

## **Mediterranean coastal pine forest stands: understorey distinctiveness or not?.**

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# 1 Mediterranean coastal pine forest stands: understorey distinctiveness or species 2 cauldron?

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6

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8

## 9 Abstract

10 A common perception of plantation forests is that they constitute an “ecological desert” and thus  
11 they are often disdained by scholars. Distribution patterns of understorey assemblages of coastal  
12 pine stands on sand dunes are still little known, despite such forests being widespread along the  
13 Mediterranean coastline, particularly in Italy. The purpose of this study of 167 plots along Italian  
14 coastlines was to analyse whether similar communities and specific species pools occur in different  
15 pine forest types dominated by *Pinus halepensis*, *P. pinea* or *P. pinaster*. Multivariate analysis was  
16 used, considering the effects of sea-inland gradient and pine canopy cover. The results indicated  
17 that pine forests do not consist of specific vegetation assemblages, suggesting the idea of a “floristic  
18 cauldron”. Understorey distinctiveness of Mediterranean coastal pine stands is limited, with  
19 psammophilous species of coastal dunes occurring mostly in *P. halepensis* stands, and forest  
20 species mainly being linked to *P. pinea* stands. Thus species-specific management is not required  
21 for different pine forest types. Like on non-forested dunes, plant species mainly followed the sea-  
22 inland gradient, maintaining the natural zonation of coastal vegetation. Moreover, higher pine  
23 canopy cover affected both herbaceous and woody natural dune vegetation in a negative way. These  
24 findings should not be disregarded since they have implications for management planning and

conservation and because understoreys of Mediterranean pine plantations, with a species reservoir of unknown value, have often hitherto been overlooked.

**Keywords:** canopy cover; dunes; Italy; plant species assemblage; sea-inland gradient; vegetation.

## 1 Introduction

Forest stands with dominance of stone pine, Aleppo pine and maritime pine (*P. pinea* L., *Pinus halepensis* Mill., *P. pinaster* Aiton) occur along almost all the low sandy coast of the Italian peninsula (Biondi et al., 2009), extending from the first back dune to the last settled innermost dune environment. Italian coastal pine forest vegetation, autochthonous or derived from ancient plantations, consists mainly of *P. pinea* or *P. halepensis* (Biondi & Blasi, 2015). Historically, the primary role of coastal pine forest stands was as a shelterbelt to protect cropland from salty sea spray and for production of pine nuts, timber and resin. These forests were mainly planted in the second half of the twentieth century or later and were maintained by humans for coastal defence against impermeabilisation waterproofing and soil erosion (Calama et al., 2003). They are well known for their rehabilitation capacity in Mediterranean dunal environments (see Bellarosa et al., 1996), as well as for recreational uses (Cutini et al., 2013) and carbon storage and sequestration services (Drius et al., 2016). Planted forests that were established a long time ago are more likely to be a habitat for biodiversity, although a common perception is that they are “ecological deserts” (Brockhoff et al., 2008). In fact, at European level they are included in “Coastal brown dunes covered with natural or almost natural thermophilous pines” (EUNIS Habitat Type Code B1.74) and since the 92/43 EEC Directive Habitat in priority habitat 2270 (“Wooded dunes with *P. pinea* and/or *P. pinaster*”), also including *P. halepensis* forests (Biondi et al., 2009). However, in recent decades, environmental concern about sandy coasts and associated pine forest have increased,

49 mainly due to direct and indirect effects of human activities, such as coastal erosion (Raddi et al.,  
50 2009), salinisation of groundwater (Antonellini & Mollema, 2010; Zanchi & Cecchi 2010),  
51 trampling (Santoro et al., 2012) and urban sprawl (Reina-Rodríguez & Soriano, 2008; Malavasi et  
52 al., 2013). These threats have been particularly intense in the last 50 years in countries bordering the  
53 Mediterranean Sea (Curr et al., 2000).

54 The flora of coastal pine forests has rarely been studied because artificial forests are not highly  
55 esteemed from a conservation viewpoint (Brockhoff et al., 2008). Although pines are the most  
56 common plantation species worldwide (about 20% of total plantation area) (FAO, 2001), pine  
57 forests have been considered “second choice” in plant community research compared with other  
58 forest types. However, pine-climate interactions (Mazza et al., 2011, 2014; Cutini et al., 2015), fire  
59 practices and their effects (Fernandes & Botelho, 2004; Rigolot, 2004; Fernandes et al., 2008) and  
60 dendrochronology are widely debated in the scientific literature (Calama et al., 2003; Calama &  
61 Montero, 2005). Although they are threatened like other dunal plant communities, the understoreys  
62 of these forests and the processes that drive them are still largely unknown and the importance of  
63 plantation forests for biodiversity conservation goals is a controversial issue.

64 Our primary objective in this study was to understand whether pine forests with different dominant  
65 pine species can harbour a particular understorey species pool or should rather be considered a  
66 “species cauldron”. We assumed that overstorey composition and structure influence understorey  
67 plant communities through modification of resources including light and soil (Messier et al. 1998,  
68 Légaré et al., 2001), with some species having special affinities for a particular overstorey type  
69 (Bartels & Chen, 2010). We analysed also the effects of sea-inland gradient and pine canopy cover  
70 on the underlying layers. Major questions were: i) Does vegetation associated with a pine forest  
71 type form distinct communities? ii) Are some plant species more likely to occur in one pine forest  
72 type than others? iii) How do distance to coastline and pine canopy cover affect pine understorey  
73 assemblages?

74 In this way, this work aims to contribute to the question whether species-specific management is  
75 required for forests dominated by different pine species and their understoreys, as a guide for  
76 vegetation management in Mediterranean coastal areas.

77

## 78 **2 Methods**

### 79 **2.1 Pine forest-types**

80 For data collection we considered the EU Directive definition of Habitat 2270 “Wooded dunes with  
81 *P. pinea* and/or *P. pinaster*” that also includes *P. halepensis* forests (Biondi et al., 2009). We then  
82 used data of three different pine forest-types dominated by: i) Stone pine (*Pinus pinea* L.); ii)  
83 Aleppo pine (*Pinus halepensis* Mill.); iii) Maritime pine (*Pinus pinaster* Aiton).

84 *Pinus pinea* is scattered throughout the Mediterranean basin, mainly in coastal areas. In Italy this  
85 “umbrella-shaped” tree is the icon of Italian coastal forests (Mazza et al., 2014) and it is reported as  
86 native to Liguria, Tuscany, Molise and the major islands, i.e. Sicily and Sardinia (Conti et al.,  
87 2005), although there is little evidence of its nativeness (Abad Viñas et al., 2016a). *Pinus halepensis*  
88 is largely present in the Western sector of the Mediterranean basin and it is the most widely  
89 distributed Mediterranean pine. In Italy the species is recognized as native to all regions except the  
90 Alps (Conti et al., 2005), although it has been widely planted (Mauri et al., 2016). *P. pinaster* has a  
91 western Mediterranean distribution; this medium-size pine mainly occurs in north and central Italy.  
92 Its presumed native distribution includes Liguria, Tuscany, Lazio and the major islands (Conti et al.,  
93 2005).

94

### 95 **2.2 Study area**

96 The study area included pine forests established on dunes along the coasts of the Italian peninsular.  
97 The forests occur in six administrative regions on the coasts of the Tyrrhenian (Toscana, Lazio and  
98 Campania) and Adriatic seas (Emilia-Romagna, Molise and Puglia), including much of the  
99 distribution of pine stands in the Italian peninsular. The sites ranged about from 0 to 5 m a.s.l. and  
100 phyto-climate depends mostly on latitude, ranging from Temperate to Mediterranean, passing through  
101 transition zones (Blasi & Michetti, 2007). The study area comprises mainly calcareous sediments,  
102 although aeolian deposits also occur from time to time (Geoportale Nazionale, 2015).

103

### 104 **2.3 Data collection**

105 For the purpose of the present study, field sampling in *Pinus pinea* stands was performed in 2014-  
106 2015, whereas an existing database of coastal dune vegetation (Acosta et al., 2009, Malavasi et al.,  
107 2016) was mainly used for *P. halepensis* and *P. pinaster* stands. Firstly, only plots with at least one  
108 of the pine species *Pinus pinea*, *P. halepensis* or *P. pinaster* were used because our interest was the  
109 role of pines. Secondly, only plots on sandy soil were included in the dataset. Thus, a dataset based  
110 on 167 plots (2 × 2 m) was defined. Each plot was assigned to a pine forest type in relation to the  
111 pine species dominant in each plot. Distance between georeferenced plot and coastline, used as a  
112 proxy of sea-inland gradient, was determined remotely by GIS. The study did not involve any  
113 experimental manipulations or disturbance of naturally developed relationships. Observed patterns  
114 should therefore reflect long-term plant–ecological interactions. The focal species of dunal  
115 vegetation were identified and selected using the list of diagnostic and characteristic species in the  
116 “Italian Interpretation Manual of the 92/43/EEC Directive Habitats” (Biondi et al., 2009; Biondi &  
117 Blasi, 2015). Autochthonous species names are according to Conti et al. (2005), alien species names  
118 are according to The Plant List (2013).

119

## 120    **2.4 Data analysis**

121    The dataset of 167 plots (94 ascribed to *Pinus pinea*, 65 to *Pinus halepensis*, and 8 to *Pinus*  
122    *pinaster*) contained 269 species. Plant values were cover percentages of each species between 0 and  
123    100. The complete species list is reported in Appendix A.

124    Evaluation of species composition distinctiveness in each forest type (with and without pine canopy  
125    covers) was performed using the following techniques:

126    1) Multi-response Permutation Procedure (MRPP), a non-parametric multivariate procedure for  
127    testing the hypothesis of no difference in species composition between two or more groups of plots  
128    chosen *a priori* (McCune & Mefford, 1999; McCune & Grace, 2002). A weighted mean within-  
129    group distance in species space is calculated using Sorensen distance. MRPP consists of two  
130    statistical tests: the *A* Statistic estimates within-group homogeneity and the *T* Statistic measures  
131    between-group separability. Higher *A* statistic values (maximum value 1) indicate a high degree of  
132    homogeneity within groups while a large negative *T* value ( $\leq -10.0$ ) indicates high separability  
133    between groups. The null hypothesis was assessed by a Monte Carlo permutation procedure with  
134    999 permutations;

135    2) Non-Metric Multidimensional Scaling (NMDS) based on Euclidean distance, used to investigate  
136    community patterns without data transformations;

137    3) INDicator SPecies ANalysis (INSPAN), performed to find species significantly associated with  
138    each forest type via 4999 randomization tests (Dufrené & Legendre, 1997).

139    To investigate whether sea-inland gradient and pine canopy cover significantly influenced  
140    understorey species distribution in coastal pine forests, two hybrid constrained CCAs were  
141    performed, with the Log ( $X+1$ )-transformed variable 'Distance'. The significance of the constrained  
142    axis was tested by a Monte Carlo randomization method, using 999 permutations. To test species  
143    response to sea-inland gradient and pine cover, for species with more than ten occurrences in the

dataset, including pines, we used General Additive Models (GAM) with binomial distribution, logit link function, 2.0 df (see Yee & Mitchell, 1991; Hájková et al., 2008; Ilunga wa Ilunga et al., 2013; Dyakov, 2016) and the quasi-distribution approach for modelling overdispersed data. GAMs were chosen because they assume a non-linear relationship between the response and each explanatory variable. Binomial distribution data was treated as binary. MRPP and INSPAN analyses were performed using the software package PCORD 6.0 (McCune and Mefford 2011), whereas NMDS, CCAs and GAMs were calculated using CANOCO v. 5.03 (ter Braak & Šmilauer 2012).

**3 Results**

Twenty-nine percent (78 out of 269) of all coastal pine stand species were focal for dune habitats (Appendix A). The MRPP results (Table 1) using the data set including pine species canopy covers suggested that forests dominated by different pine species host different plant species assemblages. The T statistic, representing separation between pine forest types, was high, negative and highly significant, while the A statistic indicated relative within-group homogeneity. However, for the data set without pine species canopy covers, the results showed few differences between vegetation plots, particularly when forest types were compared. Although the T statistic was negative and statistically significant, within-group observed average distance was high. In addition, the A statistic, a measure of within-group homogeneity, was an order of magnitude less than the value obtained when pine canopy cover data was included.

*Table 1. MRPP community comparison results*

	T statistics	Sorensen distance	A statistics
Data with pine species	-62.74 (p < 0.001)	0.68	0.21

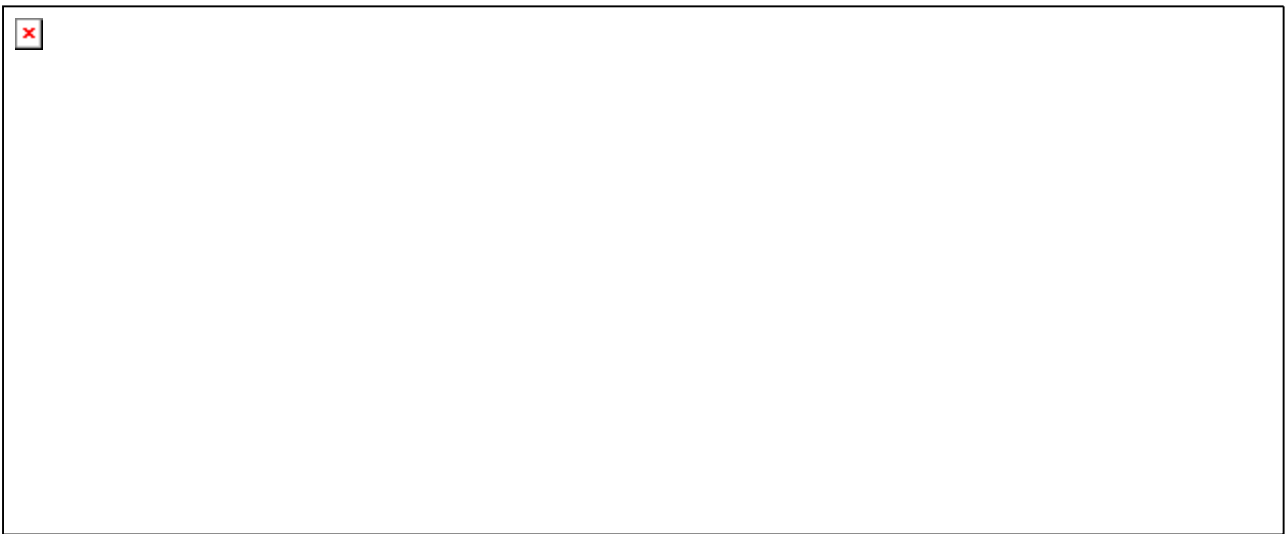


<b>Data without pine species</b>	-10.78 (p < 0.001)	0.94	0.014
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165

166 NMDS diagrams with plots grouped in three clusters obtained by *a priori* classification of forest  
 167 dominated by different pine species are shown in Figure 1. When pine cover data was included  
 168 (final stress = 0.10281), the first three axes explained 100% of community variation (axis 1  
 169 captured 60.1% of the variance, axis 2, 22.4%) and the biplot demonstrated clear disjunction of  
 170 plots dominated by different pine species (Figure 1a). In contrast, when pine canopy covers were  
 171 excluded (Figure 1b; final stress = 0.18482) the first three axes explained 100% of community  
 172 variation (axis 1 captured 38.8% of the variance, axis 2, 34.2%) and showed unclear separation of  
 173 plots dominated by different pine species.

174



175

176 *Figure 1. NMDS diagram of plots including (A) and excluding pine canopy cover data (B). Colors*  
 177 *indicate the dominant pine species. Blue diamonds are Pinus halepensis dominated plots, red stars*  
 178 *are P. pinea dominated plots and green triangles are P. pinaster dominated plots.*

179

INSPAN to detect affinity of species with the three pine forest types revealed a low percentage of indicator species (10.8%) among the total number of species (Table 2; McCune & Grace, 2002). Indicator species for *P. pinea* forest type numbered nine (3.4%) and were mainly related to forest on stabilized dunes, including *Brachypodium sylvaticum* ssp. *sylvaticum* and *Carex distachya*. Indicator species for *Pinus halepensis* forest type numbered 20 (7.4%), and were typical pioneer psammophilous species, such as *Ammophila arenaria* ssp. *australis* and *Medicago marina*, mostly associated with the forward part of the dune series. No significant indicator species for *P. pinaster* forest type were detected.

188

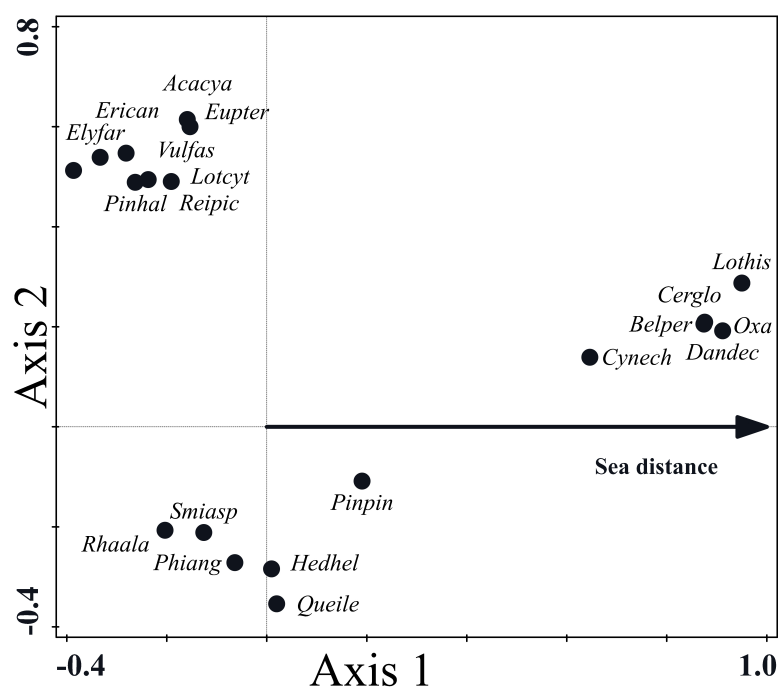
Table 2. INSPAN diagram with dominance of *Pinus halepensis*, *P. pinea* and *P. pinaster*. Only significant species are shown. Species are sorted in alphabetical order. IV = Indicator Value.

Dominant species	Indicator species	IV	p
<b><i>Pinus pinea</i></b> (p = 0.001)	<i>Arum italicum</i>	8.4	0.0484
	<i>Brachypodium sylvaticum</i> ssp. <i>sylvaticum</i>	13.8	0.0032
	<i>Carex flacca</i>	11.7	0.0072
	<i>Carex distachya</i>	8.5	0.0192
	<i>Clematis flammula</i>	9.7	0.0280
	<i>Cyclamen repandum</i>	7.4	0.0374
	<i>Euphorbia peplus</i>	10.6	0.0104
	<i>Geranium purpureum</i>	11.7	0.0066
	<i>Trachynia distachya</i>	7.4	0.0338
<b><i>Pinus halepensis</i></b> (p = 0.001)	<i>Ammophila arenaria</i> ssp. <i>australis</i>	9.4	0.0032
	<i>Artemisia campestris</i> ssp. <i>glutinosa</i>	10.9	0.0012



196 distance, such as *Phillyrea angustifolia* and *Hedera helix*, and generalist species at greater distances  
 197 from the sea, such as *Bellis perennis* and *Cerastium glomeratum*.

198

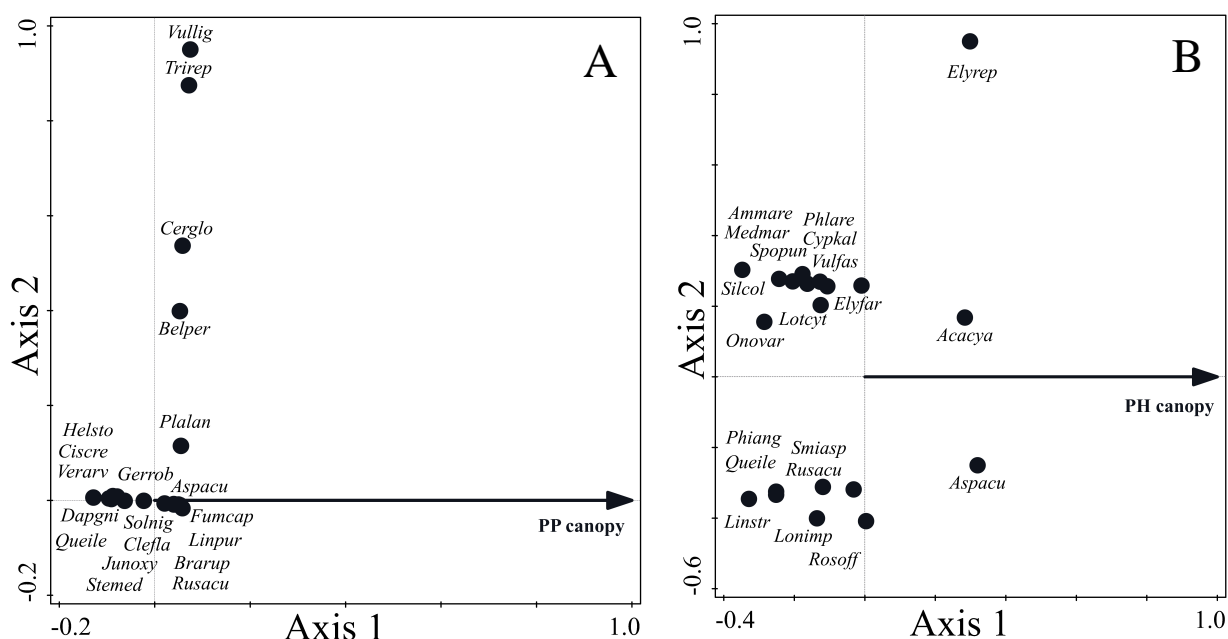


199

200 Figure 2. Hybrid constrained CCA diagram. Axis 1 captured 3.2% of the variance ( $p = 0.001$ ). The  
 201 first 20 best fitting species in the ordination spaces are shown. Plant species are designated with  
 202 the first three letters of their genus and species names as follows: Acacya = *Acacia cyanophylla*;  
 203 Belper = *Bellis perennis*; Cerglo = *Cerastium glomeratum*; Cynech = *Cynosurus echinatus*;  
 204 Dandec = *Danthonia decumbens ssp. decumbens*; Elyfar = *Elymus farctus ssp. farctus*; Erican =  
 205 *Erigeron canadensis*; Eupter = *Euphorbia terracina*; Hedhel = *Hedera helix*; Lotcyt = *Lotus*  
 206 *cytisoides*; Lothis = *Lotus hispidus*; Oxa = *Oxalis sp.*; Phiang = *Phillyrea angustifolia*; Pinhal =  
 207 *Pinus halepensis*; Pinpin = *Pinus pinea*; Queile = *Quercus ilex ssp. ilex*; Reipic = *Reichardia*  
 208 *picroides*; Rhaala = *Rhamnus alaternus ssp. alaternus*; Smiasp = *Smilax aspera*; Vulfas = *Vulpia*  
 209 *fasciculata*.

210 Hybrid constrained CCAs with canopy cover of *P. halepensis* and *P. pinea* (Figure 3) revealed the  
 211 significant effect of pine cover on the understorey. In both CCAs, lower canopy cover was  
 212 associated with herbaceous and shrub species of natural dunal successions, whereas higher canopy  
 213 cover was associated with generalist and alien species. Hybrid constrained CCA with *P. pinaster*  
 214 did not produce significant results and is therefore not shown.

215



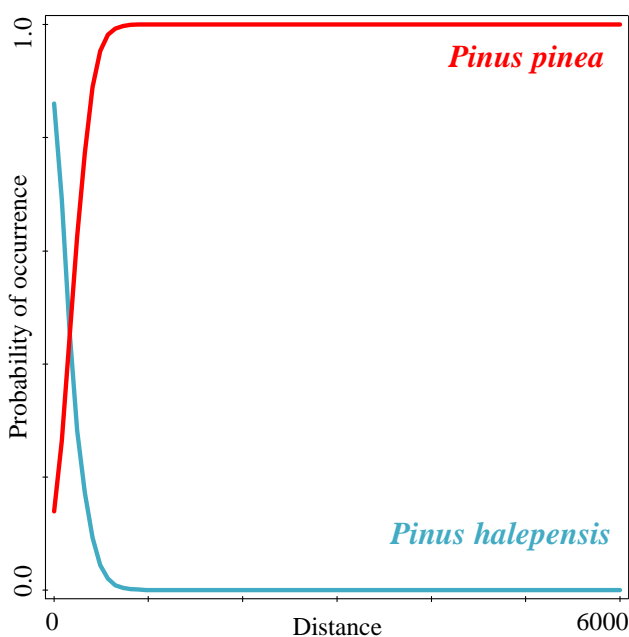
216

217 Figure 3. Hybrid constrained CCA diagrams. A) *Pinus pinea* canopy-constrained B) *P. halepensis*  
 218 canopy-constrained. Axis 1 captured 1.5% of the variance ( $p = 0.013$ ) and 3.1% ( $p = 0.001$ ),  
 219 respectively. The first 20 best fitting species in the ordination spaces are shown. Plant species are  
 220 designated with the first three letters of their genus and species names as follows: A) Aspacu =  
 221 *Asparagus acutifolius*; Belper = *Bellis perennis*; Brarup = *Brachypodium rupestre*; Cerglo =  
 222 *Cerastium glomeratum*; Ciscra = *Cistus creticus* ssp. *eriocephalus*; Clefla = *Clematis flammula*;  
 223 Dapgni = *Daphne gnidium*; Fumcap = *Fumaria capreolata* ssp. *capreolata*; Gerrob = *Geranium*  
 224 *robertianum*; Helsto = *Helichrysum stoechas*; Junoxy = *Juniperus oxycedrus* ssp. *macrocarpa*;  
 225 Linpur = *Linaria purpurea*; Plalan = *Plantago lanceolata*; Queile = *Quercus ilex* ssp. *ilex*; Rusacu

226 = *Ruscus aculeatus*; *Solnig* = *Solanum nigrum*; *Stemed* = *Stellaria media*; *Trirep* = *Trifolium*  
 227 *repens*; *Verarv* = *Veronica arvensis*; *Vullig* = *Vulpia ligustica*; B) *Acacya* = *Acacia cyanophylla*;  
 228 *Ammare* = *Ammophila arenaria* ssp. *australis*; *Aspacu* = *Asparagus acutifolius*; *Cypkal* = *Cyperus*  
 229 *capitatus*; *Elyfar* = *Elymus farctus* ssp. *farctus*; *Elyrep* = *Elymus repens* ssp. *repens*; *Linstr* =  
 230 *Linum strictum*; *Lonimp* = *Lonicera implexa* ssp. *implexa*; *Lotcyt* = *Lotus cytisoides*; *Medmar* =  
 231 *Medicago marina*; *Onovar* = *Ononis variegata*; *Phiang* = *Phillyrea angustifolia*; *Phlare* = *Phleum*  
 232 *arenarium* ssp. *caesium*; *Queile* = *Quercus ilex* ssp. *ilex*; *Rosoff* = *Rosmarinus officinalis*; *Rusacu*  
 233 = *Ruscus aculeatus*; *Silcol* = *Silene colorata*.; *Smiasp* = *Smilax aspera*; *Spopun* = *Sporobolus*  
 234 *virginicus*; *Vulfas* = *Vulpia fasciculata*.

235 GAMs on pine species revealed that *P. pinea* and *P. halepensis* were highly significant ( $p < 0.001$ ;  
 236 Appendix B). The curve trends (Figure 4) showed that *P. pinea* showed its greatest probability of  
 237 occurrence after the first 1000 m, continuing for the rest of the sea-inland gradient. On the other  
 238 hand, *P. halepensis* had the highest probability of occurrence in the first 1000 m from the coast and  
 239 then disappeared. The *P. pinaster* curve is not shown in Figure 4 because it was not significant.

240



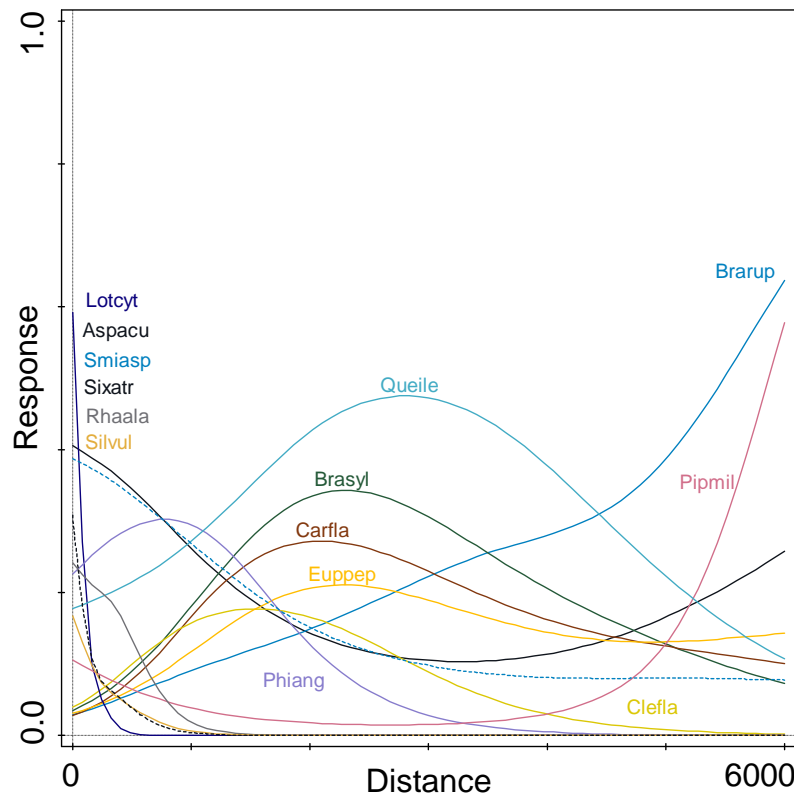
241

242 Figure 4. Species-response curves (GAMs) of pine species with respect to distance from sea  
 243 (probability of occurrence in relation to sea distance). *Pinus halepensis* and *P. pinea* were  
 244 significant ( $p < 0.001$ ). *P. pinaster* was not statistically significant.

245

246 GAMs revealed 14 species that responded significantly to binomial distribution based on CCA with  
 247 distance (Figure 5; Appendix C). Along the sea-inland gradient, dune species *sensu strictu*, such as  
 248 *Lotus cytisoides*, showed maximum probability of occurrence close to the sea, while innerdune  
 249 species (e.g. *Phillyrea angustifolia*, *Quercus ilex* and *Brachypodium sylvaticum* ssp. *sylvaticum*)  
 250 showed maximum response at intermediate distances, and species not linked to dune vegetation  
 251 succession, such as *Brachypodium rupestre*, were found at high distances.

252



253

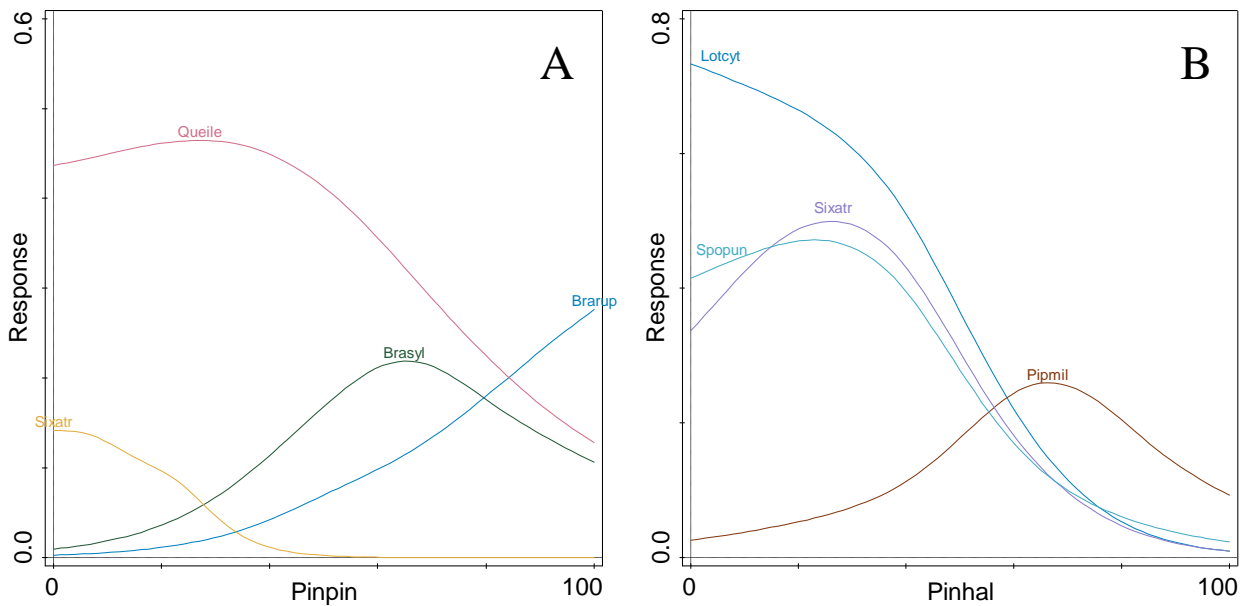
254 Figure 5. Species-response curves (GAMs) with respect to sea distance for species with more than  
255 10 occurrences in the dataset (probability of occurrence in relation to sea distance). Only  
256 significant models are shown. Plant species are designated with the first three letters of their genus  
257 and species names as follows: *Aspacu* = *Asparagus acutifolius*; *Brarup* = *Brachypodium rupestre*;  
258 *Brasyl* = *Brachypodium sylvaticum* ssp. *sylvaticum*; *Carfla* = *Carex flacca*; *Clefla* = *Clematis*  
259 *flammula*; *Euppep* = *Euphorbia peplus*; *Lotcyt* = *Lotus cytisoides*; *Phiang* = *Phillyrea angustifolia*;  
260 *Pipmil* = *Piptatherum miliaceum*; *Queile* = *Quercus ilex* ssp. *ilex*; *Rhaala* = *Rhamnus alaternus*  
261 ssp. *alaternus*; *Silvul* = *Silene vulgaris*; *Sixatr* = *Sixalix atropurpurea*; *Smiasp* = *Smilax aspera*.

262

263 GAMs to test understorey species trends in relation to *P. pinea* or *P. halepensis* canopy cover  
264 showed four species in both cases that responded significantly to binomial distribution (Appendix  
265 D). *Sixalix atropurpurea* and *Quercus ilex* showed a higher probability of occurrence at lower  
266 canopy cover of *P. pinea*, whereas species such as *Brachypodium sylvaticum* ssp. *sylvaticum* and *B.*  
267 *rupestre* preferred higher canopy cover of *P. pinea* (Figure 6a). For *P. halepensis* a common trend  
268 of focal dune species was found (*Lotus cytisoides*, *Sporobolus virginicus*), showing higher  
269 occurrence at lower canopy cover of the pine and then sharply decreasing, whereas *Piptatherum*  
270 *miliaceum*, which is not a focal dune species, showed a different trend (Figure 6b).

271





272

273 Figure 6. Species-response curves (GAMs) with respect to canopy of *P. pinea* (A) and *P. halepensis*  
 274 (B) on species with more than 10 occurrences in plots (probability of occurrence in relation to  
 275 canopy cover). Only significant models are shown. Plant species are designated with the first three  
 276 letters of their genus and species names as follows: Brarup = *Brachypodium rupestre*; Brasyl =  
 277 *Brachypodium sylvaticum ssp. sylvaticum*; Lotcyt = *Lotus cytisoides*; Pipmil = *Piptatherum*  
 278 *miliaceum*; Queile = *Quercus ilex ssp. ilex*; Sixatr = *Sixalix atropurpurea*; Spopun = *Sporobolus*  
 279 *virginicus*.

280

## 281 4 Discussion

282 Different outcomes were obtained when pine canopy cover was included in or excluded from our  
 283 dataset. When tree pine canopy cover was included, floristic differences were evident between pine  
 284 forest types. After pine canopy cover was excluded from analysis, the pattern disappeared and  
 285 communities converged into a single cluster with less difference in plant species composition. This  
 286 suggests that the different coastal pine forest types are not characterized by distinct floristic and  
 287 ecologically different understoreys. Pine stands therefore do not differentiate a specific species

288 pool. Vascular plant species can generally colonize plantation forests regardless of canopy species  
289 when habitat characteristics are appropriate (Carnus et al., 2006). Since all the pine forest stands  
290 studied shared substantially the same coastal dune environment, known to be a very selective  
291 habitat for plants (Maun, 2009), the lack of floristic differentiation between them can therefore be  
292 explained by their relatively similar environmental conditions (Frelich et al., 2003). Moreover, other  
293 authors have considered environmental conditions to be more important drivers of understorey  
294 community composition than dominant tree species (Piwczynski et al., 2016). In the same  
295 perspective, species composition may be highly variable and change substantially in response to  
296 environmental change in each pine forest type. Stands of different pine types, planted across the  
297 sea-inland gradient where vegetation zonation ranges from pioneer communities of embryonic  
298 dunes to pine plantations, have been found to host a variety of species, mainly distributed according  
299 to this gradient and often adapted to coastal environments near the sea shore (psammophilous  
300 species) (Acosta et al., 2003).

301 Although MRPP and NMDS suggested low distinctiveness at community level, T statistics  
302 indicated that different pine forest stands showed some differences in species assemblages, even  
303 when pine canopy cover was excluded from analysis. INSPAN supported this thesis, highlighting  
304 that a small pool of species was more likely to occur in one pine forest type than another. Notably,  
305 20 species showed significant affinity for *Pinus halepensis* stands, 14 of which were focal for  
306 coastal dunal habitats (Biondi et al., 2009; Biondi & Blasi, 2015) and in some cases were strictly  
307 psammophilous. Among these, *Sporobolus virginicus* and *Elymus farctus* ssp. *farctus*, typical of  
308 embryonic Mediterranean dunes (Acosta et al., 2007; Biondi et al., 2009; 2012), showed the highest  
309 indicator values for *P. halepensis* forest. On the other hand, in line with Biondi et al. (2009) and  
310 Biondi & Blasi (2015), forest species were linked to *P. pinea* stands, where *Brachypodium*  
311 *sylvaticum* ssp. *sylvaticum* was the species with the highest indicator value. This may be related to  
312 the fact that *P. halepensis* stands were often planted closer to the sea, whereas *P. pinea* stands were

313 planted relatively far from the coastline and therefore had a higher probability of occurrence along  
314 most of the sea-inland gradient. In fact, *P. pinea* has been reported to have a wide range of  
315 distribution in coastal dune habitats, mostly growing on fixed dunes and in areas with deep water  
316 table and relatively low salinity (Antonellini and Mollema, 2010; Angiolini et al. 2013). The spatial  
317 location of these two pine forest types, positioned slightly differently with respect to each other and  
318 extending from the foredunes to the innermost dunes (paleodunes), reflects the different ecology of  
319 the pine species. Indeed, *P. halepensis* is more pioneer, well adapted to drought (Mauri et al., 2016)  
320 and able to spread by seed from plantations into adjacent natural plant communities (Higgins &  
321 Richardson 1998; Lavi et al., 2005), occasionally also colonizing the inner part of the foredunes.  
322 Thus, the indicator species for *P. halepensis* forest type were largely very specialized  
323 psammophilous plants that grow exclusively on embryonic dunes, tolerating salt spray, drought and  
324 unstable substrates (Garcia-Mora et al. 1999; Acosta et al., 2000). According to Maestre & Cortina  
325 (2004), late-successional plant species are rarely observed in *P. halepensis* plantations, even after  
326 several decades. On the contrary, the species pool of *P. pinea* stands consisted of forest  
327 undergrowth species, including nemoral and basically sciaphilous plants typical of evergreen oak  
328 forest, typical of the natural vegetation of inner dunes and dune slack transition zones (Acosta et al.,  
329 2003). In fact, also Brockerhoff et al. (2003) found that some, especially older, pine stands showed  
330 affinities with nearby native forests, allowing establishment of many native forest understorey  
331 species.

332 When we tested the distance to coastline as a driving force of coastal pine forests, our results  
333 indicated that it had a significant role for pine understorey assemblages, according to its key  
334 function for the composition of natural sand dune communities (see Forey et al. 2008; Kim & Yu,  
335 2009; Angiolini et al., 2013; Ruocco et al., 2014). Like on non-forested dunes, forest pine plant  
336 species followed the natural vegetation zonation along this gradient, with dune species, such as  
337 *Elymus farctus* ssp. *farctus* and *Lotus cytisoides*, occurring closer to sea, and forest species of

338 backdune evergreen oak forests, such as *Quercus ilex* ssp. *ilex*, *Brachypodium sylvaticum* ssp.  
 339 *sylvaticum* and *Carex flacca*, in the intermediate stands (Acosta et al., 2000). On the contrary,  
 340 ruderal and generalist species such as *Brachypodium rupestre*, *Piptapterum miliaceum*, *Bellis*  
 341 *perennis* and *Cynosurus echinatus* had the highest probability of occurrence in more inland stands.  
 342 We observed a relationship between understorey assemblages and the sea-inland gradient with most  
 343 of the focal species for the natural dune zonation. Thus, these planted forests partially maintain the  
 344 previous assemblage of coastal vegetation, according to their inclusion in the EU priority habitat  
 345 2270.

346 Pine canopy is an important factor in Mediterranean forests, affecting plant species assemblages,  
 347 seedling establishment and soil fauna (McIntosh et al., 2016; Granados et al., 2016; Bonari et al.,  
 348 2016; Selvi et al., 2016). Our data confirmed that *P. halepensis* and *P. pinea* canopies significantly  
 349 affected understorey plant communities, particularly at high coverage. Thus, plant assemblages  
 350 were affected similarly by the tree canopy, regardless the pine species. Typical dunal herbaceous  
 351 and shrub species, such as *Lotus cytisoides*, *Ononis variegata*, *Sporobolus virginicus*, *Clematis*  
 352 *flammula* and *Juniperus oxycedrus* ssp. *macrocarpa*, which are heliophilous, often growing on  
 353 oligotrophic soils, had higher probability of occurrence with lower pine cover. Interestingly, not  
 354 only the herbaceous layer was affected by pine cover, as already shown by Madrigal-González et al.  
 355 (2010), but also shrub and tree species, including holm oak (*Quercus ilex* ssp. *ilex*), which had  
 356 lowest probability of occurrence under high canopy cover. As suggested by Lemenih et al. (2004),  
 357 plantations with denser canopies host lower density and richness of woody species in the  
 358 understorey. On the other hands, Bockerhoff et al. (2003; 2008) also found that understorey  
 359 vegetation beneath the canopy of pine plantations may show a successional trend towards  
 360 increasing dominance of native shade-tolerant species that are typical of natural forest understoreys.  
 361 In the pine forest stands considered in this study, an evident pool of forest species, including shade-  
 362 tolerant species, was only found *Brachypodium sylvaticum* ssp. *sylvaticum* and *Asparagus*

363 *acutifolius*, while we detected an increase in the alien invasive *Acacia cyanophylla* and for  
364 generalist species, such as *Fumaria capreolata* ssp. *capreolata*, *Brachypodium rupestre*, *Elymus*  
365 *repens* ssp. *repens*, *Piptapterum miliaceum* and *Bellis perennis* at higher canopy covers.

366

## 367 **5 Conclusion**

368 We studied Italian coastal pine forest stands, analysing the influence of different pine species, sea-  
369 inland gradient and pine canopy cover on their understoreys at community and species level. Our  
370 results support the concept of pine understoreys as a “floristic cauldron” without any clear floristic  
371 differentiation between different forest types. However, minor differences in understorey  
372 assemblage were also observed and they seem related to different pine the pine species  
373 characteristics, sea-inland gradient and canopy cover. In fact, coastal dune vegetation was relatively  
374 preserved under pine canopy. This supports the idea that coastal pine forests may maintain the  
375 “valuable” Mediterranean coastal biodiversity pool. This could be related to the fact that all the pine  
376 species planted were inside their original range of distribution, as well as to long established  
377 planting. However, since stands with higher canopy covers negatively affect understorey species  
378 assemblages, forest management can make a positive contribution. Our results provide insights into  
379 the role of Mediterranean coastal pinewoods and afforestations. Species-specific management does  
380 not seem necessary for these forests and their understoreys, whereas other factors such as sea-inland  
381 gradient and canopy cover should be taken into account. Based on our results, we could affirm that  
382 pine stands should no longer be considered a potential threat to biodiversity. In fact, Mediterranean  
383 pinewoods do not reflect an “ecological desert” but can host many focal species and a mosaic of  
384 natural habitats in the understorey, providing also ecosystem services that should be not overlooked.

385

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394

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