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Classification of the Mediterranean lowland to submontane pine forest vegetation

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Abstract

Aim: Vegetation types of Mediterranean thermophilous pine forests dominated by *Pinus brutia*, *Pinus halepensis*, *Pinus pinaster* and *Pinus pinea* were studied in various areas. However, a comprehensive formal vegetation classification of these forests based on a detailed data analysis has never been developed. Our aim is to provide the first broad-scale classification of these pine forests based on a large data set of vegetation plots.

Location: Southern Europe, North Africa, Levant, Anatolia, Crimea and the Caucasus.

Methods: We prepared a data set of European and Mediterranean pine forest vegetation plots. We selected 7,277 plots dominated by the cold-sensitive Mediterranean pine species *Pinus brutia*, *Pinus halepensis*, *Pinus pinaster* and *Pinus pinea*. We classified these plots using TWINSPAN, interpreted the ecologically and biogeographically homogeneous TWINSPAN clusters as alliances, and developed an expert system for automatic vegetation classification at the class, order and alliance levels.

Results: We described *Pinetea halepensis* as a new class for the Mediterranean lowland to submontane pine forests, included in the existing *Pinetalia halepensis* order, and distinguished 12 alliances of native thermophilous pine forests, including four newly described and three informal groups merging supposedly native stands and old-established plantations. The main gradients in species composition reflect elevational vegetation belts and the west–east, and partly north–south, biogeographical differences. Both temperature and precipitation seasonality co-vary with these gradients.

Conclusions: We provide the first formal classification at the order and alliance levels for all the Mediterranean thermophilous pine forests based on vegetation-plot data. This classification includes traditional syntaxa, which have been critically revised, and a new class and four new alliances. We also outline a methodological workflow

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that might be useful for other vegetation classification syntheses. The expert system, which is jointly based on pine dominance and species composition, is a tool for applying this classification in research and nature conservation survey, monitoring and management.

KEYWORDS
biogeography, classification, expert system, forest, Mediterranean Basin, phytosociology, pine, *Pinetea halepensis*, *Pinus*, *Quercetea ilicis*, vegetation classification, vegetation-plot database

1 | INTRODUCTION

Mediterranean coniferous tree taxa are included in the genera *Abies*, *Cedrus*, *Cupressus*, *Juniperus*, *Pinus*, and *Tetraclinis*. Especially *Pinus*, the most species-rich genus of conifers, is abundant across southern Europe and the Mediterranean Basin (Timbal et al., 2005; Farjon & Filer, 2013). There are ten pine tree species currently accepted in Europe and North Africa (Euro+Med, 2016–2020) and several infraspecific taxa. Four pine species can be considered Mediterranean in terms of their temperature requirements and distribution, which is confined to low- to mid-elevations: *Pinus brutia*, *Pinus halepensis*, *Pinus pinaster* and *Pinus pinea* (Barbéro et al., 1998; Quézel, 2000). Their distribution range lies mainly in the countries bordering the Mediterranean Sea, partly the Black Sea (*Pinus brutia*), and the Atlantic coast of the Iberian Peninsula and Morocco (*Pinus pinaster*, *Pinus pinea*; Caudullo et al., 2017). Marginally, *Pinus halepensis* is also present in the Atlantic watersheds of the Iberian Peninsula and Morocco (Caudullo et al., 2017).

Specifically, *Pinus brutia* occurs in the east of the Mediterranean Basin and some areas around the Black Sea (Crimea, northwestern Caucasus, eastern foothills of the Great Caucasus and isolated areas in the Euxinian region), Iraq and Iran (Mauri et al., 2016; Çoban & Willner, 2019). It occurs chiefly in the thermo- and mesomediterranean elevational belts, where it forms extensive stands with a dense shrub layer of sclerophyllous species (macchia, maquis), or without shrub layer (Farjon & Filer, 2013; Bonari et al., 2020).

Pinus halepensis is the most widespread Mediterranean thermophilous pine species (Mauri et al., 2016), but it is more common in the western Mediterranean Basin. In most areas, it occurs not far from the coast but reaches about 2,000 m a.s.l. in the Eastern High Atlas. It occurs in fire-prone vegetation (macchia, garrigue), but can also form a dense canopy with sparse undergrowth in places with a long absence of fire (Farjon & Filer, 2013). The distribution ranges of *Pinus halepensis* and *Pinus brutia* overlap in Greece and on the Aegean islands.

Pinus pinaster thrives in the western Mediterranean Basin (Abad Viñas et al., 2016a). It is a thermophilous species believed to be native to the Iberian Peninsula, southern France including Corsica, western Italy including Sardinia, and northwestern Africa. It also occurs on the Atlantic coast and reaches about 2,000 m a.s.l. in Morocco. This species is well adapted to fire (Fernandes & Rigolot, 2007; Farjon & Filer, 2013).

Pinus pinea is an iconic Mediterranean thermophilous tree, which occurs from the sea level up to the mountains. It has been frequently planted as an ornamental tree and for its edible seeds. It occurs at high elevations mainly in the eastern Mediterranean, where it naturally regenerates at some sites (Abad Viñas et al., 2016b).

The current distribution of the Mediterranean pines is influenced by the geological history of the Mediterranean Basin and climatic conditions during the Quaternary (Panetsos, 1981), though there were additional influences by humans. Especially the native distribution of *Pinus pinea*, and to a lesser extent of *Pinus pinaster*, is uncertain because their current distribution is highly influenced by planting, mainly in the western Mediterranean (Mazzoleni, 2004; Bonari et al., 2020). Humans have always taken advantage of the modest ecological requirements of pines and they have used them extensively in plantations for centuries (Bonari et al., 2017), although on the Iberian Peninsula most of the pine plantations were established only in the 20th century. Plantations are easily identified if they occur outside the native distribution range of the dominant pine species, but old plantations in the native range of the pine species may be difficult to distinguish from natural pine forests. Understorey species composition of pine forests varies considerably in response to many factors, including management and disturbances (Farjon & Filer, 2013; Kavgacı et al., 2017; Bonari et al., 2019a).

According to phylogenetic analyses (Gernandt et al., 2005), these four pine species (*Pinus brutia*, *Pinus halepensis*, *Pinus pinaster* and *Pinus pinea*) belong to the section *Pinus*, subsect. *Pinaster*, which has a mesogean distribution (Western Himalayas, Mediterranean region and Macaronesia), while the other European species belong to the subsect. *Pinus* or the subgenus *Strobus* (section *Quinquefoliae*). *Pinus heldreichii*, occurring in the Balkans and southern Italy, also belongs to subsect. *Pinaster* but it is a mountain pine. *Pinus halepensis* and *Pinus brutia* are more closely related to each other than to the other species of the subsect. *Pinaster*. Also, *Pinus halepensis*, *Pinus brutia* and *Pinus pinaster* show some adaptations to fire (serotinous cones, early reproductive age) lacking in *Pinus pinea*.

Besides broad overviews of forest vegetation in the Mediterranean Basin (Scarascia-Mugnozza et al., 2000; Gauquelin et al., 2018), a number of studies specifically addressed pine forest vegetation diversity in this area. Recent research focused on understanding pine forest understories and their dynamics (Zavala & Zea, 2004; Madrigal-González et al., 2010; Bonari et al., 2017), their habitat types (Bonari et al., 2018) and legislative tools for their conservation (Leone & Lovreglio, 2004). Forestry management practices in pine forests have also been in the spotlight (Granados et al., 2016; Martínez-Jauregui et al., 2018; Bonari et al., 2019a). While some studies tried to clarify the native range of pine forests (Martínez & Montero, 2004; Bonari et al., 2020), others focused on the plantations and their dynamics, for instance, the expansion of Mediterranean pines from plantations into adjacent natural non-forest plant communities (Lavi et al., 2005). Effects of pine plantations on soil, faunal communities, vegetation, biotic and abiotic gradients were also reviewed (Maestre & Cortina, 2004; Gómez-Aparicio et al., 2009).

The most important contributions to the syntaxonomy of the Mediterranean pine forests so far were made by French authors, especially Pierre Quézel and Marcel Barbéro, who performed extensive field surveys in the Mediterranean Basin from the 1970s to the 1990s. They focused mainly on the eastern Mediterranean Basin (Quézel et al., 1978), including different parts of Anatolia (Quézel & Pamukçuoğlu, 1973; Akman et al., 1978, 1979; Quézel et al., 1980), Syria (Barbéro et al., 1976), Lebanon (Chouchani et al., 1974; Abi-Saleh et al., 1976), Greece (Barbéro & Quézel, 1976) and Cyprus (Barbéro & Quézel, 1979), but also North Africa (Quézel & Barbéro, 1976; Barbéro et al., 1981; Quézel et al., 1987, 1988, 1992; Benabid, 1988) and France (Quézel & Barbéro, 1988). These contributions have created a backbone for the syntaxonomical scheme of the Mediterranean thermophilous pine forests for a long time, although significant advances have been achieved since then. The most recent comprehensive classification of European vegetation, EuroVegChecklist (Mucina et al., 2016), included the Mediterranean pine forests in the classes of broad-leaved forests, *Quercetea ilicis* and *Quercetea pubescentis*, following the established tradition (Barbéro et al., 1974; Rivas-Martínez, 1974; Quézel & Barbéro, 1986; Rivas-Martínez et al., 1986; Brullo et al., 2008).

There are open questions of paramount importance for the Mediterranean pine forests and their management, such as climate change effects, fire risk, or the dynamics of alien plant invasions. This research agenda for the near future, as well as conservation planning and management, can be significantly supported by a well-tested classification scheme for the Mediterranean pine forest types. Widely conflicting views on the syntaxonomy of the Mediterranean pine forests still exist even after the publication of EuroVegChecklist (Mucina et al., 2016) because the alliances accepted in this checklist have never been tested with a comprehensive set of vegetation-plot data. Moreover, forests dominated by Mediterranean pines were, at least in the past, not identified as independent syntaxa in spite of their distinct physiognomy and their wide distribution across the Mediterranean Basin. Due to the frequent presence of many macchia species, they were relegated into shrubland vegetation units of the order *Pistacio lentisci-Rhamnetalia alaterni*. For example, Rivas-Martínez et al. (1986) listed *Pinus halepensis* as a character species of this order. This is not consistent with the treatment of boreal or temperate pine forests which are classified in different classes than the broad-leaved forests and shrublands. This approach was partly inherited from the view of early researchers who considered the pine forests as non-climax vegetation. However, at least *Pinus brutia* and *Pinus halepensis* can form pure climax forests in a suitable climate (Feinbrun, 1959; Quézel, 2000; Boydak, 2004; Bonari et al., 2020). Another explanation lies in the fact that the native distribution of some pine species is contentious (see e.g. Martínez & Montero, 2004), and some of the extant pine forests may have originated as ancient plantations. This may be the cause for the reluctance of phytosociologists to describe syntaxa based on dominant species of uncertain origin. With increasing knowledge of the distribution of both species and communities, new syntaxonomical units of Mediterranean thermophilous pine forests were described in recent years (e.g. Pérez Latorre et al., 1998; Mucina et al., 2009; Biondi et al., 2014; Biondi & Vagge, 2015; Mucina et al., 2016; Pesaresi et al., 2017).

Currently, interest in vegetation classification and its applications is growing (Biurrun et al., 2019). The introduction of new numerical methods and formal classification approaches (De Cáceres et al., 2015) and the availability of large vegetation-plot databases (Dengler et al., 2011; Chytrý et al., 2016; Bruelheide et al., 2019) contributed to overcoming the criticism of subjectivity of the traditional Braun-Blanquet method of vegetation classification (Braun-Blanquet, 1932). This has also paved the way for synthetic international vegetation classification studies on the European scale (e.g. Douda et al., 2016; Peterka et al., 2017; Willner et al., 2017a; Marcenò et al., 2018, 2019; Landucci et al., 2020). In our case, data from the European Vegetation Archive (EVA; Chytrý et al., 2016) and from the specialized CircumMed Pine Forest Vegetation Database (Bonari et al., 2019b) made it possible to perform a detailed analysis of the Mediterranean pine forests and to accomplish the revision of their classification.

Our aim is to characterize the general diversity of pine forests in the Mediterranean Basin by providing the first comprehensive and internally consistent international classification consensus for the Mediterranean thermophilous low-elevation pine forest types at the alliance level across the Mediterranean Basin and the Black Sea region, based on an analysis of vegetation-plot data.

2 | METHODS

2.1 | Study area

The study area is the Mediterranean Basin and adjacent areas, broadly corresponding to the oceanic Mediterranean bioclimates as defined and mapped by Rivas-Martínez and Rivas Sáenz (2019) for Eurasia and North Africa. It stretches from the Atlantic coasts of Portugal to easternmost Anatolia, measuring approximately 4,300 km along its broadest longitudinal extent (9° W–42° E), and from the Caucasus to Palestine to southern Morocco, extending approximately 1,300 km along its broadest latitudinal extent (48° N–30° N). We considered all the countries bordering the Mediterranean Sea, as well as Portugal, Crimea, the Caucasus and the Euxinian region fringing the southern coast of the Black Sea. The latter three territories were included because of the disjunct native occurrence of *Pinus brutia*. In the northern part of the range of these forests, orographic features of high mountain ranges protect them from the effects of northerly winds. In addition, the proximity to the Black Sea raises air moisture and precipitation, contrasting with the arid and more continental climates of the surrounding areas. This causes the extension of the distribution range of *Pinus brutia* forests and many Mediterranean species, which reach as far north as Crimea and the foothills of the Great Caucasus (Didukh, 1992).

The physical-geographic complexity of the Mediterranean Basin needs to be taken into account when dealing with biological communities. Firstly, the Mediterranean Basin encompasses a high number of bedrock types. Limestone is by far the most common, while areas with acidic bedrock are scattered, although locally abundant. Ultramafic rock patches are also present. Bedrock diversity translates into soil diversity (Blondel et al., 2010) and thus into vegetation diversity.

Secondly, the specific Mediterranean climate is characterized by mild, wet winters and warm, dry summers. Temperatures generally increase from north to south. Mean temperatures of the summer months exceed 22 °C but are above 30 °C in some areas. Summers are characterized by the lack of rain, which in combination with high temperatures leads to marked seasonal aridity. The limited occurrence of winter frost is essential for plants. The total annual precipitation is spatially highly variable, ranging from less than 200 mm in North Africa to 2,000 mm in some northern mountainous areas (Lionello, 2012; Rundel et al., 2016).

Thirdly, numerous mountain ranges around the Mediterranean Basin show distinct elevational vegetation belts (Ozenda, 1975; Quézel, 1979; Rivas-Martínez, 1981; Blondel et al., 2010). Different pine species tend to occur at different elevations, although with some overlaps (e.g. Carrión et al., 2000). This allows a clear ecological distinction between two major groups of tree pines in the Mediterranean Basin: Mediterranean thermophilous species (*Pinus brutia*, *Pinus halepensis*, *Pinus pinaster* and *Pinus pinea*) and mountain species (*Pinus cembra*, *Pinus heldreichii*, *Pinus nigra*, *Pinus peuce*, *Pinus sylvestris* and *Pinus uncinata*). This study focuses on the former group.

2.2 | Data set and its standardization

The workflow of this study is summarized in Figure 1. We requested vegetation plots (phytosociological relevés) from EVA (Chytrý et al., 2016) from the following countries: Albania, Andorra, Austria, Belgium, Bosnia-Herzegovina, Bulgaria, Croatia, Cyprus, Czech Republic, France, Germany, Greece, Hungary, Italy, Kosovo, Luxemburg, Macedonia, Malta, Moldova, Monaco, Montenegro, The Netherlands, Poland, Portugal, Romania, San Marino, Serbia, Slovakia, Slovenia, Spain, Switzerland, Turkey, Ukraine (only the Carpathians and Crimea), North African countries (Algeria, Morocco, Tunisia), eastern Mediterranean countries (Israel, Lebanon, Syria), Georgia and Russia south of 45° N. The plots had to contain at least one of the following species (including all of their subspecies and varieties) with a cover value ≥ 15%: *Pinus brutia*, *Pinus cembra*, *Pinus halepensis*, *Pinus heldreichii*, *Pinus nigra*, *Pinus peuce*, *Pinus pinaster*, *Pinus pinea*, *Pinus sylvestris* and *Pinus uncinata*. We used a cover threshold of 15% to exclude very open vegetation with the presence of pines, but at the same time to include plots that represented forests and open pine woodlands. For a better delimitation of the vegetation types of interest, we also included vegetation with other relevant Mediterranean conifers and Mediterranean oaks (including all of their subspecies and varieties) with a cover value ≥ 30%: *Abies borisii-regis*, *Abies cephalonica*, *Abies cilicica*, *Abies marocana*, *Abies nebrodensis*, *Abies nordmanniana*, *Abies numidica*, *Abies pinsapo*, *Cedrus atlantica*, *Cedrus libani*, *Cupressus sempervirens*, *Juniperus drupacea*, *Juniperus excelsa*, *Juniperus foetidissima*, *Juniperus thurifera*, *Tetraclinis articulata*, *Quercus coccifera*, *Quercus ilex*, *Quercus rotundifolia* and *Quercus suber*. Further, we included data of the pine forest-focused CircumMed Pine Forest Vegetation Database (Bonari et al., 2019b), formerly prepared to fill the gaps in EVA in pine forest-vegetation data. We thus obtained 63,138 vegetation plots in total.

The data set contained vegetation plots sampled over several decades by many authors from different countries who used different flora

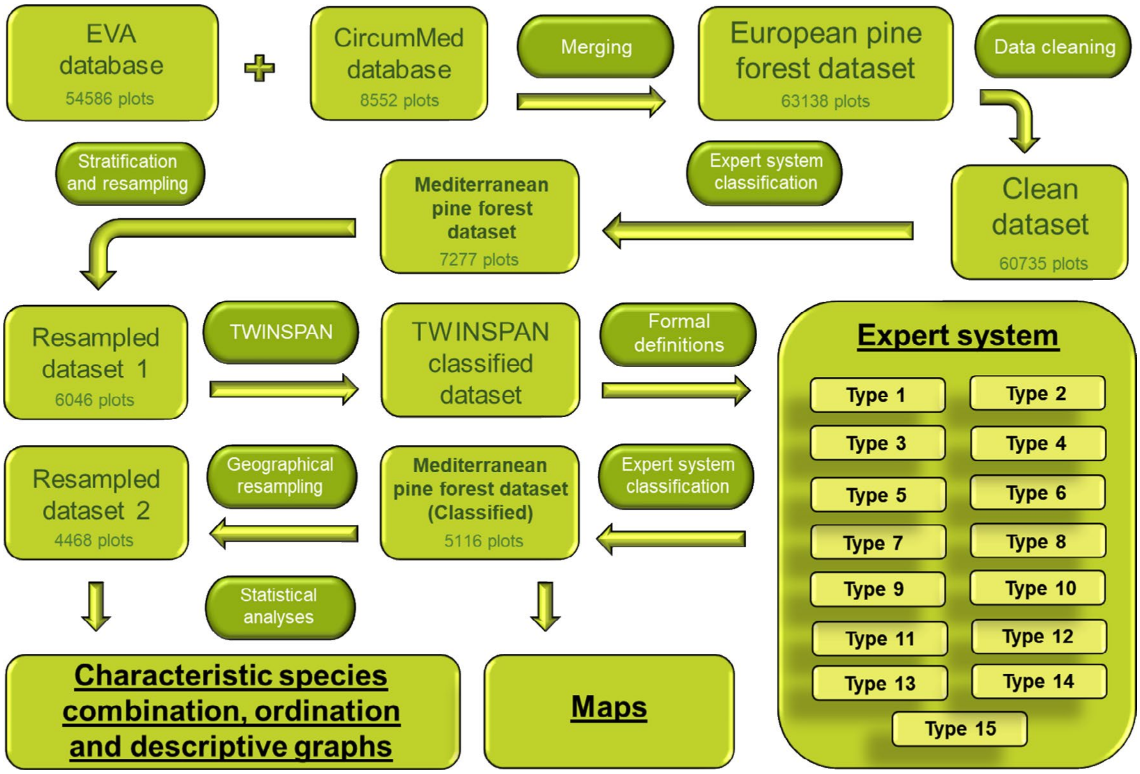

FIGURE 1 Workflow adopted in this study showing the steps from data set creation to the results (underlined), including vegetation types, characteristic species combination, maps, boxplots and elevational-density graphs. EVA = European Vegetation Archive; CircumMed database = CircumMed Pine Forest Vegetation Database; Ordination = DCA ordination superimposed with climatic variables; Plots = vegetation plots. The extraction of 5,000 random plots from the clean data set for the distinction of low-elevation pine forests from the other pine forests (see paragraph 2.2) and the classification of plots with the EUNIS expert system for the most frequent species of *Quercetea ilicis* and *Pinetea halepensis* (see paragraphs 2.4 and 3.1) are not shown in the workflow

manuals and taxon concepts. We used the SynBioSys Taxon Database in TURBOVEG 3, which matches the taxon concepts and unifies the taxon names used in different databases included in EVA (Chytrý et al., 2016). Subsequently, we adjusted the taxonomy and nomenclature to the Euro+Med PlantBase (Euro+Med, 2016–2020). The few taxa not included in Euro+Med were named according to the SynBioSys Taxon Database or using the original names given in the source publications or in individual EVA databases. The taxa recorded with different taxonomic resolution were merged into aggregates (e.g. *Achillea millefolium* aggr., *Centaurea alba* aggr., *Draba verna* aggr., *Galium mollugo* aggr.). Pines were considered at the species level because subspecies were not always identified in the data set. Also, especially for *Pinus pinaster*, there is no taxonomic agreement among authors about its subspecies.

Further, we reduced the noise and inconsistencies in the data as follows: (1) bryophytes, lichens and algae were excluded, because they were present only in a subset of vegetation plots; (2) infraspecific taxa were merged into species; (3) species with less than five occurrences in the data set were deleted; (4) tree and shrub species recorded in the herb layer or marked as seedlings or juveniles were deleted; (5) records of the same species in different layers were merged into a single layer; (6) vegetation plots with a size <50 m^2 or >1,000 m^2 were excluded, but plots without size information were retained assuming that most of them were within this size range. These steps created a data set of 60,735 vegetation plots. The data cleaning was done using the JUICE program v. 7.1 (Tichý, 2002).

To test the differentiation between the Mediterranean thermophilous and non-thermophilous pine forests, and between Mediterranean pine forests and Mediterranean oak forests, we performed an unsupervised classification of the whole data set using TWINSPAN (Hill, 1979; parameters: three pseudospecies cut levels of species percentage cover: 0%, 10%, 25%; minimum group size for division: 10 plots) on a subset of 5,000 plots that were randomly chosen to meet the technical limit of the number of plots that the TWINSPAN program could process. The result is shown in Table 1. Column 1 of this table groups Mediterranean lowland to submontane pine forests (with *Pinus brutia*, *Pinus halepensis*, *Pinus pinaster* and *Pinus pinea*), oak forests (42% constancy of *Quercus ilex*) and other Mediterranean forests. These forests strongly differ from the northern and mountain pine forests. Only *Pinus nigra* has a transitional distribution between these two groups, but it is more mountainous than the four thermophilous pines. The analysis gives support to the separation in the first division between the Mediterranean thermophilous pine forests and the other pine forests, but not to the separation between Mediterranean pine vs. oak forests (Tables 1 and 2). The floristic criterion used by TWINSPAN does not support this division, which can nevertheless

TABLE 1 Shortened synoptic table showing the result of a TWINSPAN classification into two groups of a random selection of 5,000 plots from the initial data set of the Mediterranean pine forest and their related forest types including evergreen oak forests; the numbers in columns 1 and 2 are percentage constancies and points represent species absence; the species shown include the pine species and five other species with the highest value of the phi coefficient (Φ) for one of the two groups; grey shading represents species with $\Phi > 0.2$, Constancy Ratio (CR) > 1.5 and $p < 0.05$ (based on Fisher's exact test)

Group	No. of plots	1	2
No. of plots		2,062	2,938
Species			
Pinus halepensis	422	20	.
Pinus pinaster	248	11	.
Pinus brutia	190	9	.
Pinus pinea	101	5	.
Pinus sylvestris	248	1	83
Pinus nigra	591	9	14
Pinus uncinata	91	.	3
Pinus mugo aggr.	59	.	2
Pinus cembra	59	.	2
Pinus heldreichii	25	.	1
Pinus peuce	19	1	1
Pinus × rhaetica	8	.	1
Rubia peregrina	102	48	1
Quercus ilex	898	42	1
Asparagus acutifolius	679	33	1
Smilax aspera	633	31	1
Phillyrea latifolia	605	29	1
Vaccinium myrtillus	127	.	43
Avenella flexuosa	120	1	41
Sorbus aucuparia	111	1	38
Quercus robur	108	1	36
Betula pendula	907	1	31

be based on the stand physiognomy (dominance of conifers vs. broad-leaved evergreen trees).

2.3 | Mediterranean thermophilous low-elevation pine-forest data set and resampling

As the TWINSPAN classification showed that the vegetation of forests dominated by the four low- to mid-elevation Mediterranean pines (*Pinus brutia*, *Pinus halepensis*, *Pinus pinaster* and *Pinus pinea*) differs from the mountain and temperate forests dominated by other pine species (paragraph 2.2), we analysed these forests separately (hereafter for short referred to as Mediterranean pine forests). From the total data set of 60,735 vegetation plots, we selected those in which the total cover of the four Mediterranean pine species was greater than or equal to 15% and exceeded the total cover of the other trees. Where information was available, we excluded vegetation plots sampled in recent plantations located clearly out of the alleged native distribution range of the dominant pine species, while we retained those from putative old-established plantations. Note that it is often not possible to separate native stands from old plantations, especially in the Mediterranean Basin where humans have been changing the landscape for millennia. Delineating what is natural and what is not is even more complicated when working with large vegetation-plot databases, in which more detailed information on individual plots is often missing. The selection resulted in a data set of 7,277 Mediterranean pine forest plots (Figure 2). The contributions from individual databases are reported in Appendix S1.

At this stage, we removed 381 plots with no coordinates. Vegetation plots with available coordinates ($n = 6,896$; Figure 2) were assigned to cells of a geographic grid of 0.6 longitudinal by 0.45 latitudinal minutes, i.e. approximately 50 km × 50 km in the central part of the study area. Subsequently, we performed a geographical resampling in order to overcome the bias due to uneven sampling density across the study area (Knollová et al., 2005). We resampled cells with more than 10 plots per grid cell. This operation removed 650 vegetation plots. In the grid cells that contained more than ten plots, we applied the Heterogeneity-Constrained Random (HCR) resampling algorithm (Lengyel et al., 2011) calculated with Bray–Curtis dissimilarity in plot species composition. This procedure guaranteed that the resampled data set contained, within each cell, plots that were representative of the variation in species composition within that cell. This operation removed 200 vegetation plots. The final data set was a matrix of 6,046 plots and 3,190 taxa (hereafter called “resampled data set” and “Resampled data set 1” in Figure 1). Resampling was performed using JUICE v. 7.1 (Tichý, 2002).

2.4 | Classification and determination of diagnostic species

First, unsupervised divisive classification of the resampled data set was performed using TWINSPAN (Hill, 1979; parameters: three pseudospecies cut levels of species percentage cover: 0%, 10%, 25%; minimum group size for division: 10 plots). Four division levels were used, resulting in 16 clusters. This operation allowed us to understand the coarse patterns of floristic similarity within our data set. With a few exceptions, each cluster contained plots dominated by a single pine species. When no ecologically or biogeographically interpretable dissimilarities in species composition between clusters were found, these clusters were merged. We also interpreted all the clusters syntaxonomically, comparing their floristic, ecological and biogeographical characteristics with the literature. The aim was to identify previously described alliances in our TWINSPAN groups. When the analysis supported the concepts proposed in the literature, we accepted those concepts, meaning that we took a conservative approach. When establishment of a new vegetation unit appeared to be necessary, we considered not

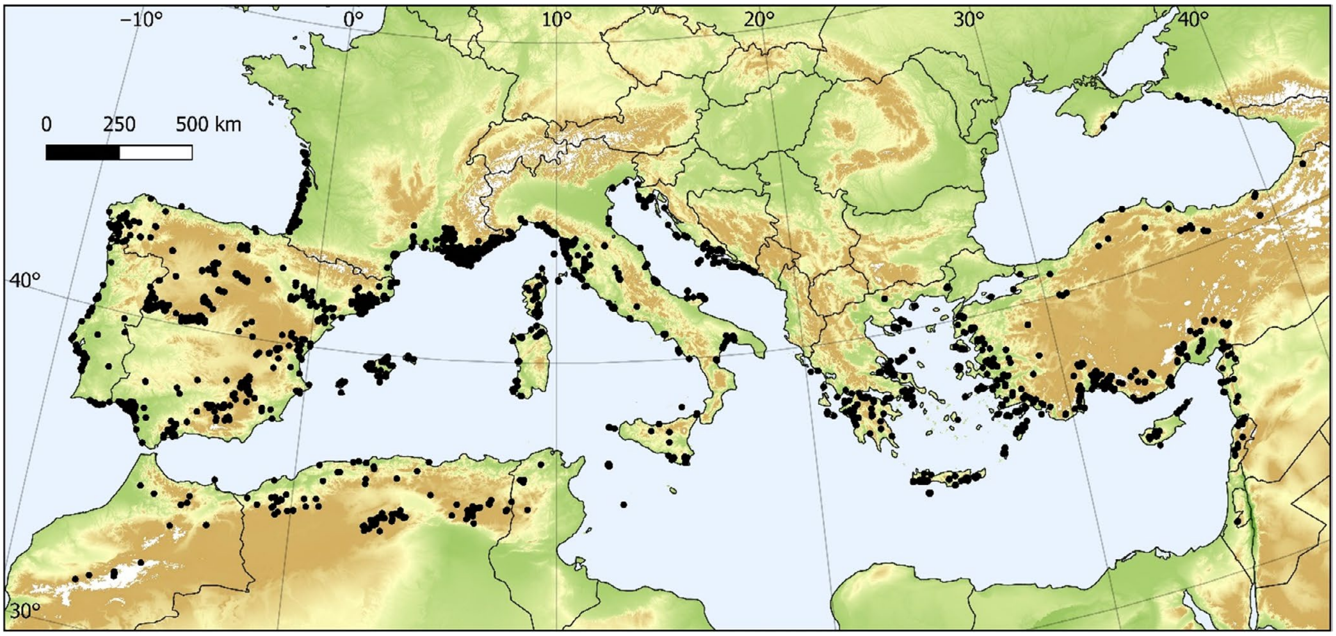

FIGURE 2 A map of 6,896 vegetation plots used in this study. Each of them is dominated by one of the four Mediterranean thermophilous low-elevation pines (*Pinus brutia*, *Pinus halepensis*, *Pinus pinaster*, *Pinus pinea*). Plots with no coordinates ($n = 381$) are not shown

only floristical but also ecological and biogeographical differences from the already established units. We also accepted two types (see paragraphs 3.1.3 and 3.1.4) that did not appear as distinct clusters in the TWINSPAN classification, given the scarcity of plots of these types in the database. We defined them by means of the expert system only. All the analyses were performed in JUICE v. 7.1 (Tichý, 2002). Phytosociological nomenclature is in agreement with the fourth edition of the International Code of Phytosociological Nomenclature (ICPN; Theurillat et al., 2021).

Formal definitions of syntaxa provide reproducible and unambiguous classification (e.g. Chytrý et al., 2020). We prepared formal definitions of the interpreted alliances and informal vegetation types based on the concept of functional species groups (Landucci et al., 2015; Tichý et al., 2019) linked by the logical operators AND, OR and NOT as proposed by Bruelheide (1997). Diagnostic species, determined based on the calculation of the phi coefficient of association (Φ), were calculated for the TWINSPAN-based clusters and used to create the functional species groups and discriminating species groups to be used in the formal definitions. Some of these groups were improved by adding a few species on the basis of expert knowledge. The phi coefficient of association was used as a fidelity measure and calculated for equalized size of clusters following Tichý and Chytrý (2006). We included formal definitions into a classification expert system that is available as TXT file (Appendix S2; for acronyms of vegetation types see paragraphs 3.1.1–3.1.15) and can be run in JUICE v. 7.1 (Tichý, 2002), TURBOVEG 3 (Hennekens, 2015) or R (Bruelheide et al., https://git.loe.auf.uni-rostock.de/misc/ESy)

We determined diagnostic species of individual alliances based on the data set resampled within grid cells defined as above, but this time nested within alliances ("Resampled data set 2" in Figure 1), meaning that unlike in the "Resampled data set 1," where the geographical resampling was applied to the whole matrix, here this operation was done within the defined alliances to produce reliable diagnostic species. For each alliance or informal group, we resampled cells with more than 10 plots per grid cell. We defined diagnostic species for a particular vegetation type as species with $\Phi \geq 0.2$, Fisher's exact test p value of the probability of the given concentration of species occurrences within the cluster < 0.05 and Constancy Ratio > 1.5. Constancy Ratio is the ratio between species constancy (relative frequency) in the cluster for which the species has the highest constancy and the maximum constancy recorded in any other cluster (Willner et al., 2017b). We defined constant species as those with relative frequency $> 20\%$ and dominant species as those occurring in at least 5% of plots with a cover $> 15\%$.

Based on "Resampled data set 2," we also prepared the ordination diagram, the elevational-density graph and the boxplots for the recognized alliances and informal groups.

To assess differences in species composition between Mediterranean pine forests and Mediterranean broad-leaved forests, we extracted 1,534 plots classified as "T3A Mediterranean lowland to submontane *Pinus* forest" and 2,826 vegetation plots as "T21 Mediterranean evergreen *Quercus* forest" from the EVA database classified by the EUNIS Habitat Classification expert system (EUNIS-ESy v. 2020-06-08; Chytrý et al., 2020). These two habitat types correspond to the classes *Pinetea halepensis* and *Quercetea ilicis*, respectively. We identified the species with the highest frequency and calculated their phi coefficient of association for these two habitat types.

All the procedures described in this section were performed using JUICE v. 7.1 (Tichý, 2002).

2.5 | Ordination

To relate the differentiation of the accepted alliances to climate, DCA ordination (Hill & Gauch, 1980) of plots was computed with log-transformed percentage covers of species using the *vegan* package (v. 2.5-6; Oksanen et al., 2019) in R (v. 3.6.1; R Core Team, 2019). Individual plot coordinates were overlaid with the CHELSA Bioclim data set v. 1.2 (Karger et al., 2017) using the "envfit" function of the *vegan* package. Climatic data consist of a downscaled model output with temperature and precipitation estimates at a horizontal resolution of 30 arc-seconds (Karger & Zimmermann, 2019). Correlations between 19 climatic variables were calculated using the Spearman correlation coefficient (Sokal & Rohlf, 1995) to reduce the number of available variables. We retained only those variables that were most clearly interpretable from an ecological point of view: mean annual temperature, temperature seasonality (standard deviation of the monthly mean temperatures), annual precipitation and precipitation seasonality (standard deviation of the monthly precipitation estimates expressed as a percentage of the annual mean). The four climatic variables were extracted from vegetation plots with help of the *raster* package (v. 3.1-5; Hijmans, 2020) using the bilinear method. Apart from the DCA, we displayed the climatic variables in boxplots for each accepted alliance and informal group.

3 | RESULTS

We interpreted TWINSPAN clusters mainly at the fourth hierarchical level of division (Figure 3) based on species composition, geographic distribution and literature. The first TWINSPAN division mainly separated the eastern and western Mediterranean pine forest communities, suggesting a biogeographic distinction between them. The divisions at the second and third hierarchical levels were mainly based on the dominance of different species of pines and elevational differences, respectively, with partial overlaps between some clusters.

Overall, we recognized 12 alliances and three informal groups of communities of supposedly native forests, including old-established plantations in the TWINSPAN clusters on the third and fourth level of division. A large majority of them were associated with the dominance of one of the four low-elevation Mediterranean pine species (*Pinus brutia*, *Pinus halepensis*, *Pinus pinaster*, *Pinus pinea*). One alliance (*Sarcopoterio spinosi-Pinion halepensis*) was identified at the fifth hierarchical level and is not shown in Figure 3. Also, it is worth mentioning that although many species of *Quercetea pubescentis* are present in the plots from the coastal areas of the northern Black Sea, TWINSPAN did not separate these plots, most likely due to their very low proportion in the data set. Therefore, these two small clusters (*Jasmino fruticantis-Juniperion excelsae* and *Campanulo sibiricae-Pinion brutiae*) represented by a few plots were separated in the expert system. However, most of the TWINSPAN clusters were accepted, either stand-alone or merged, as alliances or informal groups. When a given cluster was split in more than one accepted alliance/informal group, we used the expression "*pro parte*" ("p.p."). In contrast, we used the symbol "+" when we merged two clusters.

The diagnostic, constant and dominant species for each accepted cluster after TWINSPAN classification are shown in Appendix S3. For completeness, we also report the two clusters from Crimea and the Great Caucasus foothills in this Appendix.

3.1 | Vegetation types

We classified vegetation plots using the newly created classification expert system for the low-elevation Mediterranean pine forests. We also defined within the expert system the formulas for Crimean and Caucasian *Pinus brutia* forests. The expert system included 15 logical definitions of accepted alliances and other vegetation types. We applied this expert system to the non-resampled data set. The distribution of the plots classified as 12 accepted alliances and three informal groups is shown in Figure 4, along with the supposedly native distribution of the dominant pine species. Shortened lists of diagnostic species are shown in Table 2, while all the diagnostic, constant and dominant species for each alliance and the informal group of communities, based on the plots classified by the expert system, are listed in Appendix S4. Photos of typical stands of each alliance are provided in Figure 5. The alliances and informal groups are presented following the alphabetical order of the dominant pine species. Moreover, the floristic differences between Mediterranean thermophilous pine forests and evergreen oak forests are presented in Table 3. We include these forest in a new class and a previously described order:

Pinetea halepensis* Bonari et M. Chytrý *cl. nov.

Nomenclatural type (*holotypus*): *Pinetalia halepensis* Biondi, Blasi, Galdenzi, Pesaresi et Vagge in Biondi et al. 2014 (Biondi et al., 2014, p. 330)

Diagnostic species of the class: *Pinus brutia*, *Pinus halepensis*, *Pinus pinaster*, *Pinus pinea*.

***Pinetalia halepensis* Biondi, Blasi, Galdenzi, Pesaresi et Vagge in Biondi et al. 2014**

Nomenclatural type: *Pistacio lentisci-Pinion halepensis* Biondi, Blasi, Galdenzi, Pesaresi et Vagge in Biondi et al. 2014

3.1.1 | Thermo- to mesomediterranean *Pinus brutia* forests

***Pinion brutiae* Feinbrun 1959**

Acronym: Pin-Bru; Figures 4; 5a; 6; 7; Clusters 1 + 2

Nomenclatural type (*holotypus*): *Pinetum brutiae libanoticum* Feinbrun 1959

Synonyms: *Gonocytiso pterocladi-Pinion brutiae* Barbéro, Chalabi, Nahal et Quézel ex Quézel et al. 1993 *nom. inval.* [ICPN Art. 2b]; *Ptosimopappo-Quercion microphyllae* Barbéro, Chalabi, Nahal et

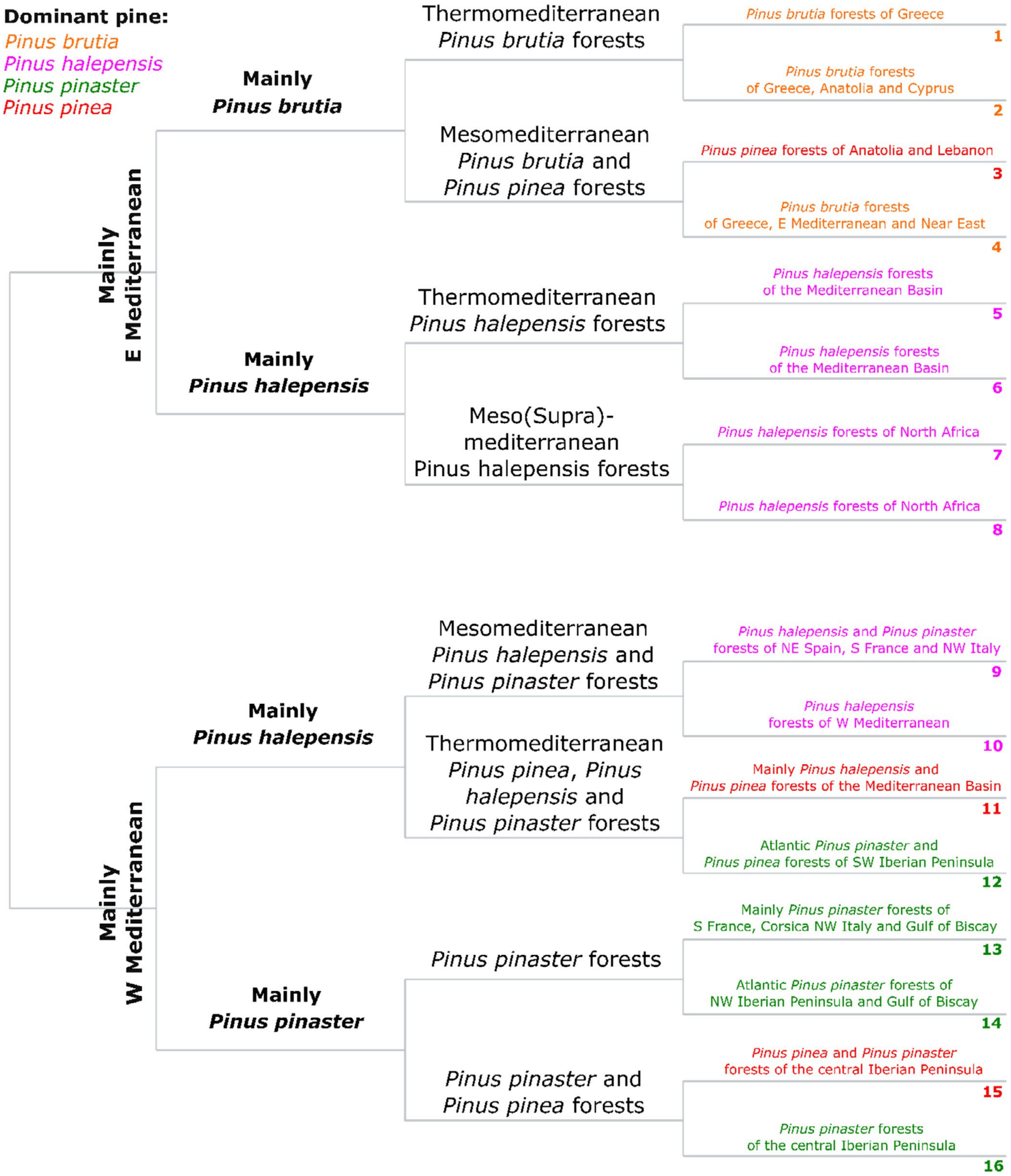

FIGURE 3 TWINSPAN dendrogram up to the fourth hierarchical level of division. In colour (right) the code of the TWINSPAN cluster (from 1 to 16) is given. The cluster approximately corresponding to *Sarcopoterio spinosi-Pinion halepensis* identified at a lower hierarchical level (i.e. within cluster 5) is not shown, as well as the Crimean and northwestern Caucasian clusters approximately corresponding to *Jasmino fruticantis-Juniperion excelsae* and *Campanulo sibiricae-Pinion brutiae* (within cluster 4)

Quézel ex Quézel et al. 1993 *nom. inval.* [ICPN Art. 2b]; *Salvio fruticosae-Pinion brutiae* Konstantinidis, Mucina et Bergmeier in Mucina et al. 2016 *nom. inval.* [ICPN Art. 5, 8].

Nomenclature comments: The invalid alliance names referred to in synonymy were proposed on the basis of geographical or lithological differences: calcareous or volcanic substrates in the

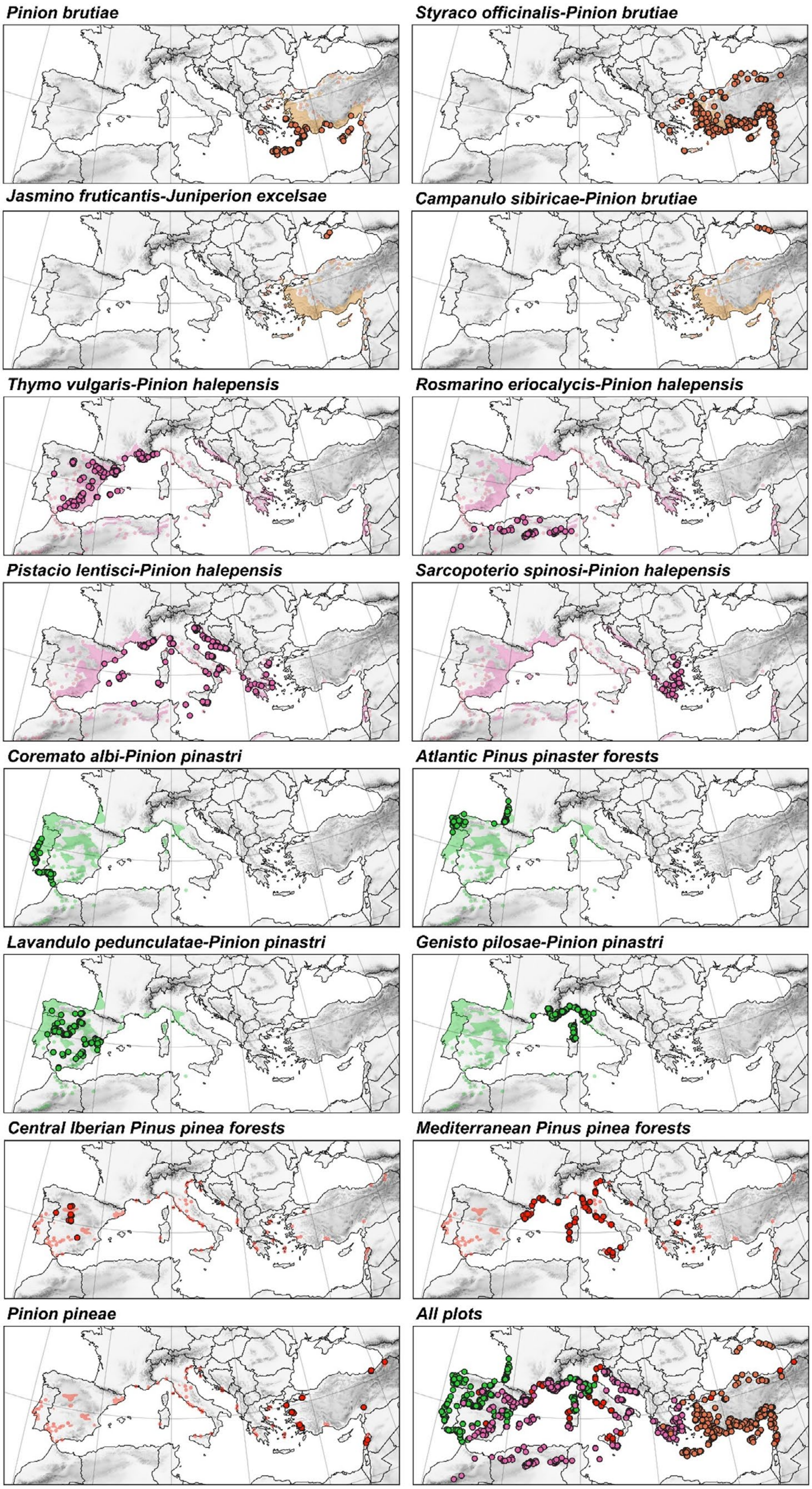

FIGURE 4 Distribution maps based on the plots assigned to alliances or informal groups of communities by the expert system ($n = 5,116$). The shaded area represents the supposed native distribution of the dominant pine species (from Caudullo et al., 2017), while dots show the position of the classified vegetation plots (orange: *Pinus brutia*; violet: *Pinus halepensis*; green: *Pinus pinaster*; red: *Pinus pinea*)

TABLE 2 Shortened synoptic table of the percentage constancies of the diagnostic and most frequent species for the vegetation plots classified at the alliance level by the expert system and geographically resampled within each alliance; diagnostic species are sorted by decreasing values of the phi coefficient (Φ) for each alliance; only species with $\Phi > 0.2$, Constancy Ratio (CR) > 1.5 and $p < 0.05$ (based on Fisher's exact test) are shown, indicated by grey shading; pines are shown at the top of the table, while non-diagnostic species with more than 300 occurrences across the whole table are reported at the bottom; the points represent species absence; see Appendix S4 for the full version of this table. See paragraphs 3.1.1–3.1.15 for alliance acronyms

Alliance	Pin-Bru	Sty-Bru	Jas-Jun	Cam-Bru	Thy-Hal	Ros-Hal	Pis-Hal	Sar-Hal	Cor-Psr	Atl-Psr	Lav-Psr	Gen-Psr	Cen-Pna	Med-Pna	Pin-Pna
No. of plots	341	1,030	12	6	239	86	494	130	140	117	650	725	81	323	94
Pines															
Pinus brutia	100	100	100	100	.	.	.	.	.	.	.	.	.	.	18
Pinus halepensis	.	1	.	.	100	100	100	100	2	.	2	14	.	2	.
Pinus pinaster	.	.	.	.	5	.	2	.	36	100	100	100	12	3	.
Pinus pinea	.	1	.	.	4	.	1	.	89	.	1	1	100	100	100
Pinion brutiae															
Asperula rigida	21	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Phlomis lanata	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Scorzonera cretica	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Teucrium microphyllum	18	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lamyropsis cynaroides	20	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Cistus parviflorus	15	.	.	.	.	.	.	2	.	.	.	.	.	.	.
Salvia fruticosa	33	3	.	.	.	.	1	5	.	.	.	.	.	.	3
Cupressus sempervirens	18	4	.	.	.	.	3	1	.	.	.	.	.	1	.
Vicia cretica	11	1	.	.	.	.	.	2	.	.	.	.	.	.	.
Satureja thymbra	33	3	.	.	.	.	.	9	.	.	.	.	.	.	2
Asphodelus ramosus	31	3	.	.	.	.	6	9	1	.	1	3	.	5	.
Leontodon tuberosus	33	3	.	.	.	1	2	10	.	1	.	1	2	1	2
Scaligeria napiformis	26	1	.	.	.	.	1	10	.	.	.	.	.	.	.
Lithodora hispidula	22	9	.	.	.	.	.	.	.	.	.	.	.	.	.
Drimia maritima aggr.	54	4	.	.	1	.	10	12	11	.	5	.	23	.	1
Thymbra capitata	35	2	.	.	.	.	10	18	.	.	.	.	.	1	15
Sonchus bulbosus	30	5	.	.	1	.	7	4	5	.	.	1	.	15	2
Phagnalon rupestre	23	2	.	.	1	.	5	12	.	.	.	.	.	.	.
Calicotome villosa	27	9	.	.	.	3	8	6	2	.	.	1	.	8	17
Rhamnus lycioides	30	7	.	.	8	1	2	1	19	.	.	.	4	.	6
Piptatherum coerulescens	19	13	.	.	.	.	1	12	.	.	.	.	.	.	5
Ceratonia siliqua	14	5	.	.	.	.	11	1	1	.	.	.	.	.	1
Rubia tenuifolia	16	9	.	.	.	.	.	13	.	.	.	.	.	.	.
Styraco officinalis-Pinion brutiae															
Eryngium falcatum	1	18	.	.	.	.	.	.	.	.	.	.	.	.	.
Quercus cerris	.	16	.	.	.	.	.	.	.	.	.	3	.	3	1
Styrax officinalis	7	40	.	.	.	.	.	.	.	.	.	.	.	.	12
Daphne sericea	3	12	.	.	.	.	.	.	.	.	.	.	.	2	4
Quercus infectoria	1	30	.	.	.	.	.	.	.	.	.	.	.	.	13
Lathyrus aphaca	5	13	.	.	.	.	1	7	.	.	1	1	.	1	1
Crucianella latifolia	9	13	.	.	.	.	1	5	.	.	.	.	.	.	.

(Continues)

TABLE 2 (Continued)

Alliance	Pin-Bru	Sty-Bru	Jas-Jun	Cam-Bru	Thy-Hal	Ros-Hal	Pis-Hal	Sar-Hal	Cor-Psr	Atl-Psr	Lav-Psr	Gen-Psr	Cen-Pna	Med-Pna	Pin-Pna
Jasmino fruticantis-Juniperion excelsae															
Jurinea ledebourii	.	.	92	.	.	.	.	.	.	.	.	.	.	.	.
Elymus nodosus	.	.	92	.	.	.	.	.	.	.	.	.	.	.	.
Linum austriacum	.	.	67	.	.	.	.	.	.	.	.	1	.	.	.
Thymus roegneri	.	.	42	.	.	.	.	.	.	.	.	.	.	.	.
Asparagus verticillatus	.	.	42	.	.	.	.	.	.	.	.	.	.	.	.
Odontarrhena tortuosa	.	.	33	.	.	.	.	.	.	.	.	.	.	.	.
Pistacia atlantica	.	1	42	.	.	.	.	.	.	.	.	.	.	.	.
Bromopsis cappadocica	.	.	33	.	.	.	.	.	.	.	.	.	.	.	.
Galatella villosa	.	.	25	.	.	.	.	.	.	.	.	.	.	.	.
Seseli dichotomum	.	.	25	.	.	.	.	.	.	.	.	.	.	.	.
Veronica multifida	.	1	42	.	.	.	.	.	.	.	.	.	.	.	.
Centaurea diffusa	.	.	50	.	.	1	.	.	.	.	.	.	.	.	.
Fumana procumbens	.	.	58	.	1	.	.	.	.	.	1	2	.	1	.
Inula ensifolia	.	.	58	.	.	.	.	.	.	.	.	.	.	.	2
Juniperus excelsa	.	4	42	.	.	.	.	.	.	.	.	.	.	.	.
Melica ciliata	1	1	33	.	.	.	.	3	.	.	1	1	2	.	3
Fumana arabica	12	6	83	.	.	.	2	6	.	.	.	.	.	.	2
Poa sterilis	.	.	75	17	.	.	.	.	.	.	.	.	.	.	.
Jasminum fruticans	1	10	42	.	1	3	1	.	.	.	.	1	.	.	.
Linum strictum aggr. (incl. *L. corymbulosum*)	9	2	33	.	3	5	5	5	.	.	1	1	.	1	5
Achnatherum bromoides (incl. *A. fallacinum*)	16	27	100	17	1	.	6	31	.	.	1	1	.	6	27
Teucrium polium aggr.	6	20	75	17	22	5	6	25	.	.	2	7	5	7	17
Teucrium chamaedrys	1	18	100	33	13	2	3	3	.	.	2	30	1	11	6
Galium biebersteinii	.	.	50	17	.	.	.	.	.	.	.	.	.	.	.
Bothriochloa ischaemum	.	1	25	.	1	.	.	.	.	.	.	1	.	1	9
Carex flacca	7	14	58	33	17	.	6	13	1	.	1	18	.	13	1
Carex halleriana	8	2	50	17	29	19	8	6	.	.	2	17	1	5	.
Salvia officinalis	.	9	17	.	10	.	2	.	.	.	1	.	1	.	4
Ruscus aculeatus	1	15	42	33	.	.	29	5	6	15	1	3	.	22	14
Rhus coriaria	.	3	17	17	.	.	.	.	.	.	1	.	.	.	9
Convolvulus cantabrica	.	2	17	17	2	.	2	2	.	.	.	2	.	2	4
Campanulo sibiricae-Pinion brutiae															
Sesleria alba	.	1	.	83	.	.	.	.	.	.	.	.	.	.	.
Echinops sphaerocephalus	.	.	.	67	.	.	.	.	.	.	.	.	.	.	.
Astragalus cicer	.	.	.	33	.	.	.	.	.	.	.	.	.	.	.
Hedera colchica	.	1	.	33	.	.	.	.	.	.	.	.	.	.	.
Argyrolobium biebersteinii	.	1	.	33	.	.	.	.	.	.	.	.	.	.	.
Smilax excelsa	.	1	.	33	.	.	.	.	.	.	.	.	.	.	.

(Continues)

TABLE 2 (Continued)

Alliance	Pin-Bru	Sty-Bru	Jas-Jun	Cam-Bru	Thy-Hal	Ros-Hal	Pis-Hal	Sar-Hal	Cor-Psr	Atl-Psr	Lav-Psr	Gen-Psr	Cen-Pna	Med-Pna	Pin-Pna
Paeonia mascula	.	1	.	33	.	.	.	.	.	.	.	.	.	.	.
Tanacetum corymbosum	.	.	.	67	.	.	.	.	.	.	1	3	.	1	.
Lonicera caprifolium	.	1	.	33	.	.	3	.	.	.	.	.	.	2	.
Carpinus orientalis	.	4	8	83	.	.	1	.	.	.	.	.	.	.	4
Clinopodium nepeta	.	1	.	33	2	.	1	2	1	.	1	1	.	4	1
Physospermum cornubiense	.	1	.	33	.	.	1	.	.	.	4	3	.	.	.
Epipactis helleborine aggr.	.	3	.	33	1	2	.	.	.	.	2	5	.	1	.
Brachypodium pinnatum	.	4	.	50	.	.	2	.	.	.	1	8	.	1	4
Sonchus asper	.	1	.	33	.	.	1	2	.	.	1	.	.	4	5
Medicago falcata	.	.	8	50	.	.	.	.	.	.	.	2	.	.	1
Viola alba	.	1	.	67	1	.	1	1	.	.	1	14	.	4	.
Bituminaria bituminosa	7	6	.	67	15	.	4	2	.	.	6	11	6	3	14
Coronilla coronata	.	.	8	33	.	.	.	.	.	.	.	.	.	.	.
Stachys recta	.	.	8	33	.	.	2	3	.	.	.	10	.	1	.
Clematis vitalba	.	1	.	33	1	.	1	.	.	.	1	10	.	4	4
Brachypodium sylvaticum	1	9	.	50	.	.	2	8	.	1	12	6	.	22	.
Hedera helix	1	3	.	67	.	.	9	.	.	29	2	20	.	31	.
Thymo vulgaris-Pinion halepensis															
Stipa juncea	.	.	.	.	14	.	.	.	.	.	.	.	.	.	.
Thymelaea tinctoria	.	.	.	.	15	.	.	.	.	.	.	.	.	.	.
Centaurea linifolia	.	.	.	.	13	.	.	.	.	.	.	.	.	.	.
Helianthemum marifolium	.	.	.	.	13	.	.	.	.	.	.	.	.	.	.
Bupleurum fruticescens	.	.	.	.	26	.	.	.	.	.	1	.	.	.	.
Fumana ericoides	.	1	.	.	27	1	1	2	.	.	1	2	.	2	.
Globularia vulgaris	.	.	.	.	15	.	.	.	.	.	1	1	.	1	.
Genista scorpius	.	.	.	.	34	.	.	.	.	.	4	1	.	2	.
Lavandula latifolia	.	.	.	.	37	.	.	.	.	.	5	2	.	1	.
Staehelina dubia	.	.	.	.	37	1	.	.	.	.	2	6	1	1	.
Koeleria vallesiana	.	.	.	.	23	.	.	.	.	.	2	1	4	1	.
Bupleurum rigidum	.	.	.	.	13	1	.	.	.	.	2	.	1	1	.
Coris monspeliensis	.	.	.	.	27	.	.	.	.	.	1	6	.	2	.
Festuca ovina aggr.	.	1	.	.	12	.	.	.	.	.	.	3	.	1	.
Argyrolobium zanonii	.	.	.	.	24	1	.	.	.	.	1	9	.	1	.
Helictochloa bromoides	.	.	.	.	46	2	1	.	.	.	3	20	.	5	.
Erica multiflora	.	.	.	.	21	1	11	.	.	.	1	1	.	7	.
Polygala rupestris	.	1	.	.	11	6	.	.	.	.	.	.	.	.	.
Helichrysum stoechas	19	1	.	.	33	3	2	8	4	.	16	14	10	12	3
Cistus albidus	.	.	.	.	24	2	2	.	1	.	2	14	1	2	.

(Continues)

TABLE 2 (Continued)

Alliance	Pin-Bru	Sty-Bru	Jas-Jun	Cam-Bru	Thy-Hal	Ros-Hal	Pis-Hal	Sar-Hal	Cor-Psr	Atl-Psr	Lav-Psr	Gen-Psr	Cen-Pna	Med-Pna	Pin-Pna
Linum suffruticosum aggr.	.	.	.	.	24	5	.	.	.	.	2	15	1	1	.
Ononis minutissima	.	.	.	.	20	.	1	.	.	.	.	13	.	1	.
Rosmarino eriocalycis-Pinion halepensis															
Rosmarinus eriocalyx	.	.	.	.	.	62	.	.	.	.	.	.	.	.	.
Thymus munbyanus	.	.	.	.	.	30	.	.	.	.	.	.	.	.	.
Centaurea boissieri	.	.	.	.	.	26	.	.	.	.	1	.	.	.	.
Helianthemum virgatum	.	.	.	.	.	13	.	.	.	.	.	.	.	.	.
Odontarrhena alpestris	.	.	.	.	.	15	.	.	.	.	.	.	.	.	.
Bombycilaena discolor	.	.	.	.	.	19	.	.	.	.	.	.	.	.	.
Bupleurum atlanticum	.	.	.	.	.	13	.	.	.	.	.	.	.	.	.
Ebenus pinnata	.	.	.	.	.	12	.	.	.	.	.	.	.	.	.
Catapodium marinum	.	.	.	.	.	24	1	.	.	.	.	.	.	1	.
Eruca vesicaria	.	.	.	.	1	19	.	.	.	.	.	.	.	.	.
Arabis nova	.	1	.	.	.	33	.	.	.	.	1	.	.	.	.
Alyssum granatense	.	.	.	.	1	12	.	.	.	.	1	.	.	.	.
Macrochloa tenacissima	.	.	.	.	5	63	.	.	.	.	1	.	1	.	.
Anisantha rubens	1	1	.	.	1	26	1	2	.	.	.	.	2	.	.
Hornungia petraea	.	1	.	.	2	13	.	.	.	.	1	.	.	.	.
Teucrium pseudochamaepitys	.	.	.	.	2	15	.	.	.	.	1	.	2	.	.
Cistus clusii	.	.	.	.	5	26	1	.	.	.	1	.	2	1	.
Filago pyramidata	1	1	.	.	1	17	.	1	.	.	.	.	4	1	.
Helianthemum cinereum	.	.	.	.	10	45	.	.	.	.	1	.	6	.	.
Globularia alypum	2	1	.	.	14	48	6	8	.	.	1	1	.	.	3
Paronychia argentea	.	.	.	.	.	14	.	.	.	.	1	.	6	.	.
Ampelodesmos mauritanicus	.	.	.	.	1	21	13	.	.	.	.	1	.	7	.
Pistacio lentisci-Pinion halepensis															
Teucrium fruticans	.	.	.	.	1	.	11	.	1	.	1	.	.	1	.
Viburnum tinus	.	.	.	.	.	.	21	1	.	.	4	2	.	5	.
Allium subhirsutum	4	.	.	.	.	.	15	2	.	.	.	1	.	4	.
Myrtus communis	10	19	.	.	.	.	52	1	15	.	1	19	.	19	1
Cistus monspeliensis	.	.	.	.	8	.	28	4	4	.	1	7	.	14	.
Lonicera implexa	.	1	.	.	1	3	39	17	1	.	2	20	.	16	.
Asparagus acutifolius	15	29	.	.	1	7	72	27	20	.	4	10	30	46	28
Smilax aspera	17	21	.	.	1	.	61	25	14	.	1	27	.	39	9
Sarcopoterio spinosi-Pinion halepensis															
Cyclamen graecum	1	.	.	.	.	.	1	34	.	.	.	.	.	.	.
Helictotrichon convolutum	1	1	.	.	.	.	1	22	.	.	.	.	.	.	.
Phlomis fruticosa	4	3	.	.	.	.	.	16	.	.	.	.	.	.	.
Luzula nodulosa	5	3	.	.	.	.	.	17	.	.	.	.	.	.	.

(Continues)

TABLE 2 (Continued)

Alliance	Pin-Bru	Sty-Bru	Jas-Jun	Cam-Bru	Thy-Hal	Ros-Hal	Pis-Hal	Sar-Hal	Cor-Psr	Atl-Psr	Lav-Psr	Gen-Psr	Cen-Pna	Med-Pna	Pin-Pna
Anthyllis hermanniae	13	1	.	.	.	.	2	45	.	.	.	1	.	.	13
Crepis fraasii	13	2	.	.	.	.	.	23	.	.	.	.	.	.	.
Hypochaeris achyrophorus	3	1	.	.	.	.	5	20	.	.	.	2	.	4	12
Teucrium divaricatum	11	2	.	.	.	.	.	17	.	.	.	.	.	.	5
Convolvulus althaeoides + elegantissimus	2	.	.	.	1	.	4	15	.	.	1	.	.	1	10
Carex distachya	5	3	.	.	.	.	9	18	1	.	3	2	1	14	1
Aira elegantissima	4	3	.	.	1	.	1	15	.	.	.	1	.	.	14
Coremato albi-Pinion pinastri															
Cistus halimifolius	.	.	.	.	.	.	1	.	56	.	1	1	.	.	.
Cistus calycinus	.	.	.	.	.	.	.	.	55	.	.	.	.	.	.
Ulex genistoides	.	.	.	.	.	.	.	.	35	.	.	.	.	.	.
Corema album	.	.	.	.	.	.	.	.	29	.	.	.	.	.	.
Cytisus grandiflorus	.	.	.	.	.	.	.	.	30	.	1	.	.	.	.
Aristolochia baetica	.	.	.	.	.	.	.	.	11	.	.	.	.	.	.
Cistus crispus	.	.	.	.	.	.	1	.	22	.	1	.	.	1	.
Osyris lanceolata	.	.	.	.	.	1	.	.	16	.	1	.	.	.	.
Carpobrotus edulis	.	.	.	.	.	.	.	.	16	.	.	.	.	2	.
Helichrysum italicum	2	.	.	.	.	.	4	.	44	.	1	2	6	1	.
Chamaerops humilis	.	.	.	.	1	2	5	.	24	.	1	.	.	2	.
Cistus libanotis	.	.	.	.	2	3	.	.	17	.	.	.	.	1	.
Ulex parviflorus	.	.	.	.	10	.	1	.	29	.	3	.	.	2	.
Genista triacanthos	.	.	.	.	.	.	.	.	11	6	1	.	.	.	.
Cistus salviifolius	34	15	.	.	8	14	31	32	56	9	8	33	.	38	13
Lavandula stoechas	5	4	.	.	3	.	6	3	39	.	5	12	.	15	28
Juniperus phoenicea	22	.	.	.	21	22	27	4	36	.	1	1	.	14	.
Lagurus ovatus	1	1	.	.	.	.	8	3	16	.	.	1	.	15	2
Atlantic *Pinus pinaster* forests															
Ulex minor	.	.	.	.	.	.	.	.	.	44	.	.	.	.	.
Pseudarrhenatherum longifolium	.	.	.	.	.	.	.	.	.	36	.	.	.	.	.
Daboecia cantabrica	.	.	.	.	.	.	.	.	.	30	.	.	.	.	.
Melampyrum pratense	.	.	.	.	.	.	.	.	.	11	1	.	.	.	.
Agrostis curtisii	.	.	.	.	.	.	.	.	1	31	.	.	.	.	.
Erica cinerea	.	.	.	.	.	.	.	.	.	65	2	1	.	1	.
Pedicularis sylvatica	.	.	.	.	.	.	.	.	.	11	1	.	.	.	.
Glandora diffusa	.	.	.	.	.	.	.	.	.	11	1	.	.	.	.
Quercus robur	.	.	.	.	.	.	1	.	.	67	1	1	.	3	.
Ulex europaeus	.	.	.	.	.	.	.	.	6	76	.	5	.	.	.
Digitalis purpurea	.	.	.	.	.	.	.	.	.	15	1	1	.	.	.
Potentilla erecta	.	.	.	.	.	.	.	.	.	27	1	3	.	1	.
Frangula alnus	.	.	.	.	.	.	.	.	.	22	2	3	.	1	.
Lonicera periclymenum	.	.	.	.	.	.	.	.	.	34	5	1	.	.	.

(Continues)

TABLE 2 (Continued)

Alliance	Pin-Bru	Sty-Bru	Jas-Jun	Cam-Bru	Thy-Hal	Ros-Hal	Pis-Hal	Sar-Hal	Cor-Psr	Atl-Psr	Lav-Psr	Gen-Psr	Cen-Pna	Med-Pna	Pin-Pna
Ilex aquifolium	.	1	.	.	.	.	.	.	.	19	1	4	.	.	.
Glandora prostrata	.	.	.	.	.	.	.	.	5	18	2	.	.	.	.
Erica umbellata	.	.	.	.	1	.	.	.	3	32	10	.	.	.	.
Molinia caerulea aggr.	.	.	.	.	.	.	.	.	.	20	.	8	.	1	.
Corynephorus canescens	.	.	.	.	.	.	.	.	8	20	7	1	9	.	.
Simethis planifolia	.	.	.	.	1	.	2	.	1	22	10	1	.	1	.
Quercus suber	.	.	.	.	2	.	3	.	4	33	3	16	.	10	.
Lavandulo pedunculatae-Pinion pinastri															
Cistus populifolius	.	.	.	.	.	.	.	.	.	.	14	.	.	.	.
Festuca elegans	.	.	.	.	.	.	.	.	.	.	12	.	.	.	.
Erica australis	.	.	.	.	1	.	.	.	1	.	29	.	.	.	.
Digitalis thapsi	.	.	.	.	.	.	.	.	.	.	23	.	1	.	.
Aristolochia paucinervis	.	.	.	.	.	.	.	.	.	.	13	.	1	.	.
Genista tridentata	.	.	.	.	1	.	.	.	2	2	22	.	.	.	.
Cytisus multiflorus	.	.	.	.	.	.	.	.	.	2	16	.	1	.	.
Quercus pyrenaica	.	.	.	.	.	.	.	.	.	8	36	.	.	.	.
Anarrhinum bellidifolium	.	.	.	.	1	.	.	.	.	4	14	.	.	.	.
Hypochaeris radicata	.	.	.	.	3	.	1	.	.	7	37	1	12	4	.
Tuberaria lignosa	.	.	.	.	2	.	3	.	.	3	11	4	.	1	.
Arrhenatherum elatius	.	1	.	.	6	.	.	.	1	.	21	3	7	2	.
Holcus lanatus	.	.	.	.	.	.	1	.	.	1	13	5	.	5	.
Cytisus striatus	.	.	.	.	.	.	.	.	.	8	19	.	.	.	.
Agrostis castellana + tenuis	.	.	.	17	.	.	.	.	1	8	38	6	15	5	.
Clinopodium vulgare	.	8	.	.	.	.	.	2	.	.	24	3	.	.	12
Centaurea alba aggr.	.	.	.	.	.	.	.	.	.	.	20	.	11	1	.
Cistus umbellatus	.	.	.	.	.	.	.	.	1	.	17	.	10	.	1
Micropyrum tenellum	.	.	.	.	.	.	.	.	.	.	16	.	10	.	1
Cistus psilosepalus	.	.	.	.	.	.	.	.	1	12	18	.	.	.	.
Filago minima	.	.	.	.	.	.	.	.	1	.	16	.	11	.	.
Cytisus scoparius	.	.	.	.	1	.	.	.	.	19	24	3	12	3	.
Genisto pilosae-Pinion pinastri															
Knautia purpurea	.	.	.	.	1	.	.	.	.	.	.	20	.	.	.
Sesleria autumnalis	.	.	.	.	1	.	1	.	.	.	.	14	.	.	.
Rosa agrestis	.	.	.	.	1	.	.	.	.	.	1	12	.	1	.
Cytisophyllum sessilifolium	.	.	.	.	1	.	.	.	.	.	.	12	.	.	.
Polygala nicaeensis aggr.	.	.	.	.	1	.	.	2	.	.	.	13	.	.	.
Prunella hyssopifolia	.	.	.	.	2	.	.	.	.	.	.	14	.	.	.
Teucrium montanum	.	.	.	.	4	.	.	.	.	.	.	26	.	.	.
Centaurea jacea	.	.	.	.	2	.	.	.	.	.	1	11	1	1	.
Sorbus domestica	.	.	.	.	1	.	1	.	.	.	1	14	.	2	.

(Continues)

TABLE 2 (Continued)

Alliance	Pin-Bru	Sty-Bru	Jas-Jun	Cam-Bru	Thy-Hal	Ros-Hal	Pis-Hal	Sar-Hal	Cor-Psr	Atl-Psr	Lav-Psr	Gen-Psr	Cen-Pna	Med-Pna	Pin-Pna
Lavandula angustifolia	.	.	.	.	4	.	.	.	.	.	.	24	.	.	.
Asperula purpurea	.	.	.	.	3	.	1	.	.	.	.	20	.	.	.
Ostrya carpinifolia	.	3	.	.	.	.	.	.	.	.	.	15	.	1	.
Scabiosa triandra	.	.	.	.	3	.	.	.	.	.	.	14	.	1	.
Amelanchier ovalis	.	.	.	.	4	.	.	.	.	.	1	18	.	.	.
Bromopsis erecta	.	1	.	.	5	.	1	.	.	.	1	29	.	1	6
Genista pilosa	.	.	.	.	6	.	1	.	.	.	.	25	.	1	.
Thesium divaricatum	.	.	.	.	3	.	1	.	.	.	.	14	.	.	.
Juniperus communis	.	.	.	.	3	.	1	.	.	.	4	21	.	5	.
Cytisus villosus	.	1	.	.	.	.	1	.	.	.	.	11	.	3	.
Euphorbia spinosa	.	.	.	.	6	.	3	.	.	.	.	19	.	.	.
Fraxinus ornus	1	5	.	.	.	.	5	1	.	.	.	22	.	7	.
Leucanthemum pallens	.	.	.	.	4	.	.	.	.	.	1	11	.	.	.
Catananche caerulea	.	.	.	.	7	5	.	.	.	.	3	20	.	.	.
Ononis spinosa	2	1	.	.	7	.	.	.	.	.	3	19	.	1	2
Carlina vulgaris	.	.	.	.	4	.	.	.	.	2	1	11	.	2	.
Cephalaria leucantha	.	.	.	.	7	.	.	.	.	.	.	18	2	1	.
Festuca rubra aggr.	.	.	.	.	11	.	.	.	.	1	1	26	.	1	.
Castanea sativa	.	1	.	.	.	.	.	.	.	2	9	20	.	1	2
Genista cinerea	.	.	.	.	2	9	.	.	.	.	4	18	.	1	.
Dianthus sylvestris	.	.	.	.	7	.	1	.	.	.	.	14	.	1	.
Galium corrudifolium	.	.	.	.	7	3	1	.	.	.	.	13	.	1	.
Onobrychis supina	.	.	.	.	8	.	.	.	.	.	.	16	.	1	.
Pulicaria odora	.	.	.	.	.	.	8	.	5	.	1	14	.	5	.
Rubus ulmifolius (incl. *R. sanctus*)	.	1	.	.	2	.	5	.	4	15	28	44	.	27	.
Asperula cynanchica	.	.	.	.	10	.	1	.	.	.	1	16	1	2	.
Pilosella officinarum aggr.	.	.	.	.	13	.	.	.	.	.	6	20	7	6	.
Coriaria myrtifolia	.	.	.	.	7	.	.	.	.	.	.	11	.	2	.
Lotus corniculatus	2	1	.	.	5	.	1	1	.	12	5	17	1	1	.
Sanguisorba minor	1	5	.	.	16	.	2	11	1	1	18	25	10	5	3
Arbutus unedo	10	5	.	.	2	1	35	30	9	13	12	49	2	9	12
Calicotome spinosa	.	1	.	.	5	1	11	.	.	.	1	15	.	4	.
Echinops ritro	.	2	.	.	11	.	.	1	.	.	1	15	1	1	1
Erica scoparia	.	1	.	.	2	.	3	.	11	22	5	29	.	12	.
Solidago virgaurea	.	.	.	17	.	.	.	.	.	1	4	17	.	1	.
Central Iberian *Pinus pinea* forests															
Calendula arvensis	.	1	.	.	.	.	1	.	.	.	.	.	19	.	.
Asphodelus serotinus	.	.	.	.	.	.	.	.	.	.	2	.	43	.	.
Silene nocturna	1	.	.	.	.	.	.	.	.	.	1	.	14	1	.
Plantago lagopus	1	1	.	.	.	.	1	.	.	.	.	1	14	1	.
Daucus durieua	.	.	.	.	.	.	.	.	1	.	1	.	14	.	.
Vicia disperma	.	1	.	.	.	.	.	.	.	.	2	1	38	.	.
Holcus annuus	.	.	.	.	.	.	.	.	.	.	1	.	14	.	.

(Continues)

TABLE 2 (Continued)

Alliance	Pin-Bru	Sty-Bru	Jas-Jun	Cam-Bru	Thy-Hal	Ros-Hal	Pis-Hal	Sar-Hal	Cor-Psr	Atl-Psr	Lav-Psr	Gen-Psr	Cen-Pna	Med-Pna	Pin-Pna
Anisantha diandra	1	1	.	.	.	.	.	.	1	.	1	.	30	2	.
Echium plantagineum	.	1	.	.	.	.	1	.	.	.	1	.	14	1	.
Silene gallica	.	1	.	.	.	.	1	.	.	.	1	1	11	1	.
Carduus pycnocephalus	1	1	.	.	.	.	1	1	.	.	.	1	25	1	2
Leontodon saxatilis	.	.	.	.	1	.	1	.	.	.	4	.	48	1	.
Centaurea aristata	.	.	.	.	.	.	.	.	.	.	2	.	21	.	.
Anthemis arvensis	.	1	.	.	.	.	1	1	.	.	4	1	32	1	.
Jasione sessiliflora	.	.	.	.	.	.	.	.	.	.	1	.	11	.	.
Crepis vesicaria	1	.	.	.	6	.	6	.	.	.	2	1	47	3	.
Viola kitaibeliana	.	.	.	.	1	.	.	.	.	.	2	.	14	.	.
Mibora minima	.	.	.	.	.	.	.	.	.	2	1	.	12	.	.
Arrhenatherum album	.	.	.	.	.	.	.	.	5	.	1	.	32	.	.
Retama sphaerocarpa	.	.	.	.	2	1	1	.	.	.	5	.	26	.	.
Hypochaeris glabra	.	.	.	.	.	.	1	.	7	5	5	1	32	3	1
Silene scabriflora	.	.	.	.	.	.	.	.	1	.	3	.	11	.	.
Tragopogon porrifolius	2	2	.	.	.	.	.	1	.	.	1	1	12	.	3
Centranthus calcitrapae	3	.	.	.	1	.	1	1	4	.	4	.	15	1	.
Lupinus angustifolius	.	.	.	.	.	.	.	.	.	.	4	.	12	.	1
Anisantha madritensis	1	1	.	.	1	.	2	3	1	.	1	.	12	4	.
Asterolinon linum-stellatum	6	1	.	.	2	12	4	3	9	1	3	.	38	3	1
Vicia lathyroides	2	1	.	.	.	.	.	.	.	.	4	1	17	.	5
Sanguisorba verrucosa	.	1	.	.	4	.	.	.	.	.	17	1	52	.	.
Urospermum picroides	8	3	.	.	.	.	2	2	1	.	1	.	25	1	3
Crepis capillaris	.	.	.	.	.	.	.	.	1	1	5	.	15	.	.
Lathyrus angulatus	.	.	.	.	.	.	.	.	.	.	4	.	11	.	.
Trachynia distachya	8	4	.	.	2	7	4	14	1	.	3	1	37	7	2
Aira caryophyllea	.	1	.	.	.	.	2	.	1	.	9	1	23	7	4
Campanula rapunculus	.	1	.	.	1	.	1	.	.	.	4	6	15	1	.
Linaria spartea	.	.	.	.	.	.	.	.	4	.	4	.	11	.	.
Senecio lividus	.	.	.	.	.	.	.	.	1	6	2	5	14	1	.
Vulpia myuros	.	1	.	.	.	.	1	.	1	2	12	1	26	1	4
Thapsia villosa	.	.	.	.	2	.	.	.	25	.	16	1	53	2	.
Avena barbata	3	3	.	.	.	.	2	5	1	.	4	1	42	5	20
Leopoldia comosa	6	4	.	.	.	.	2	8	.	.	1	.	17	2	9
Umbilicus rupestris	.	1	.	.	.	.	.	.	.	2	6	3	11	1	1
Anisantha tectorum	.	1	8	.	.	.	.	.	.	.	3	.	16	.	6
Carlina corymbosa	10	1	.	.	8	1	1	2	6	.	23	6	43	1	22
Briza maxima	9	3	.	.	1	.	11	2	28	.	25	4	53	13	28
Tuberaria guttata	1	1	.	.	1	1	1	.	16	2	21	2	38	5	13
Coronilla scorpioides	4	3	17	17	1	3	7	1	.	.	.	.	27	1	2
Anthyllis lotoides	.	.	.	.	.	.	.	.	.	.	11	.	16	.	.
Teesdalia coronopifolia	.	.	.	.	.	.	.	.	.	.	8	1	11	.	.

(Continues)

TABLE 2 (Continued)

Alliance	Pin-Bru	Sty-Bru	Jas-Jun	Cam-Bru	Thy-Hal	Ros-Hal	Pis-Hal	Sar-Hal	Cor-Psr	Atl-Psr	Lav-Psr	Gen-Psr	Cen-Pna	Med-Pna	Pin-Pna
Eryngium campestre	.	1	17	.	21	.	1	2	.	.	6	20	27	2	.
Dactylis glomerata	40	42	25	50	18	21	15	18	23	2	38	25	73	23	55
Mediterranean *Pinus pinea* forests															
Phillyrea angustifolia	.	.	.	.	11	19	30	.	35	1	14	26	.	36	.
Pinion pineae															
Eremopoa capillaris	.	1	.	.	.	.	.	.	.	.	.	.	.	.	17
Trifolium tomentosum	1	1	.	.	.	.	.	.	.	.	.	.	.	.	12
Petrorhagia dubia	1	1	.	.	.	.	.	.	.	.	.	.	1	.	18
Filago arvensis	.	1	.	.	.	.	.	1	.	.	1	.	.	.	14
Trifolium glomeratum	.	.	.	.	.	.	.	.	.	.	2	.	.	1	15
Aegilops triuncialis	.	3	.	.	.	2	.	.	.	.	1	.	.	1	14
Anisantha sterilis	6	5	.	.	.	.	2	8	.	.	4	.	5	.	35
Trifolium arvense	1	7	.	.	.	.	1	3	1	.	9	1	15	3	50
Trifolium campestre	20	23	.	.	1	.	3	8	2	.	9	3	26	3	70
Campanula lyrata	1	7	.	.	.	.	.	.	.	.	.	.	.	.	15
Poa bulbosa	5	16	.	.	1	21	2	15	.	.	6	.	17	1	30
Silene italica	1	7	.	17	2	.	2	2	.	.	.	10	.	3	22
Micromeria myrtifolia	4	11	.	.	.	.	.	.	.	.	.	.	.	.	14
Diagnostic species for more than one alliance/community type															
Arisarum vulgare	23	3	.	.	1	.	21	3	.	2	.	1	.	1	.
Prasium majus	38	1	.	.	.	.	22	8	.	.	.	.	.	4	.
Olea europaea	29	10	.	.	1	.	31	13	17	.	2	2	.	6	3
Centaurea raphanina	20	1	.	.	.	.	.	29	.	.	.	.	.	.	.
Hypericum empetrifolium	29	2	.	.	.	.	1	45	.	.	.	.	.	.	.
Genista acanthoclada	22	3	.	.	.	.	1	22	.	.	.	.	.	.	.
Erica manipuliflora	24	7	.	.	.	.	6	28	.	.	.	.	.	.	11
Sarcopoterium spinosum	19	4	.	.	.	.	2	18	.	.	.	.	.	.	10
Asparagus aphyllus	39	1	.	.	.	.	.	16	34	.	.	.	.	.	.
Quercus coccifera aggr.	39	50	.	.	32	6	9	79	11	.	3	1	.	5	41
Arbutus andrachne	9	28	25	.	.	.	1	32	.	.	.	.	.	.	6
Pistacia terebinthus	7	49	.	.	3	.	6	24	.	.	2	9	2	.	31
Campanula sibirica	.	.	25	67	.	.	.	.	.	.	.	.	.	.	.
Dictamnus gymnostylis	.	.	25	17	.	.	.	.	.	.	.	.	.	.	.
Aegonychon purpurocaeruleum	.	1	25	67	.	.	1	.	.	.	.	.	.	1	.
Asphodeline lutea	4	.	25	17	.	.	.	2	.	.	.	1	.	.	.
Paliurus spina-christi	1	8	42	33	.	.	2	.	.	.	.	.	.	.	2
Galium mollugo aggr.	2	4	33	50	8	.	2	.	.	1	1	15	.	1	.
Cotinus coggygria	.	19	33	83	.	.	.	5	.	.	.	10	.	.	.
Dorycnium pentaphyllum aggr.	.	18	42	.	53	5	1	4	.	.	5	29	1	7	2
Hippocrepis emerus	.	5	50	.	.	.	25	5	.	.	.	6	.	3	.
Quercus pubescens	.	8	58	33	5	.	4	9	.	.	.	41	.	22	9

(Continues)

TABLE 2 (Continued)

Alliance	Pin-Bru	Sty-Bru	Jas-Jun	Cam-Bru	Thy-Hal	Ros-Hal	Pis-Hal	Sar-Hal	Cor-Psr	Atl-Psr	Lav-Psr	Gen-Psr	Cen-Pna	Med-Pna	Pin-Pna
Rhaponticum coniferum	.	.	.	.	30	24	.	.	.	.	3	8	10	1	.
Brachypodium retusum	36	1	.	.	51	1	39	63	.	.	4	19	.	7	.
Rosmarinus officinalis	.	1	.	.	69	12	32	.	46	.	11	9	31	15	.
Genista hispanica	.	.	.	.	17	.	.	.	.	.	1	20	.	.	.
Coronilla minima	.	.	.	.	30	1	.	.	.	.	1	22	1	1	.
Fumana ericifolia	.	.	.	.	19	.	.	.	.	.	1	14	.	1	.
Helianthemum italicum	.	.	.	.	16	.	1	.	.	.	.	18	.	1	.
Astragalus monspessulanus	.	.	.	.	14	.	1	2	.	.	.	17	.	.	.
Aphyllanthes monspeliensis	.	.	.	.	43	.	1	.	.	.	3	28	1	1	.
Brachypodium phoenicoides	.	.	.	.	27	.	2	.	3	.	1	32	1	5	.
Thymus vulgaris	.	.	.	.	59	.	3	.	.	.	4	26	4	6	.
Odontites luteus	.	.	.	.	15	.	1	.	.	.	.	13	.	4	.
Pistacia lentiscus	48	5	.	.	14	.	89	36	57	.	1	10	.	41	.
Erica arborea	.	2	.	.	3	.	39	3	3	3	13	56	.	24	.
Rubia peregrina	1	2	.	.	21	1	56	15	39	19	29	71	.	51	.
Clematis flammula	.	2	.	.	2	1	20	1	.	.	1	9	.	20	1
Rhamnus alaternus	3	1	.	.	6	.	25	3	9	.	1	12	.	26	.
Daphne gnidium	.	1	.	.	10	.	9	2	49	7	38	13	.	14	.
Neoschischkinia truncatula	.	.	.	.	.	.	.	.	.	18	20	.	.	.	.
Cistus lasianthus	.	.	.	.	1	.	.	.	.	27	20	.	.	.	.
Arenaria montana	.	.	.	.	1	.	.	.	.	18	19	.	.	.	.
Teucrium scorodonia	.	.	.	.	1	.	.	.	.	23	8	17	.	1	.
Calluna vulgaris	.	.	.	.	1	.	1	.	15	57	9	28	.	4	.
Andryala integrifolia	.	.	.	.	.	.	.	.	1	2	36	3	42	5	9
Jasione montana	.	.	.	.	1	.	1	.	1	9	44	3	25	1	.
Rumex acetosella	.	1	.	.	.	.	.	.	1	3	21	1	25	3	9
Lavandula pedunculata	.	.	.	.	1	.	.	.	13	.	37	.	44	.	15
Cistus ladanifer	.	.	.	.	2	.	.	.	16	.	32	.	40	.	.
Thymus mastichina	.	.	.	.	3	.	1	.	16	.	27	.	28	.	.
Trifolium cherleri	1	2	.	.	.	.	.	.	.	.	1	.	30	.	34
Trifolium stellatum	9	5	.	.	1	.	3	3	.	.	1	.	30	1	32
Cynosurus echinatus	1	11	.	.	.	.	4	8	1	.	23	1	33	6	63
Ornithopus compressus	.	1	.	.	.	.	.	1	1	.	22	.	59	2	28
Phillyrea latifolia	13	42	.	.	.	3	46	59	.	.	.	6	.	13	16
Cistus creticus	43	54	17	.	.	16	22	68	.	.	.	3	.	15	93
Pteridium aquilinum	1	4	.	.	1	.	1	2	4	68	40	36	.	4	14
Quercus ilex	1	2	.	.	15	42	46	13	.	3	34	57	81	58	.
Species occurring in > 300 plots across the whole table except those already listed above															
Juniperus oxycedrus	20	318	6	1	136	41	99	17	25	.	108	225	29	65	21
Teucrium polium aggr.	19	205	9	1	53	4	32	32	.	.	12	51	4	22	16
Briza maxima	29	34	.	.	2	.	53	2	39	.	161	26	43	41	26

(Continues)

TABLE 2 (Continued)

Alliance	Pin-Bru	Sty-Bru	Jas-Jun	Cam-Bru	Thy-Hal	Ros-Hal	Pis-Hal	Sar-Hal	Cor-Psr	Atl-Psr	Lav-Psr	Gen-Psr	Cen-Pna	Med-Pna	Pin-Pna
Crataegus monogyna	5	115	.	.	9	1	15	5	.	20	62	142	4	39	11
Geranium robertianum aggr. (incl. *Geranium purpureum*)	56	59	.	.	.	.	49	13	9	.	30	35	19	29	7

Aegean (*Salvio fruticosae-Pinion brutiae*), Anatolia and the Levant (*Gonocytiso pterocladi-Pinion brutiae*) and ultramafic substrates in southern Anatolia and Syria (*Ptosimopappo-Quercion microphyllae*). As these differences are not supported in our analysis, we include them in our geographically more widely conceived *Pinion brutiae*.

This alliance includes eastern Mediterranean *Pinus brutia* forests of the thermo- and mesomediterranean belts of Greece (mainland and Aegean islands), western and southern Anatolia, Cyprus, Lebanon and Syria, thriving on various substrates. Old-established reforestations within the supposed native distribution range of the dominant species can also occur, especially in mainland Greece and Anatolia. Besides *Pinus brutia*, also *Cupressus sempervirens*, *Olea europaea* and *Quercus coccifera* aggr. can be found in the tree layer. The shrub layer includes *Juniperus phoenicea* and *Rhamnus lycioides*. The herb and dwarf-shrub species with eastern Mediterranean distributions are numerous.

3.1.2 | Meso- to supramediterranean *Pinus brutia* forests

Styraco officinalis-Pinion brutiae **Bonari, M. Chytrý, Çoban, Kavgacı et Sağlam *all. nov.***
Acronym: Sty-Bru; Figures 4; 5b; 6; 7; Cluster 4 p.p.
Nomenclatural type (*holotypus*): *Verbasco pseudoholotrichi-Pinetum brutiae* Vural, Akman et Quézel 1999 (Vural et al., 1999, p. 8)
Diagnostic species of the alliance: *Alyssum strigosum*, *Brizochloa humilis*, *Crucianella latifolia*, *Daphne sericea*, *Eryngium falcatum*, *Fontanesia phillyreoides*, *Lathyrus aphaca*, *Lens ervoides*, *Phlomis samia*, *Quercus alnifolia*, *Quercus cerris*, *Quercus infectoria*, *Salvia tomentosa*, *Styrax officinalis*, *Thymbra spicata*, *Vicia tenuifolia + dalmatica*.

This alliance includes the meso- and supramediterranean *Pinus brutia* forests of Anatolia, Levant, Cyprus, Crete and marginally also Greek mainland. Oak species such as *Quercus alnifolia* (in Cyprus), *Quercus cerris* and *Quercus infectoria* can be present in the tree layer. *Arbutus andrachne*, *Daphne sericea*, *Fontanesia phillyreoides*, *Phillyrea latifolia*, *Quercus coccifera*, *Pistacia terebinthus*, *Styrax officinalis* and *Juniperus oxycedrus* occur in the shrub layer. Mediterranean and eastern Mediterranean elements such as *Alyssum strigosum* and *Eryngium falcatum* characterize this alliance in the herb layer, which has a variable understorey due to the occurrence over a large area. It occurs on various substrates such as limestones, conglomerates, schists, marls and serpentinites. In the Taurus mountains, it is generally found up to 1,300–1,400 m a.s.l., extending inland through deep valleys in western and northern Anatolia reaching up to 800–1,000 m a.s.l. The forests of this alliance differ from the vicariant alliance *Pinion brutiae*, which is confined to lower elevations. *Styraco-Pinion brutiae* occurs in more favourable climatic conditions such as shorter summer drought, lower temperature and higher precipitation within meso- to supramediterranean elevational belts (Mayer & Aksoy, 1998; Boydak et al., 2006).

3.1.3 | Crimean *Pinus brutia* forests

Jasmino fruticantis-Juniperion excelsae **Didukh, Vakarenko et Shelyag-Sosonko ex Bonari et al. *all. nov.***
Acronym: Jas-Jun; Figures 4; 5c; 6; 7; Cluster 4 p.p.
Original diagnosis and diagnostic species: Didukh (1996, pp. 66–74)
Nomenclatural type (*holotypus*): *Phleo phleoidis-Juniperetum excelsae* Didukh, Vakarenko et Shelyag-Sosonko in Didukh 1996 (Didukh, 1996, p. 73)
Synonyms: *Jasmino-Juniperion excelsae* Didukh, Vakarenko et Shelyag-Sosonko 1986 *nom. inval.* [ICPN Art. 2b]; *Jasmino-Juniperion excelsae* Didukh, Vakarenko et Shelyag-Sosonko ex Didukh 1996 *nom. inval.* [ICPN Art. 5]
Nomenclature comments: The proposal of the name *Jasmino-Juniperion excelsae* in Didukh et al. (1986) is invalid because the diagnosis does not contain any valid association name (i.e. types were not designated for the associations nor for the alliance). Didukh (1996) validated several associations within this alliance, most of them corresponding to *Juniperus excelsa* forests, but did not designate the type of the alliance, which remained invalid. The alliance was originally included in *Fraxino orni-Cotinetalia* (*Quercetea pubescentis*) but Mucina et al. (2016) moved it to *Berberido creticae-Juniperetalia excelsae* (*Junipero-Pinetea sylvestris*). The only association of the alliance including pine forests is the *Achnathero bromoidis-Pinetum pityusae* Didukh 1996 (*Pinetum pityusae tauricum* Didukh, Vakarenko et Shelyag-Sosonko 1986 *nom. inval.*). Although *Achnatherum bromoides* is not in the holotype of this association, the name is valid because this species is present in all the relevés ascribed to the association in Didukh et al. (1986), as part of the original diagnosis by unambiguous reference (hence ICPN Art. 3f and Art. 16 do not apply). The name must be corrected [ICPN Art. 44] if we consider, following e.g. Euro+Med (2016–2020) and many other authors, that *Pinus pityusa*

is a later synonym of *Pinus brutia*: *Achnathero bromoidis-Pinetum brutiae* Didukh 1996 *nom. corr.* (=*Achnathero bromoidis-Pinetum pityusae* Didukh 1996 *nom. inept*.). Only the *Pinus brutia* forests belonging to this association have been included and analysed in this study.

Diagnostic species of the alliance: *Achnatherum bromoides*, *Allium carinatum*, *Asparagus verticillatus*, *Asperula tenella*, *Astragalus hamosus*, *Bothriochloa ischaemum*, *Bromopsis cappadocica*, *Bupleurum falcatum*, *Carex caryophyllea*, *Carex flacca*, *Carex halleriana*, *Centaurea diffusa*, *Centaurea sterilis*, *Cleistogenes serotina*, *Convolvulus cantabrica*, *Convolvulus lineatus*, *Diplotaxis tenuifolia*, *Elymus nodosus*, *Erysimum cuspidatum*, *Festuca stricta*, *Fibigia clypeata*, *Fumana arabica*, *Fumana procumbens*, *Galatella villosa*, *Galium biebersteinii*, *Gaudiniopsis macra*, *Helianthemum stevenii*, *Hieracium* × *brachiatum*, *Inula aspera*, *Inula ensifolia*, *Inula oculus-christi*, *Iris pumila*, *Jasminum fruticans*, *Juniperus excelsa*, *Jurinea ledebourii*, *Linum austriacum*, *Linum nodiflorum*, *Linum strictum* aggr. (incl. *Linum corymbulosum*), *Melica ciliata*, *Melica transsilvanica*, *Odontarrhena tortuosa*, *Orchis simia*, *Ornithogalum pyrenaicum*, *Piptatherum holciforme*, *Pistacia atlantica*, *Pistorinia hispanica*, *Poa sterilis*, *Podospermum laciniatum*, *Polygala major*, *Psephellus declinatus*, *Reseda lutea*, *Rhus coriaria*, *Ruscus aculeatus*, *Salvia officinalis*, *Scorzonera crispa*, *Seseli dichotomum*, *Sorbus aucuparia*, *Stipa lessingiana*, *Stipa pennata* aggr. (incl. *Stipa eriocaulis*), *Teucrium chamaedrys*, *Teucrium polium* aggr., *Thymus roegneri*, *Veronica multifida*, *Viola odorata*.

The Crimean *Pinus brutia* forests occur in few localities along a narrow coastal belt on the southern slopes of the Crimean Mountains. They are characterized by a mixture of Mediterranean and non-Mediterranean elements. *Juniperus excelsa*, *Pistacia atlantica* and *Quercus pubescens* are found in the tree layer. *Jasminum fruticans* and *Paliurus spina-christi* frequently occur in the shrub layer. The herb layer is rich in both annual and perennial species, containing Mediterranean elements such as *Achnatherum bromoides* and *Carex halleriana*. These forests show floristic relations with the other two alliances that occur in the Black Sea area (*Styraco officinalis-Pinion brutiae* and *Campanulo sibiricae-Pinion brutiae*) although showing differential elements. Further analyses including the other local forest types are needed to clarify the contentious hierarchical position of the alliance *Jasmino fruticantis-Juniperion excelsae*.

3.1.4 | Caucasian *Pinus brutia* forests

Campanulo sibiricae-Pinion brutiae **Litvinskaya et Postarnak ex Mucina in Mucina et al. 2016**

Acronym: Cam-Bru; Figures 4; 5d; 6; 7; Cluster 4 p.p.

Nomenclatural type (*holotypus*): *Epimedio colchici-Pinetum pythiusae* Litvinskaya et Postarnak ex Mucina in Mucina et al. 2016

Synonym: *Campanulo longistylae-Pinion pithyusae* Litvinskaya et Postarnak 2002 *nom. inval.* [ICPN Art. 5]

This alliance groups the *Pinus brutia* forests occurring on calcareous substrates in a narrow belt along the northwest Caucasian Black Sea coast. The alliance is characterized by non-Mediterranean elements. *Carpinus orientalis* and *Quercus pubescens* are found in the tree layer. *Cotinus coggygria* and *Epimedium pinnatum* frequently occur in the shrub layer. The herb layer is rich in Colchic elements.

3.1.5 | Mesomediterranean *Pinus halepensis* forests

Thymo vulgaris-Pinion halepensis **Biondi et Pesaresi in Pesaresi et al. 2017**

Acronym: Thy-Hal; Figures 4; 5e; 6; 7; Clusters 9 + 10

Nomenclatural type (*holotypus*): *Cisto albidi-Pinetum halepensis* Vagge, Biondi et Pesaresi in Pesaresi et al. 2017

This alliance comprises *Pinus halepensis* forests widely distributed in eastern Spain and extending to southeastern France (Languedoc-Roussillon and Provence), northeastern Italy (Liguria) and the Balearic Islands, mainly on base-rich substrates. Its distribution matches well with the Mediterranean basophilous scrub, rich in perennial herbs, of the order *Rosmarinetalia*, and in part with the sclerophyllous forests of the alliance *Quercion ilicis*. The climatic conditions in this area allow the development under the pine canopy of the scrub and some perennial herbs of the alliance *Brachypodion phoenicoidis*. The tree layer is dominated by *Pinus halepensis*. *Juniperus phoenicea* and *Juniperus oxycedrus* can occur in the shrub layer. Species of the western mesomediterranean element are more common than in the *Pistacio lentisci-Pinion halepensis*, with which this alliance partially overlaps. *Aphyllanthes monspeliensis*, *Brachypodium phoenicoides*, *Cistus albidus*, *Genista scorpius*, *Helichrysum stoechas*, *Lavandula latifolia* and *Thymus vulgaris* are frequent in the low shrub and herb layers.

3.1.6 | Meso- to supramediterranean forests and pre-forests of North Africa

Rosmarino eriocalycis-Pinion halepensis **Bonari, M. Chytrý et Fernández-González *all. nov.***

Acronym: Ros-Hal; Figures 4; 5f; 6; 7; Clusters 7 + 8

Nomenclatural type (*holotypus*): *Genisto quadriflorae-Pinetum halepensis* Meddour, Meddour-Sahar, Zeraia et Mucina in Bonari et al. 2021

Diagnostic species of the alliance: *Alyssum granatense*, *Ammoides atlantica*, *Ampelodesmos mauritanicus*, *Anisantha rubens*, *Arabis nova*, *Bombycilaena discolor*, *Bufonia tenuifolia*, *Bupleurum atlanticum*, *Catapodium marinum*, *Centaurea boissieri*, *Cistus clusii*, *Dianthus caryophyllus*, *Ebenus pinnata*, *Echinaria capitata*, *Eruca vesicaria*, *Filago pyramidata*, *Fumana fontanesii*, *Genista capitellata*, *Globularia alypum*, *Helianthemum cinereum*, *Helianthemum virgatum*, *Herniaria hirsuta*, *Hornungia petraea*, *Macrochloa tenacissima*, *Minuartia montana*, *Odontarrhena alpestris*, *Papaver hybridum*, *Paronychia argentea*, *Petrorhagia illyrica*, *Pilosella pseudopilosella*, *Rosmarinus eriocalyx*, *Schismus barbatus*, *Tetraclinis articulata*, *Teucrium pseudochamaepitys*, *Thymelaea virescens*, *Thymus algeriensis*, *Thymus munbyanus*.

Type relevé (*holotypus*) of *Genisto quadriflorae-Pinetum halepensis* Meddour, Meddour-Sahar, Zeraia et Mucina *ass. nov.*: Benabdeli (1996, p. 110, Table 4, relevé 3)

This alliance includes forests and pre-forests dominated by *Pinus halepensis* in Algeria, Morocco and partly Tunisia. It occurs in semiarid and subhumid climates. Most of the stands occur in the mesomediterranean belt, but some are reaching the supramediterranean belt, in particular in the eastern part of the Atlas. The tree layer is dominated by *Pinus halepensis*. Junipers (*Juniperus oxycedrus* and *Juniperus phoenicea*) can occur in the shrub layer. The understorey is characterized by *Cistus clusii*, *Globularia alypum*, *Helianthemum cinereum*, *Macrochloa tenacissima*, *Rosmarinus eriocalyx* and *Thymus munbyanus*.

The European vegetation checklist (Mucina et al., 2016) does not include Algeria, Morocco and Tunisia, where these pine (pre-)forests occur. As highlighted first by Fennane (2003) and then by Meddour et al. (2017), the syntaxonomical status of *Quercetea ilicis* and low-grown matorral, macchia and garrigue (*Pistacio lentisci-Rhamnetalia alaterni*) is unclear for the whole of North Africa, and a critical revision is needed. This alliance contributes to closing this gap. These (pre-)forest formations with tall *Pinus halepensis* individuals occur over a large area of North Africa. This alliance, with the presence of North African species, is the African vicariant of the *Pistacio lentisci-Pinion halepensis* and *Thymo vulgaris-Pinion halepensis*.

3.1.7 | Thermomediterranean *Pinus halepensis* forests

***Pistacio lentisci-Pinion halepensis* Biondi, Blasi, Galdenzi, Pesaresi et Vagge in Biondi et al. 2014**

Acronym: Pis-Hal; Figures 4; 5g; 6; 7; Clusters 5 p.p. + 6

Nomenclatural type (*holotypus*): *Pistacio lentisci-Pinetum halepensis* De Marco, Veri et Caneva 1984

Synonym: *Rosmarino officinalis-Pinion halepensis* Biondi et Pesaresi in Pesaresi et al. 2017

Nomenclature comments: De Marco et al. (1984) did not designate a holotype for the association, but as they designated holotypes for the three subassociations and they said (p. 29) that the subassociation *pinetosum* "represents the typical aspect of the association," the holotype of the subassociation *pinetosum* automatically becomes the holotype of the association [ICPN Art. 5b, §3]. We consider the alliance *Rosmarino officinalis-Pinion halepensis* as a synonym of *Pistacio lentisci-Pinion halepensis*, because we did not support it by numerical analysis of a much larger data set than the one used in the study containing the original description of this alliance (Pesaresi et al., 2017).

This broadly distributed Mediterranean alliance includes *Pinus halepensis* forests of the thermomediterranean belt, from mainland Greece to eastern Spain and probably also some Mediterranean coastal areas of northwestern Africa. These forests thrive on various substrates, mostly calcareous, and can be locally co-dominated by other thermophilous pine species. This vegetation type also includes pine plantations. *Quercus ilex* may occur beside *Pinus halepensis*. Common Mediterranean shrubs and dwarf shrubs such as *Myrtus communis*, *Pistacia lentiscus*, *Rhamnus alaternus* and *Rosmarinus officinalis* are present, often with lianas such as *Rubia peregrina* and *Smilax aspera*. The herb layer is generally species-poor, but Mediterranean elements such as *Brachypodium retusum* are common.

3.1.8 | Thermo- to mesomediterranean *Pinus halepensis* forests of Greece

***Sarcopoterio spinosi-Pinion halepensis* Biondi et Pesaresi in Pesaresi et al. 2017**

Acronym: Sar-Hal; Figures 4; 5h; 6; 7; Cluster 5 p.p.

Nomenclatural type (*holotypus*): *Anthyllido hermanniae-Pinetum halepensis* Biondi et Pesaresi in Pesaresi et al., 2017

Nomenclature comments: There is a prior valid alliance name (*Alkanno baeoticae-Pinion halepensis* Mucina et Dimopoulos in Mucina et al. 2009) described for the Aegean *Pinus halepensis* forests on ultramafic substrates. However, our database did not give support to the differentiation of edaphic alliances, possibly due to the underrepresentation of plots from ultramafic substrates. Therefore, we prefer to adopt the alliance *Sarcopoterio spinosi-Pinion halepensis* for the Aegean *Pinus halepensis* forests included here, assuming that the independence of the *Alkanno baeoticae-Pinion halepensis* can be corroborated with new data.

This alliance includes thermo- to mesomediterranean *Pinus halepensis* forests in mainland Greece and in some Aegean islands (Konstantinidis et al., 2012). Besides *Pinus halepensis*, *Quercus coccifera* can occur in the low tree layer. In the shrub layer, Mediterranean elements such as *Arbutus andrachne*, *Arbutus unedo*, *Pistacia lentiscus* and *Pistacia terebinthus* occur. *Anthyllis hermanniae*, *Centaurea raphanina*, *Cistus creticus*, *Crepis fraasii*, *Cyclamen graecum*, *Erica manipuliflora*, *Genista acanthoclada* and *Hypericum empetrifolium* are present in the herb layer. These pine forests grow mainly on calcareous substrates.

3.1.9 | Atlantic *Pinus pinaster* and *Pinus pinea* forests on sand

Corematо albi-Pinion pinastri* J.C. Costa, Neto, Capelo, Aguiar, Monteiro-Henriques et Bonari *all. nov.

Acronym: Cor-Psr; Figures 4; 5i; 6; 7; Cluster 12

Nomenclatural type (*holotypus*): *Pinetum pinastro-pineae* J.C. Costa et Neto in Bonari et al. 2021

Diagnostic species of the alliance: *Acacia longifolia*, *Andryala arenaria*, *Aristolochia baetica*, *Armeria macrophylla*, *Armeria velutina*, *Asparagus albus*, *Carlina hispanica*, *Carpobrotus edulis*, *Centaurea sphaerocephala*, *Chamaerops humilis*, *Cistus calycinus*, *Cistus crispus*, *Cistus halimifolius*, *Cistus libanotis*, *Cistus salviifolius*, *Corema album*, *Cytisus grandiflorus*, *Euphorbia baetica*, *Euphorbia portlandica*, *Galium minutulum*, *Genista triacanthos*, *Helichrysum italicum*, *Iris xiphium*, *Juniperus phoenicea*, *Lagurus ovatus*, *Lavandula stoechas*, *Morella faya*, *Osyris lanceolata*, *Retama monosperma*, *Scrophularia canina*, *Seseli tortuosum*, *Thymus albicans*, *Thymus capitellatus*, *Ulex argenteus*, *Ulex boivinii*, *Ulex genistoides*, *Ulex parviflorus*.

Type relevé (*holotypus*) of *Pinetum pinastro-pineae* J.C. Costa et Neto *ass. nov.*: *Pinus pinea* 4, *Pinus pinaster* 2, *Pistacia lentiscus* 2, *Ulex parviflorus* subsp. *parviflorus* 2, *Daphne gnidium* 2, *Corema album* 2, *Juniperus phoenicea* subsp. *turbinata* 1, *Cistus halimifolius* 1, *Ulex genistoides* +, *Cistus calycinus* +, *Seseli tortuosum* +, *Helichrysum italicum* subsp. *picardii* +, *Cistus salviifolius* 1, *Asparagus aphyllus* 1, *Thymus capitellatus* 1, *Lavandula pedunculata* subsp. *lusitanica* 1, *Carpobrotus edulis* +, *Carlina hispanica* +, *Corynephorus canescens* +, *Dactylis glomerata* subsp. *hispanica* +, *Sedum sediforme* +, *Centaurea sphaerocephala* +, *Calluna vulgaris* +. Area: 60 m^2; elevation: 10 m a.s.l.; aspect: W; slope: 6°; locality: Praia das Bicas, Meco (Sesimbra, Portugal); coordinates: WGS84 38.49041° N, 9.18135° W.

This alliance includes Atlantic southwestern Iberian natural forests dominated by *Pinus pinaster* and/or *Pinus pinea* occurring mostly on sandy soils close to the coast, although our data show a higher constancy of *Pinus pinea* over *Pinus pinaster*. This is related to a disproportion of vegetation plots in the data set that deviate from reality. *Pistacia lentiscus* and *Juniperus phoenicea* (subsp. *turbinata*) can occur in the shrub layer. *Cistus calycinus*, *Corema album*, *Cytisus grandiflorus*, *Helichrysum italicum*, *Morella faya*, *Osyris lanceolata*, *Seseli tortuosum* and *Ulex genistoides* are taxa relatively restricted to such coastal areas and present in the understorey. By studying in situ macroremains, García-Amorena et al. (2007) showed that communities dominated by *Pinus pinaster* thrived in these sandy coastal sites at least during the first half of the Holocene (7,930–7,430 cal years BP). Co-occurring with *Pinus pinaster*, *Pinus pinea* macroremains and charcoals are more frequent in the region to the south of Lisbon and have been dated as far back as 6,300–6,400 ^{14}C years BP (Carrión Marco, 2005). Old-established plantations in these coastal environments are indistinguishable from naturally established communities based on their floristic composition. We hypothesize that for long these communities have been shaped by the effect of the cold water of the Atlantic Ocean, which influences local temperature and summer fogginess. Furthermore, strong sea currents and powerful storms support sand deposition, which extends far inland. However, inland plantations, even if old-established, lack the above-mentioned taxa and cannot be considered a part of this alliance. Although *Pinus pinaster* (and possibly *Pinus pinea*) was common in inland communities in pre-Holocene times, it declined during the Holocene, being progressively replaced by other Mediterranean species (Figueiral, 1995). *Acacia longifolia* and *Carpobrotus edulis* are alien species invading these native communities and displacing native plant taxa. The new association describes communities dominated by *Pinus pinaster* and *Pinus pinea*, enduring strong maritime influence, on deep sandy soils of southwestern Portugal, under an upper thermomediterranean, dry to subhumid bioclimate.

3.1.10 | Atlantic *Pinus pinaster* forests

Acronym: Atl-Psr; Figures 4; 5j; 6; 7; Cluster 14

This group includes Atlantic acidophilous *Pinus pinaster* forests of the northwestern Iberian Peninsula and along the Gulf of Biscay. They are largely old-established plantations. The tree layer is dominated by *Pinus pinaster*, but *Quercus robur*, *Quercus suber* or *Frangula alnus* can also occur. The shrub layer can contain *Erica cinerea*, *Erica scoparia* and *Ulex europaeus*, while the low shrub and herb layer comprises *Calluna vulgaris*, *Daboecia cantabrica*, *Erica umbellata*, *Pteridium aquilinum* and *Ulex minor*.

3.1.11 | Meso- to supramediterranean Central Iberian *Pinus pinaster* forests

Lavandulo pedunculatae-Pinion pinastri* Fernández-González, Bonari et M. Chytrý *all. nov.

Acronym: Lav-Psr; Figures 4; 5k; 6; 7; Cluster 16

Nomenclatural type (*holotypus*): *Centaureo albae-Pinetum pinastri* Fernández-González, Bonari et Chytrý in Bonari et al. 2021

Nomenclature comments: The alliance "*Pino pinastri-Juniperion phoeniceae* Pérez Latorre et Cabezudo in Pérez Latorre et al. 1998" ("*Junipero phoeniceae-Pinion acutisquamae* Pérez Latorre et Cabezudo in Pérez Latorre et al. 1998 *corr.* Rivas-Martínez et al. 2002 *nom. inv. propos.*") is accepted by Mucina et al. (2016) for "southern Iberian shrublands on dolomitic and ultramafic substrates" and by Rivas-Martínez et al. (2011) for "Betic juniper shrublands and pine forests" on the same substrates. Nevertheless, this alliance name is invalid because the holotype designated (*Pino pinastri-Quercetum cocciferae* Cabezudo et al., 1989) is an invalid association as the authors (Cabezudo et al., 1989) wrongly designated two different holotype relevés (ICPN Art. 5). Moreover, most of the relevés of this thermomediterranean association do not correspond to pine forests and their floristic composition differs considerably from the alliance we are proposing here.

Diagnostic species of the alliance: *Agrostis castellana* + *tenuis*, *Anarrhinum bellidifolium*, *Aristolochia paucinervis*, *Arnoseris minima*, *Arrhenatherum elatius*, *Campanula lusitanica*, *Centaurea alba* aggr., *Centaurea langei*, *Cistus ocymoides*, *Cistus populifolius*, *Cistus psilosepalus*, *Cistus umbellatus*, *Clinopodium vulgare*, *Coronilla repanda*, *Cytisus multiflorus*, *Cytisus scoparius*, *Cytisus striatus*, *Digitalis thapsi*, *Erica australis*, *Festuca elegans*, *Filago minima*, *Genista falcata*, *Genista florida*, *Genista tridentata*, *Geum sylvaticum*, *Holcus lanatus*, *Holcus mollis*, *Hypericum linarifolium*, *Hypochaeris radicata*, *Lotus parviflorus*, *Luzula lactea*, *Micropyrum tenellum*, *Quercus faginea*, *Quercus pyrenaica*, *Teesdalia nudicaulis*, *Thapsia minor*, *Tuberaria lignosa*.

Type relevé (*holotypus*) of *Centaureo albae-Pinetum pinastri* Fernández-González, Bonari et M. Chytrý *ass. nov.* (Braun-Blanquet scale): *Pinus pinaster* 4, *Cistus ladanifer* subsp. *ladanifer* 2, *Lavandula pedunculata* 1, *Origanum vulgare* subsp. *virens* 1, *Rosmarinus officinalis* 1, *Daphne gnidium* 1, *Phillyrea angustifolia* +, *Pistacia terebinthus* +, *Cytisus scoparius* +, *Quercus faginea* subsp. *broteroi* +, *Quercus pyrenaica* +, *Retama sphaerocarpa* +, *Rubia peregrina* +, *Thymus mastichina* subsp. *mastichina* +, *Agrostis castellana* +, *Andryala integrifolia* +, *Bituminaria bituminosa* +, *Briza maxima* +, *Carex distachya* +, *Carlina hispanica* +, *Centaurea alba*

FIGURE 5 Typical stands of each alliance or informal group of communities. a = *Pinion brutiae* (Yamanlar Dağı, Izmir, Turkey); b = *Styraco officinalis-Pinion brutiae* (Cehennemdere, Mersin, Turkey); c = *Jasmino fruticantis-Juniperion excelsae* (Cape Aya Reserve, Sevastopol, Crimea); d = *Campanulo sibiricae-Pinion brutiae* (Golubaya Dolina, Krasnodar, Russian Federation); e = *Thymo vulgaris-Pinion halepensis* (Combe des Pins, Le Triadou, France); f = *Rosmarino eriocalycis-Pinion halepensis* (Tamga forest, High Atlas of M'goun, Morocco); g = *Pistacio lentisci-Pinion halepensis* (Mattinata, Foggia, Italy); h = *Sarcopoterio spinosi-Pinion halepensis* (Neos Marmaras, Sithonia Peninsula, Greece); i = *Coremato albi-Pinion pinastri* (Praia do Pedrógão, Leiria, Portugal); j = Atlantic *Pinus pinaster* forests (Dune of Pilat, Landes, France); k = *Lavandulo pedunculatae-Pinion pinastri* (Pedro Bernardo, Ávila, Spain); l = *Genisto pilosae-Pinion pinastri* (Monticiano, Siena, Italy); m = Central Iberian *Pinus pinea* forests (Almorox, Toledo, Spain); n = Mediterranean *Pinus pinea* forests (Castiglione della Pescaia, Grosseto, Italy); o = *Pinion pineae* (Kozak-Kaplan Köyü, Bergama, Turkey). Photo credits: O. Argagnon (e), M. Beskaravayny (c), G. Bonari (a, g, h, l, n), A. Çalışkan (b), M. Chytrý (o), J. El Oualidi (f), P. M. Fernandes (j), F. Fernández-González (k, m), Maxar Technologies, Google Earth 2020© (d), T. Monteiro-Henriques (i)

subsp. *alba* +, *Dactylis glomerata* subsp. *hispanica* +, *Holcus lanatus* +, *Hypericum linarifolium* +, *Plantago lanceolata* +, *Pteridium aquilinum* +, *Sanguisorba verrucosa* +, *Trifolium arvense* +. Area: 150 m^2; elevation: 740 m a.s.l.; aspect: S; slope: 10°; locality: Piedralaves (Ávila, Spain), coordinates: WGS84 40.3146° N; 4.7255° W.

This group comprises meso- and supramediterranean *Pinus pinaster* forests in the central Iberian Peninsula, distributed mainly on the northern Castilian plateau and the adjacent mountain systems (Central System and Iberian System), extending south to some Andalusian mountains. The elevational range is 400–1,500 m. They thrive mainly on siliceous substrates (granite, sandstone, quartzite and other metamorphic rocks, as well as sedimentary deposits related to them) or partially decalcified soils on limestones. The tree layer is dominated by *Pinus pinaster*, but *Quercus rotundifolia* and *Quercus pyrenaica* can occur and are the main competing trees. *Cistus ladanifer*, *Cytisus scoparius*, *Daphne gnidium*, *Erica australis*, *Genista tridentata*, *Lavandula pedunculata and Thymus mastichina* are frequent in the shrub layer. *Hypochaeris radicata*, *Jasione montana* or *Pteridium aquilinum* are present in the herb layer. Although *Pinus pinaster* is considered native in most of these areas, it has also been used often in forestry plantations in Spain for the last 80 years. The association *Centaureo albae-Pinetum pinastri* corresponds to the maritime pine forests of the southern, mesomediterranean slopes of the Sierra de Gredos (Central System), where a continuous pine cover is documented in the palaeopalynological record for at least the last 2,500 years (López-Sáez et al., 2010).

3.1.12 | Thermo- to mesomediterranean *Pinus pinaster* forests

***Genisto pilosae-Pinion pinastri* Biondi et Vagge 2015**

Acronym: Gen-Psr; Figures 4; 5l; 6; 7; Cluster 13

Nomenclatural type (*holotypus*): *Erico scopariae-Pinetum pinastri* Biondi et Vagge 2015

This alliance includes thermo- to mesomediterranean forests of *Pinus pinaster* of the Ligurian, Provencal and Languedoc seaboards and Corsica. It is characterized by a mixture of Mediterranean and non-Mediterranean species, but an impoverishment in Mediterranean sclerophyllous shrubs is noteworthy. It occurs on a variety of soils, including those on serpentinite, but mainly acidic or decalcified. The tree layer can contain an admixture of broad-leaved trees such as *Castanea sativa*, *Fraxinus ornus*, *Quercus ilex* and *Quercus pubescens*. In the shrub layer, *Arbutus unedo*, *Erica arborea*, *Erica scoparia*, *Juniperus communis* and *Juniperus oxycedrus* can be found. *Brachypodium phoenicoides*, *Calluna vulgaris*, *Cistus salviifolius*, *Pteridium aquilinum* and *Teucrium chamaedrys* are frequent in the low shrub and herb layers.

3.1.13 | Mesomediterranean Central Iberian *Pinus pinea* forests

Acronym: Cen-Pna; Figures 4; 5m; 6; 7; Cluster 15

This group includes *Pinus pinea* forests of the central Iberian Peninsula (Castilian plateaus and low hills of the Central System), mostly in the mesomediterranean belt (elevations of 500–1,000 m). They grow mainly on fluvial or aeolian sand deposits and other coarse-textured soils on siliceous rocks. *Pinus pinea* is considered native here, as in the southwestern and western coast of the Iberian Peninsula (Loidi, 2017; Mutke et al., 2019), although most of these forests have been intensively managed for wood, pine seed harvesting and livestock grazing. The tree layer is dominated by *Pinus pinea*, sometimes with *Pinus pinaster*, but *Quercus rotundifolia* is common in the understorey. *Juniperus oxycedrus* and *Retama sphaerocarpa* can occur in the shrub layer. Dwarf shrubs such as *Lavandula pedunculata*, *Rosmarinus officinalis*, or rockroses (*Cistus ladanifer*) are present. In the open and grazed stands, the herb layer is rich in Mediterranean annuals, which dominate among the diagnostic species of the group as differentiated by TWINSPAN, but otherwise it is floristically and biogeographically related to the herb layers of the Central Iberian *Pinus pinaster* forests. Indeed, *Pinus pinaster* forests (see paragraph 3.1.11) are much more extended in this large area of central Spain, overlapping their distribution with *Pinus pinea* forests, and there are mixed forests with both pines at low elevations of the Central System and on the sedimentary deposits of the Castilian plateaus. Hence the distinction between *Pinus pinea* and *Pinus pinaster* forests in central Iberia could be reflected at the level of associations rather than of alliances.

3.1.14 | Thermomediterranean *Pinus pinea* forests

Acronym: Med-Pna; Figures 4; 5n; 6; 7; Cluster 11 p.p.

This group includes thermomediterranean, partly supposedly native forests but largely old-established plantations of *Pinus pinea* in Catalonia, France, the Italian Peninsula, Sicily and Sardinia. *Pinus pinea* old-established plantations on the Italian Peninsula occur at the sea level on sand. In the hinterland, reforested areas with this pine species are few. Catalonian, Provencal and Languedoc forests can reach up to 800 m. The populations of *Pinus pinea* on sandstone in the Provence are likely native (Quézel, 1979), as well as those at one site in Sardinia (Arrigoni, 1967). However, the areas currently occupied by *Pinus pinea* have been artificially extended (and often heavily managed) in recent times. The structure and floristic composition of these forests is highly influenced by management and human impact (Bonari et al., 2019a). In the tree layer, *Quercus ilex* and *Quercus pubescens* can occur. More frequent species in the shrub layer include *Erica arborea*, *Phillyrea angustifolia*, *Pistacia lentiscus* and *Rhamnus alaternus*, but also lianas (*Rubia peregrina*, *Smilax aspera*). The herb layer contains *Asparagus acutifolius*, *Brachypodium sylvaticum* and *Cistus salviifolius*.

3.1.15 | Eastern thermo- to mesomediterranean *Pinus pinea* forests

***Pinion pineae* Feinbrun 1959**

Acronym: Pin-Pna; Figures 4; 5o; 6; 7; Cluster 3

TABLE 3 Shortened synoptic table of the percentage constancies of the diagnostic and most frequent species for the vegetation plots classified to the EUNIS habitat types corresponding to the classes *Pinetea halepensis* and *Quercetea ilicis*

Species	No. of plots	*Pinetea halepensis* (T3A)	*Quercetea ilicis* (T21)
No. of plots		1,534	2,826
Tree species			
Pinus brutia	332	19	1
Pinus halepensis	973	48	8
Pinus pinaster	563	29	4
Pinus pinea	238	12	2
Quercus coccifera	1,127	31	23
Quercus ilex	2,158	32	59
Quercus rotundifolia	806	7	25
Quercus suber	525	6	15
Acer monspessulanum	185	1	6
Fraxinus ornus	591	6	17
Diagnostic species for *Pinetea halepensis* (T3A)			
Rosmarinus officinalis	580	25	7
Cistus creticus	491	18	7
Teucrium polium aggr.	344	14	5
Dorycnium pentaphyllum	486	18	7
Helichrysum stoechas	298	12	4
Diagnostic species for *Quercetea ilicis* (T21)			
Ruscus aculeatus	1,277	10	40
Asplenium adiantum-nigrum	817	4	27
Hedera helix aggr.	1,136	11	34
Rubia peregrina	2,555	41	68
Dioscorea communis	616	4	20
Crataegus monogyna	901	10	26
Rosa sempervirens	412	2	13
Viola alba	377	2	12
Carex distachya	476	4	15
Asplenium trichomanes	216	1	7
Phillyrea latifolia	1,407	23	38
Cyclamen repandum	288	2	9
Helleborus foetidus	150	1	5
Luzula forsteri	250	2	8
Species occurring in > 1,000 plots across the whole table except the species already listed above			
Asparagus acutifolius	1,652	32	41
Smilax aspera	1,573	31	39
Arbutus unedo	1,235	22	32
Brachypodium retusum	1,231	32	26
Juniperus oxycedrus aggr.	1,211	34	24
Pistacia lentiscus	1,150	32	23
Erica arborea	1,009	17	26

Nomenclatural type (*holotypus*): *Pinetum pineae libanoticum* Feinbrun 1959

This alliance includes native forests of *Pinus pinea* in the eastern Mediterranean and the eastern Euxinian region, occurring in the thermo- to mesomediterranean belts. These forests are chiefly present on acidic rocky substrates. The shrub layer includes *Arbutus unedo*, *Cistus creticus*, *Erica manipuliflora*, *Lavandula stoechas* and *Quercus coccifera*. As in other *Pinus pinea* forests, the herb layer is rich in annual species. However, perennial species are also present (*Dianthus strictus*, *Genista lydia*, *Micromeria myrtifolia*).

3.2 | Climatic and elevational patterns

The individual alliances of Mediterranean pine forests mostly occupy distinct elevational ranges (Figure 6) and are related to different climatic features (Figures 7 and 8). The climatic conditions relate to thermo-, meso- and supramediterranean belts. Precipitation seasonality, temperature and temperature seasonality are related to the differentiation of the alliances along the first ordination (DCA) axis of species composition, while precipitation is related to the second axis.

The alliances of the *Pinus brutia* forests differ in their typical elevations, with *Pinion brutiae* being confined to the thermo- and mesomediterranean belts (Figure 6), with high temperature and low precipitation (Figure 7a and c), as opposed to the *Styraco officinalis-Pinion brutiae*, which tends to be more frequent at higher elevations (Figure 6). The *Jasmino fruticantis-Juniperion excelsae* is restricted to a small area, but its climatic relationships seem to be intermediate between those of the other two alliances, while *Campanulo sibiricae-Pinion halepensis* shows a relationship to higher precipitation (Figure 7a). The alliances dominated by *Pinus halepensis* also differ in their elevational range, although *Sarcopoterio spinosi-Pinion halepensis* occurs in similar elevational belts as *Pistacio lentisci-Pinion halepensis* and *Thymo vulgaris-Pinion halepensis*, but differs in terms of precipitation seasonality (Figures 6 and 7b). The *Pistacio lentisci-Pinion halepensis* is typical of the thermomediterranean belt with a warmer climate and more seasonal precipitation, while *Thymo vulgaris-Pinion halepensis* occurs mainly in the mesomediterranean belt (Figures 6 and 7b). *Rosmarino eriocalycis-Pinion halepensis* occurs mainly in the meso- to supramediterranean belts, with a high temperature seasonality (Figures 6 and 7d). Non-coastal alliances of *Pinus pinaster* forests (*Genisto pilosae-Pinion pinastri* and *Lavandulo pedunculatae-Pinion pinastri*) show a different elevational pattern between the thermo- and mesomediterranean belts, respectively. Their climatic patterns are similar, while *Coremato albi-Pinion pinastri* and the Atlantic *Pinus pinaster* forests show opposite trends of precipitation and precipitation seasonality at low elevations (Figures 6, 7a and b). Also, *Pinus pinea* alliances occur at different elevations, but while the Mediterranean *Pinus pinea* communities, including old-established plantations, are concentrated in coastal areas, native forests of *Pinion pineae* in the eastern Mediterranean are more frequently found at higher elevations of the meso- (to supra-)mediterranean belt with high precipitation seasonality (Figures 6 and 7b).

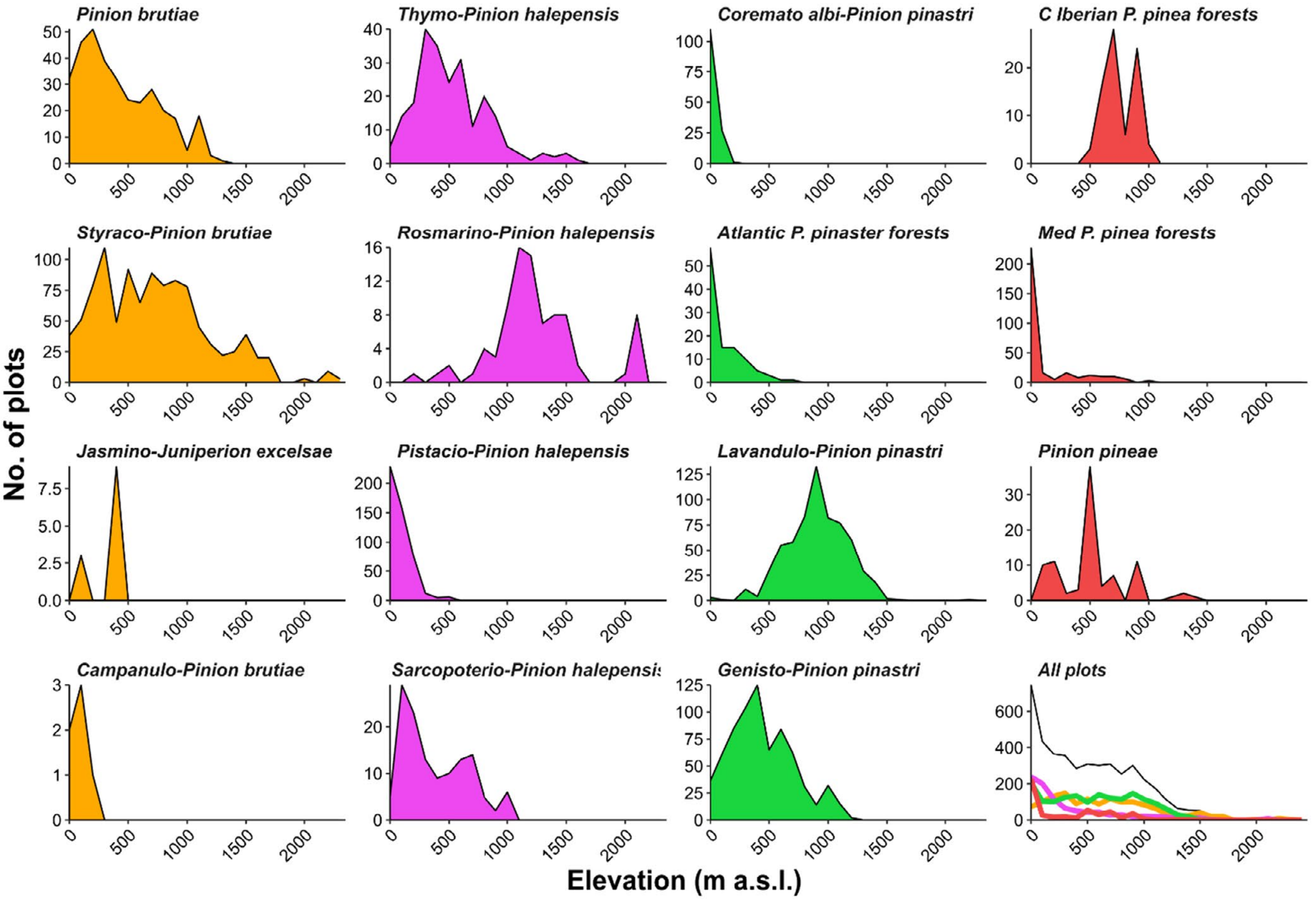

FIGURE 6 Elevational-density graphs for the resampled data set of vegetation plots classified by the expert system to individual alliances (n = 4,468; a subset of plots with an indication of elevation). Alliances dominated by individual pine species are shown in different colours. C = central; Med = Mediterranean. All plots = cumulative curve of all plots (in black) and of each pine species (orange = *Pinus brutia*; violet = *Pinus halepensis*; green = *Pinus pinaster*; red = *Pinus pinea*). Full names of alliances and informal groups are reported in paragraphs 3.1.1–3.1.15

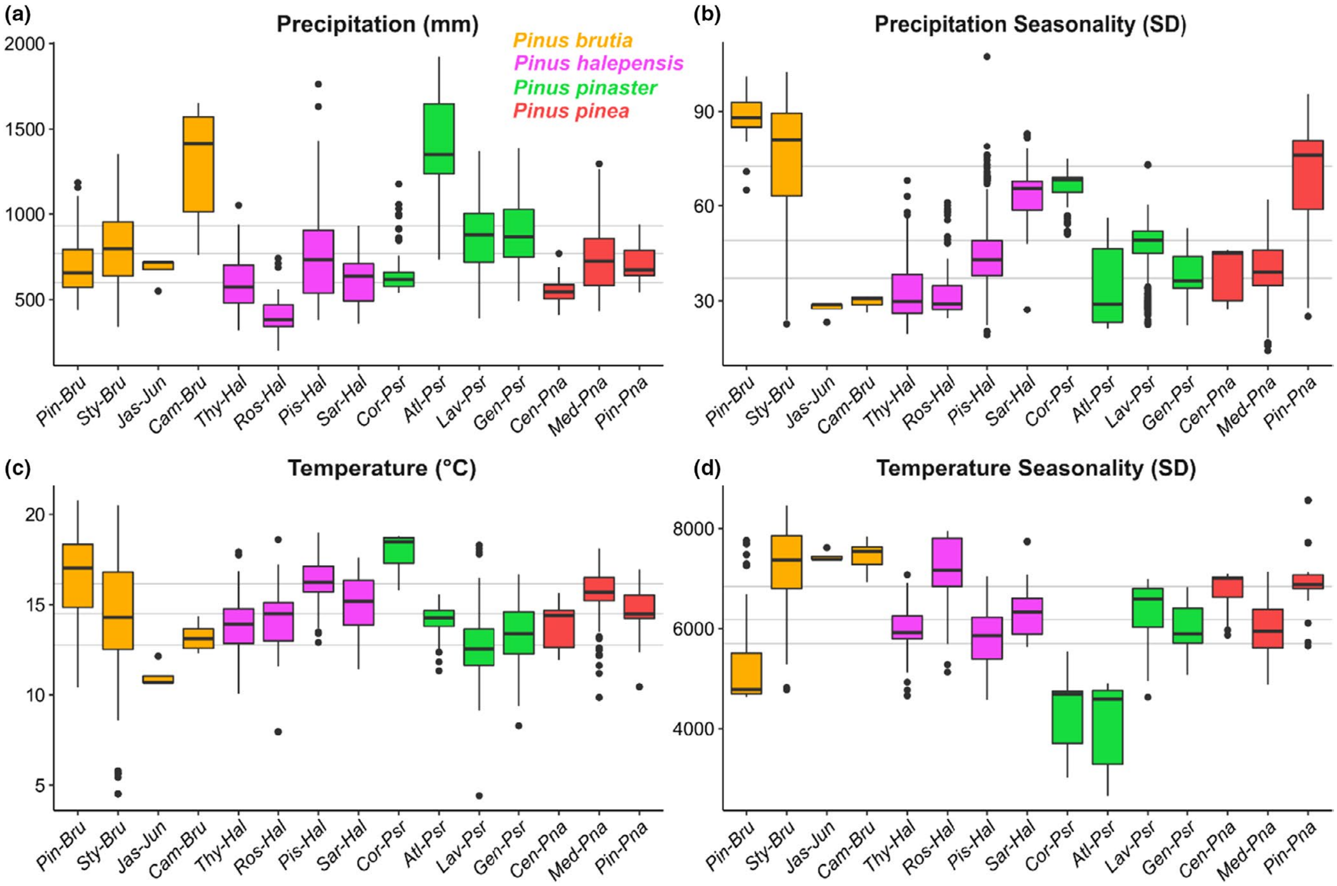

FIGURE 7 Boxplots of climatic variables for the data set of resampled vegetation plots (*n* = 4,468) classified by the expert system to individual alliances and informal groups. See paragraphs 3.1.1–3.1.15 for alliance acronyms. Grey lines represent the upper quartile, the median and the lower quartile for all plots (*n* = 4,468)

4 | DISCUSSION

4.1 | Mediterranean and non-Mediterranean pine forest alliances

We propose some changes in the system of alliances published in EuroVegChecklist (Mucina et al., 2016) for Europe, but also for North Africa, for which we identified a new alliance of pine (pre-)forests. Following the physiognomic classification approach at the class and order level, we assigned the alliances of the vegetation dominated by Mediterranean thermophilous pine species to the order *Pinetalia halepensis*. We placed in this order the alliances *Pinion brutiae*, *Styraco officinalis-Pinion brutiae*, *Jasmino fruticantis-Juniperion excelsae*, *Campanulo sibiricae-Pinion brutiae*, *Thymo vulgaris-Pinion halepensis*, *Rosmarino eriocalycis-Pinion halepensis*, *Pistacio lentisci-Pinion halepensis*, *Sarcopoterio spinosi-Pinion halepensis*, *Coremato albi-Pinion pinastri*, *Lavandulo pedunculatae-Pinion pinastri*, *Genisto pilosae-Pinion pinastri* and *Pinion pineae*. We also included here three informal groups: Atlantic *Pinus pinaster* forests, Central Iberian *Pinus pinea* forests and Mediterranean *Pinus pinea* forests. Data analysis showed that some of the earlier described alliances are not supported, or cannot be separated. For example, the diagnostic species of the alliance *Pistacio lentisci-Pinion halepensis* largely overlap with those of *Rosmarino officinalis-Pinion halepensis*. Therefore, we synonymized these two alliances.

The alliance *Alkanno baeoticae-Pinion halepensis* was described by Mucina et al. (2009) but not recognized in our study since it is documented by very few plots. It was described from a small area with ultramafic bedrock (peridotite) on the Greek island of Evvia (Euboea), but the authors of the original description were uncertain about the distribution of this alliance ("we presume its occurrence also in the adjacent Greek mainland on appropriate geological substrates"). Further studies in the field are needed to understand the syntaxonomical status of this vegetation unit.

In the EuroVegChecklist, the Crimean alliance *Jasmino fruticantis-Juniperion excelsae* was assigned to the *Berberido creticae-Juniperetalia excelsae* order of the *Junipero-Pinetea sylvestris* class. Based on physiognomy and species composition, it is better to accommodate Crimean *Pinus brutia* forests (*Jasmino fruticantis-Juniperion excelsae*) in *Pinetalia halepensis*. However, further analyses are needed to disentangle the hierarchical status of *Jasmino fruticantis-Juniperion excelsae* as these forests grow only at two relatively small sites mixed with sparse forests of *Juniperus excelsa*, which are much more widespread.

For completeness, our expert system and syntaxonomical scheme also report the alliance *Campanulo sibiricae-Pinion brutiae*, which comprises *Pinus brutia*-dominated forests on the south-facing slopes of the western Great Caucasus above the Black Sea near Novorossiysk (Litvinskaya & Postarnak, 2002; Mucina et al., 2016). The species composition of these forests is close to that of the deciduous forests of the alliance *Carpino orientalis-Quercion pubescentis* and they were classified to the syntaxa of deciduous thermophilous oak forests in EuroVegChecklist: *Quercetalia pubescenti-petraeae* and *Quercetea pubescentis* (but see also Didukh, 1996). Although the *Pinus brutia* forests in southern Crimea (*Jasmino fruticantis-Juniperion excelsae*) also contain several species of deciduous oak forests, they harbour more Mediterranean species and structural features than their counterparts in the western Caucasus. Further studies are needed to clarify the position of the latter forests. In particular, they will need to be compared with forests of *Erico-Pinetea*, *Brachypodio pinnati-Betuletea pendulae* and *Quercetea pubescentis*.

4.2 | *Pinetea halepensis*: a new class of the Mediterranean thermophilous pine forests

The current European vegetation classification (Mucina et al., 2016) puts a strong emphasis on the physiognomy of the dominant layer in the definitions of vegetation classes. For example, it separates the class of temperate broad-leaved acidophilous forests (*Quercetea robori-petraeae*) from that of boreal to temperate coniferous forests (*Vaccinio-Piceetea*) in spite of considerable overlap in species composition, especially in Central European lowland oak and pine forests (Heinken, 2008; Leuschner & Ellenberg, 2017). Similarly, also the non-Mediterranean southern European deciduous oak and pine forests are separated at the class level (*Quercetea pubescentis* vs. *Erico-Pinetea*). In this context, the inclusion of the Mediterranean sclerophyllous oak and pine forests in a single class *Quercetea ilicis*, as proposed by Mucina et al. (2016), is inconsistent, hard to convey to practitioners and difficult to apply in remote sensing of vegetation and land-cover classifications. It also has no clear links to the broadly used systems of habitats or forest types, which usually in the first place make a distinction between broad-leaved and coniferous forests (Barbati et al., 2006; Chytrý et al., 2020).

With this in mind, we establish here a new class named *Pinetea halepensis* to accommodate the Mediterranean thermophilous pine forests addressed in this paper. This class corresponds to the EUNIS habitat type “T3A Mediterranean lowland to submontane *Pinus* forest,” and partly also to “N1G Mediterranean coniferous coastal dune forest” (Chytrý et al., 2020). The new syntaxonomic solution, uniting all of these pine forests in one class, is justified especially by the structural and physiognomic criteria. Also ecologically, natural pine forests are united by their occurrence in either climatically or edaphically extreme environments, such as the most exposed, warm and dry rocky slopes, often on ultramafic bedrocks, marls, dolomites or limestones. This new concept is well supported by the comparative analysis of the phi coefficients for the most frequent species of the classes *Pinetea halepensis* and *Quercetea ilicis* (Table 3). Narrow-leaved xerophytes are chiefly present in *Pinetea halepensis* (e.g. *Helichrysum stoechas*, *Rosmarinus officinalis*, *Teucrium polium* aggr.), as opposed to several broad-leaved or "broad-phyllocladian" species mainly present in *Quercetea ilicis* (e.g. *Asplenium adiantum-nigrum*, *Asplenium trichomanes*, *Dioscorea communis*, *Rosa sempervirens*, *Ruscus aculeatus*). Beside showing the drier nature of the pine forest understorey, the presence of narrow-leaved xerophytes can also be tentatively interpreted as an adaptation/response of the species composition to different degrees of insolation between the open (*Pinetea halepensis*) vs. closed canopy (*Quercetea ilicis*), a further

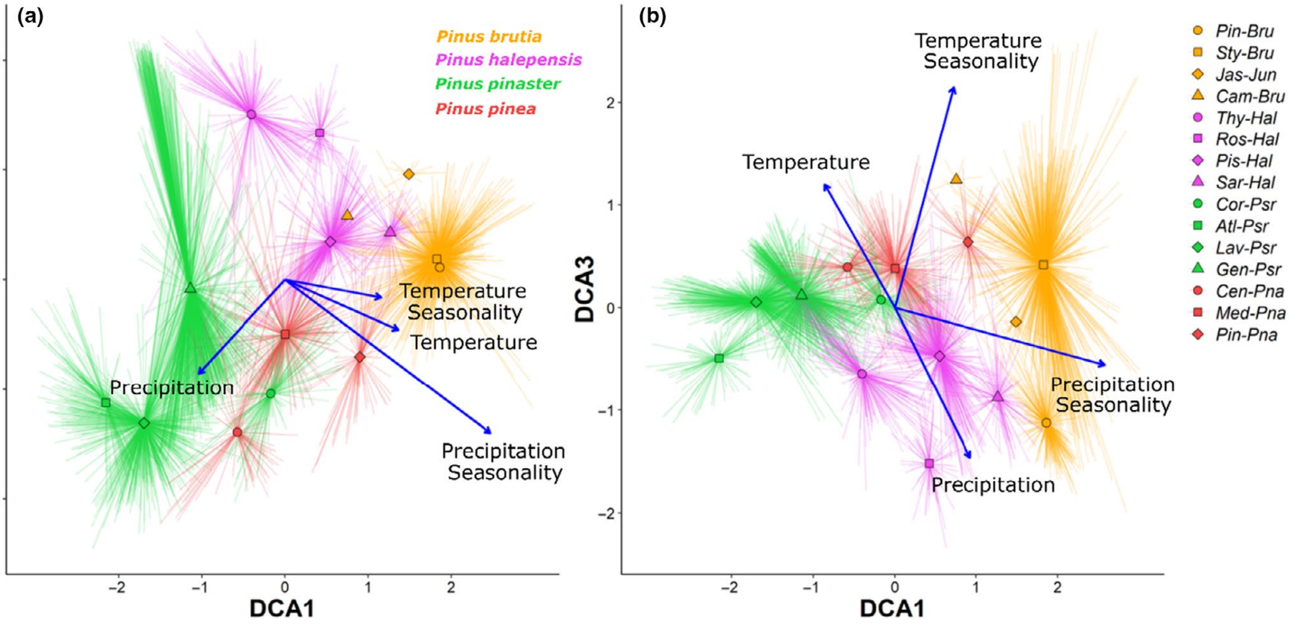

FIGURE 8 DCA ordinations (A = axes 1–2; B = axes 1–3) of the resampled data set of vegetation plots (n = 4,468) classified by the expert system to individual alliances/informal group. Plots are grouped by alliances, with tips of the lines connecting the positions of individual vegetation plots with alliance centroids. The blue arrows represent climatic variables. See paragraphs 3.1.1–3.1.15 for acronyms

TABLE 4 The new syntaxonomical scheme for low-elevation Mediterranean pine forests

Syntaxonomic scheme
Pinetea halepensis Bonari et Chytrý in Bonari et al. 2021
Pinetalia halepensis Biondi, Blasi, Galdenzi, Pesaresi et Vagge in Biondi et al. 2014
● ***Pinion brutiae*** Feinbrun 1959
● ***Styraco officinalis-Pinion brutiae*** Bonari, Chytrý, Çoban, Kavgacı et Sağlam in Bonari et al. 2021 (New)
● ***Jasmino fruticantis-Juniperion excelsae*** Didukh, Vakarenko et Shelyag-Sosonko ex Bonari et al. 2021 (EVC/More research/Validated)
○ ***Thymo vulgaris-Pinion halepensis*** Biondi et Pesaresi in Pesaresi et al. 2017
○ ***Rosmarino eriocalycis-Pinion halepensis*** Bonari, Chytrý et Fernández-González in Bonari et al. 2021 (New)
○ ***Pistacio lentisci-Pinion halepensis*** Biondi, Blasi, Galdenzi, Pesaresi et Vagge in Biondi et al. 2014 (EVC)
○ ***Sarcopoterio spinosi-Pinion halepensis*** Biondi et Pesaresi in Pesaresi et al. 2017
○ ***Alkanno baeoticae-Pinion halepensis*** Mucina et Dimopoulos in Mucina et al. 2009 (EVC/More research)
◆ ***Coremato albi-Pinion pinastri*** J.C. Costa, Neto, Capelo, Aguiar, Monteiro-Henriques et Bonari in Bonari et al. 2021 (New)
◆ Atlantic *Pinus pinaster* forests (Informal)
◆ ***Lavandulo pedunculatae-Pinion pinastri*** Fernández-González, Bonari et Chytrý in Bonari et al. 2021 (New)
◆ ***Genisto pilosae-Pinion pinastri*** Biondi et Vagge 2015 (EVC)
◇ Central Iberian *Pinus pinea* forests (Informal)
◇ Mediterranean *Pinus pinea* forests (Informal)
◇ ***Pinion pineae*** Feinbrun 1959 (EVC)
Quercetea pubescentis Doing-Kraft ex Scamoni et Passarge 1959
Quercetalia pubescenti-petraeae Klika 1933 corr.
● ***Campanulo sibiricae-Pinion brutiae*** Litvinskaya et Postarnak ex Mucina in Mucina et al. 2016 (EVC/More research/Unresolved)

Units at syntaxonomical levels lower than order are sorted by the dominance of different pine species that is indicated by a solid circle (*Pinus brutia*), empty circle (*Pinus halepensis*), solid diamond (*Pinus pinaster*) and empty diamond (*Pinus pinea*). Abbreviations in parentheses add information for each given alliance or informal group. EVC = alliance present in the EuroVegChecklist (Mucina et al., 2016); Informal = informal group; More research = more research is needed for the alliance; New = alliance newly described in this paper; Unresolved = the syntaxonomical position of the syntaxon is unresolved; Validated = alliance validated in this paper.

difference between the two classes. The observation that pine forests of the Mediterranean Basin are confined to specific edaphic conditions under which oaks do not develop into canopy dominants or are entirely absent is not novel (see e.g. Feinbrun, 1959). In some areas such as Anatolia, there is no evidence of vegetation development towards sclerophyllous oak formations in *Pinus brutia* forests (Akman et al., 1978; Quézel, 1986). Another example of no evidence of succession towards sclerophyllous oak forests is also found in arid areas with annual precipitation below 350 mm in southeastern Spain, in the lower Ebro valley and other scattered spots along the Mediterranean coast. The only tree species able to grow in these areas is *Pinus halepensis* (except for the very localized *Tetraclinis articulata* and *Juniperus thurifera* formations). Nevertheless, in the more natural landscapes of these semiarid areas, sclerophyllous shrublands are more common than *Pinus halepensis* forests.

Support for the concept of this new class also comes from palaeopalynology, palaeoanthracology and archaeology. *Pinus pinaster* has been shown to dominate a well-developed forest type on the Iberian Peninsula at certain time windows in the period between 31,000 and 3,000 ^{14}C year BP (Carrión et al., 2000 and references therein). Also, the presence of *Pinus pinaster* on the coastal dunes of Portugal has been reported during the first half of the Holocene (Mateus & Queiroz, 1993; García-Amorena et al., 2007), but also charcoal remains dating from 33,000 years BP were found in the Lisbon region, making up 93% of all the remains present (Figueiral, 1993). Similarly, there is evidence about the native status of *Pinus pinea* on the Iberian Peninsula, both on the southern coast (from 40,000 years ago to pre-Roman times) and in central Spain (northern Castilian plateau, 2,600–2,500 years BP, i.e. pre-Roman time). The problem with this species is that its pollen cannot always be differentiated morphologically from the pollen of the widespread *Pinus pinaster*, therefore, macrofossils (pine nuts, cones, wood) are needed to confirm the presence of *Pinus pinea* in old deposits. The existence of the low-elevation Mediterranean pine forests for millennia is an argument in support of considering them as a separate vegetation unit of high hierarchical rank.

The nomenclatural type of this class is the order *Pinetalia halepensis* Biondi, Blasi, Galdenzi, Pesaresi et Vagge in Biondi et al. 2014, previously included in the class *Quercetea ilicis*. Its most important diagnostic feature is the dominance of one of the four low-elevation Mediterranean pines. The character species of the new class (based on Biondi et al., 2014; Pesaresi et al., 2017 and the results of the present study) include *Pinus brutia*, *Pinus halepensis*, *Pinus pinaster* and *Pinus pinea*, while many typical Mediterranean woody species such as *Arbutus unedo*, *Asparagus acutifolius*, *Ceratonia siliqua*, *Cistus creticus*, *Cistus salviifolius*, *Erica arborea*, *Juniperus oxycedrus*, *Myrtus communis*, *Olea europaea*, *Phillyrea latifolia*, *Pistacia lentiscus*, *Pistacia terebinthus*, *Rhamnus alaternus*, *Rubia peregrina* and *Smilax aspera* are joint character species of the *Pinetea halepensis* and other classes of Mediterranean vegetation, mainly *Quercetea ilicis* but also *Cisto-Lavanduletea stoechadis* and *Ononido-Rosmarinetea*. This reflects the very close floristic and often dynamic relationship between many of the pine forests analysed in this study and communities of broad-leaved sclerophyllous woodlands and shrublands of macchia and garrigue.

Mediterranean thermophilous pine forests have recently undergone profound classification reinterpretations at the order level. *Pinus halepensis* communities have been traditionally considered as a part of the order of Mediterranean sclerophyllous scrub (macchia, maquis), *Pistacio lentisci-Rhamnetalia alaterni* (e.g. Rivas-Martínez et al., 1986) or evergreen Mediterranean oak forests and macchia, *Quercetalia ilicis* (e.g. Horvat et al., 1974; Rodwell et al., 2002). Recently, a new order of the Mediterranean thermophilous pine forests was established by Biondi et al. (2014). These authors defined it as native forests of *Pinus halepensis* and *Pinus pinea* of the Mediterranean, including old-established plantations present within their native distribution range. Besides the diagnostic species reported by Biondi et al. (2014; i.e. *Erica arborea*, *Juniperus oxycedrus*, *Juniperus phoenicea* subsp. *turbinata*, *Myrtus communis*, *Pinus halepensis*, *Pinus pinea*, *Pistacia lentiscus*, *Rosmarinus officinalis*), here we also add *Pinus brutia* and *Pinus pinaster* and extend the original definition of this order by including also native and old-established plantations dominated by the four low-elevation Mediterranean pines.

4.3 | Old-established coastal pine plantations: to be or not be (a phytosociological unit)?

Mediterranean pine forests have not traditionally received much attention from phytosociologists, because pines have been planted throughout the Mediterranean Basin for millennia (Bonari et al., 2017). Although most plantations were established in the 20th century (especially on the Iberian Peninsula), in many cases, it is challenging to trace whether or not a pine forest is natural.

Our classification includes informal vegetation types comprising old-established plantations of native pine species, in which natural species composition can develop in the understorey (Bonari et al., 2017, 2019a, 2020). This is in contrast to what happens in the plantations of most non-native trees (e.g. *Eucalyptus* spp.). The old pine plantations then resemble natural pine forests, but establishing syntaxonomical units for them would deviate from the tradition of the phytosociological classification of forests, which is focused on natural forests or at least on the vegetation dominated by spontaneously-established native trees. For these reasons, we do not establish formal syntaxa for pine plantations in habitats and areas where particular pines are considered non-native or plantations are likely more common than native communities. Still, we distinguish informal units including old-established plantations, because they were recognized in the unsupervised classification in our study and have, to some extent, a distinct species composition. These units may also include some supposedly native forests. Beside the localities where they were undoubtedly planted, e.g. along the Italian Peninsula coast, especially *Pinus pinea* communities require further research at the local scale using palaeobotanical evidence, old written documents and other sources, to assess the origin of each population. Irrespective of their origin, these forests largely correspond to the priority habitat 2270 “Wooded dunes with *Pinus pinea* and/or *Pinus pinaster*” of Annex I of the EU Habitats Directive (92/43/EEC) and to “T3A Mediterranean lowland to submontane *Pinus* forest” and “N1G Mediterranean coniferous coastal dune forest” in the EUNIS Habitat Classification (Chytrý et al., 2020) and they are considered valuable for nature conservation (Bonari et al., 2018).

4.4 | Data limitations and recommendations for future vegetation surveys

We have laid down a classification which does not pretend to be perfect. We are aware of the fact that some areas were underrepresented in our analyses because of the lower density of plots, meaning that we might have overlooked some vegetation types or some diagnostic species. Nevertheless, a clear advantage of our classification is that it is formally described and reproducible. Also, by covering the full distribution range of the studied dominant pine species, we encompass the full species pool of these forests, so that the alliances can acquire a relevant biogeographical meaning. The expert system (Appendix S2) contains groups of species and decision rules that enable identification of each of the pine forest alliances recognized here.

Some pine-dominated vegetation plots remained unclassified after running the expert system. For example, a considerable proportion of *Pinus halepensis*-dominated plots, equally distributed around the Mediterranean Basin, remained unclassified at the alliance level, although they were correctly classified at the class and order level. Because of the open-canopy structure of pine forests, which allows the occurrence of species from various habitats, these plots contained a mixture of species with different ecology. Nevertheless, our expert system showed that there is a large portion of plots with *Pinus halepensis* that can be classified. The unclassified plots are more or less equally distributed across the study area, which points to local-scale effects (including disturbance such as fire, forestry management or trampling) that make the classification of Mediterranean pine forests challenging.

Further, some areas in our data set are represented by very species-poor plots, in some cases with one to three species only (e.g. in the Levant). Such plots are problematic because they were perhaps sampled in very disturbed areas, but sometimes they were the only data available from a broader area. Disturbances may have influenced the classification results. For instance, if vegetation plots in biogeographically contrasting areas experienced more intensive forestry management (plantation, re/afforestation, timber extraction), they can become species-poor and the overall effect is weakening of the biogeographical patterns in the classification. This fact contrasts with clearer biogeographical patterns of other alliances identified in this study. Also, the open canopy allows the entry of many generalist (e.g. ruderal and annual) species. We suggest that with the increasing availability of large vegetation-plot databases and detailed revisions of vegetation classification, broadly conceived geographically defined alliances will be delineated more often than in the past.

Other Mediterranean conifer forests dominated by *Juniperus*, *Cupressus*, or *Tetraclinis* share some structural aspects with pine forests (e.g. relatively open canopies, litter decomposition), but in general, have not been managed so heavily. Some of them reach heights much lower than the pines, but others can be comparable in height when the forest is undisturbed. Their right position in the syntaxonomical scheme of Mediterranean forests should be revised through a large-scale analysis.

Collecting new data in scarcely surveyed areas is needed in the future. In particular, for *Pinus brutia*, we miss data from the easternmost limit of its distribution (Azerbaijan, Armenia, Iran and Iraq) and also from Israel. For *Pinus halepensis*, we miss data from northern Libya and Albania. For *Pinus pinaster*, we miss mainly data from North African countries. For *Pinus pinea*, we miss data from Southern

Balkans and some Mediterranean islands. These new data could provide evidence for recognizing new syntaxa or reinterpreting and redefining the earlier proposed vegetation units.

Despite the Food and Agriculture Organization (FAO) and most of the national forest inventories usually using 20% canopy cover as a threshold for forest, we used a cover of 15%. We advocate that the traditional Braun-Blanquet cover value 2, including covers of 5%–25%, is relatively broad for our purposes and does not ensure by itself that a given plot belongs to a "forest" or shrubland with a few pines. Therefore, the decision to use 15% represents a compromise for not excluding too many pine (pre-)forests plots with an open canopy. For such large-scale analyses, old sampled plots are also crucial, and we used them. However, for sampling new plots, we recommend that at least a cover value of 3 should apply when selecting plot areas for pine forests. Another related problem is that in many old plots the growth form (either shrub or tree) is not indicated for woody plants. Therefore, we also recommend an indication of the height of the strata to recognize the forest structure properly and to evaluate whether or not pines are the dominant trees.

5 | CONCLUSIONS

We propose a new syntaxonomical scheme for the low-elevation Mediterranean pine forests (Table 4) with 15 alliances (or informal groups), four of them described as new. Generally, each alliance is dominated by one of the Mediterranean thermophilous pine species (*Pinus brutia*, *Pinus halepensis*, *Pinus pinaster*, *Pinus pinea*) and is largely related to specific elevational belts (thermo-, meso- or supra-mediterranean) and a position on the west–east, and partly north–south, biogeographical gradients.

Our broad-scale classification of the Mediterranean thermophilous pine forests distinguished and documented 12 alliances of native forests and three informal groups. Conceptual considerations have allowed us to include the recognized units into a newly-established class (*Pinetea halepensis*) and its subordinate order (*Pinetalia halepensis*).

In comparison with EuroVegChecklist (Mucina et al., 2016), this study has enriched the syntaxonomical system of Europe by four newly recognized alliances (*Coremato albi-Pinion pinastri*, *Lavandulo pedunculatae-Pinion pinastri*, *Styraco officinalis-Pinion brutiae*) and one newly recognized alliance for North Africa (*Rosmarino eriocalycis-Pinion halepensis*). One previously invalidly described alliance was validated (*Jasmino-Juniperion excelsae*). In contrast, a previously described alliance (*Rosmarino officinalis-Pinion halepensis*) was not supported by the analysis of a large data set. The alliances *Alkanno baeoticae-Pinion halepensis*, *Campanulo sibiricae-Pinion brutiae* and *Jasmino fruticantis-Juniperion excelsae* with restricted geographic distribution will require further research.

The results of this study provide information on the compositional and distributional patterns of Mediterranean thermophilous pine forests, offering a list of statistically derived combinations of diagnostic species for the major eco-geographical vegetation units. Further, the workflow adopted in this study, but also its pitfalls and limitations, might be useful as a pathway for similar broad-scale vegetation classification studies.

This classification study sheds light on the biodiversity, biogeography and environment of the Mediterranean thermophilous pine forests. It complements the existing systems of habitat classification used for nature conservation such as the EUNIS Habitat Classification and the EU Habitats Directive, thus providing a tool for better conservation planning, monitoring and management at both the international and national level.

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AUTHOR CONTRIBUTIONS

GB and MC conceived the idea; GB, IK and MC developed the database; GB conducted the analysis, under the supervision of MC; SMH and LT provided support for data processing in TURBOVEG 3 and JUICE; JD helped with the interpretation of plant names; KC prepared maps and graphs; GB led the writing, with substantial inputs from MC; all the co-authors participated in discussions and syntaxonomic interpretations.

DATA AVAILABILITY STATEMENT

Vegetation-plot data used in this study are available in the CircumMed Pine Forest Vegetation Database (GIVD ID: EU-00-026) and European Vegetation Archive (EVA). They can be obtained upon request from the EVA database administrator with reference to EVA project no. 57.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1 Databases, countries and plot sizes used for the analysis.

Appendix S2 Expert system (script v. 2020-09-22) for classification of the phytosociological alliances and informal groups of plant communities of the Mediterranean thermophilous pine forests.

Appendix S3 Diagnostic, constant and dominant species for the accepted clusters based on TWINSPAN classification.

Appendix S4 Diagnostic, constant and dominant species for the alliances and informal groups of plant communities classified by the expert system.

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