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Forest edge herbaceous vegetation (Trifolio–Geranietea) of northern Spain

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A survey of the vegetation of forest (and hedge) fringes, classified within the Trifolio–Geranietea, in the Basque Country and the western and central Pyrenees (northern Spain) is presented. Three plant associations can be distinguished: the Centaureo nemoralis–Origanetum vulgaris, the Agrimonio–Trifolietum medii (both on lime-rich substrates) and the Hyperico androsaemi–Teucrietum scorodoniae (typical of siliceous soils). The Centaureo nemoralis–Origanetum vulgaris has already been known from the Atlantic zone of France. The Agrimonio-Trifolietum medii was described for Central Europe and it was also found to be widespread in the Pyrenees. The Hyperico androsaemi–Teucrietum scorodoniae is a new syntaxon (described in this paper) and occurs in coastal regions of the Atlantic Basque Country (Santanderino–Vizcaino Subsector).

Introduction

Forest fringe (saum) communities

Between natural forests and neighbouring grasslands, meadows or other types of vegetation, there is a narrow fringe — a transitional habitat (in terms of light conditions and nutrient status), in which forbs often dominate and form special communities. This medium-sized, tall, dense vegetation, called 'saum' in German (the term was adopted by recent English vegetation–ecological terminology), forms linear structures along these semi-shaded woodland and hedge edges. Phenological optimum of this vegetation is between late spring and mid summer.

The primary habitats (i.e. the sites in which a community occurs in natural conditions not linked to any disturbance) of the saum vegetation are the edges of forests, along which they usually form fringes (Dierschke 1974a). They usually became established also along edges of shrubby formations accompanying forest edges (here they are often addressed as forest mantels) or they are found along hedges fringing roads and meadow plots. The shrubby vegetation is mainly classified within communities of the Prunetalia order. The saum communities are very often in contact with meso-xerophilous grasslands of the Brometalia erecti, with hay meadows of the Arrhenatheretalia or with nitrophilous herb-rich communities of the Artemisietea vulgaris and the Galio–Urticetea. In modern landscapes, secondary habitats are usually more frequent than primary ones, especially in regions where woodlands or thickets have disappeared due to intensive farming activity. Disturbed edges of scattered shrubbery in these cultural landscapes are a typical habitat where nitrophilous herb-rich vegetation meets the saum vegetation. This phenomenon is encountered especially in landscapes where grazing and mowing activities cease in neighbouring grassland, as happens when rural abandonment occurs — a typical agricultural practice in contemporary Europe. The invasion of species typical of saum habitats into habitats formerly occupied by another herbaceous vegetation types has been called 'verasumung' (see Mucina and Kolbek 1993). In any case, the ecotonal character of this vegetation becomes evident even in the primary habitats, when it occurs at the edge of forests as these support shade-tolerant species typical of the forest together with light-demanding ones originated from outside of the forest.

In areas where natural forests disappeared and have been replaced by shrublands, low-growing scrub vegetation or by artificial tree plantations, saum communities occupy small patches in close contact with other plant communities (small woodland lots, shrubby mantels, heathlands, grasslands, meadows, nitrophilous ruderal vegetation, etc.). This results in a highly diverse complex of plant communities (mosaic), making the differentation of stands of the saum communities difficult.

The saum vegetation has been traditionally classified within the Trifolio–Geranietea sanguinei by most European phytosociologists (Müller 1962, 1978, Dierschke 1974a, 1974b, Mucina and Kolbek 1993, Pignatti *et al.* 1995, Mucina 1997, Rivas-Martínez *et al.* 2002a). In comparison with the nitrophilous forest-fringe communities of the Galio–Urticetea and the Cardamino hirsutae–Geranietea purpurei (limited to Submediterranean and Mediterranean regions), the Trifolio-Geranietea saum does not show high requirements for nutrients or soil humidity.

Sampling considerations

The sampling procedure to study these communities has to be adapted to the particular modern-time conditions they are experiencing. In a stable agrarian society, such as Europe several decades ago, these communities were clearly distinguishable in the country as they occupied the habitats described above. Nowadays, the abandonment of land is quickly taking place and many meadows and grasslands are being transformed into thickets, heathlands or tree plantations. This profound and extensive land-use change alters the previous organisation and distribution of plant communities, particularly those which occupy narrow ecological niches. Initially, following the release of the grazing pressure, an invasion of the saum plants into the grasslands takes place. In later stages of vegetation development the Trifolio-Geranietea plants become extinct and shrubby or woody vegetation takes over. As a result, after three decades of this process in northern Spain, a mass extinction of this vegetation type took place in many parts of the region. In addition, modern road building destroys fringes of these communities on the border of woodlands or hedges. In heavily populated areas it is therefore difficult to find places where this vegetation would be well represented. More often, fragmented places where the Trifolio–Geranietea species would be found in mix with plenty of ruderal nitrophilous elements are found. Therefore, in the sampling carried out in the surveyed area, secondary habitats with a certain degree of mixture with other vegetation types are more represented than the primary ones, hence our relevés score high numbers of companion plants. In almost all the cases, the sampling plots are linear in shape, ordinarily 30–50m long and 1m broad.

Distribution

This vegetation class of the Trifolio–Geranietea has a wide distribution in Europe — it is mostly found in temperate Central and Western Europe, in the zone occupied by deciduous broad-leaved forests. To the north it reaches southern Scandinavia and to the south it is limited by the dry areas of the Mediterranean region. The Trifolio–Geranietea communities are known to be thermophilous, hence their stands would prefer the south-facing slopes and edges of forests. This feature was formerly established out in central Europe, but it has ever been an issue of much discussion. It now seems clear that these communities are not indicative of warm climates in the southern part of the continent (Dierschke 1977). As far as we know, they are certainly missing in the coldest areas such as high mountains (oro- and cryorotemperate thermotypes) or in the Boreal Zone, as well as in the extreme south of the continent — in the dry and semi-arid thermomediterranean and mesomediterranean regions.

The Iberian Peninsula is one of the three southern peninsulas of Europe, with a humid temperate north and a dry to semi-arid Mediterranean centre and south, characterised by severe summer drought. Hence the plant communities of the Trifolio–Geranietea, known to be better adapted to temperate moist climates, have mainly northern distribution in the Iberian Peninsula and are usually associated with deciduous or semi-deciduous forests and to a lesser extent with the Mediterranean evergreen formations, especially in regions having high local rainfall.

Syntaxonomical framework

Two orders have been recently accepted for the Trifolio–Geranietea in Europe: the order of the Origanetalia vulgaris for the meso-eutrophic soils and the order of Melampyro–Holcetalia for the base poor substrata (Mucina and Kolbek 1993, Mucina 1997, Rivas-Martínez *et al.* 2001). However, at least in the Iberian Peninsula, there are no true character taxa for Melampyro–Holcetalia and in the latest synthesis for this area by Rivas-Martínez *et al.* (2002a) the Melampyro–Holcetalia is no longer recognised as an independent unit and it is included within the Origanetalia (which appears to be the only order of the class in the Iberian Peninsula). In any case, no character taxa for the Melampyro–Holcetalia were found in communities studied in this paper.

This vegetation has been extensively, although not evenly studied in the Iberian Peninsula; most of the data come from the north-east or the western part of the region. So far 30 associations have been described from the Iberian Peninsula (Rivas-Martínez *et al.* 2001) — an indication of the high diversity of this vegetation in the area. In the western part of the Iberian Peninsula, dominated by siliceous substrates, a large set of endemic species characterise these communities. This enables the differentiation of two phytosociological alliances which are particular to these regions, i.e. the Origanion virentis and the Linarion triornithophorae (including in total 16 associations). The characteristic taxa of these alliances are listed in Rivas-Martínez *et al.* (2002a).

Aims

The aim of this study is to describe the variability of the saum vegetation in northern Spain, and to relate the saum-vegetation patterns to the climatic and biogeographic diversity of the surveyed area.

Materials and Methods

Studied area

In this work the central regions of the northern Iberian Peninsula, from the Basque Country to the central Pyrenees (Figure 1) have been sampled. This mountainous area has not been well-studied, however the fringe vegetation is a common phenomenon here as the landscape presents plenty of forested areas with many bushes and hedges. The relevés have been collected on both siliceous and calcareous substrata under humid to hyperhumid conditions in the temperate climatic zone, with little or no Mediterranean influence.

The climate of northern Spain is rainy, with precipitation ranging between 1 000mm and 2 000mm. Temperature varies with altitude. The lower coastal areas are warm and frost-free (13–14°C) and the mean temperatures of the coldest month (m) is around 6°C. The montane areas have cold

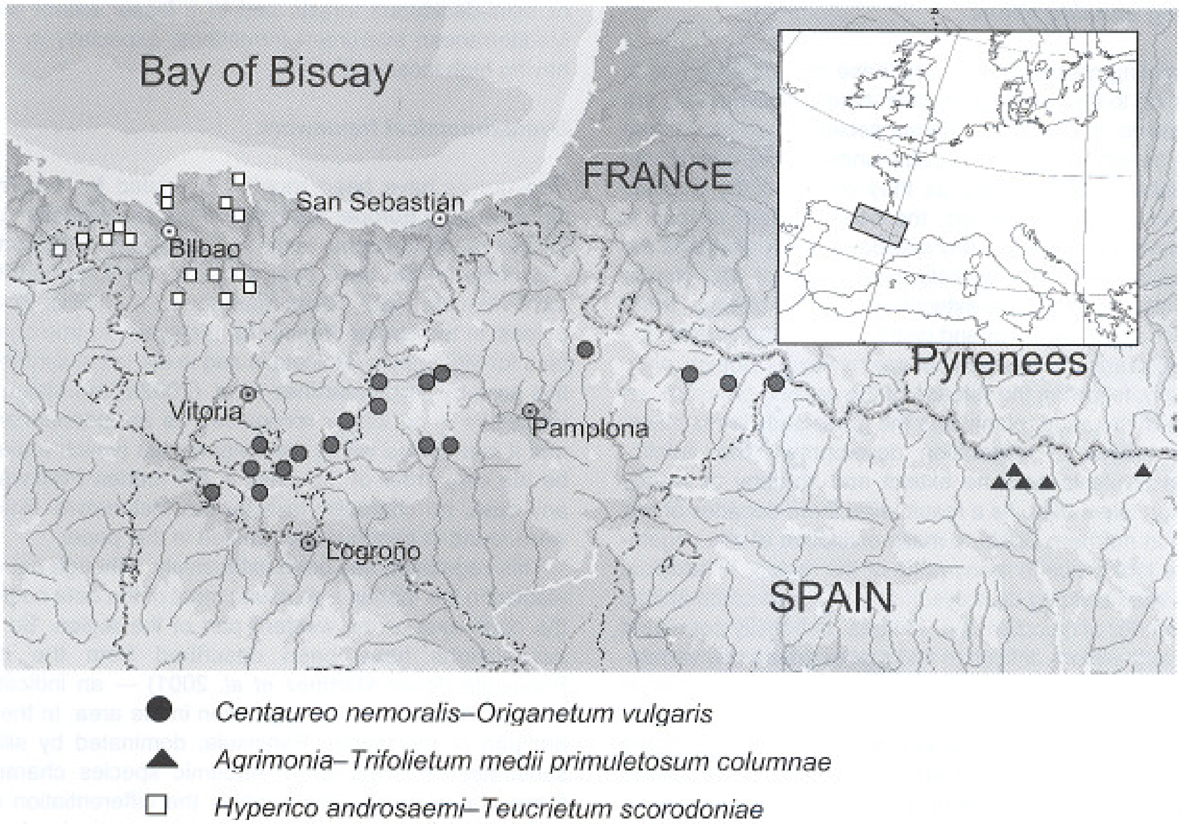

Figure 1: Map showing the location of relevés of Tables 1, 2 and 3

winters (7–9°C and m: +1°C to –2°C). The studied area is strongly influenced by the neighbouring Atlantic Ocean — marked attenuation of the seasonal temperature variations being one of the major climatic characteristics. The oceanic character vanishes in an eastward direction towards the Pyrenees. According to the bioclimatic classification by Rivas-Martínez and Loidi (1999) for the Iberian Peninsula, the studied area belongs to the temperate macroclimate; the ombrotypes range between subhumid to hyperhumid and the thermotypes range between thermotemperate to supra-temperate. A more complete climatic description of the area is given by Loidi *et al.* (1997).

The biogeographical division of the territory is given in Berastegi *et al.* (1997) and Rivas-Martínez *et al.* (2002b). The surveyed communities occur in the temperate area belonging to the Eurosiberian Region — to the Atlantic European Province (Cantabrian-Basque Sector) and the Cévennean–Pyrenean Province (Central Pyrenean Sector). The Cantabrian–Basque Sector has a strong Atlantic (maritime/oceanic) character. The Central Pyrenean Sector is influenced by the Alpine and central European flora and vegetation, and its climate is of a more continental character. The low-rank subdivisions reflect the variability of the climate and substrates of the region. The warmest and more oceanic regions of the Cantabrian–Basque Sector belong to the Santanderino–Vizcaino and Eastern Euskaldun Subsectors, while colder and slightly more continental conditions predominate in the Navarro–Alavés Subsector. In the study area, the Central Pyrenean Sector is divided into the Western Pyrenean and the High Pyrenean Subsectors; the former receives strong maritime influence from the Atlantic Ocean, whereas the latter is more continental in nature.

Methods

The analysis carried out has been performed in order to establish a solid classification of the surveyed communities in the syntaxonomic system, through comparison with the published data from neighbouring territories. A set of 51 relevés have been collected using the Braun-Blanquet approach (Braun-Blanquet 1964, Westhoff and Van der Maarel 1973). These relevés have been captured into a database managed by TURBOVEG software (Hennekens 2000). Exports of data from the database were made to construct phytosociological tables and to submit the data to further data-analytic procedures. Van der Maarel's (1979) transformation was applied to the species cover-abundance values prior to numerical analyses. A Detrended Correspondence Analysis (DCA) was carried out in order to glimpse the structure of the data set and the grouping tendencies of the relevés in their projection onto the ordination space (Ter Braak and Smilauer 1998). Graphic outputs have been completed using the program CANODRAW 3.1 (Smilauer 1992).

The phytosociological tables (Tables 1–3) constructed from relevés were subject to comparison with bibliographical infor-

Table 1: *Centaureo nemoralis–Origanetum vulgaris*

Relevé number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Characteristic species of associaton and higher units:																										
Origanum vulgare subsp. *vulgare*	.	2	2	.	2	2	2	+	.	.	2	3	1	2	3	3	2	.	1	2	2	2	3	3	1	2
Agrimonia eupatoria subsp. *eupatoria*	.	.	.	.	.	1	.	+	.	.	.	.	+	.	.	+	+	.	.	1	.	1	1	+	.	+
Lathyrus latifolius	.	.	.	.	.	1	2	2	.	.	.	3	2	3	.	.	.	.	.	+	.	.	.	1	3	.
Centaurea jacea	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	2	1	.	3	3	+	.	2	1	.	.
Satureja vulgaris	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	3	3	.	2	+	2	1	1	1	.	.
Centaurea scabiosa	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	1	.	.	.	+	.	+	+	+	.	.
Fragaria vesca	2	.	+	.	.	.	.	.	3	.	2	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.
Centaurea debeauxii subsp. *nemoralis*	.	.	2	3	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	3	.	+	.	.
Trifolium medium subsp. *medium*	2	1	1	2	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cruciata glabra	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	+
Campanula patula	1	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	+	.
Teucrium scorodonia	.	.	.	1	2	2	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.	.
Campanula rapunculus	.	.	.	.	1	+	+	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.
Trifolium ochroleucon	2	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Satureja calamintha agg.	.	.	.	.	+	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Silene nutans subsp. *nutans*	.	.	.	.	.	+	+	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vicia cracca subsp. *cracca*	+	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Astragalus glycyphyllos	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
Vicia sepium	.	.	.	.	.	.	.	.	1	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Inula conyza	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.
Aquilegia vulgaris subsp. *vulgaris*	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Geranium sanguineum	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lathyrus sylvestris	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
Vicia orobus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Campanula persicifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
Other species:																										
Brachypodium pinnatum subsp. *rupestre*	3	2	2	2	.	3	3	3	.	4	1	1	2	2	1	2	1	2	2	3	1	1	1	3	2	1
Picris hieracioides	.	.	.	1	1	1	.	1	.	.	.	+	+	1	1	1	+	+	.	1	2	1	1	1	.	.
Sanguisorba minor	+	1	+	.	.	.	1	1	.	.	.	1	1	.	.	1	2	.	+	.	.	1	1	+	1	.
Hypericum perforatum	.	.	2	1	1	1	+	1	.	.	.	+	1	+	.	+	.	.	1	.	1	.	1	1	.	.
Daucus carota subsp. *carota*	.	.	+	.	+	.	+	1	.	+	.	.	+	+	.	2	.	.	+	1	+	1	1	1	.	.
Lotus corniculatus subsp. *corniculatus*	1	2	1	1	.	.	+	.	.	1	1	2	.	.	1	.	+	.	+	.	.	+	1	.	.	.
Dactylis glomerata subsp. *glomerata*	.	.	.	.	.	.	.	1	.	.	1	1	1	1	.	1	1	1	1	1	.	.	.	+	1	1
Carex flacca	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	+	+	+	+	1	.	+	+	.	1	.
Scabiosa columbaria	.	.	.	.	+	.	+	.	.	.	.	.	+	.	.	.	1	+	.	+	.	1	1	2	.	.
Galium verum subsp. *verum*	1	.	1	.	.	.	.	1	.	1	.	.	1	.	.	.	+	.	.	.	.	.	+	+	.	.
Briza media subsp. *media*	.	+	.	.	.	.	.	.	.	+	.	.	1	.	.	.	+	.	+	1	.	.	1	.	1	.
Vicia villosa	.	.	1	.	.	1	1	+	1	+	.	1	.	.	.	.	.	.	.	.	.	.	2	.	.	.
Ononis spinosa	.	.	.	.	.	1	+	+	.	.	.	1	.	.	.	.	2	.	.	.	.	1	1	1	.	.
Galium mollugo	.	.	.	.	.	+	.	.	.	.	.	.	.	2	1	1	.	3	+	+	.	2	.	.	.	.
Blackstonia perfoliata	.	.	.	.	.	.	.	.	.	+	.	.	+	.	+	.	+	.	.	+	.	+	+	+	.	.
Hypochoeris radicata	.	1	+	+	+	.	+	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	+	.	.
Holcus lanatus	.	.	.	+	2	.	.	.	.	.	.	1	.	.	.	.	+	.	.	.	.	1	1	.	.	2
Anthoxanthum odoratum	1	1	.	.	.	.	.	.	.	.	.	.	.	2	2	.	.	1	.	.	.	.	.	.	+	.
Medicago lupulina	1	.	.	.	.	1	.	.	.	.	.	1	.	.	.	1	1	.	.	.	1	.	.	.	.	.
Bromus erectus subsp. *erectus*	.	1	.	.	.	.	.	2	.	.	.	.	2	1	+	.	.	.	.	.	.	.	.	.	+	.
Silene vulgaris	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	1	.	+	+	+	.	.	.	.
Potentilla montana	+	+	1	+	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Galium pumilum subsp. *pinetorum*	+	.	1	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.

Table 1 cont.

Centaurium erythraea	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	1	.	.
Cruciata laevipes	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	1	.	.	.	.	.	.	.	+	.	2
Anthyllis vulneraria	.	.	.	.	.	.	+	.	.	1	.	.	.	.	+	.	.	1	.	.	.	.	.	+	.	.
Genista hispanica subsp. *occidentalis*	.	.	.	.	.	.	.	.	.	+	.	1	.	.	.	.	.	.	.	+	.	1	.	+	.	.
Trifolium pratense	.	.	.	.	.	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	1	.	.	.	1	1
Hypericum pulchrum	+	+	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Prunella grandiflora	2	2	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Helianthemum nummularium	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	.
Agrostis capillaris	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	2
Crepis capillaris	.	.	+	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	1	.	.	.	.	.
Vicia sativa agg.	.	.	.	.	1	.	.	.	.	.	.	1	+	+	.	.	.	.	.	.	.	.	.	.	.	.
Linum viscosum	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	+	.	1	.	.
Leucanthemum pallens	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	1	.	.	.	.	.	.
Plantago lanceolata	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	.	.	.	+	.	.	.	.	.
Brachypodium sylvaticum subsp. *sylvaticum*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	+	+	.	.	.	.
Polygala vulgaris	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Danthonia decumbens	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stachys officinalis subsp. *officinalis*	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.
Lathyrus pratensis	.	1	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Erica vagans	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Linum catharticum	.	1	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.
Campanula trachelium	.	.	.	.	+	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
Achillea millefolium	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Malva moschata	.	.	.	.	.	+	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	+	.	.	.	.
Lapsana communis subsp. *communis*	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.
Arrhenatherum elatius subsp. *bulbosum*	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
Hieracium murorum	.	.	.	.	.	.	.	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Carduus argemone subsp. *argemone*	.	.	.	.	.	.	.	.	2	.	.	.	.	.	1	.	.	2	.	.	.	.	.	.	.	.
Lotus maritimus	.	.	.	.	.	.	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Dorycnium pentaphyllum	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.
Cirsium tuberosum	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	1	.	.	+	.	.	.
Knautia arvernensis	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	+	.	.	+	.	.	.

Species occurring in 1 or 2 rels. only: Rel. 1: *Hypericum hirsutum* 1, *Potentilla erecta* 1, *Potentilla sterilis* +, *Pteridium aquilinum* subsp. *aquilinum* +, *Linum strictum* subsp. *strictum* +, *Plantago media* +, *Ranunculus tuberosus* +. Rel. 2: *Teucrium pyrenaicum* subsp. *pyrenaicum* +, *Hippocrepis comosa* +, *Medicago suffruticosa* +, *Rubus caesius* +. Rel. 3: *Seseli cantabricum* +, *Arenaria montana* subsp. *montana* +, *Thymus pulegioides* +. Rel. 4: *Genista tinctoria* 1, *Solidago virgaurea* subsp. *virgaurea* +, *Daboecia cantabrica* +, *Prunella vulgaris* +. Rel. 5: *Lathyrus hirsutus* 1, *Trifolium campestre* 1, *Dianthus armeria* subsp. *armeria* +, *Lathyrus aphaca* +, *Vicia hirsuta* +, *Jasione montana* subsp. *montana* +. Rel. 7: *Prunella laciniata* +, *Sedum sediforme* +. Rel. 8: *Crepis vesicaria* subsp. *haenseleri* +, *Dianthus armeria* subsp. *armeria* +, *Lathyrus aphaca* +, *Trisetum flavescens* subsp. *flavescens* +. Rel. 9: *Poa nemoralis* subsp. *nemoralis* 1, *Potentilla sterilis* 1, *Ajuga reptans* 1, *Bromus ramosus* 1, *Lilium martagon* +, *Mycelis muralis* +, *Scrophularia alpestris* +. Rel. 10: *Helictotrichon cantabricum* 2, *Crepis vesicaria* subsp. *haenseleri* +, *Euphorbia flavicoma* subsp. *occidentalis* +. Rel. 11: *Sesleria argentea* 2, *Arrhenatherum elatius* subsp. *sardoum* 1, *Festuca rubra* subsp. *rubra* 1, *Dianthus hyssopifolius* subsp. *hyssopifolius* +, *Euphorbia amygdaloides* subsp. *amygdaloides* +, *Hepatica nobilis* +, *Viola silvestris* agg. +. Rel. 12: *Pteridium aquilinum* subsp. *aquilinum* +, *Sesleria argentea* +. Rel. 13: *Onobrychis argentea* subsp. *hispanica* +. Rel. 14: *Seseli cantabricum* 1, *Pimpinella saxifraga* +, *Senecio jacobaea* +. Rel. 15: *Solidago virgaurea* subsp. *virgaurea* 2, *Euphorbia amygdaloides* subsp. *amygdaloides* +, *Teucrium pyrenaicum* ssp. *pyrenaicum* +. Rel. 16: *Catananche caerulea* +, *Phleum pratense* subsp. *bertolonii* +, *Verbena officinalis* +, *Bupleurum rigidum* subsp. *rigidum* +, *Jasonia tuberosa* +. Rel. 17: *Tordylium maximum* 1, *Potentilla reptans* 1. Rel. 18: *Vincetoxicum hirundinaria* 2, *Vicia pyrenaica* 1, *Astrantia major* 1, *Senecio adonidifolius* 1, *Dianthus hyssopifolius* subsp. *hyssopifolius* +, *Bromus diandrus* +. Rel. 19: *Lathyrus linifolius* 1, *Geranium columbinum* +, *Tordylium maximum* +. Rel. 20: *Senecio jacobaea* 1, *Pulicaria dysenterica* 1, *Campanula glomerata* +, *Lathyrus linifolius* +, *Heracleum sphondylium* subsp. *sphondylium* +, *Silaum silaus* +. Rel. 21: *Verbena officinalis* 2, *Anthriscus caucalis* 1, *Elymus caninus* 1, *Melica ciliata* +, *Geranium columbinum* +, *Odontites verna* subsp. *serotina* +. Rel. 22: *Vicia pubescens* 1, *Eupatorium cannabinum* subsp. *cannabinum* +, *Sonchus oleraceus* +. Rel. 23: *Vicia hirsuta* 1, *Phleum pratense* subsp. *bertolonii* +, *Pimpinella saxifraga* +. Rel. 24: *Carlina vulgaris* subsp. *vulgaris* +, *Hypericum montanum* +. Rel. 25: *Leucanthemum vulgare* agg. 1, *Catananche caerulea* +, *Bituminaria bituminosa* +. Rel. 26: *Cynosurus echinatus* +, *Ranunculus acris* subsp. *despectus* +

Table 2: *Agrimonio–Trifolietum medii primuletosum columnae*

Relevé number	1	2	3	4	5	6
Characteristic species of association and higher units:						
Campanula trachelium	3	1	1	2	1	+
Origanum vulgare subsp. *vulgare*	2	1	3	1	2	2
Satureja vulgaris	1	1	2	2	2	+
Fragaria vesca	2	.	2	1	1	2
Vicia orobus	1	2	.	.	+	.
Silene nutans subsp. *nutans*	+	.	+	.	.	+
Vicia sepium	.	.	1	+	.	1
Hypericum montanum	.	.	.	+	1	+
Trifolium medium subsp. *medium*	+	.	.	.	.	2
Lathyrus sylvestris	.	1	1	.	.	.
Agrimonia eupatoria subsp. *eupatoria*	.	1	.	+	.	.
Campanula rapunculus	.	1	.	+	.	.
Inula conyza	.	.	.	.	+	+
Stachys recta subsp. *recta*	2	.	.	.	.	.
Centaurea debeauxii subsp. *nemoralis*	.	+	.	.	.	.
Teucrium scorodonia	.	.	1	.	.	.
Astragalus glycyphyllos	.	.	.	.	+	.
Satureja ascendens	.	.	.	.	+	.
Geranium sanguineum	.	.	.	.	.	+
Other species:						
Picris hieracioides	1	2	1	1	+	.
Brachypodium sylvaticum subsp. *sylvaticum*	.	1	2	2	2	1
Hypericum perforatum	+	2	1	.	.	+
Scabiosa columbaria	+	1	+	.	.	+
Daucus carota subsp. *carota*	.	1	+	1	+	.
Anthyllis vulneraria	1	+	+	.	.	.
Helianthemum nummularium	+	.	.	1	+	.
Pimpinella saxifraga	.	+	+	.	1	.
Crepis capillaris	.	.	+	+	+	.
Emerus major	.	.	1	.	2	2
Onobrychis argentea subsp. *hispanica*	1	+	.	.	.	.
Brachypodium pinnatum subsp. *rupestre*	2	.	.	1	.	.
Dactylis glomerata subsp. *glomerata*	1	.	.	+	.	.
Centaurea scabiosa	.	1	+	.	.	.
Ononis spinosa	.	2	.	1	.	.
Galium verum subsp. *verum*	.	1	.	+	.	.
Silene vulgaris	.	+	.	.	+	.
Agrostis capillaris	.	1	.	.	.	1
Prunella grandiflora	.	1	.	.	.	1
Plantago lanceolata	.	.	.	+	.	+
Holcus lanatus	.	.	.	.	1	1
Solidago virgaurea subsp. *virgaurea*	.	.	.	.	+	+

Species with 1 occurrence only: Rel. 1: *Festuca rubra* subsp. *rubra* 2, *Euphorbia cyparissias* +, *Lathyrus vernus* subsp. *vernus* +, *Teucrium chamaedrys* subsp. *chamaedrys* +. Rel. 2: *Elymus caninus* 1, *Phleum pratense* subsp. *bertolonii* 1, *Sanguisorba minor* +. Rel. 3: *Bupleurum falcatum* subsp. *falcatum* 1, *Achillea millefolium* +, *Helleborus foetidus* +, *Lapsana communis* subsp. *communis* +, *Poa nemoralis* subsp. *nemoralis* +. Rel. 4: *Hypochoeris radicata* +, *Prunella vulgaris* +. Rel. 5: *Vicia sativa* agg. 1, *Bromus diandrus* +, *Geranium robertianum* subsp. *robertianum* +, *Medicago lupulina* +, *Mycelis muralis* +. Rel. 6: *Stachys officinalis* subsp. *officinalis* 1, *Viola reichenbachiana* 1, *Anthoxanthum odoratum* +, *Centaurium erythraea* +, *Lathyrus linifolius* +, *Linum catharticum* +

mation in the form of a synthetic table (Table 4). A data set containing 380 relevés from bibliographic sources and 51 relevés from our study was used to construct the synthetic table.

Nomenclature of plants and syntaxa

For species nomenclature Castroviejo *et al.* (1986–2001), Greuter *et al.* (1984–1989) and Tutin *et al.* (1964–1980) were followed, and Rivas-Martínez *et al.* (2001) and Rivas-Martínez *et al.* (2002a) for the syntaxonomy. The rules of the Code of Phytosociological Nomenclature (Weber *et al.* 2000) have been followed to name the syntaxa.

Results

Major syntaxonomic patterns

A first analysis of the entire data set reveals that none of the relevés could be assigned to the Geranion sanguinei, which is well represented in Catalonia and the central and eastern Pyrenees (Bolòs 1967, 1983, Rivas-Martínez 1968, Carrillo *et al.* 1984). Only one relevé from the literature (Loidi *et al.* 1997: 399, tab. 47, rel. 1) can be clearly assigned to the central Pyrenean Sileno nutantis–Geranietum sanguinei (Rivas-Martínez 1968). This indicates a poor presence of the Geranion sanguinei communities in the Cantabrian–Atlantic Subprovince; the latter are present in the Basque Country, but they have never been found further to the west (Rivas-Martínez *et al.* 1984, Díaz and Fernández Prieto 1994). The recorded communities completely lack the western Iberian endemic element previously mentioned (Tables 1–3). It became obvious that they should not be classified in the Iberian alliances of the Origanion virentis or of the Linarion triornithophorae.

The vegetation relevés were initially divided into three categories according to their geographic origin: (1) a group from the Pyrenees, (2) a group from the Navarro–Alavés Subsector and (3) a group from the Santanderino–Vizcaino Subsector (Figure 1). In order to test if they segregate into the same groups in a numerical ordination, a Detrended Correspondence Analysis was carried out with the total set of relevés. The DCA (Figure 2) shows a clear segregation of the relevés along Axes I and III, separating the relevés of the respective three geographic groups. The 19 relevés of the Santanderino–Vizcaino Subsector concentrate on the left side of Axis I and lower part of Axis III, the 26 relevés from the Navarro–Alavés Subsector concentrate in the central part of the graph and the six central Pyrenean relevés are located in the positive sector along both axes. Each of the respective groups was then shown in a separate table (Tables 1–3). The distribution of the relevé sites is shown in Figure 1.

As a further step of the analysis, our data have been subjected to comparison with similar vegetation in the form of a synoptic table (Table 4) which presents vegetation already described from the studied area as well as surrounding regions. The synthetic table includes data sets attributed to the Agrimonio–Trifolietum medii (from the Pyrenees and Germany), to the Valeriano–Fragarietum vescae and the Trifolio–Lithospermetum officinalis (from the Pyrenees), to

Table 3: *Hyperico androsaemi–Teucrietum scorodoniae*

Relevé number										1	1	1	1	1	1	1	1	1	1
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
Characteristic and differential species of association and higher units:																			
Centaurea debeauxii subsp. *nemoralis*	1	1	2	2	2	1	2	2	2	2	2	3	2	2	2	1	4	2	·
Teucrium scorodonia	2	2	3	2	2	2	+	+	3	2	3	·	·	·	4	2	1	·	1
Origanum vulgare subsp. *vulgare*	2	3	2	3	1	3	3	3	·	·	·	3	3	2	·	·	·	2	2
Fragaria vesca	1	1	·	·	2	·	·	·	2	1	1	·	·	·	1	·	·	·	·
Hypericum androsaemum	1	·	·	·	·	·	+	·	+	1	+	+	·	·	·	·	·	·	·
Hypericum pulchrum	·	·	·	+	1	·	·	·	·	+	1	·	·	·	·	1	+	·	·
Vicia bithynica	+	1	1	·	·	3	1	·	·	·	·	·	·	·	·	·	·	·	·
Digitalis purpurea subsp. *purpurea*	1	·	·	·	·	·	·	·	·	1	1	·	·	·	1	2	·	·	·
Inula conyza	·	1	·	1	·	·	·	·	+	·	·	·	·	1	+	·	·	·	·
Satureja vulgaris	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	+
Aquilegia vulgaris subsp. *vulgaris*	·	·	1	·	·	·	·	·	·	1	·	1	·	·	·	·	·	·	·
Jasione montana subsp. *montana*	·	·	1	·	·	·	·	·	·	1	·	·	·	·	·	+	·	·	·
Campanula rapunculus	·	·	·	+	·	·	·	·	·	2	·	·	·	·	·	·	·	·	·
Silene nutans subsp. *nutans*	·	·	·	·	·	·	1	·	·	·	·	·	+	·	·	·	·	·	·
Veronica chamaedrys subsp. *chamaedrys*	·	·	·	·	·	·	·	+	·	+	·	·	·	·	·	·	·	·	·
Campanula patula	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·
Companion species:																			
Lotus corniculatus subsp. *corniculatus*	2	2	1	1	1	2	2	1	1	1	·	·	1	1	1	2	+	1	·
Brachypodium pinnatum subsp. *rupestre*	3	2	1	2	1	2	2	1	·	·	2	2	1	3	·	1	3	2	2
Picris hieracioides	1	+	1	·	+	·	·	+	1	1	+	·	·	1	1	1	1	+	1
Dactylis glomerata subsp. *glomerata*	1	+	·	1	+	·	·	+	1	+	+	+	+	1	·	·	1	·	+
Medicago lupulina	1	1	+	+	+	1	2	·	1	·	·	·	·	1	1	·	·	1	+
Daucus carota subsp. *carota*	+	2	1	1	·	2	1	·	·	·	·	1	·	1	1	·	1	1	1
Anthoxanthum odoratum	1	·	1	·	1	1	·	+	1	2	2	·	·	·	1	1	·	·	+
Hypochoeris radicata	+	+	1	·	1	·	·	1	·	+	+	1	·	·	1	2	·	·	·
Hypericum perforatum	+	+	+	+	1	·	·	·	+	·	·	+	1	2	·	·	·	·	·
Sonchus oleraceus	+	+	·	·	·	+	+	·	·	·	+	+	·	+	·	·	·	+	+
Leucanthemum pallens	·	·	·	1	·	1	1	+	1	·	1	1	+	·	·	·	·	1	·
Sanguisorba minor	·	1	·	·	·	·	·	1	·	·	·	+	1	+	·	·	·	1	+
Plantago lanceolata	·	·	1	·	+	·	1	+	·	·	·	·	+	·	+	+	·	·	·
Galium mollugo	2	·	1	2	·	·	+	·	·	1	·	+	·	·	·	·	·	·	·
Centaurium erythraea	+	·	·	+	+	·	·	·	1	·	·	+	·	·	1	·	·	·	·
Agrostis capillaris	·	·	2	·	1	·	·	·	1	1	·	·	·	·	1	1	·	·	·
Festuca rubra subsp. *rubra*	·	·	1	·	·	·	1	2	1	·	1	·	·	·	·	+	·	·	·
Blackstonia perfoliata	·	·	·	+	+	1	+	·	·	·	·	·	·	+	·	·	+	·	·
Polygala vulgaris	+	·	·	·	·	+	·	+	+	·	·	·	·	·	·	+	·	·	·
Lapsana communis subsp. *communis*	·	+	·	+	·	+	+	·	·	·	·	·	·	·	·	·	·	·	2
Vicia pubescens	·	1	·	·	1	·	·	1	·	+	+	·	·	·	·	·	·	·	·
Daboecia cantabrica	·	·	+	+	+	·	·	·	·	·	1	·	·	·	·	+	·	·	·
Solidago virgaurea subsp. *virgaurea*	·	·	1	·	1	·	·	·	+	1	1	·	·	·	·	·	·	·	·
Pteridium aquilinum subsp. *aquilinum*	·	·	·	+	·	·	·	·	+	1	·	·	·	·	+	·	1	·	·
Crepis capillaris	·	·	·	·	·	·	+	·	·	·	1	·	1	·	+	1	·	·	·
Vicia sativa agg.	+	·	·	·	+	·	·	·	·	·	·	·	·	·	·	+	·	·	2
Holcus lanatus	·	+	·	·	1	·	·	·	·	·	+	·	·	·	·	·	+	·	·
Carex flacca	·	·	·	·	·	+	·	+	·	·	·	1	·	·	·	·	·	+	·
Geranium columbinum	·	·	·	·	·	2	·	·	+	·	·	·	+	·	·	·	·	·	2
Vicia hirsuta	+	1	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·
Andryala integrifolia	·	1	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	3
Linum bienne	·	·	·	·	+	1	·	·	·	·	·	·	+	·	·	·	·	·	·
Pulicaria dysenterica	·	·	·	·	1	·	·	·	·	·	+	·	·	+	·	·	·	·	·
Reichardia picroides	·	·	·	·	1	·	·	·	·	·	·	1	1	·	·	·	·	·	·
Prunella grandiflora	·	·	·	·	·	·	+	1	·	·	·	·	·	·	·	·	+	·	·
Stachys officinalis subsp. *officinalis*	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	·	+	·
Galium pumilum subsp. *pinetorum*	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	1	1	·
Campanula glomerata	·	·	·	·	·	·	·	·	·	·	·	·	1	+	·	·	·	+	·
Briza maxima	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+
Avena barbata	·	+	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·
Trifolium pratense	·	·	1	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·
Cytisus commutatus	·	·	+	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·
Euphorbia amygdaloides subsp. *amygdaloides*	·	·	·	+	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·
Blechnum spicant	·	·	·	·	+	·	·	·	·	+	·	·	·	·	·	·	·	·	·

Table 3 cont.

Osmunda regalis	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Potentilla erecta	.	.	.	.	1	.	.	.	.	.	+	.	.	.	.	.	.	.	.
Erica vagans	.	.	.	.	.	.	+	.	.	.	.	1	.	.	.	.	.	.	.
Vicia tetrasperma	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	+	.
Danthonia decumbens	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.
Linum catharticum	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	.	.
Rhinanthus mediterraneus	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.
Lathyrus pannonicus	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	+	.
Potentilla sterilis	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.
Torilis arvensis	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.
Geranium robertianum subsp. *robertianum*	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1
Eupatorium cannabinum subsp. *cannabinum*	.	.	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.
Carlina vulgaris subsp. *vulgaris*	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+
Ononis spinosa	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	+	.	.
Rubus ulmifolius	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1
Pseudarrhenatherum longifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	.	.	.
Lathyrus linifolius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.

Other species: Rel. 1: *Vicia pannonica* 2, *Dianthus armeria* subsp. *armeria* +, *Trifolium campestre* +. Rel. 2: *Cruciata laevipes* +. Rel. 4: *Galium aparine* +. Rel. 5: *Athyrium filix–femina* +, *Ulex gallii* +. Rel. 6: *Festuca arundinacea* 1, *Cynosurus echinatus* +. Rel. 7: *Asplenium onopteris* +. Rel. 8: *Euphorbia dulcis* +, *Gaudinia fragilis* +, *Ranunculus acris* subsp. *despectus* +. Rel. 9: *Brachypodium sylvaticum* subsp. *sylvaticum* 1, *Carex divulsa* subsp. *divulsa* +. Rel. 10: *Silene vulgaris* 1, *Ranunculus tuberosus* +, *Rumex acetosa* subsp. *acetosa* +, *Wahlenbergia hederacea* +. Rel. 11: *Angelica sylvestris* +. Rel. 12: *Euphorbia hyberna* 1, *Briza media* subsp. *media* +, *Cirsium tuberosum* +. Rel. 13: *Melica ciliata* 1, *Sedum sediforme* 1, *Centaurea calcitrapa* +, *Lactuca tenerrima* +, *Sonchus arvensis* +. Rel. 14: *Foeniculum vulgare* 1, *Eryngium campestre* +, *Picris echioides* +. Rel. 15: *Geum urbanum* +, *Prunella vulgaris* +, *Stachys alpina* +. Rel. 16: *Avenella flexuosa* 1. Rel. 17: *Seseli cantabricum* 1. Rel. 18: *Bromus erectus* subsp. *erectus* +, *Helianthemum nummularium* +, *Hypericum montanum* +, *Teucrium pyrenaicum* subsp. *pyrenaicum* +. Rel. 19: *Bromus hordeaceus* +, *Quercus robur* subsp. *robur* +, *Verbena officinalis* +

the Lathyro latifolii–Centaureetum nemoralis (from the Cantabrian mountains), to the Centaureo–Origanetum vulgaris and the Hyperico pulchri–Melampyretum pratensis (from western France). Two of our vegetation units can be identified as already described syntaxa (Centaureo–Origanetum vulgaris and Agrimonio–Trifolietum medii primuletosum columnae) while the saum vegetation from the Santanderino–Vizcaino Subsector is described here as a new association (Hyperico androsaemi–Teucrietum scorodoniae).

Description of the syntaxa

Centaureo nemoralis–Origanetum vulgaris Foucault, Frileux and Wattez in Foucault and Frileux 1983
(Syn. Lathyro latifolii–Centaureetum nemoralis Rivas-Martínez T.E. Díaz, Fernández Prieto, Loidi and Penas 1984) (Table 1 and Table 4, Column 3)

This vegetation unit is represented by 26 relevés made in the Navarro–Alavés and Western Pyrenean Subsectors on base-rich substrates (mostly marl and limestone). It shows a considerably higher share of the Trifolio–Geranietea floristic elements such as *Origanum vulgare* and *Lathyrus latifolius*. This community is found in forested regions dominated by *Quercus robur* (Crataego laevigatae–Quercetum roboris), *Q. faginea* (Pulmonario) longifoliae–Quercetum fagineae and *Fagus sylvatica* (Carici sylvaticae–Fagetum and Epipactido helleborines–Fagetum).

Only a small number of relevés (13) were published from Cantabria (Rivas-Martínez *et al.* 1984, López Pacheco 1988, Pérez Morales 1988, Puente 1988, Herrero 1989) under the name of Lathyro latifolii–Centaureetum nemoralis — most of them were sampled in the mountainous territories of the Orocantabrian Subprovince (Table 4, Column 2). 41 relevés from Table X in Foucault and Frileux (1983), which represent a wide sample of these communities in north-west France, have been summarised in Column 1. Several species link Cantabrian communities with those of France, and separate them from the central Pyrenean and central European ones: *Campanula rapunculus, Centaurea nemoralis, Galium mollugo* etc. (Table 4). Comparison with more oceanic and silicicolous communities of Column 10 (the Hyperico androsaemi–Teucrietum scorodoniae) highlights important floristic differences in the table, particularly the scarcity of some silicicolous plants such as *Teucrium scorodonia* and the presence of some basiphilous species such as *Centaurea jacea, C. scabiosa* and *Lathyrus latifolius*. The strong similarities of the Centaureo–Origanetum with the French association suggest the inclusion of the studied communities of Table 1 (Table 4, Column 3), and those of the Orocantabrian territories (Table 4, Column 2) into the Centaureo nemoralis–Origanetum vulgaris.

Agrimonio–Trifolietum medii Müller 1961 *primuletosum columnae* Carrillo, Ninot and Vigo 1984
(Syn. Trifolio–Lithospermetum Rivas-Martínez, Báscones, T.E. Díaz, Fernández-González and Loidi 1991) (Table 2 and Table 4, Column 5)

The six relevés made in the Central Pyrenees, mostly linked to the occurrence of *Quercus pubescens* (Buxo–Quercetum pubescentis), *Fraxinus excelsior* (Brachypodio sylvatici–Fraxinetum excelsioris) and *Fagus sylvatica* (Scillo lilio–hyacinthi–Fagetum) forests are presented in Table 2 and summarised as Column 5 of Table 4. They also show a

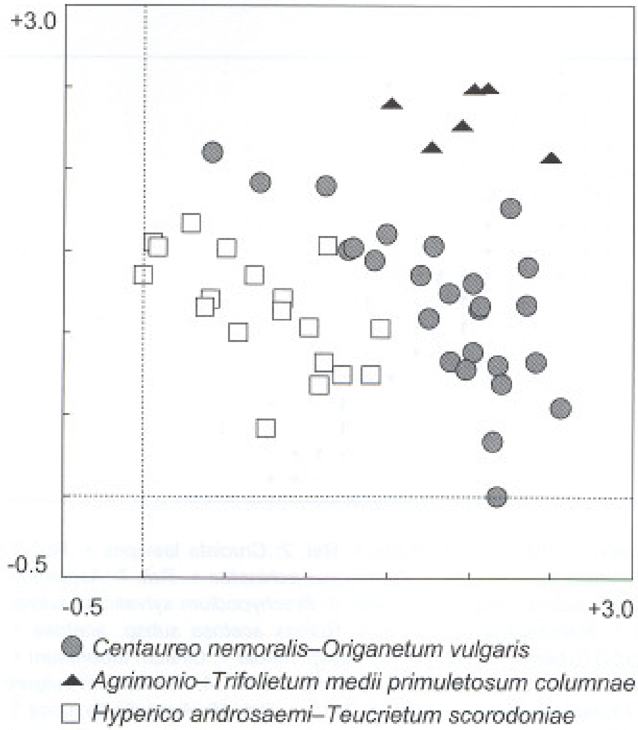

Figure 2: Detrended Correspondence Analysis (Axes I–III)

high participation of the Origanetalia vulgaris taxa as well as occurrence of species such as *Trifolium medium, Campanula trachelium* and *Lathyrus sylvestris* which are lacking in the similar Cantabrian communities. The only similar vegetation data published are those by Rivas-Martínez *et al.* (1991) from the Ordesa Valley. These data are peculiar because of the dominance of *Lithospermum officinale*. The dominance of the latter species led the authors to call this vegetation unit Trifolio medii–Lithospermetum officinalis. It is very likely that the three relevés by Rivas-Martínez *et al.* (l.c.) were made within a short distance and represent a local version of our community. We maintain that the most widespread saum association in the Pyrenees is the Agrimonio-Trifolietum medii (Carrillo *et al.* 1984, Carrillo and Ninot 1992, Soriano 1992, Carreras 1993, Villegas 1993, Carreras *et al.* 1995) described originally in southern Germany and found to be widespread throughout the entire central Europe (Müller 1961, 1978, Dierschke 1974a). In the Pyrenees it is represented by the subassociation primuletosum columnae, described by Carrillo *et al.* (1984) for the eastern Pyrenees, and differentiated by the presence of *Campanula trachelium, Prunella grandiflora* and *Primula veris* subsp. *columnae*. The central Pyrenean Valeriano officinalis–Fragarietum vescae O. Bolòs 1977, typical of wet habitats, is clearly differentiated from Agrimonio–Trifolietum by the dominance of *Valeriana officinalis* (Bolòs 1977, Romo 1989, Soriano 1992, Viñas 1993).

Hyperico androsaemi–Teucrietum scorodoniae
(Table 3 and Table 4, Column 10)

This new association is represented by 19 relevés sampled in the Santanderino–Vizcaino Subsector, i.e. on the northern fringe between the watershed mountains and the coast, at low elevation and under very oceanic climatic conditions (low temperature oscillation and high rainfall throughout all the seasons). In this area, substrates are predominantly base-poor due to lithology (sandstone, flysch, argillite) and/or due to intensive leaching of soils by high rainfall. Many of the relevés were made in secondary habitats, hence they contain a high proportion of companion plants found usually in grassland, meadow and ruderal communities, with which this saum vegetation is found in contact. The group of plants typical of the Trifolio–Geranietea is small; they have broad ecological valency and they appear as dominant or co-dominant elements (*Origanum vulgare, Centaurea debeauxii* subsp. *nemoralis* and *Teucrium scorodonia*). Among the companions, the grassland element *Brachypodium pinnatum* subsp. *rupestre* is prominent — it is very abundant in the region in general. The stands of this community accompany forests of *Quercus robur* (Polysticho setiferi–Fraxinetum excelsioris and Hyperico pulchri–Quercetum roboris) and *Q. pyrenaica* (Melampyro pratensis–Quercetum pyrenaicae) as well as their mantel shrub formations (Prunetalia spinosae).

From the syntaxonomic point of view, this community poses some difficulties as to its position in the current classification system (Loidi *et al.* 1997, Díaz and Fernández Prieto 1994, Rivas-Martínez *et al.* 2001). In 1979 Passarge described the Melampyro–Holcetalia (including the Melampyrion pratensis) for the non-nitrophilous herbaceous forest border communities on acidic substrates. Later, Foucault *et al.* (1983) proposed the Teucrion scorodoniae — a concept to a great extent overlapping with the Melampyrion pratensis. These silicicolous syntaxa are ecologically well justified, but from the floristic point of view they are known to contain no character taxa. Therefore, we choose not to consider them valid units or to recognise them as independent syntaxa.

The dominance of *Centaurea debeauxii* subsp. *nemoralis* and *Teucrium scorodonia* and the relatively high frequency of *Hypericum pulchrum, Digitalis purpurea* and *Jasione montana* (all indicators of acidic soils), are the main floristic features of this community. The silicicolous communities known from western France and the British Isles, which presumably are comparable to those sampled in this study, are mostly included in the Hyperico pulchri–Melampyretum described by Foucault and Frileux (1983). However, the original table of these authors (summarised in Table 4, Column 11) does not include *Centaurea debeauxii* subsp. *nemoralis* and *Origanum vulgare*, two constant species in the Cantabrian communities. Hence we maintain that our communities cannot be included within the Hyperico–Melampyretum. [Regarding the nomenclature of the Hyperico pulchri–Melampyretum, the authors designated in their description the relevé no. 20 of Table II as the holotype. However, a typographic error has erased most of that relevé from the printed table, thus, the association has been invalidly published according to the CPN rules (nomen dubium, arts. 16 and 37). In this paper, we designate relevé no. 21 of the same table as the holotype of the Hyperico pulchri–Melampyretum pratensis Foucault and Frileux ass. nova

Table 4: Synthetic table. 1–3: Centaureo nemoralis–Origanetum vulgaris; 4: Valeriano–Fragarietum vescae; 5–9: Agrimonio–Trifolietum medii (5–7: primuletosum columnae, 8–9: typicum); 10: Hyperico androsaemi–Teucrietum scorodoniae; 11: Hyperico pulchri–Melampyretum pratensis

No. of column	1	2	3	4	5	6	7	8	9	10	11
No. of relevés	41	13	26	27	6	3	39	176	66	19	15
Differentials of basophilous associations:											
Centaurea scabiosa	I	II	II	+	II	·	+	I	I	·	·
Astragalus glycyphyllos	·	II	+	+	I	2	II	III	II	·	·
Tanacetum corymbosum subsp. *corymbosum*	·	II	·	+	·	·	+	II	·	·	·
Centaurea jacea	·	·	II	·	·	·	+	II	IV	·	·
Differentials of acidophilous associations:											
Teucrium scorodonia	+	II	I	I	I	·	+	·	+	IV	IV
Potentilla erecta	·	·	+	+	·	·	·	·	+	I	IV
Hypericum pulchrum	·	I	I	·	·	·	·	·	·	II	V
Avenella flexuosa	·	·	·	·	·	·	I	·	+	+	III
Differentials of *Centaureo–Origanetum* vs *Agrimonio–Trifolietum:*											
Campanula rapunculus	+	II	I	+	II	·	·	·	·	I	·
Centaurea debeauxii subsp. *nemoralis*	IV	II	II	·	I	·	·	·	·	V	·
Galium mollugo	III	I	II	·	·	·	·	·	·	II	III
Cruciata laevipes	II	+	I	·	·	·	·	·	·	+	I
Malva moschata	+	II	I	·	·	·	·	·	·	·	·
Differential of *Valeriano–Fragarietum vescae:*											
Valeriana officinalis	·	·	·	IV	·	·	I	II	II	·	·
Differentials of *Agrimonio–Trifolietum* vs *Centaureo–Origanetum:*											
Veronica chamaedrys subsp. *chamaedrys*	II	·	·	III	·	2	III	IV	III	I	III
Vicia sepium	+	·	+	IV	III	·	IV	IV	IV	·	III
Euphorbia cyparissias	+	·	·	+	I	3	+	III	I	·	·
Lathyrus sylvestris	·	·	+	·	II	·	+	II	+	·	·
Helleborus foetidus	·	·	·	+	I	1	+	·	·	·	·
Emerus major	·	·	·	+	III	·	I	·	·	·	·
Differentials of *Agrimonio–Trifolietum primuletosum columnae:*											
Brachypodium pinnatum subsp. *rupestre*	V	+	V	·	II	·	+	·	·	V	IV
Campanula trachelium	+	·	I	III	V	3	I	·	·	·	·
Prunella grandiflora	·	I	I	·	II	·	II	+	·	I	·
Vicia cracca agg.	+	II	+	·	·	·	II	·	·	·	·
Prunella hastifolia	·	I	·	II	·	·	II	·	·	·	·
Hepatica nobilis	·	·	+	I	·	·	III	·	·	·	·
Primula veris subsp. *columnae*	·	·	·	+	·	·	II	·	·	·	·
Differentials of *Agrimonio–Trifolietum typicum:*											
Geranium pratense	·	·	·	·	·	·	·	I	II	·	·
Brachypodium pinnatum subsp. *pinnatum*	·	·	·	·	·	·	·	V	·	·	·
Differentials of *Hyperico–Teucrietum* vs *Hyperico pulchri–Melampyretum:*											
Origanum vulgare subsp. *vulgare*	V	I	V	II	V	·	II	V	IV	IV	·
Hypericum androsaemum	·	·	·	I	·	·	·	·	·	II	·
Differentials of *Hyperico pulchri–Melampyretum* vs *Hyperico–Teucrietum:*											
Holcus mollis subsp. *mollis*	+	+	·	·	·	·	·	·	+	·	IV
Melampyrum pratense	·	·	·	·	·	·	I	+	+	·	V

Table 4 cont.

Characteristic species of *Trifolio–Geranietea*:											
Fragaria vesca	I	II	II	V	V	3	IV	III	III	II	IV
Satureja vulgaris	III	IV	II	III	V	2	III	IV	IV	I	·
Trifolium medium subsp. *medium*	+	V	I	I	II	2	V	IV	IV	·	II
Agrimonia eupatoria subsp. *eupatoria*	IV	+	II	III	II	1	I	V	·	·	+
Aquilegia vulgaris subsp. *vulgaris*	·	II	+	III	·	2	+	·	·	I	·
Silene nutans subsp. *nutans*	·	I	I	·	III	·	II	I	·	I	·
Inula conyza	I	·	+	·	II	·	·	II	·	II	·
Trifolium ochroleucon	·	+	I	+	·	·	+	+	·	·	·
Geranium sanguineum	·	II	+	·	I	·	·	I	I	·	·
Satureja calamintha agg.	·	·	I	+	I	·	+	+	·	·	·
Campanula persicifolia	·	·	+	I	·	·	I	+	+	·	·
Vicia orobus	·	+	+	·	III	·	+	·	·	·	·
Vincetoxicum hirundinaria	·	·	+	+	·	·	·	+	+	·	·
Campanula patula	·	·	I	·	·	·	+	+	·	+	·
Lathyrus latifolius	·	II	II	+	·	·	·	·	·	·	·
Cruciata glabra	·	·	I	+	·	·	IV	·	·	·	·
Stachys recta subsp. *recta*	·	·	·	·	I	·	·	+	·	·	·
Lithospermum officinale	·	·	·	·	·	3	+	·	·	·	·
Verbascum lychnitis	·	·	·	·	·	·	·	II	I	·	·
Vicia tenuifolia	·	·	·	·	·	·	·	I	+	·	·
Companion species:											
Hypericum perforatum	IV	+	III	II	IV	1	II	IV	V	III	II
Dactylis glomerata subsp. *glomerata*	IV	+	III	II	II	·	III	IV	IV	IV	IV
Brachypodium sylvaticum subsp. *sylvaticum*	I	I	I	IV	V	·	II	+	IV	+	I
Prunella vulgaris	I	+	+	II	I	1	I	·	·	+	II
Sanguisorba minor	II	I	III	I	I	·	+	II	III	II	·
Achillea millefolium	V	II	I	I	I	·	III	IV	IV	·	II
Poa nemoralis subsp. *nemoralis*	+	II	+	+	I	·	III	+	III	·	II
Lathyrus pratensis	II	II	I	+	·	1	II	IV	IV	·	I
Agrostis capillaris	I	·	I	III	II	·	II	+	II	II	IV
Lotus corniculatus subsp. *corniculatus*	IV	·	III	I	·	·	II	II	I	V	+
Arrhenatherum elatius	IV	+	I	+	·	·	+	II	III	·	III
Galium verum subsp. *verum*	II	·	II	+	II	2	+	IV	IV	·	·
Daucus carota subsp. *carota*	III	·	III	I	IV	·	+	III	II	IV	·
Anthoxanthum odoratum	+	·	II	+	I	·	+	·	I	III	IV
Solidago virgaurea subsp. *virgaurea*	+	·	+	·	II	·	II	III	IV	II	V
Stachys officinalis subsp. *officinalis*	·	·	I	III	I	·	I	+	II	I	V
Festuca rubra agg.	·	·	+	+	I	·	I	+	+	II	II
Briza media subsp. *media*	+	I	II	·	·	·	I	+	I	+	·
Silene vulgaris	+	III	II	·	II	·	+	+	·	+	·
Leucanthemum vulgare agg.	III	II	+	·	·	·	+	II	III	·	II
Geranium robertianum subsp. *robertianum*	+	I	·	II	I	·	+	+	·	I	·
Viola silvestris agg.	+	·	+	III	I	2	III	·	·	·	V
Plantago lanceolata	II	·	I	+	II	·	I	·	·	II	II
Linum catharticum	+	·	I	+	I	·	+	·	·	I	+
Carex flacca	I	·	II	I	·	·	+	I	·	II	+
Lapsana communis subsp. *communis*	·	·	I	+	I	·	+	I	+	II	·
Lathyrus linifolius	·	·	+	+	I	·	I	+	·	I	V
Trifolium pratense	II	I	I	I		·	II	·	·	I	·
Holcus lanatus	I	+	II	III	II	·	·	·	·	II	·
Potentilla sterilis	+	I	+	I	·	·	·	·	·	I	V

Table 4 cont.

Stellaria holostea	I	II	·	+	·	·	I	·	III	·	V
Pimpinella saxifraga	IV	·	+	+	III	·	II	II	·	·	·
Scabiosa columbaria	+	·	II	+	IV	·	+	+	·	·	·
Medicago lupulina	III	·	II	+	I	·	+	·	·	IV	·
Vicia hirsuta	II	·	+	+	·	·	+	·	·	I	·
Ononis spinosa	I	·	II	+	II	·	I	·	·	I	·
Helianthemum nummularium	+	·	I	I	III	·	I	·	·	+	·
Phleum pratense	I	·	+	·	I	·	+	+	+	·	·
Euphorbia amygdaloides subsp. *amygdaloides*	·	+	+	II	·	·	I	·	·	I	III
Picris hieracioides	·	+	IV	·	V	·	I	+	·	IV	·
Centaurium erythraea	·	·	I	+	I	·	+	·	·	II	+
Ranunculus tuberosus	·	·	+	·	·	1	I	+	+	+	·

***Centaureo nemoralis–Origanetum vulgaris*: 1.** Foucault and Frileux (1983): tab. X, 41 rels.; **2.** Herrero (1989): tab. 66, 2 rels., López Pacheco (1988): tab. 8, 1 rel., Pérez Morales (1988): tab. 60, 7 rels., Puente (1988): tab. 16, 2 rels., Rivas-Martínez *et al.* (1984): tab. 11, 1 rel. (all sub *Lathyro latifoliae–Centaureetum nemoralis*); **3.** Table 1 (in this work). ***Valeriano officinalis–Fragarietum vescae*: 4.** Bolòs (1977): tab. 1, rel. 1–10, 12–24, Romo (1989): tab. 35, 1 rel., Soriano (1992): tab. 3.91, rel. 7–8, Viñas (1993): tab. TXT, 1 rel. ***Agrimonio–Trifolietum medii primuletosum columnae*: 5.** Table 2 (in this work); **6.** Rivas-Martinez *et al.* (1991): tab. 34, 3 rels., sub *Trifolio medii–Lithospermetum officinalis*; **7.** Carreras (1993): tab. 50, 3 rels., Carreras *et al.* (1995): tab. TX5, 1 rel., Carrillo and Ninot (1992): tab. 61, 3 rels., Carrillo *et al.* (1984): tab. 1, 20 rels., Soriano (1992): tab. 3.91, rel. 1–6, Villegas (1993): tab. 36, 6 rels.; ***typicum*: 8.** Müller (1978): tab. 128, rel. 11a, *sub* planar–submontane Form, subass. gruppe mit *Brachypodium pinnatum*; **9.** Müller (1978): tab. 128, rel. 11b, sub planar–submontane Form, subass. gruppe mit *Poa nemoralis*. ***Hyperico androsaemi–eucrietum scorodoniae*: 10.** Table 3 (in this work). ***Hyperico pulchri-Melampyretum pratensis*: 11.** Foucault and Frileux (1983): tab. II, rel. 21–35, sub *Hyperico–Melampyretum potentilletosum sterilis*

(Syn: Hyperico pulchri–Melampyretum pratensis Foucault and Frileux 1983 nom. dub. propos.; Arts. 16, 37)]

The floristic composition of this Cantabrian community type is original and different to those already described in western and south western France (Foucault *et al.* l.c.), and therefore a new association is described here: the Hyperico androsaemi–Teucrietum scorodoniae ass. nova hoc loco; the relevé no. 1 in Table 3 is designated as its holotype.

Syntaxonomic scheme

The syntaxonomy for the plant communities represented in the synthetic table is as follows (asterisk indicates the associations of the communities studied in this paper):

Trifolio–Geranietea Müller 1962
Origanetalia vulgaris Müller 1962
Trifolion medii Müller 1962
* Centaureo nemoralis–Origanetum vulgaris Foucault, Frileux and Wattez in Foucault and Frileux 1983
(Syn. Lathyro latifolii–Centaureetum nemoralis Rivas-Martínez *et al.* 1984)
Valeriano officinalis–Fragarietum vescae O. Bolòs 1977
* Agrimonio–Trifolietum medii Müller 1961 primuletosum columnae Carrillo, Ninot and Vigo 1984
(Syn. Trifolio–Lithospermetum Rivas-Martínez *et al.* 1991)
* Hyperico androsaemi–Teucrietum scorodoniae ass. nova hoc loco
Hyperico pulchri–Melampyretum pratensis Foucault and Frileux ass. nova
(Syn. Hyperico pulchri–Melampyretum pratensis Foucault and Frileux 1983 nom. dub. propos. Art. 16, 37)

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Appendix: Header data for relevés in Tables 1, 2 and 3

No.	Locality	Altitude (m)	UTM coord	Area (m²)	Richness
Table 1: Centaureo nemoralis–Origanetum vulgaris					
1	Alava: From Opacua to Pto. Opacua	750	30TWN5241	20	28
2	Alava: From Sta. Teodosia to S Vicente de Arana	920	30TWN5234	10	22
3	Alava: From S Vicente de Arana to Sabando	780	30TWN5032	30	23
4	Alava: From S Vicente de Arana to Sabando	770	30TWN4933	20	18
5	Alava: Urturi	780	30TWN4021	25	19
6	Alava: From Urturi to Obecuri (Treviño)	770	30TWN3821	40	22
7	Alava: From Lagrán to Pipaón	820	30TWN3219	10	18
8	Alava: Pipaón	890	30TWN2918	20	20
9	Alava: From Pipaón to Pto. Herrera	1 010	30TWN2716	20	14
10	Alava: From Pto. Berrostegieta to Treviño	780	30TWN2137	20	20
11	Alava: Pto. Rivas de Tereso	950	30TWN2218	15	20
12	Alava: Pto. Rivas de Tereso	950	30TWN2218	20	20
13	Alava: Pto. Rivas de Tereso	800	30TWN2219	20	21
14	Navarra: Olazagutia	610	30TWN6648	30	25
15	Navarra: Pto. Urbasa	900	30TWN6645	15	19
16	Navarra: Amézcoa Baja	650	30TWN7036	15	25
17	Navarra: Abárzuza	640	30TWN7833	10	23
18	Navarra: From Pto. Lizarraga to Etxarri-Aranaz	960	30TWN8146	15	17
19	Navarra: Lizarraga	550	30TWN7847	10	16
20	Navarra: From Unanua to Dorrao	590	30TWN8048	50	30
21	Huesca: Zuriza	1 040	30TXN7848	10	23
22	Navarra: From Isaba to Uztarroz	820	30TXN6948	30	30
23	Navarra: From Izalzu to Ochagavia	900	30TXN5853	20	29
24	Navarra: From Erro to Pto. Erro	720	30TXN2555	30	27
25	Alava: Korres	750	30TWN4627	10	17
26	Alava: Korres	650	30TWN4627	10	14
Table 2: Agrimonio–Trifolietum medii primuletosum columnae					
1	Huesca: Benasque	1 300	31TBH9822	30	20
2	Huesca: La Sarra	1 200	31TBH6426	20	25
3	Huesca: Bielsa	1 100	31TBH7124	20	23
4	Huesca: Escuain	1 210	31TBH6419	10	20
5	Huesca: Añisclo	910	31TBH6013	10	24
6	Huesca: Añisclo	960	31TBH6014	15	25
Table 3: Hyperico androsaemi–Teucrietum scorodoniae					
1	Bizkaia: Agirre (Holotypus ass.)	180	30TWN1899	50	26
2	Bizkaia: Sopuerta	100	30TVN8789	20	24
3	Bizkaia: Agirre, Arrieta	200	30TWN1899	40	22
4	Bizkaia: Zeberio	130	30TWN1377	30	21
5	Bizkaia: Orozko	100	30TWN0773	30	30
6	Bizkaia: Güeñes	40	30TVN9284	20	21
7	Bizkaia: Carranza	150	30TVN7184	30	24
8	Bizkaia: Güeñes	40	30TVN9284	40	28
9	Bizkaia: Zeanuri	180	30TWN2071	40	25
10	Bizkaia: Agirre, Arrieta	200	30TWN1899	100	29
11	Bizkaia: Bermeo	80	30TWP2105	60	23
12	Bizkaia: Morga	120	30TWN2194	30	23
13	Bizkaia: Dima	250	30TWN2273	30	21
14	Bizkaia: Berango	70	30TWP0001	50	20
15	Bizkaia: Artea	150	30TWN1775	40	21
16	Bizkaia: Pto. Dima	570	30TWN2570	20	20
17	Bizkaia: Mte. Unbe	100	30TWN0598	30	17
18	Bizkaia: From Avellaneda to Sopuerta	50	30TVN8788	40	21
19	Bizkaia: Arcentales	80	30TVN8287	50	22