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

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Abstract

A common perception of plantation forests is that they constitute an "ecological desert" and thus they are often disdained by scholars. Distribution patterns of understorey assemblages of coastal pine stands on sand dunes are still little known, despite such forests being widespread along the Mediterranean coastline, particularly in Italy. The purpose of this study of 167 plots along Italian coastlines was to analyse whether similar communities and specific species pools occur in different pine forest types dominated by *Pinus halepensis*, *P. pinea* or *P. pinaster*. Multivariate analysis was used, considering the effects of sea-inland gradient and pine canopy cover. The results indicated that pine forests do not consist of specific vegetation assemblages, suggesting the idea of a "floristic cauldron". Understorey distinctiveness of Mediterranean coastal pine stands is limited, with psammophilous species of coastal dunes occurring mostly in *P. halepensis* stands, and forest species mainly being linked to *P. pinea* stands. Thus species-specific management is not required for different pine forest types. Like on non-forested dunes, plant species mainly followed the sea-inland gradient, maintaining the natural zonation of coastal vegetation. Moreover, higher pine canopy cover affected both herbaceous and woody natural dune vegetation in a negative way. These 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” (Brockerhoff 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, mainly due to direct and indirect effects of human activities, such as coastal erosion (Raddi et al., 2009), salinisation of groundwater (Antonellini & Mollema, 2010; Zanchi & Cecchi 2010), trampling (Santoro et al., 2012) and urban sprawl (Reina-Rodríguez & Soriano, 2008; Malavasi et al., 2013). These threats have been particularly intense in the last 50 years in countries bordering the Mediterranean Sea (Curr et al., 2000).

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

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

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

2 Methods

2.1 Pine forest-types

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

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

2.2 Study area

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

2.3 Data collection

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

2.4 Data analysis

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

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

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

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

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

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

Data without pine species	−10.78 ($p < 0.001$)	0.94	0.014

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

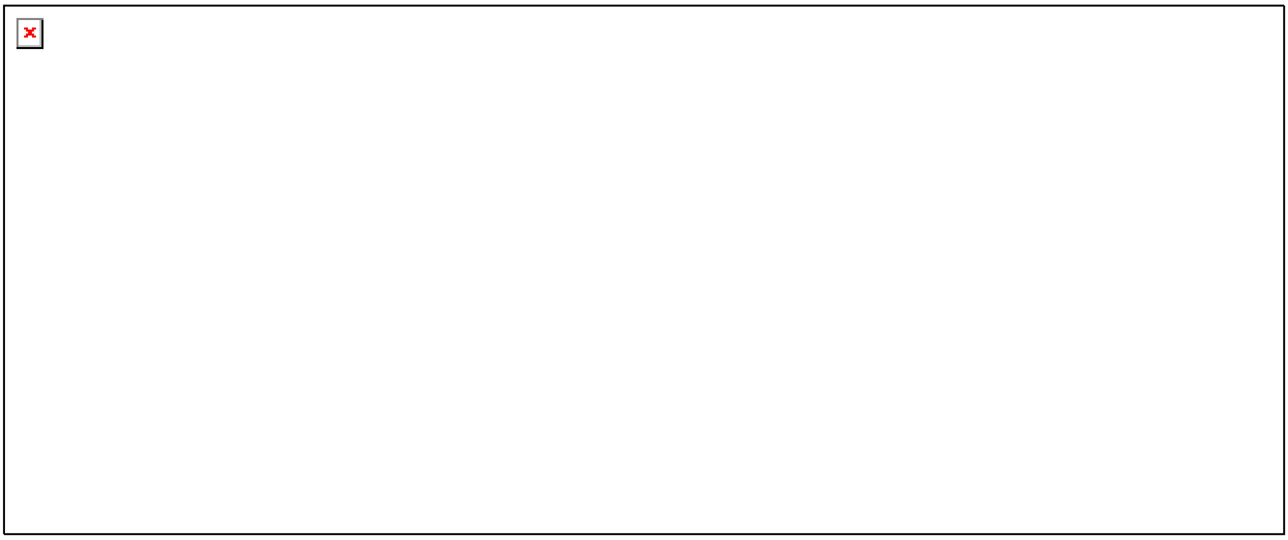

Figure 1. NMDS diagram of plots including (A) and excluding pine canopy cover data (B). Colors indicate the dominant pine species. Blue diamonds are Pinus halepensis dominated plots, red stars are P. pinea dominated plots and green triangles are P. pinaster dominated plots.

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.

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

	Cyperus capitatus	15.6	0.0004
	Echinophora spinosa	6.2	0.0226
	Elymus farctus ssp. *farctus*	21.9	0.0002
	Elymus repens ssp. *repens*	7.8	0.0072
	Erigeron canadensis	6.2	0.0200
	Erodium laciniatum	12.5	0.0002
	Eryngium maritimum	6.2	0.0216
	Euphorbia terracina	17.2	0.0002
	Medicago marina	10.9	0.0006
	Ononis variegata	9.4	0.0034
	Phleum arenarium ssp. *caesium*	12.5	0.0006
	Reichardia picroides	17.1	0.0004
	Silene colorata	17.2	0.0002
	Silene vulgaris	17.7	0.0004
	Sixalix atropurpurea	20.9	0.0002
	Sporobolus virginicus	25.0	0.0002
	Verbascum niveum ssp. *garganicum*	12.5	0.0004
	Vulpia fasciculata	17.2	0.0002
Pinus pinaster (n.s.)	/	/	/

Hybrid CCA (Figure 2) with first axis constrained by sea distance significantly discriminated three clusters of coastal pine forest species: typical dunal species closer to the sea, such as *Elymus farctus* ssp. *farctus* and *Vulpia fasciculata,* species typical of Mediterranean maquis at intermediate distance, such as *Phillyrea angustifolia* and *Hedera helix*, and generalist species at greater distances from the sea, such as *Bellis perennis* and *Cerastium glomeratum*.

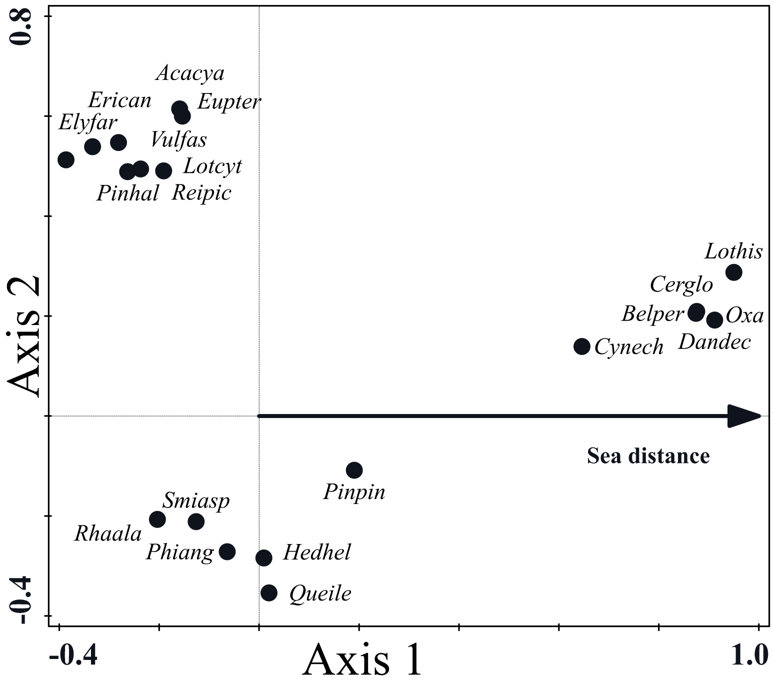

Figure 2. Hybrid constrained CCA diagram. Axis 1 captured 3.2% of the variance (p = 0.001). The first 20 best fitting species in the ordination spaces are shown. Plant species are designated with the first three letters of their genus and species names as follows: Acacya = Acacia cyanophylla; Belper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

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

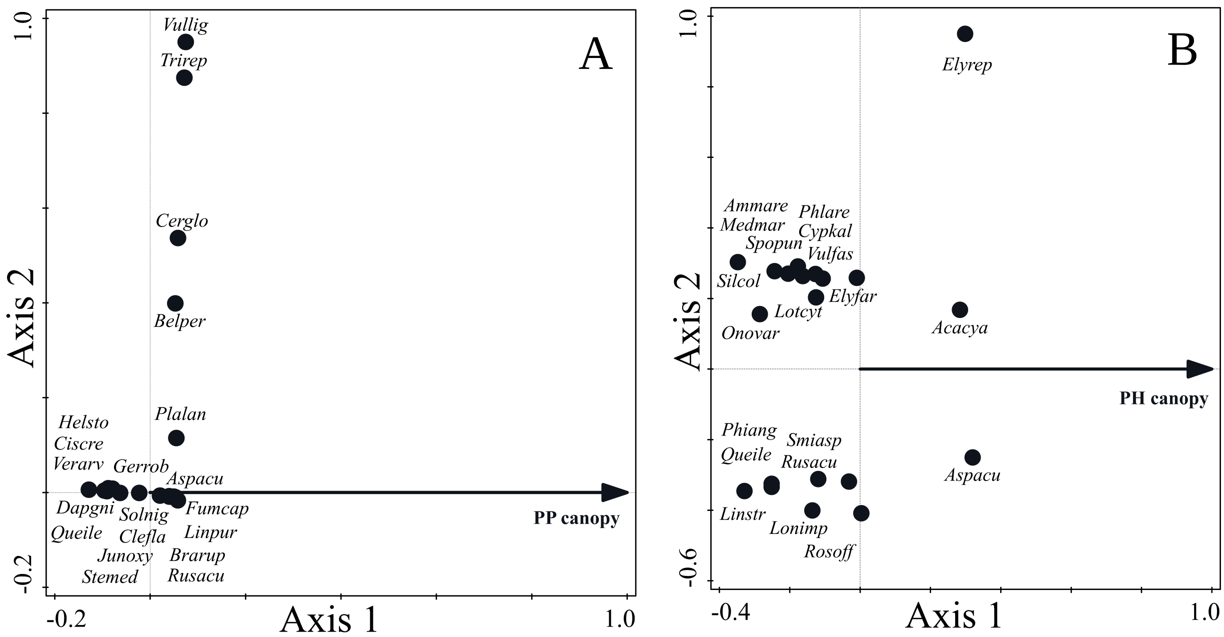

Figure 3. Hybrid constrained CCA diagrams. A) Pinus pinea canopy-constrained B) P. halepensis canopy-constrained. Axis 1 captured 1.5% of the variance (p = 0.013) and 3.1% (p = 0.001), respectively. The first 20 best fitting species in the ordination spaces are shown. Plant species are designated with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

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

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

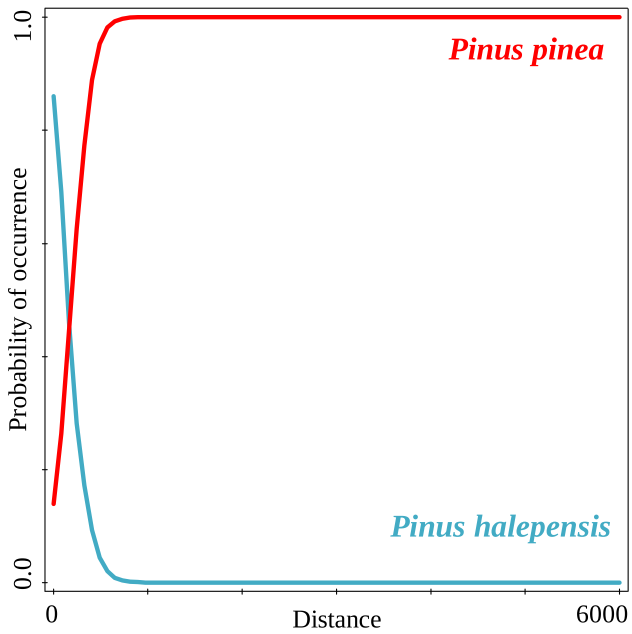

Figure 4. Species-response curves (GAMs) of pine species with respect to distance from sea (probability of occurrence in relation to sea distance). Pinus halepensis and P. pinea were significant ($p < 0.001$). P. pinaster was not statistically significant.

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

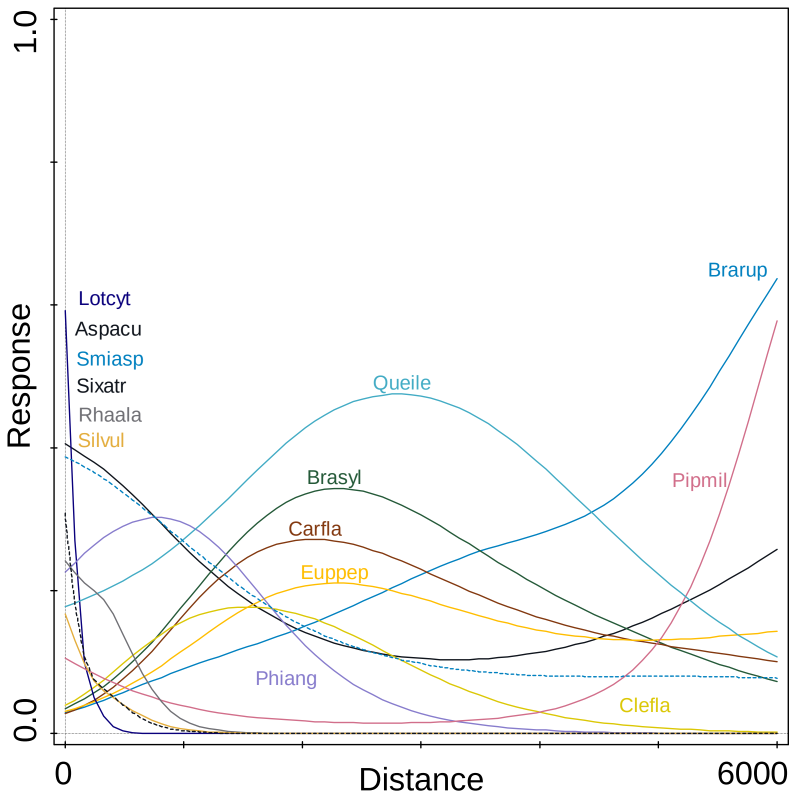

Figure 5. Species-response curves (GAMs) with respect to sea distance for species with more than 10 occurrences in the dataset (probability of occurrence in relation to sea distance). Only significant models are shown. Plant species are designated with the first three letters of their genus and species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

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

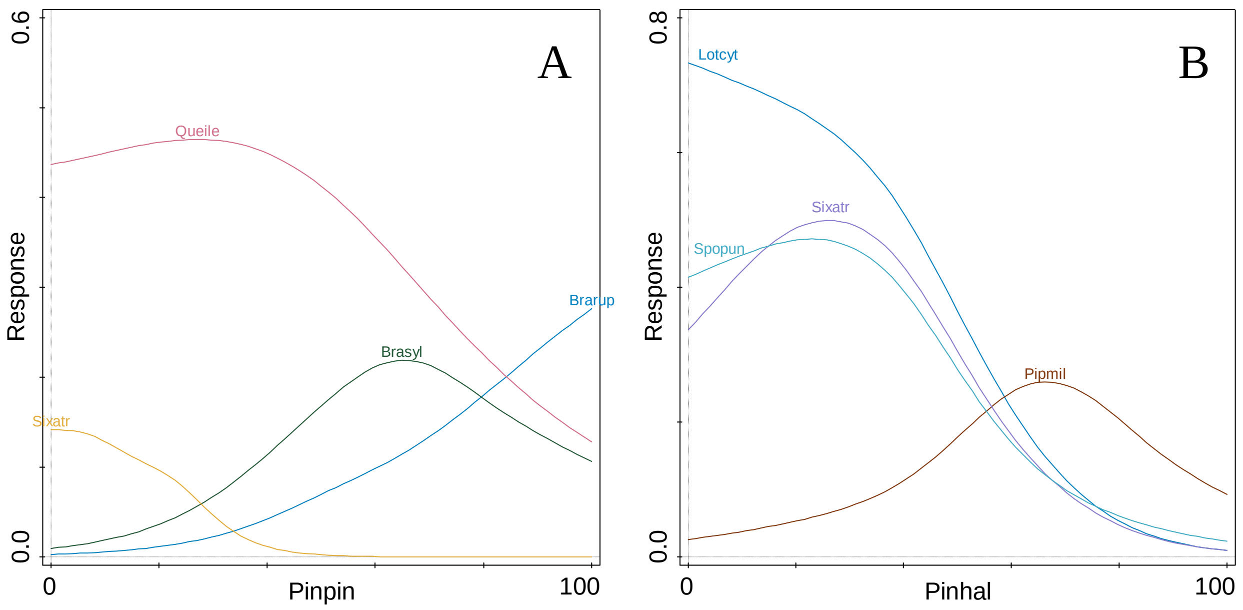

Figure 6. Species-response curves (GAMs) with respect to canopy of P. pinea (A) and P. halepensis (B) on species with more than 10 occurrences in plots (probability of occurrence in relation to canopy cover). Only significant models are shown. Plant species are designated with the first three letters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

4 Discussion

Different outcomes were obtained when pine canopy cover was included in or excluded from our dataset. When tree pine canopy cover was included, floristic differences were evident between pine forest types. After pine canopy cover was excluded from analysis, the pattern disappeared and communities converged into a single cluster with less difference in plant species composition. This suggests that the different coastal pine forest types are not characterized by distinct floristic and ecologically different understoreys. Pine stands therefore do not differentiate a specific species pool. Vascular plant species can generally colonize plantation forests regardless of canopy species when habitat characteristics are appropriate (Carnus et al., 2006). Since all the pine forest stands studied shared substantially the same coastal dune environment, known to be a very selective habitat for plants (Maun, 2009), the lack of floristic differentiation between them can therefore be explained by their relatively similar environmental conditions (Frelich et al., 2003). Moreover, other authors have considered environmental conditions to be more important drivers of understorey community composition than dominant tree species (Piwczynski et al., 2016). In the same perspective, species composition may be highly variable and change substantially in response to environmental change in each pine forest type. Stands of different pine types, planted across the sea-inland gradient where vegetation zonation ranges from pioneer communities of embryonic dunes to pine plantations, have been found to host a variety of species, mainly distributed according to this gradient and often adapted to coastal environments near the sea shore (psammophilous species) (Acosta et al., 2003).

Although MRPP and NMDS suggested low distinctiveness at community level, T statistics indicated that different pine forest stands showed some differences in species assemblages, even when pine canopy cover was excluded from analysis. INSPAN supported this thesis, highlighting that a small pool of species was more likely to occur in one pine forest type than another. Notably, 20 species showed significant affinity for *Pinus halepensis* stands, 14 of which were focal for coastal dunal habitats (Biondi et al., 2009; Biondi & Blasi, 2015) and in some cases were strictly psammophilous. Among these, *Sporobolus virginicus* and *Elymus farctus* ssp. *farctus*, typical of embryonic Mediterranean dunes (Acosta et al., 2007; Biondi et al., 2009; 2012), showed the highest indicator values for *P. halepensis* forest. On the other hand, in line with Biondi et al. (2009) and Biondi & Blasi (2015), forest species were linked to *P. pinea* stands, where *Brachypodium sylvaticum* ssp. *sylvaticum* was the species with the highest indicator value. This may be related to the fact that *P. halepensis* stands were often planted closer to the sea, whereas *P. pinea* stands were planted relatively far from the coastline and therefore had a higher probability of occurrence along most of the sea-inland gradient. In fact, *P. pinea* has been reported to have a wide range of distribution in coastal dune habitats, mostly growing on fixed dunes and in areas with deep water table and relatively low salinity (Antonellini and Mollema, 2010; Angiolini et al. 2013). The spatial location of these two pine forest types, positioned slightly differently with respect to each other and extending from the foredunes to the innermost dunes (paleodunes), reflects the different ecology of the pine species. Indeed, *P. halepensis* is more pioneer, well adapted to drought (Mauri et al., 2016) and able to spread by seed from plantations into adjacent natural plant communities (Higgins & Richardson 1998; Lavi et al., 2005), occasionally also colonizing the inner part of the foredunes. Thus, the indicator species for *P. halepensis* forest type were largely very specialized psammophilous plants that grow exclusively on embryonic dunes, tolerating salt spray, drought and unstable substrates (Garcia-Mora et al. 1999; Acosta et al., 2000). According to Maestre & Cortina (2004), late-successional plant species are rarely observed in *P. halepensis* plantations, even after several decades. On the contrary, the species pool of *P. pinea* stands consisted of forest undergrowth species, including nemoral and basically sciaphilous plants typical of evergreen oak forest, typical of the natural vegetation of inner dunes and dune slack transition zones (Acosta et al., 2003). In fact, also Brockerhoff et al. (2003) found that some, especially older, pine stands showed affinities with nearby native forests, allowing establishment of many native forest understorey species.

When we tested the distance to coastline as a driving force of coastal pine forests, our results indicated that it had a significant role for pine understorey assemblages, according to its key function for the composition of natural sand dune communities (see Forey et al. 2008; Kim & Yu, 2009; Angiolini et al., 2013; Ruocco et al., 2014). Like on non-forested dunes, forest pine plant species followed the natural vegetation zonation along this gradient, with dune species, such as *Elymus farctus* ssp. *farctus* and *Lotus cytisoides*, occurring closer to sea, and forest species of backdune evergreen oak forests, such as *Quercus ilex* ssp. *ilex*, *Brachypodium sylvaticum* ssp. *sylvaticum* and *Carex flacca,* in the intermediate stands (Acosta et al., 2000). On the contrary, ruderal and generalist species such as *Brachypodium rupestre*, *Piptapterum miliaceum*, *Bellis perennis* and *Cynosurus echinatus* had the highest probability of occurrence in more inland stands. We observed a relationship between understorey assemblages and the sea-inland gradient with most of the focal species for the natural dune zonation. Thus, these planted forests partially maintain the previous assemblage of coastal vegetation, according to their inclusion in the EU priority habitat 2270.

Pine canopy is an important factor in Mediterranean forests, affecting plant species assemblages, seedling establishment and soil fauna (McIntosh et al., 2016; Granados et al., 2016; Bonari et al., 2016; Selvi et al., 2016). Our data confirmed that *P. halepensis* and *P. pinea* canopies significantly affected understorey plant communities, particularly at high coverage. Thus, plant assemblages were affected similarly by the tree canopy, regardless the pine species. Typical dunal herbaceous and shrub species, such as *Lotus cytisoides*, *Ononis variegata*, *Sporobolus virginicus*, *Clematis flammula* and *Juniperus oxycedrus* ssp. *macrocarpa*, which are heliophilous, often growing on oligotrophic soils, had higher probability of occurrence with lower pine cover. Interestingly, not only the herbaceous layer was affected by pine cover, as already shown by Madrigal-Gonzaléz et al. (2010), but also shrub and tree species, including holm oak (*Quercus ilex* ssp. *ilex*), which had lowest probability of occurrence under high canopy cover. As suggested by Lemenih et al. (2004), plantations with denser canopies host lower density and richness of woody species in the understorey. On the other hands, Brockerhoff et al. (2003; 2008) also found that understorey vegetation beneath the canopy of pine plantations may show a successional trend towards increasing dominance of native shade-tolerant species that are typical of natural forest understoreys. In the pine forest stands considered in this study, an evident pool of forest species, including shade-tolerant species, was only found *Brachypodium sylvaticum* ssp. *sylvaticum* and *Asparagus* *acutifolius*, while we detected an increase in the alien invasive *Acacia cyanophylla* and for generalist species, such as *Fumaria capreolata* ssp. *capreolata*, *Brachypodium rupestre*, *Elymus repens* ssp. *repens*, *Piptapterum miliaceum* and *Bellis perennis* at higher canopy covers.

5 Conclusion

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

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