



Vegetation classification and conservation aspects of Atlantic dune pine forests in the southwest of the Iberian Peninsula

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Abstract

This study refines the classification framework for Portuguese dune pine forests included in the alliance *Coremato albi-Pinion pinastri* at the association level after the syntaxonomic revision of Mediterranean pine forests of the class *Pinetea halepensis*. We collected 61 original vegetation plots between 2017 and 2022 in the southwestern Iberian Peninsula, analysing them through Principal Coordinate Analysis (PCoA) and UPGMA clustering. Numerical analysis identified four associations within the alliance *Coremato albi-Pinion pinastri*, specific to the sandy Atlantic coast of the Iberian Peninsula. Of these, three associations are newly described (*Cytiso grandiflori-Pinetum pinastri*, *Aristolochio baeticae-Pinetum pineae*, and *Ulici australis-Pinetum pineae*). Our study classified pine forests on sand in southwestern Iberia and identifies conservation-significant species in their understory. The floristic diversity in these psammophilous pine forests is enhanced by numerous endemics and relic species from the Tertiary period, shaped by past climatic refugia and multiple floristic migration routes, including Atlantic, Mediterranean, and North African pathways. This has resulted in a unique blend of thermophilic, oceanic, and xeric species with high conservation value. Our study contributes to the understanding of Atlantic dune pine forest ecology and inform habitat conservation efforts.

Keywords

Flora, psammophilous pine forests, phytosociology, *Pinetea halepensis*, *Pinus pinaster*, *Pinus pinea*, vegetation, sand dunes

Introduction

Pine forests are a widespread vegetation type across the Mediterranean Basin. Numerous studies have focused on these communities dominated by *Pinus pinaster* and/or *Pinus pinea* in various regions (Desole 1964; Arrigoni 1967; Agostini 1973; Brullo et al. 1977, 2002; Barbéro et al. 1998;

Gianguzzi 1999; Biondi and Vagge 2015; Bonari et al. 2017, 2018, 2020; Calvia et al. 2022a, 2022b; Ciaramella et al. 2024).

During the early Holocene, forest communities dominated by *Pinus pinaster* thrived in sandy coastal areas of the southwestern Iberian Peninsula, with macrofossil evidence dated between 7,930 and 7,430 cal years BP (García-Amorena et al. 2007). In regions south of Lisbon,

Pinus pinea is also well represented in the paleoecological record – particularly through macroremains and charcoal – dating back to approximately 6,300–6,400 ^{14}C years BP (Carrión et al. 2000; Carrión Marco 2005). These data suggest that both species were key components of coastal vegetation during the early-mid Holocene, even after their decline inland, where Mediterranean taxa became more dominant (Figueiral 1995).

Paleoecological and historical evidence confirm that both *Pinus pinaster* and *Pinus pinea* are native to Portugal (Teixeira and Pais 1976; Mateus 1992; Van Leeuwaarden and Queiroz 2003; Aguiar and Capelo 2008). Its consistent presence in Portuguese coastal areas since the Holocene (Rego 2001; Reboredo and Pais 2014), along with its ecophysiological and phenological traits, supports its long-standing adaptation to dynamic dune ecosystems, particularly at elevations below 500 meters (Aguiar and Capelo 2008).

Ecological differences between the two species are notable, especially in their fire responses. *Pinus pinaster* is a pyrophytic species, typically associated with high-biomass, flammable communities dominated by ericaceous and other fire-adapted taxa on western coastal sands. In contrast, *Pinus pinea* forms less flammable communities, often with sparse understories and few ericaceous species. Its reproductive biology and resin production traits indicate a lower adaptation to frequent, short-interval fires (Aguiar and Capelo 2008). These differences support the hypothesis of an originally allopatric distribution in the western and southwestern Iberian Peninsula, with each species occupying distinct ecological niches. Currently, pine forest communities are (co-)dominated by these two species that define both the structure and physiognomy of the vegetation.

Along the coast, forests of *Pinus pinaster* subsp. *pinaster* and *Pinus pinea* are designated as priority habitats on dunes under the EU Habitats Directive 92/43/EEC (Costa et al. 2007). According to the Interpretation Manual of EU Habitats (European Commission 2013), these formations are classified as priority habitat 2270, defined as current or ancient dune systems supporting forests of *Pinus pinaster* and/or *Pinus pinea*. In the EUNIS habitat classification system, these forests fall under type T3A, “Mediterranean lowland to submontane *Pinus* forest”, and are found across southern European countries (Chytrý et al. 2020).

However, Mediterranean pine forests lacked a well-defined phytosociological framework. Formerly, *Pinus pinaster* dune forests of southwestern Iberian peninsula had been variably assigned to the classes *Quercetea ilicis*, *Calluno-Ulicetea*, and *Cisto-Lavanduletea stoechadis*. The study by Bonari et al. (2021) represents the first attempt to formally classify these dune pine forests within a revised phytosociological framework at the class and alliance levels. Within the recently defined phytosociological class *Pinetalia halepensis* Bonari et Chytrý in Bonari et al. (2021), forests in the southwestern Atlantic region of the Iberian Peninsula – dominated by *Pinus pinaster* and/or *Pinus pinea* and primarily

occurring on sandy coastal soils – have been classified under the alliance *Coremato albi-Pinion pinastri* J.C. Costa, Neto, Capelo, Aguiar, Monteiro Henriques et Bonari in Bonari et al. (2021). This alliance encompasses pine forests of *Pinus pinaster* and *Pinus pinea* with a psammophilous understory rich in species restricted to southwestern Iberia. It is distributed along the coast within the thermo- to meso-Mediterranean bioclimatic zones of the western and southwestern Iberian Peninsula (Lusitanian coast and West Andalusia province; Preislerová et al. 2022). Nevertheless, subordinate syntaxonomic levels (i.e. associations) remain undefined, a knowledge gap that the present study seeks to address.

This study presents a phytosociological analysis of dune pine forests classified in the alliance *Coremato albi-Pinion pinastri* within priority habitat 2270 along the Atlantic coast of the Iberian Peninsula. It aims to i) describe and characterise the distinct plant communities of this habitat in Portugal and ii) underscore the conservation value of these forest formations and related flora.

Material and methods

Study area

The psammophilous pine forests studied here occupy a coastal region extending from the Ria de Aveiro in Portugal to the sands of the Costa del Sol in southwestern Spain. Influenced heavily by the Atlantic Ocean, this area is predominantly characterised by sandy and limestone substrates (Neto et al. 2007; Espírito-Santo et al. 2017). This coastal area faces west toward the Atlantic Ocean, where summer advection fogs are common (Daveau 1985).

Data collection and preparation

From 2017 to 2022, we conducted a phytosociological survey of pine forests on coastal sand dunes, collecting a total of 61 original vegetation plots (Suppl. material 1: table S1–S5) in habitat 2270, including both mature and newly stabilised dunes along the Iberian Atlantic coast, from Esmoriz to the Algarve. Fieldwork was concentrated in locations that were either previously documented in phytosociological literature or identified through a prior habitat mapping project.

The nomenclature for vascular plants in this study adheres to Flora Iberica (Castroviejo 1986–2012; Cubas 2000) and Flora-On (2023). Syntaxonomic nomenclature for associations outside of pine forests is based on Costa et al. (2012), while higher taxonomic ranks follow Mucina et al. (2016), apart from pine forests, for which we adhere to Bonari et al. (2021). Syntaxonomy aligns with the fourth edition of the International Code of Phytosociological Nomenclature (ICPN; Theurillat et al. 2021). All vegetation data are maintained in the CircumMed Forest Database (Bonari et al. 2019).

Bioclimatic classification for the description of the associations is based on Rivas-Martínez et al. (2011) and Monteiro-Henriques et al. (2016), while biogeographic units follow the system by Rivas-Martínez et al. (2011, 2017).

Analysis

To investigate differences in species composition among coastal sand dune pine forest types, we analysed the 61 original vegetation plots (relevés) collected in our survey. Transformation of cover-abundance values for numerical treatment follows van der Maarel (1979, 2007). The data were subjected to Principal Coordinate Analysis (PCoA) using the Bray-Curtis coefficient with CANOCO 5.5 software (ter Braak and Šmilauer 2012) and a UPGMA hierarchical clustering also based on Bray-Curtis coefficients, conducted with SYNTAX 2000 software (Podani 2001). We interpreted the UPGMA clusters by comparing species composition and analysing ecological gradients using literature-based references. Community definitions and synthetic table arrangements were developed using floristic-statistical group analysis following Müller-Dombois and Ellenberg (1974).

To emphasise the conservation significance of the vegetation and associated flora of pine forests (priority habitat 2270) in the Southwestern Iberian Peninsula, we prepared a list of taxa with conservation value based on their inclusion in the Habitats Directive annexes and their IUCN extinction risk category for mainland Portugal (IUCN conservation status; Carapeto et al. 2020), and level of endemism (Carapeto et al. 2020).

Results

The floristic composition analysis of the vegetation plots enabled us to distinguish four pine forest associations, of which three are newly described. The results of the Principal Coordinate Analysis (PCoA) are presented in Figure 1.

The PCoA shows plant community patterns on axis 1 according to latitude, reflecting the change in climatic conditions along the coast from north to south. Total rainfall values decrease from north to south and temperature

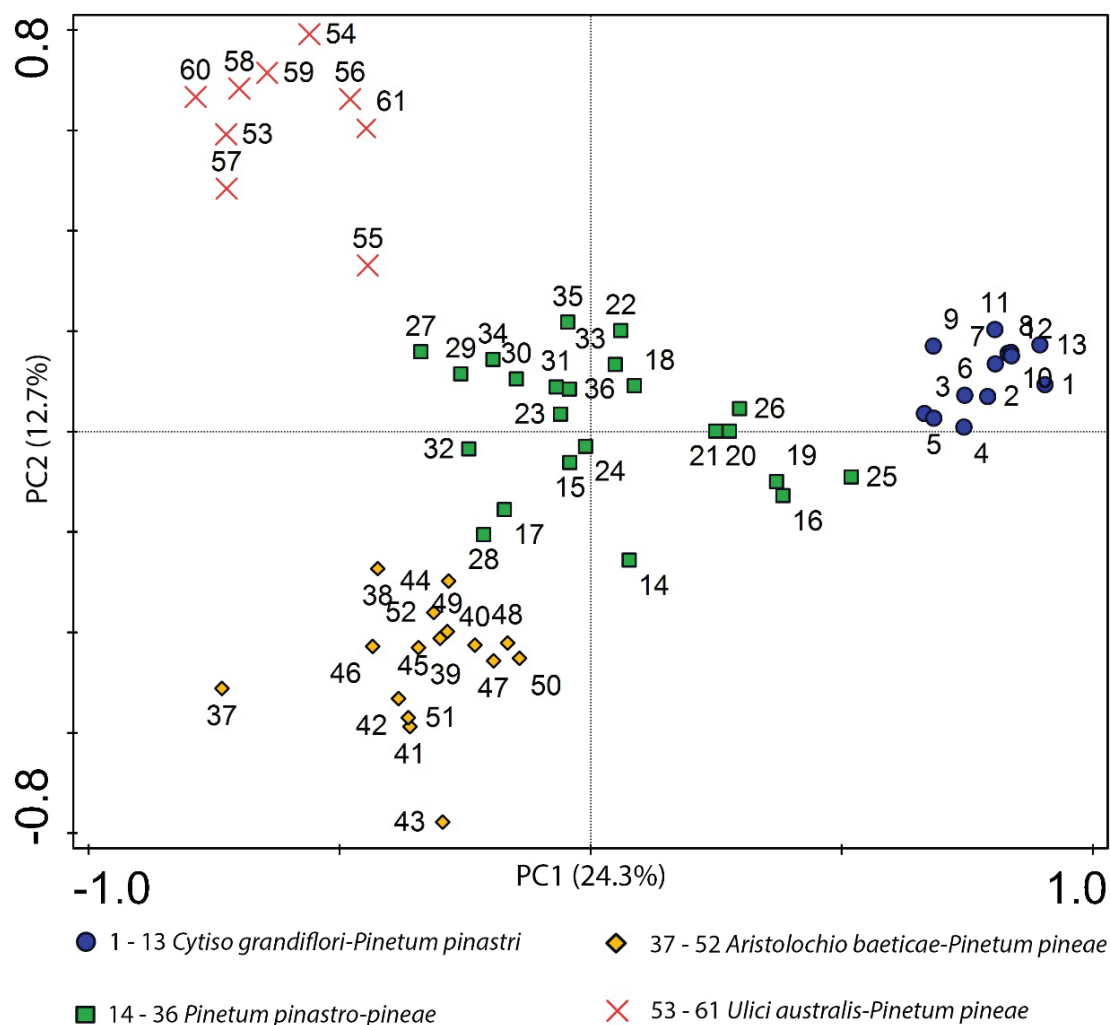


Figure 1. Principal Coordinate Analysis (PCoA) with Bray-Curtis coefficient, generated using CANOCO 5.5 software, based on 61 vegetation plots. Four distinct groups are evident, corresponding to the associations identified in this study. The spatial distribution of the associations is depicted in Figure 3.

values increase from north to south, in combination with summer fogs, which are very frequent north of Lisbon and gradually decrease southwards. These fogs are very important because they provide plants with water in the driest season. Thus, the associations found on axis 1 are organised according to this gradient, with the northernmost community (*Cytiso grandiflori*-*Pinetum pinastri*) occupying the highest values on axis 1, the *Pinetum pinastro-pineae* community occupying south-west Portugal and the other two associations (*Aristolochio*-*Pinetum pineae* and *Ulici*-*Pinetum pineae*) having a more southerly distribution, occupying the negative values on axis 1.

Our hierarchical clustering analysis highlights the separation among our pine forest communities (Figure 2). The first division can be interpreted as the distinction between the mesomediterranean community and the other thermomediterranean communities.

Figure 3 shows the distribution of the four pine forest communities. The abbreviated synthetic table (Table 1) presents species percentages across the four pine forest communities. The full table is reported in Suppl. material 1: table S6.

Pine forest communities

We describe the four pine forest communities (Figure 4) and provide information on the holotype for three newly described communities, diagnostic species, structure, ecology, dynamics, and chorology.

Cytiso grandiflori*-*Pinetum pinastri J.C. Costa, Monteiro-Henriques et Neto ass. nova (typus relevé no. 12, Suppl. material 1: table S1)

Type relevé (holotypus): *Pinus pinaster* 4, *Cytisus grandiflorus* subsp. *grandiflorus* 2, *Corema album* 2,

Halimium calycinum 2, *Myrica faya* 1, *Phillyrea angustifolia* 1, *Rubia peregrina* 1, *Ulex latebracteatus* +, *Arbutus unedo* +, *Cistus salviifolius* +, *Pinus pinaster* (juvenile) +, Other species: *Calluna vulgaris*. 1. Area: 200 m², Aspect: W; Locality: between Praia de Vieira and São Pedro de Muel, Leiria, Portugal.

Diagnostic species: *Cytisus grandiflorus* subsp. *grandiflorus*, *Erica arborea*, *Myrica faya*, *Ulex latebracteatus*.

Structure: A pine forest dominated by *Pinus pinaster*, ranging from 5 to 15 m in height, with a dense understorey of psammophilous and sclerophyllous shrubs, as well as some lianas and herbs. Typical species include *Corema album*, *Cytisus grandiflorus*, *Phillyrea angustifolia*, *Halimium calycinum*, *Cistus salviifolius*, *Ulex latebracteatus*, *Myrica faya*, *Arbutus unedo*, *Rubia peregrina*, *Halimium halimifolium* subsp. *multiflorum*, *Ruscus aculeatus*, *Helichrysum picardii*, *Daphne gnidium*, *Stauracanthus genistoides*, *Lavandula pedunculata* subsp. *lusitanica*, *Erica arborea*, *Scilla monophyllos*, *Pistacia lentiscus*, and *Calluna vulgaris*. In many areas, this association has been replaced by *Acacia longifolia*, an invasive species that has spread significantly in recent decades, particularly following fires.

Ecology: Found on recent and ancient Quaternary dunes at elevations of 5–60 m above sea level, within a lower sub-humid upper mesomediterranean bioclimate.

Dynamics: Generally situated as a vegetation strip adjacent to the dune interiors and *Juniperus* series (*Osyrio quadripartitae*-*Juniperetum turbinatae*, *Rubio longifoliae*-*Coremetum albi*). Further inland, *Cytiso grandiflori*-*Pinetum pinastri* may border *Lauro nobilis*-*Quercetum rivasmartinezii* or *Myrico fayae*-*Arbutetum unedonis*, which occupy thin dune sands, often overlaying Miocene-Pliocene formations in the innermost dune complex areas (Henriques and Neto 2002; Neto 2012). Subserial stages include the scrubland *Ulici latebracteati*-*Cytisetum striati*, the psammophilic thicket *Stauracantho genistoidis*-*Corematetum albi*, and the annual

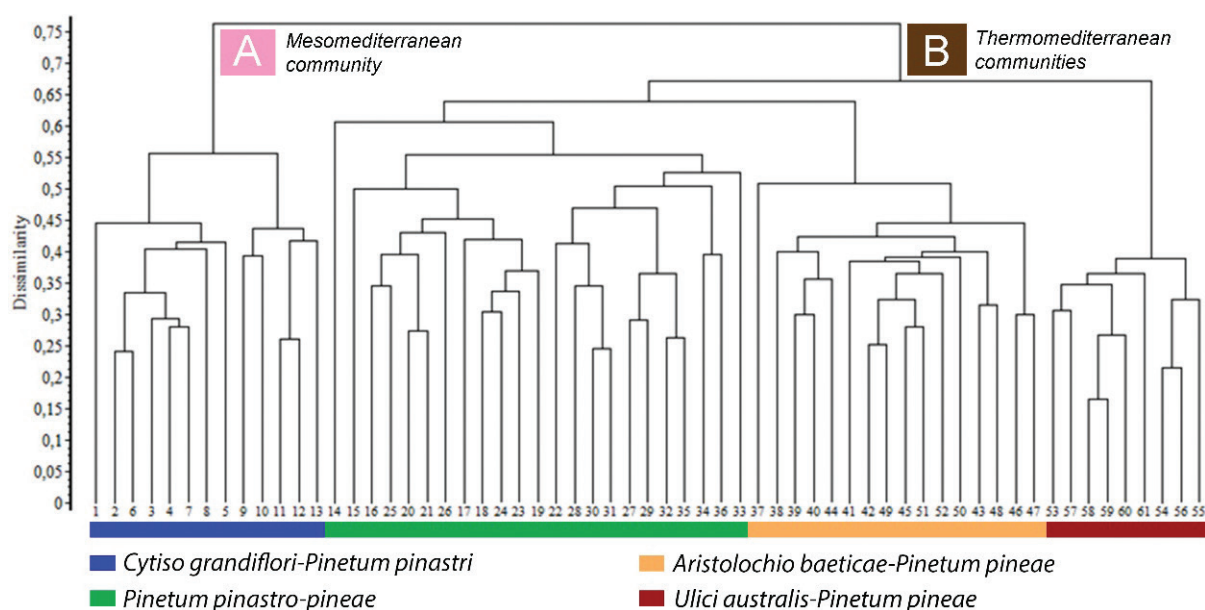


Figure 2. UPGMA dendrogram using the Bray-Curtis coefficient based on 61 vegetation plots.

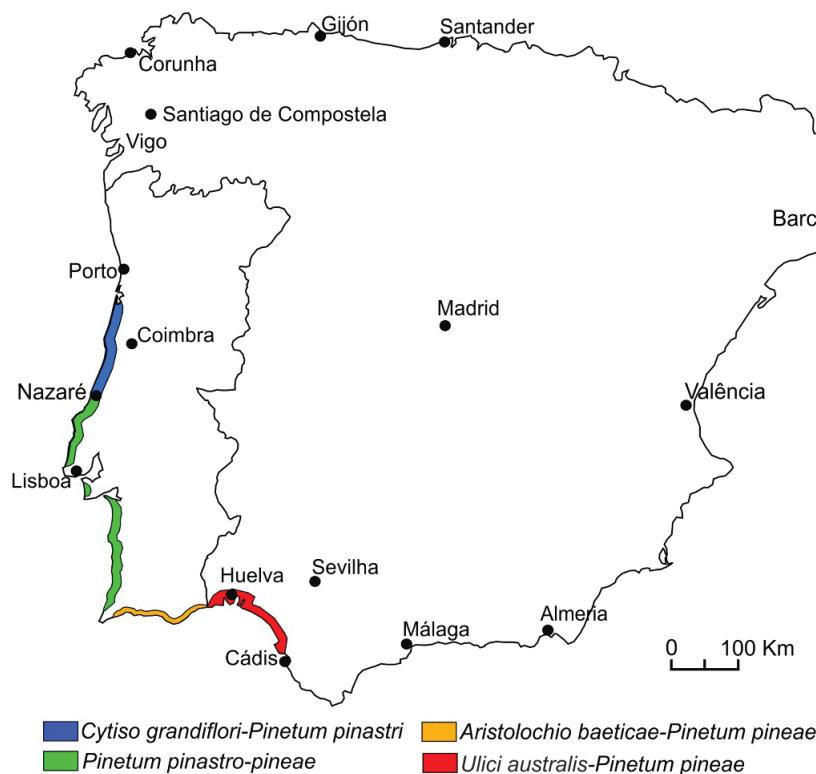


Figure 3. Distribution of plant communities in the western and southwestern regions of the Iberian Peninsula.

grasslands *Cerastio diffusi-Vulpietum fontqueranae* and *Herniario robustae-Corynephorum maritimi*.

Chorology: Ranges from south of Espinho to Nazaré, covering Porto and Low Douro District (Galicia and North Portugal sector, Cantabrian-Atlantic subprovince, Atlantic European province, Eurosiberian region, and Littoral Beira district, Lusitanian coast, and West Andalusia province, Mediterranean region).

***Pinetum pinastro-pineae* J.C. Costa et Neto in Bonari et al. 2021** (Suppl. material 1: table S2)

Diagnostic species: *Juniperus navicularis*, *Ulex jussiaei*, *U. australis* subsp. *welwitschianus*, *Armeria rouyana*, *Santolina rosmarinifolia*, *Stauracanthus spectabilis*, *Thymus camphoratus*, *Thymus capitellatus*.

Note: In the type relevé (holotypus) published in Bonari et al. (2021), *Ulex parviflorus* subsp. *parviflorus* is reported. However, this taxon is a complex of species including *U. jussiaei*, *U. australis* subsp. *australis*, *U. australis* subsp. *welwitschianus*, and *U. airensis*.

Structure: Mixed pine forest of *Pinus pinea* and *Pinus pinaster*, reaching heights of 5–20 m, characterised by a dense understorey of psammophilous, thermophilous, and sclerophyllous shrubs, vines, and herbs. Species include *Asparagus aphyllus*, *Pistacia lentiscus*, *Cistus salviifolius*, *Juniperus turbinata*, *Daphne gnidium*, *Helichrysum picardii*, *Corema album*, *Rubia peregrina*, *Ulex australis* subsp. *welwitschianus*, *Lavandula pedunculata* subsp. *lusitanica*, *Halimium calycinum*, *Phillyrea angustifolia*, *Rhamnus alaternus*, *Halimium halimifolium*

subsp. *multiflorum*, *Olea europaea* var. *sylvestris*, *Thymus capitellatus*, *Juniperus navicularis*, *Stauracanthus spectabilis*, *S. genistoides*, *Smilax aspera*, *Thapsia villosa* var. *platyphyllos*, *Quercus rivasmartinezii*, and other dune species such as *Corynephorus canescens* var. *maritimus*, *Ononis ramosissima*, and *Euphorbia portlandica*. The diagnostic species of this community include several endemic taxa, many of which are exclusive to Portugal and listed in Annexes II and IV of the Habitats Directive.

Ecology: Located on sandy soils of recent and ancient Quaternary dunes, at elevations of 5–60 m above sea level, within an upper dry to lower sub-humid thermomediterranean bioclimate.

Dynamics: The *Pinetum pinastro-pineae* represents the potential natural vegetation in most areas of recent dunes, with many species from *Juniperus turbinata* and *Corema album* shrub formations in the understorey, and primarily in ancient dunes where species of the *Juniperus navicularis* series are prevalent. Inland, it borders cork oak forests (*Aro neglecti-Quercetum suberis*). The subserial stages are primarily psammophilous plant communities, such as *Thymo capitellati-Stauracanthetum genistoidis* (Sado District), *Thymo camphorati-Stauracanthetum spectabilis* (São Vicente Coastal District), *Erico umbellatae-Ulicetum welwitschiani* (Sado and São Vicente Coasts), *Euphorbio transtaganae-Celticetum giganteae* (Sadense and Costeiro Vicentino), *Lavandulo luisieri-Ulicetum jussiaei* (Estremadura, Coimbra, and Lisbon Districts), *Omphalodo kuzinskyanae-Evacetum ramosissimae* (Lisbon), *Corynephoromacrantheri-Arenarietum algarbiensis* (Sado and São Vicente Coasts), *Herniario maritimae-Corynephorum maritimi*

Table 1. Shortened synthetic table of the four pine forest communities: 1 = *Cytisus grandiflori*-*Pinetum pinastri*; 2 = *Pinetum pinastro-pineae*; 3 = *Aristolochia baeticae*-*Pinetum pineae*; 4 = *Ulici australis*-*Pinetum pineae*. Cells in grey represent the diagnostic species of each plant community.

Pine forest community	1	2	3	4
N° of vegetation plots	13	22	16	9
Pine species				
<i>Pinus pinaster</i>	100	100	88	11
<i>Pinus pinea</i>	.	100	100	100
Diagnostic species				
<i>Cytisus grandiflorus</i> subsp. <i>grandiflorus</i>	92	.	.	.
<i>Ulex latebracteatus</i>	85	.	.	.
<i>Myrica faya</i>	69	.	.	.
<i>Erica arborea</i>	38	.	.	.
<i>Ulex australis</i> subsp. <i>welwitschianus</i>	.	52	.	.
<i>Juniperus navicularis</i>	.	26	.	.
<i>Thymus capitellatus</i>	.	30	.	.
<i>Stauracanthus spectabilis</i>	.	26	.	.
<i>Santolina rosmarinifolia</i>	.	22	.	.
<i>Ulex jussiaei</i>	.	13	.	.
<i>Thymus camphoratus</i>	.	9	.	.
<i>Armeria rouyana</i>	.	9	.	.
<i>Chamaerops humilis</i>	.	.	100	.
<i>Aristolochia baetica</i>	.	.	81	.
<i>Stauracanthus boivinii</i>	.	.	81	.
<i>Asphodelus serotinus</i>	.	.	81	.
<i>Ulex argenteus</i> subsp. <i>subsericeus</i>	.	.	75	.
<i>Asparagus albus</i>	.	.	63	.
<i>Centaurea aspera</i> subsp. <i>stenophylla</i>	.	.	38	.
<i>Genista hirsuta</i> subsp. <i>algarbiensis</i>	.	.	25	.
<i>Cistus libanotis</i>	.	.	19	.
<i>Thymus lotocephalus</i>	.	.	19	.
<i>Tuberaria major</i>	.	.	13	.
<i>Juniperus macrocarpa</i>	.	.	.	100
<i>Ulex australis</i> subsp. <i>australis</i>	.	.	.	56
<i>Thymus mastichina</i> subsp. <i>donyaea</i>	.	.	.	11
Other species				
<i>Juniperus turbinata</i>	8	87	.	100
<i>Corema album</i>	100	61	.	33
<i>Rosmarinus officinalis</i>	.	17	.	100
<i>Asparagus aphyllus</i>	15	96	100	22
<i>Pistacia lentiscus</i>	46	91	94	89
<i>Daphne gnidium</i>	54	83	94	56
<i>Helichrysum picardii</i>	54	70	69	100
<i>Rubia peregrina</i>	69	61	63	67
<i>Lavandula pedunculata</i> subsp. <i>lusitanica</i>	38	57	75	44
<i>Halimium calycinum</i>	92	52	56	67
<i>Stauracanthus genistoides</i>	38	26	.	56
<i>Asparagus acutifolius</i>	8	.	31	100
<i>Rhamnus oleoides</i>	.	17	38	89
<i>Osyris quadripartita</i>	.	13	44	56
<i>Myrtus communis</i>	.	4	38	11
<i>Halimium halimifolium</i> subsp. <i>multiflorum</i>	62	48	.	.
<i>Ruscus aculeatus</i>	54	9	.	.
<i>Scilla monophyllos</i>	54	22	.	.
<i>Cytisus grandiflorus</i> subsp. <i>cabezudo</i>	.	.	81	78
<i>Halimium halimifolium</i> subsp. <i>halimifolium</i>	.	.	56	100
<i>Thymus albicans</i>	.	.	56	11
<i>Armeria macrophylla</i>	.	.	31	11
<i>Euphorbia boetica</i>	.	.	31	11
<i>Corynephorus canescens</i> var. <i>maritimus</i>	38	57	6	11
<i>Scrophularia frutescens</i>	23	22	.	11
<i>Artemisia crithmifolia</i>	15	17	.	.

(Lisbon and Sado), and *Herniario unamunoanae*-*Corynephorum maritimi* (Sado and São Vicente Coasts).

Chorology: Extending from Nazaré to Cabo São Vicente, covering the Estremadura and Coimbra, Lisbon, Sado, and São Vicente Coastal Districts (including Ribatejo and Sado in the Portuguese sector, Cádiz and Sado subprovince, Lusitanian coast, and West Andalusia province, Mediterranean region).

***Aristolochia baeticae*-*Pinetum pineae* J.C. Costa, Neto et A.R. Pina ass. nova** (typus relevé no. 42, Suppl. material 1: table S3)

Type relevé (holotypus): *Pinus pinea* 4, *Pinus pinaster* 2, *Pistacia lentiscus* 3, *Ulex argenteus* subsp. *subsericeus* 3, *Chamaerops humilis* 2, *Osyris quadripartita* 2, *Daphne gnidium* 2, *Pinus pinea* (juvenile) 2, *Aristolochia baetica* 1, *Rhamnus oleoides* 1, *Asparagus aphyllus* 1, *Stauracanthus boivinii* 1, *Olea europaea* var. *sylvestris* +, *Phillyrea angustifolia* +, *Cytisus grandiflorus* subsp. *cabezudo* +, *Rubia peregrina* +, *Cistus salviifolius* +, *Lavandula pedunculata* subsp. *lusitanica* +, *Lavandula luisieri* +, *Halimium calycinum* +, *Helichrysum picardii* +, *Lithodora lusitanica* +, *Thapsia villosa* var. *platyphyllos* +, *Asphodelus serotinus* +; Other species: *Cistus ladanifer* 1, *Calluna vulgaris* +, *Genista triacanthos* +, *Carlina hispanica* +, *Dactylis hispanica* +, *Hyparrhenia hirta* +, *Tulipa australis* +. Area: 200 m²; Aspect: SW; Location: Ancão, Loulé, Portugal.

Diagnostic species: *Aristolochia baetica*, *Asparagus albus*, *Asphodelus serotinus*, *Centaurea aspera* subsp. *stenophylla*, *Chamaerops humilis*, *Cistus libanotis*, *Genista hirsuta* subsp. *algarbiensis*, *Stauracanthus boivinii*, *Thymus lotocephalus*, *Tuberaria major*, *Ulex argenteus* subsp. *subsericeus*.

Structure: *Pinus pinea* forest with *Pinus pinaster*, 10–20 m in height, supported by a dense understorey of psammophilous, thermophilous, and sclerophyllous shrubs, vines, and herbs, including *Asparagus aphyllus*, *Chamaerops humilis*, *Pistacia lentiscus*, *Cistus salviifolius*, *Daphne gnidium*, *Olea europaea* var. *sylvestris*, *Thapsia villosa* var. *platyphyllos*, *Aristolochia baetica*, *Cytisus grandiflorus* subsp. *cabezudo*, *Stauracanthus boivinii*, *Asphodelus serotinus*, *Ulex argenteus* subsp. *subsericeus*, and more. This forest is rich in endemic and rare taxa, some listed in Annexes II and IV of the Habitats Directive.

Ecology: Sandy soils, sometimes with gravel beds near the coast, at 0–20 m a.s.l., within a dry lower thermomediterranean bioclimate.

Dynamics: Represents the potential natural vegetation of the Algarve's sandy coastal soils. Substitution stages include: *Cytisetum cabezudo*, *Cistetum libanotidis*, *Tuberario majoris*-*Stauracanthetum boivinii*, *Armerio macrophyllae*-*Celticetum giganteae*, and *Tolpido barbatiae*-*Tuberarietum bupleurifoliae*. Inland, it transitions to cork oak forests (*Aro neglecti*-*Quercetum suberis*).

Chorology: Distributed in the Algarve district (Algarve and Monchique sector, Cádiz and Sado subprovince, Lusitanian coast, and West Andalusia province, Mediterranean region).



Figure 4. Photographs of the four pine forest communities. **A)** *Cytiso grandiflori-Pinetum pinastri* at Pinhal de Leiria (Portugal) – Pine forest of *Pinus pinaster* with an understorey of *Myrica faya*. **B)** *Pinetum pinastro-pineae* at Comporta (west coast, south of Lisbon) – Pine forest of *Pinus pinaster* with an understorey of *Corema album*, *Juniperus turbinata*, among others. **C)** *Aristolochio baeticae-Pinetum pineae* at Faro near Ria Formosa (southern coast, eastern Algarve) – Pine forest of *Pinus pinea* with an understorey of *Ulex argenteus* subsp. *subsericeus*, *Osyris quadripartita*, *Daphne gnidium*, *Halimium halimifolium* subsp. *halimifolium*, *Stauracanthus boivinii*, among others. **D)** *Ulici australis-Pinetum pineae* near Huelva (southwestern Spain) – Pine forest of *Pinus pinea* with an understorey of *Juniperus macrocarpa*, among others. Photo credits: A: J. C. Costa; B and C: C. Neto; D: A. R. Pina.

***Ulici australis-Pinetum pineae* J.C. Costa et A.R. Pina ass. nova** (typus relevé no. 54, Suppl. material 1: table S4)

Type relevé (holotypus): *Pinus pinea* 5, *Juniperus turbinata* 3, *Corema album* 3, *Juniperus macrocarpa* 2, *Osyris quadripartita* 2, *Pistacia lentiscus* 1, *Asparagus acutifolius* 1, *Cytisus grandiflorus* subsp. *cabezudo* 1, *Ulex australis* subsp. *australis* 1, *Stauracanthus genistoides* 1, *Rosmarinus officinalis* 1, *Rhamnus oleoides* +, *Daphne gnidium* +, *Halimium halimifolium* subsp. *halimifolium* +, *Halimium calycinum* +, *Helichrysum picardii* +, *Pinus pinea* (juvenile) +, *Lavandula pedunculata* subsp. *lusitanica* +, *Lavandula luisieri* +; Other species: *Celtica gigantea* +. Area: 400 m²; Aspect: S; Location: Torre de Higuera, Huelva, Spain.

Diagnostic species: *Juniperus macrocarpa*, *Rosmarinus officinalis*, *Thymus mastichina* subsp. *donyaea*, *Ulex australis* subsp. *australis*.

Structure: A *Pinus pinea* forest, 10–20 m in height, with a dense understorey of psammophilous, thermophilous, and sclerophyllous shrubs, vines, and herbs, such as *Juniperus turbinata*, *Asparagus acutifolius*, *Halimium halimifolium* subsp. *halimifolium*, *Helichrysum picardii*, *Rosmarinus officinalis*, *Juniperus macrocarpa*, *Pistacia lentiscus*, *Rhamnus oleoides*, and others.

Ecology: Within a dry lower thermomediterranean bioclimate at elevation between 5 and 30 m a.s.l.

Dynamics: On the coast, *Ulici australis-Pinetum pineae* contacts *Juniperus turbinata* communities (*Osyris quadripartitae-Juniperetum turbinatae*) and other coastal communities, transitioning inland to cork oak forests (*Aro neglecti-Quercetum suberis*). Substitution stages include *Halimio halimifolii-Stauracanthetum genistoidis*, *Asphodelo aestivi-Armerietum gaditanae*, and *Linario donyanae-Loeflingietum baeticae*.

Chorology: Cadiz and Littoral Huelva sector (Cádiz and Sado subprovinces, Lusitanian coast, and West Andalusia province, Mediterranean region).

We found 19 taxa of conservation concern with reference to Habitats Directive annexes (17 Annex I species, of which 4 of priority importance, and 18 Annex IV species), IUCN conservation status (2 critically endangered, 1 endangered, 2 vulnerable, 4 near threatened, and 10 least concern) in mainland Portugal and endemism levels (17 endemic to mainland Portugal, 2 endemic to Iberian Peninsula) (Table 2).

Discussion

We identified distinct pine forest communities in southwestern Iberia, including new associations on ancient coastal dunes. Their rich, psammophilous flora is shaped

Table 2. Flora of conservation concern in the understory of Atlantic dune pine forests in the southwestern Iberian Peninsula (priority habitat 2270), with reference to Habitats Directive annexes, extinction risk category in mainland Portugal (IUCN conservation status; Carapeto et al. 2020), and level of endemism. Species are listed in alphabetical order. The asterisk indicates a species present in our vegetation plots.

Species	Habitats Directive annex	Extinction risk in Portugal according to IUCN category	Level of endemism
<i>Armeria rouyana</i> *	Annex II (priority), IV	Near Threatened	Endemic to mainland Portugal
<i>Armeria velutina</i>	Annex II, IV	Critically endangered	Endemic to mainland Portugal
<i>Avenula hackelii</i>	Annex II, IV	Vulnerable	Endemic to mainland Portugal
<i>Euphorbia transtagana</i>	Annex II, IV	Least Concern	Endemic to mainland Portugal
<i>Herniaria algarvica</i>	Annex II, IV	Endangered	Endemic to mainland Portugal
<i>Herniaria maritima</i>	Annex II, IV	Least Concern	Endemic to mainland Portugal
<i>Hyacinthoides vicentina</i>	Annex II, IV	Least Concern	Endemic to mainland Portugal
<i>Jasione maritima</i> var. <i>sabularia</i> (J. <i>lusitanica</i>)	Annex II, IV	Near Threatened	Endemic to mainland Portugal
<i>Jonopsidium acaule</i>	Annex II, IV	Least Concern	Endemic to mainland Portugal
<i>Juniperus navicularis</i> *	-	Near Threatened	Endemic to Iberian Peninsula
<i>Linaria algarviana</i>	Annex II, IV	Near Threatened	Endemic to mainland Portugal
<i>Linaria bipunctata</i> subsp. <i>glutinosa</i> (L. <i>ficalhoana</i>)	Annex II (priority), IV	Least Concern	Endemic to mainland Portugal
<i>Omphalodes kuzinskyanae</i>	Annex II, IV	Critically endangered	Endemic to mainland Portugal
<i>Ononis hackelii</i>	Annex II (priority), IV	Vulnerable	Endemic to mainland Portugal
<i>Santolina impressa</i>	Annex II, IV	Least Concern	Endemic to mainland Portugal
<i>Thymus camphoratus</i> *	Annex II (priority), IV	Least Concern	Endemic to mainland Portugal
<i>Thymus capitellatus</i> *	Annex IV	Least Concern	Endemic to mainland Portugal
<i>Thymus carnosus</i>	Annex II, IV	Least Concern	Endemic to Iberian Peninsula
<i>Verbascum litigiosum</i>	Annex II, IV	Least Concern	Endemic to mainland Portugal

by climate and biogeographic boundaries. This region hosts many endemic and relict species due to its role as a climatic refuge and intersection of Mediterranean, Atlantic, and North African migration routes.

Pine forests associations

A recent large-scale study examined pine forest communities across lowland and submontane areas in 20 Mediterranean countries, resulting in the classification of Mediterranean pine forests within the class *Pinetea halepensis* (Bonari et al. 2021). In the Iberian Peninsula, pine forests are a dominant forest type, ranging from mountainous to lower elevations. In southwestern Iberia, these forests are classified within the alliance *Coremato albi-Pinion pinastri* J.C. Costa, Neto, Capelo, Aguiar, Monteiro Henriques et Bonari in Bonari et al. 2021. Our analysis of vegetation plots of the alliance *Coremato albi-Pinion pinastri* identified four associations, of which three of them are new, within these ancient dunes, formed during the Pleistocene glaciations and often subject to podzolisation.

North of Nazaré to Porto, summer fog significantly reduces water stress for coastal plants, unlike the southern coastal regions. As a result, many thermophilic coastal psammophilous species with southern distributions are absent in this sector, leading to a separation between mesomediterranean and thermomediterranean communities. This separation reflects the biogeographic boundary between the Eurosiberian and Mediterranean regions, located between Aveiro and Lisbon, where flora and vegetation from both regions converge due to the lack of biogeographic barriers.

Flora of conservation concern

The floristic composition of the psammophilous understory in pine forests varies along a coastal-to-inland gradient, influenced by soil and air salinity, sandy substrate mobility, temperature, wind, and soil chemistry, as well as latitudinal changes in climate. An important ecological factor along the western Iberian coast is horizontal precipitation from coastal summer fog, which declines in frequency from north to south (Daveau 1977, 1985). This fog supplies water to plants during the crucial summer months, influencing the distribution of species and communities. Thus, topography, climate, and biogeographical history contribute to the understory composition, resulting in a diverse flora with numerous Portuguese and Iberian endemics along the sandy coast (Costa 1992; Costa et al. 1997; Neto 2002; Neto et al. 2004, 2005).

The coastal vegetation in southwestern Iberia is notably rich in endemic Paleomediterranean and Paleotropical lianoid and lauroid species with leathery leaves (Costa et al. 1998; Costa et al. 2000; Espírito-Santo et al. 2017; Fernández-Palacios et al. 2017; Neto et al. 2019). This region's oceanic or hyperoceanic climate, with mild winters, has provided a refuge for numerous thermophilic and naked bud plants, which were relatively unaffected by Pleistocene glaciations and Holocene climatic shifts (Médail and Diadema 2009; Minkley et al. 2015; Gómez-Orellana et al. 2021). Such plants, typical of oceanic thermophilic forests, are absent in the more continental forests of holm and cork oaks, likely due to their inability to recolonise colder inland regions of Iberia during the Holocene.

This unique climatic and palaeoecological context also facilitated the persistence of palaeomediterranean Tertiary elements with affinities to the Macaronesian Subregion (e.g., *Myrica faya*, *Convolvulus fernandesii*, *Cheilantes guanchica*, *Polypodium macaronesicum*, *Woodwardia radicans*) and allowed the arrival of Mauritanian and Pontic-Indian flora (Costa et al. 1998; Vargas et al. 2018; Ramos-Capón et al. 2024). This area lies at the intersection of several floristic migration routes, primarily the Mediterranean coastal route and the Betic limestone range (from the Sierra Nevada to the Algarve Barrocal).

Broadleaved, soft-leaved Atlantic taxa of the class *Carpino-Fagetea sylvaticae*, including species of the genera *Acer*, deciduous *Quercus*, and *Sorbus*, also reached this territory from the north when the temperate macrobioclimate extended to lower latitudes (Alarcón et al. 2013; Vargas 2020), along with various *Ericaceae* species. The nanophanerophytic scrubland vegetation, represented by the alliance *Asparago albi-Rhamnion oleoidis* (order *Pistacio lentisci-Rhamnetalia alaterni*), contains a diversity of xeric paleotropical shrubs (*Olea*, *Pistacia*, *Rhamnus*, *Myrtus*, *Asparagus*), which endured the climatic shift from tropical to Mediterranean during the Miocene (Guzmán et al. 2009; Fiz-Palacios and Valcárcel 2013; López-Villalta 2014; Coello et al. 2021; Martín-Hernanz et al. 2023). These species now persist as either stable communities or as successional stages in low-rainfall, warm territories.

This region has also served as a significant area for speciation from ancient genotypes distinct from those in non-coastal western Iberia (e.g., *Stauracanthus* spp.). Various floristic migration routes have enriched the gene pool here, particularly two main coastal routes: an ascending route over mobile, halophilic dune substrates facilitating Mediterranean taxa migration, and a descending sublit-toral route supporting Atlantic taxa displacement. Additionally, this region shows evidence of contributions from a North African migratory route, evidenced by the presence of Iberian-Mauritanian taxa (Suc 1984; Palamarev 1989; Costa et al. 1998; Verdú et al. 2003; Jiménez-Moreno et al. 2010; Suc et al. 2018).

Conclusions

We present an updated vegetation classification of psam-mophilous pine forests in western and southwestern Iberian Peninsula, identifying three newly described syntaxa dominated by sand dune-exclusive plants. Each of the four associations analysed in this study is distinct, with a unique floristic composition. Our findings indicate a clear distinction between the mesomediterranean community and the thermomediterranean community group, influenced by the biogeographic boundary between the Eurosiberian and Mediterranean regions, which lies between Aveiro and Lisbon. This diffuse boundary, without biogeographic barriers, allows the convergence of flora and vegetation from both regions. Consequently, the

thermomediterranean plant communities contain a high number of taxa with predominantly Mediterranean distributions, particularly those native to southwestern Iberian sand habitats. The floristic assemblages, often hosting taxa previously considered diagnostic of other habitats – many of which are protected – highlights the conservation importance of these coastal Atlantic pine forests.

Syntaxonomic scheme

Class *Pinetea halepensis* Bonari et Chytrý in Bonari et al. 2021

Order *Pinetalia halepensis* Biondi, Blasi, Galdenzi, Pesaresi et Vagge 2014

Alliance *Coremato albi-Pinion pinastri* J.C. Costa, Neto, Capelo, Aguiar, Monteiro Henriques et Bonari in Bonari et al. 2021

Association *Cytiso grandiflora-Pinetum pinastri* J.C. Costa, Monteiro-Henriques et Neto ass. nova

Association *Pinetum pinastro-pineae* J.C. Costa et Neto in Bonari et al. 2021

Association *Aristolochio baeticae-Pinetum pineae* J.C. Costa, Neto et A.R. Pina ass. nova

Association *Ulici australis-Pinetum pineae* J.C. Costa et A.R. Pina ass. nova

Data availability

The data used in this article are accessible through the CircumMed Forest Database (GIVD Code: EU-00026).

Author contributions

JCC, CN, and TMH designed and conducted the survey; JCC and CN identified the plant specimens. CN, GB, and JCC wrote the manuscript. All authors contributed to the manuscript and approved the final submission.

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Supplementary material 1

Phytosociological tables of the Atlantic dune pine forests in the southwest of the Iberian Peninsula

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Data type: docx

Explanation note: We report the phytosociological tables of the Atlantic dune pine forests in the Southwest of the Iberian Peninsula; table S1 = *Cytiso grandiflori-Pinetum pinastri*; table S2 = *Pinetum pinastro-pineae*; table S3 = *Aristolochio baeticae-Pinetum pineae*; table S4 = *Ulici australis-Pinetum pineae*; table S5 = Coordinates of the original vegetation plots; table S6 = Synthetic table of the four pine forest communities.

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