corsican endemics are not bound to specific and restricted territories. They indeed display the same abundance pattern as the other native taxa. The abundance pattern of the endemic taxa s.l. and that of the strictly Corsican endemics are however dissimilar ($\chi^2 = 10.1$, df = 4, $P = 0.039$).

Comparing the different categories of endemics (Fig. 4), various patterns of abundance can be observed: it is obvious that the strictly Corsican endemics are rarer (R and RR: 47.5%) than subendemics (21.6%; z-ratio = 4.61, $P < 0.001$). From a patrimonial and conservation perspective, the strictly Corsican endemics are therefore the most interesting species.

Table 8. – Number of endemic taxa in each abundance class, proportion on the whole endemic flora, compared to the proportion of the native flora in the same classes. Significant differences are indicated in bold.
[D? = probably extinct; RR = very rare; R = rare; PF = infrequent or disseminated; LOC = localised; C = common; CC = very common]

	D?	RR	R	LOC	PF	C	CC	Total
Number of endemic taxa	3	59	34	25	72	68	23	**284**
Endemic flora [%]	1.1	20.8	12.0	8.8	25.4	23.9	8.1	
Number of native taxa	72	446	292	85	576	570	196	**2237**
Native flora [%][1]	3.2	19.9	13.1	3.8	25.7	25.5	8.8	
***P*(z-ratio)**	>0.05[2]	0.74	0.609	**<0.001**	0.886	0.575	0.708	

[1] According to Jeanmonod et al. (2011a) on 2237 taxa.
[2] Because the number of endemics was too low (< 5) we calculated the 95% confidence interval for both percentages: 0.4% < 1.1% < 3.1% and 2.6% ≤ 3.2% ≤ 4%.

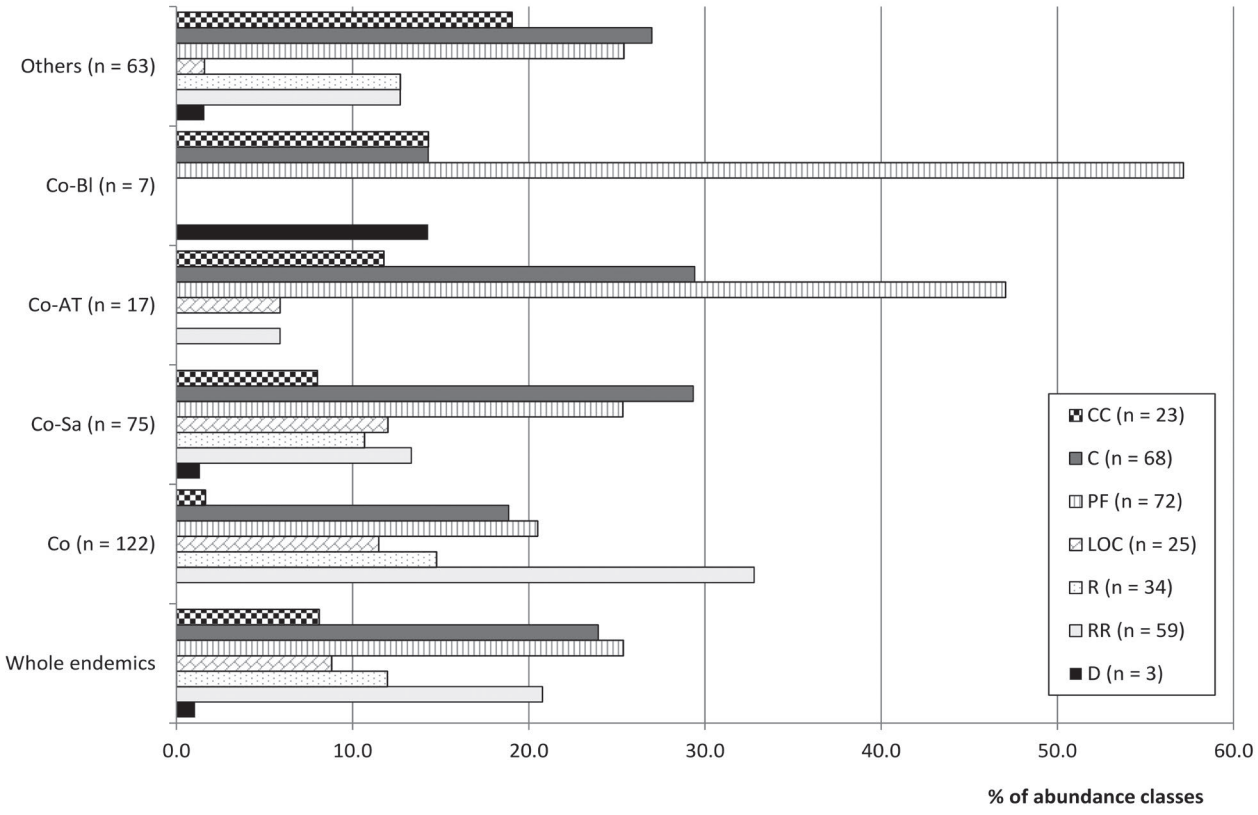

Fig. 4. – Relative Relative proportion of abundance classes in each endemic element.
[n = number of taxa in each category; CC = very common; C = common; PF = infrequent or disseminated; LOC = localised; R = rare; RR = very rare; D = probably extinct]

Vegetation belts

In the various vegetation belts (Table 9), the proportion of endemics s.l. and the proportion of taxa belonging to the native flora are not the same (as already highlighted by Schlüssel et al., 2014). For instance, 73% of the native flora lives in the mesomediterranean belt, compared to 47.9% for endemics. Conversely, only 6.1% of the native flora can be found in the alpine belt, compared to 20.8% for the endemic flora. Table 9 shows that the proportion of the native and endemic flora increases with altitude. The endemics represent almost half (43.1%) of the native flora in the alpine and cryo-oromediterranean belts (36.8% for the treeless belts: Or + Sa + Al), whereas they only make 8.3% of the mesomediterranean flora. However, due to varying number of taxa in the different categories, the montane belt houses the highest number of endemics with 149 taxa, followed by the supramediterranean belt with 141 taxa and the mesomediterranean one with 136 taxa. Conversely, the alpine and the subalpine belts shelter only 59 and 88 taxa, respectively.

Table 9. – In each vegetation belt, number of endemic taxa and their proportion in the whole endemic flora compared to the number of native taxa and their proportion in the whole native flora (*P1*). *P2* refers to the comparison of the proportion of endemic taxa in the endemic flora vs. the native flora; Significant differences are indicated in bold.
[Li: costal; Tm: thermomediterranean; Me: mesomediterranean; Sm: supramediterranean; Mo: montane; Or: cryo-oromediterranean; Sa: subalpine; Al: alpine]

	Li	Tm	Me	Sm	Mo	Or	Sa	Al	Total
Number of endemic taxa	54	70	136	141	149	66	88	59	**284**
Endemic flora [%]	19.0	24.6	47.9	49.6	52.5	23.2	31.0	20.8	
Number of native taxa	508	868	1634	1031	715	153	289	137	**2237**
Native flora [%]	22.7	38.8	73.0	46.1	32.0	6.8	12.9	6.1	
***P1*(z-ratio)**	0.159	**<0.001**	**<0.001**	0.257	**<0.001**	**<0.001**	**<0.001**	**<0.001**	
Endemic/native flora [%]	10.6	8.1	8.3	13.7	20.8	43.1	30.4	43.1	
***P2*(z-ratio)**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.89	**<0.001**	

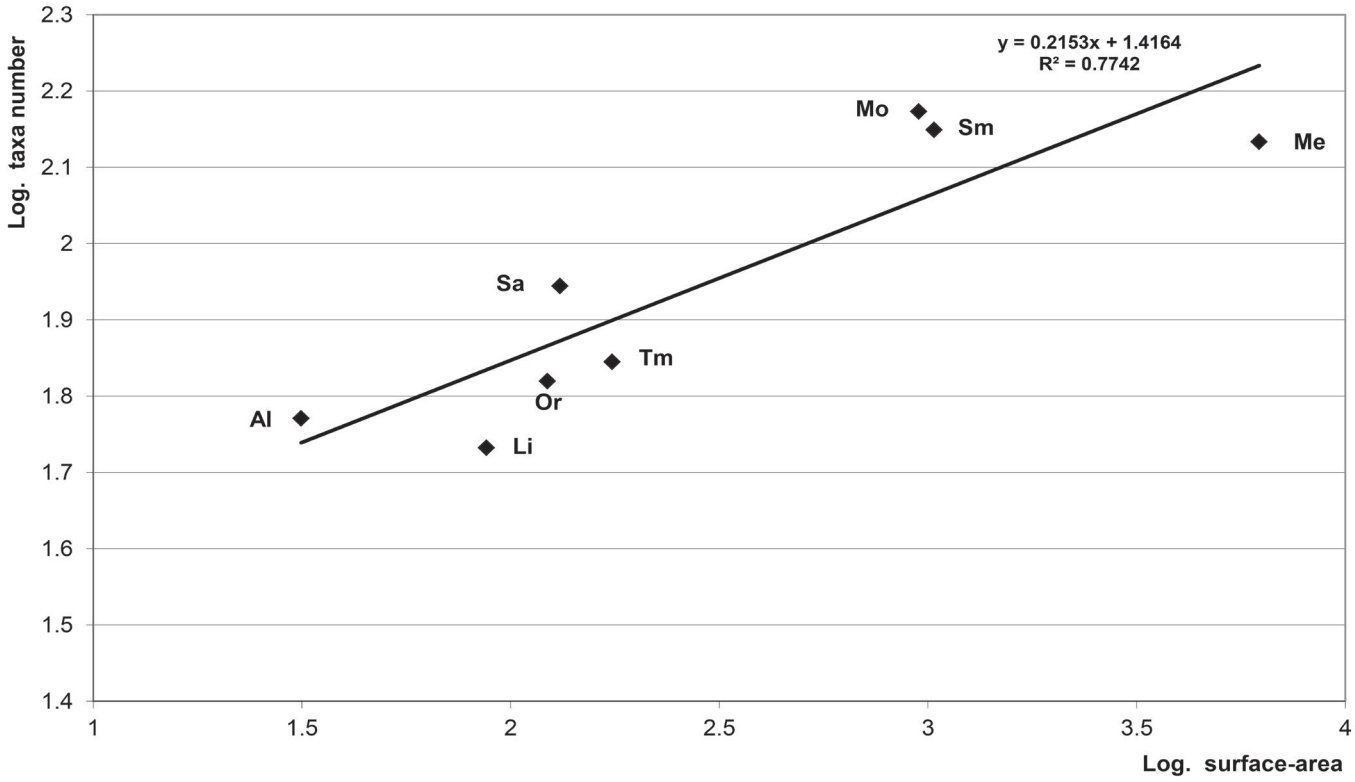

Fig. 5. – Relationship (logarithmic mode) between species richness (endemic taxa) of each vegetation belt and their surface area.
[Li: coastal zone; Tm: thermomediterranean; Me: mesomediterranean; Sm: supramediterranean; Mo: montane; Or: cryo-oromediterranean; Sa: subalpine; Al: alpine]

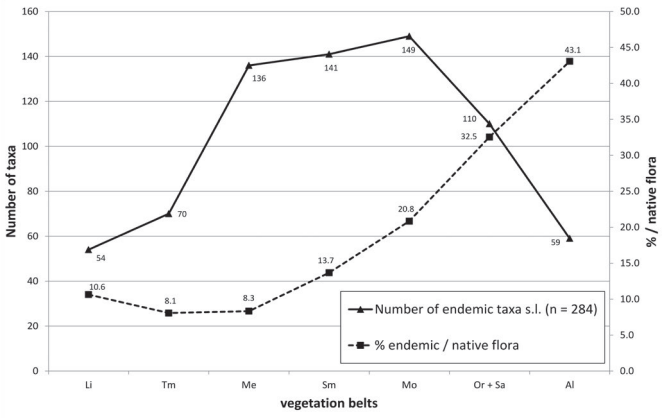

Fig. 6A – Relationship between the number of taxa and the altitude (as expressed by vegetation belts).
[Li: coastal zone; Tm: thermomediterranean; Me: mesomediterranean; Sm: supramediterranean; Mo: montane; Or: cryo-oromediterranean; Sa: subalpine; Al: alpine]

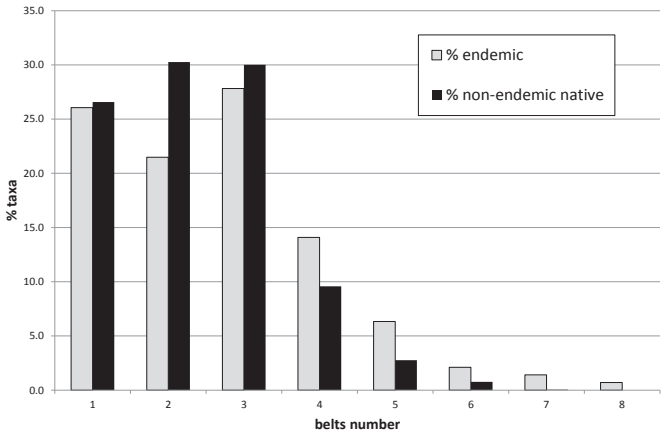

Fig. 6B – Comparison of the number of vegetation belts occupied by the endemic taxa and the non-endemic native taxa.
[% total taxa of each category]

Additional analyses were conducted to better understand the distribution of endemic taxa. The first one was to highlight the alpha- diversity for endemics in the different vegetation belts, and more precisely to confront the number of species with the surface they occupy in each belt (Fig. 5), as did Schlüssel et al. (2014) for native species. In the latter analysis, species richness for the different vegetation belts was found highly significantly different when calculated on the native or the endemic flora for all categories except the littoral and the supramediterranean belts (z-ratio = -1.409, P = 0.159 and z-ratio = 1.133, P = 0.257, respectively; Table 9). More specifically, Schlüssel et al. (2014) showed that species richness was particularly high for low altitudes (littoral and thermomediterranean belts), and particulatly low for high altitudes (cryo-oromediterranean and alpine belts). For endemic taxa, it is the reverse, with a low alpha-diversity in the littoral and the mesomediterranean belts (but also for the thermomediterranean and the cryo-oromediterranean belts) and a high alpha-diversity for the alpine, the subalpine and the mountane belts. As for Schlüssel et al. (2014) the proportions of endemics and native taxa in the different vegetation belts are all different (P < 0.001), except for the subalpine belt for which the two proportions are the same (z-ratio = 0.139, P = 0.89; Table 9).

The second analysis was to correlate the number of endemic taxa with altitude, by grouping the cryo-oromediterranean and the subalpine belts since they correspond to the same altitudinal range, one on southern-oriented slopes and the other one on northern-oriented slopes. Figure 6A shows that the number of non-endemic taxa follows a unimodal asymmetric distribution, with a maximum found in the montane belt, a result that was also retrieved from Table 9. Conversely the proportion of endemics increases with altitude in an exponential way. It should however be noticed that this trend is more due to a drastic decrease of non endemic species more than to an increase of endemics themselves with altitude (only 18 endemic species are exclusively found in the three upper belts, the cryo-oromediterranean, the subalpine and the alpine ones).

Endemic taxa indeed display an adaptation spectrum that is proportionnaly wider than the one of native species, since they occupy a higher number of vegetation belts (Fig. 6B). Only two species, both endemics (*Brimeura fastigiata* (Viv.) Chouard and *Galium corsicum* Spreng.), occupy all eight vegetation belts that exist in Corsica, and five species, among them four endemics (*Bellium bellidioides* L., *Crocus corsicus* Maw, *Sedum brevifolium* DC., and *Stachys corsica* Pers.) are found in seven vegetation belts. This pattern was already evidenced by Gamisans (1981) who pointed out ubiquist endemics and who wrote "it is tempting to envisionne that empty ecological niches once existed in Corsica and that these endemics were able to colonize at nearly all vegetation belts". Our data support such a hypothesis, but suggest that there might be a shift of empty niches to high altitude belts. For southeast France, Médail & Verlaque (1997) showed that 87% of the endemic flora is restricted to one or two vegetation belts and only 1% of this flora occupies four to six belts. In Corsica, these proportions are 47.5% and 24.6%, respectively. A great difference then exists between the continent and the island, which confirms the widening of ecological niches in island environments as already suggested by Médail & Verlaque (1997).

The distribution of endemic taxa according to their origin is illustrated on Figure 7 and shows that it is different among the strictly Corsican endemic species (Co) and the ones that are restricted to Corsica and Sardinia (Co-Sa; χ^2 = 33, P < 0.001). The situation is similar for the Corsican endemics on the one hand, and the Corsican-Tuscanian ones

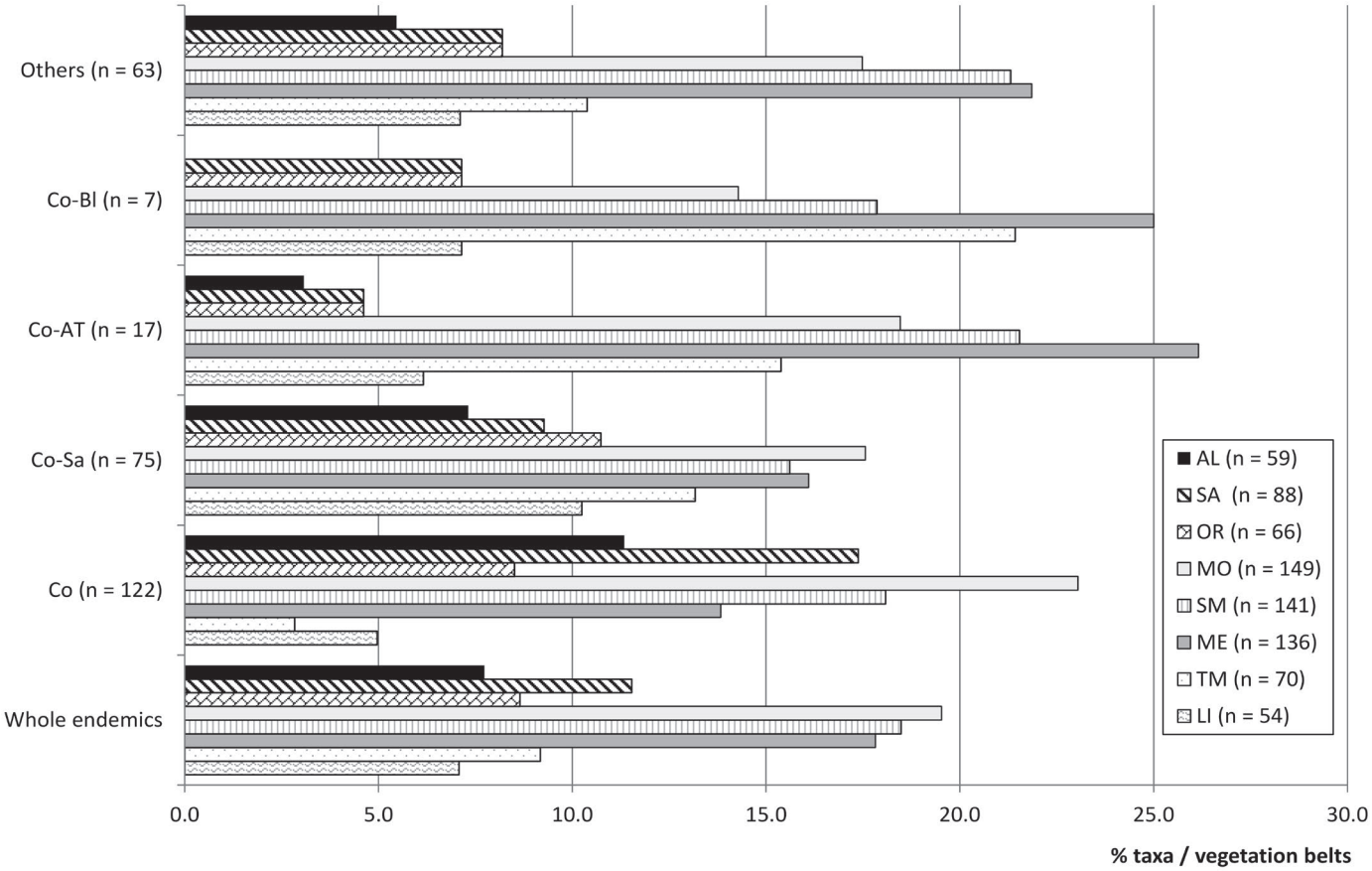

Fig. 7. – Proportion of taxa in each vegetation belt, for each endemic element.
[Al: alpine; Sa: subalpine; Or: cryo-oromediterranean; Mo: montane; Sm: supramediterranean; Me: mesomediterranean; Tm: thermomediterranean; Li: coastal zone]

(Co-AT; $\chi^2 = 26.8$, $P < 0.001$) or the Corsican-Balearic ones on the other (Co-Bl; $\chi^2 = 20.8$, $P = 0.004$). The strictly Corsican endemics are proportionally more often found at upper altitudes, more specifically in the alpine and subalpine belts were they account for half on the taxa growing there. This is congruent with the results obtained for Co-Sa, Co-AT and Co-Bl endemics, since Sardinia as well as the Tuscan Archipelago and the Balearic Island do not possess as elevated belts as Corsica. Indeed, when some sub-endemic taxa are found in the subalpine or the alpine belt in Corsica, this is because they grow there at the upper margin of their respective distribution ranges which, otherwise, are centered at lower altitudes. The thermomediterranean belts exhibit the reverse tendency with a high rate of Co-Sa, Co-AT and Co-Bl subendemic taxa and a low rate of strictly Corsican taxa. By comparison, in the southern Iberian Peninsula, the number of endemic taxa reaches a maximum in the mesomediterranean belt and displays a quite different distribution spectrum than the one recorded for Corsica (Giménez et al., 2004).

Vegetation belts and family spectrum

The family spectrum was calculated within each vegetation belts (Table 10) and it appears to be different among belts. In each belt, the family spectrum for endemics is different from the one recorded for the native taxa (Schlüssel et al., 2014). Moreover, each vegetation belt presents a specific family spectrum that is not the one recorded for all taxa, nor for all endemics (Jeanmonod et al., 2011a)., The thermomediterranean belt is dominated by *Orchidaceae*, the cryo-oromediterranean belt by *Caryophyllaceae* and *Asteraceae*, whereas the littoral one is dominated by *Plumbaginaceae*. The remaining belts are characterized by a high proportion of *Asteraceae*. The temperate-type (montane, subalpine and alpine) belts are characterized by a significant presence of *Ranunculaceae* (between 6% and 9.1%). The comparison of the latter stages with the ones of the Alpine Flora (Aeschimann et al., 2011b) shows again notable differencies. As for Corsica, *Asteraceae* comes first but the following families are found in different orders, although some leading ones are also found in both floras (*Caryophyllaceae* and *Poaceae* in the montane and subalpine belts, *Caryophyllaceae* and *Scrophulariaceae* in the alpine belt; Aeschimann et al., 2011b).

Table 10. – The five first ranks of the most important families for endemic taxa in each vegetation belt with, between brackets, the percentage of endemic taxa from this family on the whole endemic taxa of the vegetation belt. When necessary, all families with the same number of taxa are mentioned together.
[Li: coastal zone; Tm: thermomediterranean; Me: mesomediterranean; Sm: supramediterranean; Mo: montane; Or: cryo-oromediterranean; Sa: subalpine; Al: alpine; All: all belts]

	1	2	3	4	5
Li	*Plumbaginaceae* (27.8)	*Asteraceae* (18.5)	*Caryophyllaceae* (9.3)	*Liliaceae* (7.4) *Rubiaceae* (7.4)	*Iridaceae* (5.6)
Tm	*Orchidaceae* (17.1)	*Liliaceae* (11.4)	*Asteraceae* (10.0)	*Iridaceae* (7.1)	*Lamiaceae* (5.7)
Me	*Asteraceae* (17.6)	*Orchidaceae* (8.1)	*Liliaceae* (5.9) *Lamiaceae* (5.9)	*Caryophyllaceae* (5.1) *Scrophulariaceae* (5.1) *Apiaceae* (5.1)	*Brassicaceae* (4.4)
Sm	*Asteraceae* (25.5)	*Caryophyllaceae* (7.1)	*Poaceae* (6.4)	*Scrophulariaceae* (5.7)	*Lamiaceae* (5.0)
Mo	*Asteraceae* (23.5)	*Caryophyllaceae* (8.1)	*Scrophulariaceae* (7.4)	*Poaceae* (6.0) *Ranunculaceae* (6.0)	*Apiaceae* (5.7)
Or	*Asteraceae* (13.6) *Caryophyllaceae* (13.6)	*Poaceae* (10.6)	*Scrophulariaceae* (7.6) *Apiaceae* (7.6) *Lamiaceae* (7.6)	*Ranunculaceae* (4.6) *Liliaceae* (4.6)	*Brassicaceae* (3.0) *Fabaceae* (3.0) *Crassulaceae* (3.0) *Plumbaginaceae* (3.0) *Santalaceae* (3.0)
Sa	*Asteraceae* (27.3)	*Ranunculaceae* (9.1)	*Caryophyllaceae* (6.8)	*Poaceae* (5.7) *Scrophulariaceae* (5.7)	*Apiaceae* (4.5)
Al	*Asteraceae* (25.4)	*Caryophyllaceae* (11.9)	*Ranunculaceae* (6.8) *Apiaceae* (6.8)	*Poaceae* (5.1) *Lamiaceae* (5.1)	*Scrophulariaceae* (3.4) *Liliaceae* (3.4) *Brassicaceae* (3.4) *Plumbaginaceae* (3.4) *Juncaceae* (3.4) *Rubiaceae* (3.4)
All	*Asteraceae* (23.6)	*Caryophyllaceae* (6.7)	*Plumbaginaceae* (6.0)	*Orchidaceae* (5.6)	*Scrophulariaceae* (4.9)

Table 11. – Number of endemic taxa in each habitat; proportion on the whole endemic flora compared to the proportion of the native flora in the same habitat. Significant differences are indicated in bold.
[D? = probably extinct; RR = very rare; R = rare; PF = infrequent or disseminated; LOC = localised; C = common; CC = very common]

	sandy	rocky	aquatic	semi-aquatic	wet herbs	meadows	mega-phorbs	bushy/ shrubby	forests	riparian	ruderals	cropping
Number of endemic taxa	33	129	1	35	34	126	6	110	58	19	17	0
Endemic flora [%]	11.6	45.4	0.4	12.3	12.0	44.4	2.1	38.7	20.4	6.7	6.0	0
Number of native taxa	242	548	60	330	295	932	30	694	457	195	558	204
Native flora [%][1]	10.8	24.5	2.7	14.8	13.2	41.7	1.3	31.0	20.4	8.7	24.9	9.1
***P* (z-ratio)**	0.683	**<0.001**	**<0.05**[2]	0.274	0.567	0.384	0.302	**0.009**	0.998	0.249	**<0.001**	**<0.05**[2]

[1] According to Schlüssel et al. (2014) on a total of 2237 taxa.
[2] Because the number of endemics was too low (<5) we only calculated the 95% confidence interval for the two proportions of aquatic taxa: 0.06% <0.4% < 1.96% and 2.09% ≤ 2,7% ≤ 3.43%, and for the proportion of cropping taxa: 8% ≤ 9.1% ≤ 10.38%.

Habitats

The distribution of endemic taxa in the different Corsican habitats is different from the one of the native flora (Table 11). Significantly higher percentages were found for the endemic flora vs. the native one in rocky habitats (45.4% vs. 24.5%, z-ratio = 7.495, $P < 0.001$) and in bushy/shrubby environments (38.7% vs. 31%, z-ratio = 2.626, $P = 0.009$), but significantly lower percentages were recorded in aquatic habitats (0.4% [0.06-1.96] vs. 2,7% [2.09-3.43], respectively, $P < 0.05$), in cultivated fields (0% [0-1.33] vs. 9.1% [8.00-10.38], $P < 0.05$) and in ruderal places (6% vs. 24.9%, z-ratio = -7.172, $P < 0.001$). Habitats that show the highest richness in endemics are rocky environments, meadows and bushy/shrubby habitats (45.4%, 44.4%, and 38.7%, respectively), whereas the highest richness for the indigeneous taxa is found in meadows, bushy/shrubby habitats and ruderal places

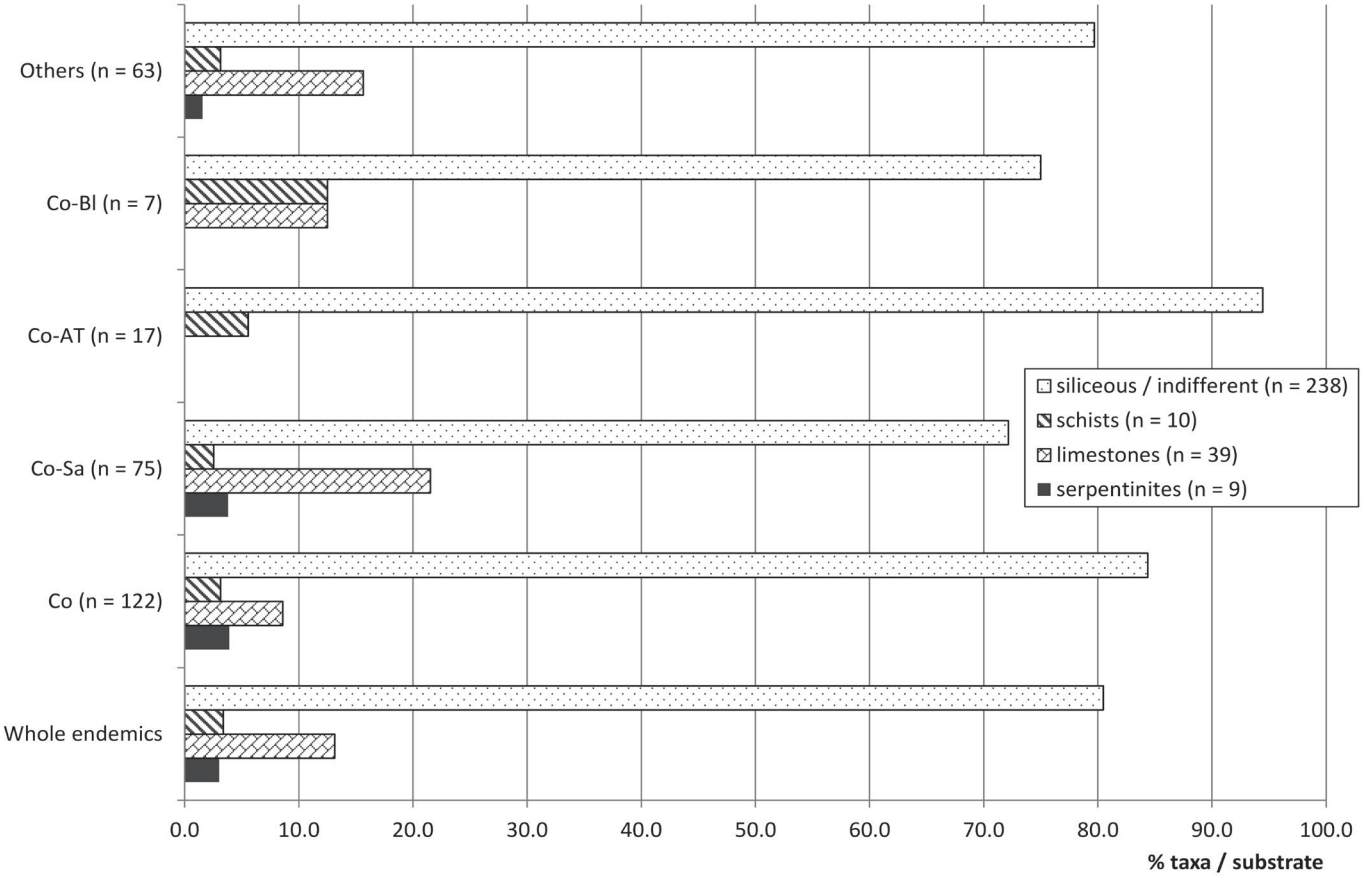

Fig. 8. – Proportion of taxa in each substrate type, for each endemic element. [n = number of taxa in each category]

(41.7%, 31%, and 24.9%, respectively). Although the rocky habitats host a large proportion of endemics in Corsica, it is still far from what is recorded by Casazza et al. (2005) for the Italian Maritime Alps, with 67.6% of the endemic taxa found in rocky habitats, 27.1% in meadows and only 2.8% in bushy/shrubby habitats. In Sardinia Bacchetta et al. (2012a) showed that 23.1% of the endemic taxa are found in rocky environments and caves, 19.2% in coastal and halophytic habitats, 16.2% in sclerophyllous scrubs (matorral) and temperate heath and scrubs, and 15.7% in natural and semi-natural grassland formations.

Substrates

Endemic taxa are found in all substrates in similar proportions than for the native flora ($P > 0.05$ for all categories, Table 12). A closer analysis, taking into account the different origins of endemic taxa (Fig. 8), shows that all endemics growing on serpentinites, except one, are strictly Corsican or Cyrno-Sardinian. On calcareous substrates, the Cyrno-Sardinian sub-endemics dominates (21.5% vs. 8.6% for strictly Corsican endemics, z-ratio = -2.641, $P = 0.008$), which is awaitened since Sardinia is much more calcareous than Corsica. The existence of nine strictly Corsican endemics limited to calcareous substrates is, therefore, surprising. They are mostly found in *Limonium* (2), *Hieracium* (2) and *Orchidaceae* (2). In their analysis of the alpine

Table 12. – Number of endemic taxa in each substrate type, proportion on the whole endemic taxa compared with the proportion of native flora in the same substrate.

	serpentinites	limestones	schists	siliceous or indifferent	Total
Number of endemic taxa	9	39	10	239	**284**
Endemic flora (n = 284) [%]	3.2	13.7	3.5	84.2	
Number of native taxa	44	307	56	1906	**2237**
Native flora (n = 2237) [%][1]	2.0	13.7	2.5	85.2	
***P* (z-ratio)**	0.184	0.997	0.312	0.641	

[1] According to Schlüssel et al. (2014).

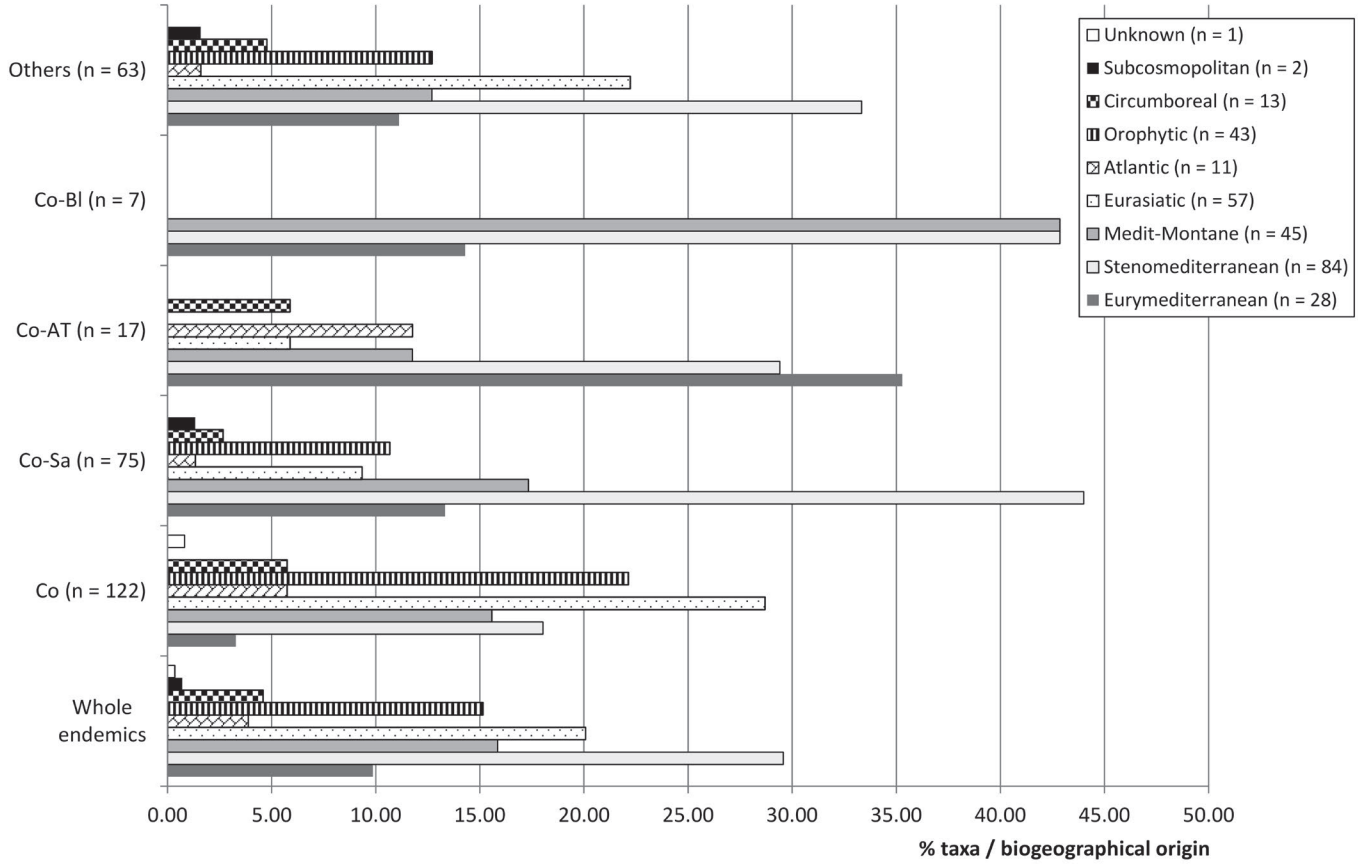

Fig. 9. – Proportion of taxa of the various biogeographical origins for each endemic element. [n = number of taxa in each category]

Flora, Aeschimann et al. (2012b) show that 83.2% of the alpine endemics are found on calcareous substrates (with 33.3% being calcareous exclusive). For southeast France, 60% of the endemic taxa are calcicolous whereas only 18% are siliceaous, the remaining 22% being indifferent (Médail & Verlaque, 1997). These comparisons confirm the scarcity of the calcicolous flora in Corsica, due to the low and discontinuous surface occupied by this type of substrate, and highlight the role that calcareous habitats have played in speciation events. This confirms the results of Fenu et al. (2014) in Sardinia who showed that regions in which limestone and dolomitic substrates are found have played a key role in the evolution of endemic species.

Flowering

Comparing flowering spectrums of endemic taxa s.l. and indigeneous ones shows a delay of about 15 days for the former, with a peak that remains however in June (data not shown). This is due to endemics being proportionnally less numerous than indigeneous taxa in the lower vegetation belts, as already shown before. Therefore, it is not surprising that the strictly Corsican endemics display an even more delayed flowering with a peak in July, since they concentrate in the upper vegetation belts. The graph of the number of flowering months for endemics (data not shown) resembles the one for native species, with a first maximum at three months followed by a second one at two months and a third one at four months. No significant difference was found when analysing the flowering periods according to the type of endemism.

Biogeographical origin

The origin of endemic species is quite different from the one of the total flora, with a dominance of the Mediterranean elements (Table 13; see chapter 1, "Biogeographical types"). The Mediterranean group (55.3%) is indeed more numerous than the Holarctic one (43.7%) by 11.6% (z-ratio = 2.769, $P = 0.006$), whereas this difference only reaches 1% for the native flora (39.2% vs. 38.2%, respectively, z-ratio = 0.737, $P = 0.461$, Table 1).

Within the endemic taxa (Fig. 9), this spectrum varies significantly between the strict Corsican endemics (36.9% of

Mediterranean elements vs. 62.3% of Holarctic ones, z-ratio = -3.969, $P < 0.001$), the Cyrno-Sardinian endemics (74.7% vs. 24%, respectively, z-ratio = 6.206, $P < 0.001$), the Cyrno-Tuscanian endemics (76.5% [52.7-90.4] vs. 23.5% [9.6-47.3], respectively, $P < 0.05$) and the Cyrno Balearic endemics (100% [64.6-1.0] vs. 0% [0.0-35.4], respectively, $P < 0.05$). This is due to the strict Corsican endemics growing essentially at high altitudes (subalpine and alpine belts) as already highlighted before.

Conclusions

The former analyses highlight several original charateristics of the Corsican flora. We were able to show the following features about the geographic origin of the native Corsican flora:

- in contradiction with other Mediterranean islands, Corsica hosts native species for which the Mediterranean origin (39.2%) is only slightly higher than the Holarctic origin (38.2%). This is explained by the mountaneous lanscape of the island and by its septentrional geographical position;
- although the Mediterranean elements dominate in the thermo- and mesomediterranean belts, as the Holarctic elements do in the montane, subalpine and alpine belts, it is surprising to notice that the supramediterranean and the cryo-oromediterranean belts are dominated by Holarctic elements. This must however be downweighted by the fact that in these stages, the Mediterranean elements comprise more frequent species than the Holarctic ones;
- within the Mediterranean Corsican element, the taxonomic spectrum is not different from that recorded in other typically Mediterranean islands with a dominance of *Fabaceae, Asteraceae, Poaceae, Apiaceae* and *Caryophyllaceae*. Similarly, within the Holarctic Corsican element, a dominance of *Asteraceae, Poaceae, Cyperaceae, Fabaceae* and *Rosaceae* was found, as in other temperate regions.

Regarding the endemic Corsican flora, we have shown the following:

- Corsica displays the highest endemism (12.7% of the indigeneous flora) of all Mediterranean islands and other adjacent continental areas analysed here, excepting Greece and Italy. This is likely due to its mountaneous lanscape and long-standing isolation;
- the endemic flora shows patterns that depart partly from that of the native one. This is the case for the taxonomic representativeness, the distribution of biological types and the altitudinal distribution. Conversely, patterns related to ecology (substrates and habitats) and to abundance frequencies are very similar;
- the five families that comprise the highest number of endemic taxa s.l. are, in decreasing order, *Asteraceae, Caryophyllaceae, Plumbaginaceae, Orchidaceae* and *Scrophulariaceae,* whereas the five families, among those comprising more than 10 taxa, that display the highest rate of endemics are *Plumbaginaceae, Iridaceae, Scrophulariaceae, Orchidaceae* and *Ranunculaceae*. These patterns do not correspond to the one recorded for the native Corsican flora nor for any other Mediterranean or temperate regions, as far as we know;
- the biological types of the endemic taxa do not show the same distribution pattern than the one recorded for the Corsican native taxa. The rates of hemicryptophytes and chamaephytes are higher than the ones found for the native flora whereas the rate of therophytes is lower. These rates are quite similar to those recorded in Sardinia, but rather different from those of other Mediterranean islands. This difference comes, once again, from the montaneous lanscape of Corsica since the biological type rates are directly influenced by altitude, which also influences the rate of endemism;
- the abundance pattern of endemics s.l. is not that different from the one of native species, which indicates that in Corsica, endemics are not, on average, rarer than all

Table 13. – Number of taxa and proportion of the biogeographical elements of the endemic Corsican flora, with percentages calculated on the whole endemic flora.

	Mediterranean			Holarctic-eurosiberian				Others	
	Stenomediter.	Eurymediter.	Medit-Montane	Eurasiatic	Atlantic	Orophytic	Circumboreal	Cosmopolitan	Uunknown
Number of endemic taxa	28	84	45	57	11	43	13	2	1
Endemic flora [%]	9.9	29.6	15.8	20.1	3.9	15.1	4.6	0.7	0.4
Group [%]		55.3			43.7			1.1	

other taxa. A meaningful distinction in terms of patrimonial heritage and conservation should however be made between the strictly Corsican endemics that are on average rare to very rare and the subendemics that are usually more widely distributed;

- the endemic flora s.l. is not uniformly distributed among the different vegetation belts. The number of endemics increases with altitudes, reaches a maximum in the montane belt, and decreases in the subalpine and the alpine belts. However, the percentage of endemics increases regularly until the alpine belt where it reaches 43.1% of the native taxa. Our analyses also highlighted the fact that endemics s.l. occupy a larger altitudinal spectrum than the native taxa. Finally, it is worth noticing that the strict Corsican endemics largely dominate the subendemic taxa in the higher temperate belts (subalpine and alpine);
- the endemic flora of the different vegetation belts is clearly caracterized by its taxonomic spectrum, with a dominance of *Plumbaginaceae* on the coasts, *Orchidaceae* in the thermomediterranean belt, *Caryophyllaceae* and *Asteraceae* in the cryo-oromediterranean belt, and *Asteraceae* in all other belts;
- noticably, serpentinites, which surface is very small on Corsica, display a higher (although non significant) proportion of the endemic flora than of the indigeneous one. This might be explained by the stress-tolerance strategy of endemics already described by Médail & Verlaque (1997);
- the endemic taxa that grow on serpentinites are essentially Corsican or Corsico-sardinian endemics;
- the distribution of endemic species s.l. in the various Corsican habitats is slightly different from the one recorded for the native taxa. Endemics are however preferentially found in rocky habitats rather than in meadows; they are absent or nearly so in cultivated fields and aquatic habitats and only seldomly found in ruderal places. The distribution of endemics according to substrates is the same that for the native taxa. In opposition with other surrounding regions, the calcareous substrats do not host a higher rate of endemic taxa vs. native taxa;
- the biogeographical origin of endemic taxa s.l. is not the same as for the native flora. In opposition with the latter, the Mediterranean origin is predominant (55.3%). However, this trend is more marked in subendemics (69.3%) than in the strict Corsican endemics (36.4%) for which a Holarctic origin is dominating (62.8%);
- within the endemic taxa s.l., there is a marked difference between the strict Corsican endemics and the subendemics. The strict Corsican endemics are on average rarer, more often found at high altitudes, they are essentially hemicryptophytes and chamaephytes (82.7%), they have a mostly Holarctic origin, and encompass proportionnally more species than the subendemics that mostly grow in megaphorbs and meadows.

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