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Conservation of the Mediterranean coastal pine forests: how can management support biodiversity?

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Highlights

- Dune woodland is an important habitat for conservation
- Fencing has a significant effect on both plant and mite community composition
- Unlike plants, fencing does not affect species richness of mites
- Combination of fenced and non-fenced forest areas is important for creating heterogeneity
- Fencing of small areas is an effective conservation measure for enhancing biodiversity

Abstract

Forest management decisions may have unintentional effects on what they were originally not designed for, including effects on woodland species and communities. In protected areas of coastal forests, some sites are fenced as a part of forestry management. In this study, we hypothesised that different states of disturbance (disturbed vs non-disturbed) created by fencing generate unintentional heterogeneity in species composition (and possibly richness) in both plant communities and soil biota. We surveyed vascular plants, oribatid mites and soil properties in fenced and nearby non-fenced places in protected coastal pine forests in Italy. The fenced areas were undisturbed for at least 30 years, whereas the non-fenced areas were subjected to thinning and trampling. Effects of fencing on community composition and soil properties were assessed by (distance based) redundancy analysis. Congruence between plant and mite community composition in response to fencing was tested by a series of (partial) Mantel tests. Finally, linear mixed-effects models were used to study species richness. Fencing had a significant effect on community composition of both plant and mite communities. A significant congruent response to fencing between plant and oribatid community composition was found. Moreover, species richness of plants decreased due to fencing, while that of mites was unaffected. We conclude that fencing of small areas creates biotic heterogeneity and increases beta diversity in the Mediterranean coastal woodlands. Therefore, we support the use of

fencing as a relatively cheap and effective method of conservation management for maintaining the biodiversity of both above- and belowground communities in the coastal pine forests of the Mediterranean area.

Keywords

Biodiversity; Community ecology; Conservation; Disturbance; EU Habitat; Forest; Management; Mediterranean Basin; Oribatida; *Pinus*; Protected areas; Soil; Vascular plants.

Abbreviations

EC = Electrical Conductivity

F = Fenced plots

NF = Non-fenced plots

SOM = Soil Organic Matter

1. Introduction

Dune woodland, a forest type scattered along the Mediterranean Sea coast, is an important habitat for nature conservation. The dominant species of these dune woodlands are often pines, including *Pinus brutia*, *P. halepensis*, *P. pinaster* and *P. pinea*. They largely belong to the priority habitat “Wooded dunes with *Pinus pinea* and/or *P. pinaster*”^{2270*} of Annex I of the EU Habitats Directive (92/43/EEC). Most of these forests are the result of large reforestations that took place in the second half of the twentieth century in Italy and other Mediterranean countries, mainly for pine nut, resin and timber production and as a shelterbelt for crops (Martínez & Montero, 2004). In spite of this, they are protected since they resemble the structure and plant composition of the original

forests, hosting specialist species of coastal environments (Leone & Lovreglio, 2004; Bonari et al., 2017a; Bonari et al., 2018).

Mediterranean forests have been under long-lasting human impact (Scarascia-Mugnozza et al., 2000). Generally, the following characteristics can be considered signs of a well-maintained pine forest for conservation purposes: natural composition of the canopy (including high cover of *Pinus* individuals in reproductive age), structural complexity with heterogeneous age structure or completeness of layers (including a well-developed shrub layer), resprouting of canopy trees and shrubs, the scarce presence of non-native species, presence of old trees and a variety of dead wood (lying or standing), low levels of soil compactness and human trampling (Dimopoulos, 2016). Unfortunately, coastal pine forests are highly disturbed at many sites due to urban sprawl, coastal erosion and increasing tourism. One way of maintaining their biological diversity is creating heterogeneity in the understorey, which might support heterogeneous plant and animal communities. Silvicultural treatments have been often proposed for enhancing the diversity of pine forests, e.g. by thinning in high-density or homogeneous stands (Ruiz-Benito et al., 2012).

Alternatively, one possible way of creating heterogeneity is the fencing of smaller areas, which creates differences in disturbance between fenced and non-fenced places. Forest parcels are used by foresters to physically separate areas with different forestry treatments. They are currently adopted in many of the protected areas hosting this forest type, having unknown implications for conservation although originally they were not designed as a conservation measure. Since the effects of fencing of pine dune woodlands on biodiversity are poorly known, scientific studies are needed to understand the effect of this practice (Coll et al., 2018).

It is relatively easy to observe how plants react to fencing management, but there are other components of the ecosystem that may respond to a reduction of disturbance by fencing. For example, the effects of fencing on soil mesofauna are poorly known. Still, conservation management should be optimized to take into account both flora and fauna (Bonari et al., 2017b). Therefore, we studied the effect of fencing on plants and oribatids, the latter being an

important indicator of the state of soil, with effects on the ecosystem such as decomposition and nutrient cycling, as well as one of the most abundant groups among soil fauna (e.g. [Salmon, 2018](#)). Moreover, even though to a lesser extent than plants, also soil fauna has been used as an indicator for management practices (e.g. [Zhao et al., 2013](#)).

In our previous study, we tested the hypothesis of concordance between vascular plants and oribatid mites under the same disturbance regime ([Bonari et al., 2017c](#)). In the present study, we studied the protected Mediterranean coastal pine forests with mixed management including fenced areas with no silvicultural treatment since decades and non-fenced areas subject to various disturbances. Our hypotheses are that (1) fencing creates heterogeneity in species composition and richness in both plant communities and soil biota, and (2) observed heterogeneity in a plant community can indicate a parallel heterogeneity in soil community.

2. Materials & methods

2.1. Study area and habitat

The study area comprises the Tyrrhenian and Adriatic coastlines of the Italian Peninsula where stone pine (*Pinus pinea*) dominated forests occur. These woodlands cover approximately 46,290 ha in Italy ([Tabacchi et al., 2007](#)). They are listed in the European Red List of Habitats where they are qualified as Least Concern ([Janssen et al., 2016](#)). *P. pinea*, one of the dominant pine species forming these forests, currently occurs in most of the countries bordering the Mediterranean Sea. However, the natural range is unknown because it has been introduced throughout the Mediterranean basin since antiquity ([Martínez & Montero, 2004](#)). Typically, an open-canopy upper tree layer is formed by *P. pinea*, while the occurrence of scattered *Quercus* spp. individuals or other thermophilous tree species is usually limited to the lower tree layer. The character of the shrub layer is heavily dependent on disturbance (and management) but it includes species typical of holm oak (*Quercus ilex*) forests and

the Mediterranean macchia. The herb layer is heterogeneous and generally poor, although richer patches with light-demanding species are present. As in the shrub layer, the disturbance is decisive in determining the occurrence of individual herb species and their abundances. These forests grow in the inland zone of the coastal dune systems, i.e. on stabilized dunes, mainly on moderately acidic soils, but different levels of pH are found also at the same site (see e.g. [Bonari et al., 2017c](#)). Climate varies with latitude and encompasses both the Mediterranean and temperate macro-bioclimate ([Pesaresi et al., 2014](#)). From the syntaxonomic point of view, these forests are currently classified in the *Pinetalia halepensis* order of the *Quercetea ilicis* class ([Mucina et al., 2016](#)).

2.2. Sampling design

We collected original data during springs of 2014 and 2015 to analyse the effects of fencing on vascular plants and oribatid mites, which were surveyed simultaneously at the same sites ([Fig. 1](#)). In [Figure 1](#) the distribution of coastal stone pine forests in peninsular Italy is also shown, using data extracted from the *CircumMed Pine Forest Database* (GIVD: EU-00-26; [Bonari et al., 2019](#)). We selected seven homogeneous sites ([Appendix A, Table S1](#)) with stone pine forests along the coastline of the Italian Peninsula fulfilling the following criteria: (i) being a part of a protected area (i.e. National Park, Nature Reserve, Regional Park or Site of Community Importance); (ii) being attributable to the priority habitat 2270* “Wooded dunes with *Pinus pinea* and/or *Pinus pinaster*” of Annex I of the EU 92/43/EEC Directive ([Gigante et al., 2016](#)); (iii) growing on sandy soils; (iv) with the presence of fenced areas (F), in which forestry practices, e.g. thinning, were not performed for at least 30–50 years depending on the site and where high fences prevent the access of people and ungulates—such as deer and wild boars—into these enclosures for prolonged periods of time, and non-fenced areas (NF) subjected, on the contrary, to various disturbances such as thinning and trampling by humans and large animals (see examples in [Appendix A, Figure S1](#)).



Figure 1. Sampled sites (circles) and the distribution of the stone pine (*Pinus pinea*) dominated dune woodlands (stripes) in peninsular Italy. Distribution data are extracted from the *CircumMed Pine Forest Database* (GIVD: EU-00-26; Bonari et al., 2019).

Our stratified random sampling design is shown in Fig. 2. At each of the seven sites, we randomly chose six points (three in F and three in NF areas). Starting from the centre of these points, we delimited an area of 100 m². Within this area, we placed three plots (1 m × 1 m; A, B, C) in the opposite corners and in its centre (corresponding to the above-mentioned random point). Firstly, all vascular plants were recorded with an estimation of their percentage cover, i.e. the vertical ground

projection of each species in each 1 m² plot. Secondly, mites were collected as follows: after removal of the undecomposed organic matter including branches, twigs and pine needles, namely the litter layer, we sampled, in the opposite corners of each plot and in its centre, to the depth of 10 cm, three replicates as cubic soil blocks by means of a corer (1000 cm³; not shown in [Figure 2](#)). Thirdly, the same procedure used for mites was repeated for soil samples (1000 cm³; not shown in [Figure 2](#)). They represent the upper-most part of soil profile (topsoil) including both the organic layer, when present, and the underlying mineral soil.

Mite community composition was recorded as numbers of individuals for each species. Our sampling design can be therefore outlined as 3 plots (1, 2, 3) × 3 replicates (A, B, C) × 2 treatments (F, NF) × 7 sites, resulting in a total of 126 plots. Soil fauna was extracted in the lab by means of Berlese-Tullgren funnels. Extractions were conducted at ambient temperature for 15 days and preserved in 75% ethanol for subsequent identification. Upon separation from other taxonomic groups, mites were identified to species using different keys ([Perez-Iñigo, 1993; 1997; Subías & Arillo, 2001; Subías, 2004; Weigmann, 2006](#)). All the information related to the chorological and autecological traits of the collected species of mites was extracted from the same literature. Vascular plant nomenclature follows [Conti et al. \(2005\)](#).

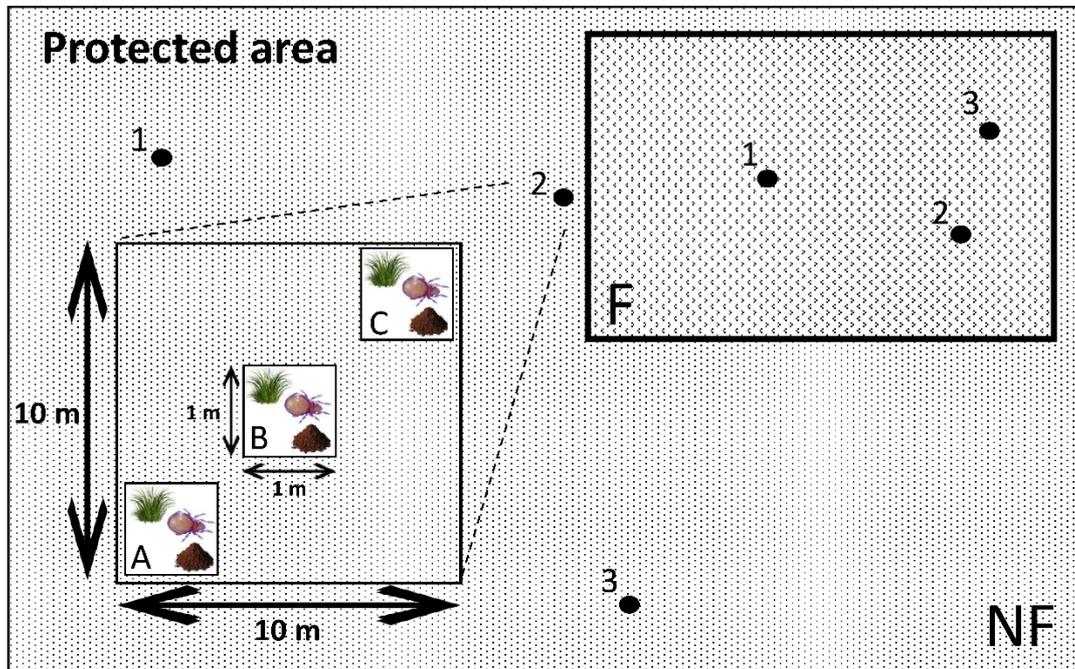


Figure 2. A scheme of the stratified sampling design adopted in this study showing random points (1, 2, 3), in fenced (F) and non-fenced (NF) parts of a protected area. The magnification shows the position of plots (A, B, C) in within an area of 100 m². Replicates of cubic soil blocks used for sampling mites and soil within the plots of 1 m² are not shown. The position of icons of plants, mites and soil within the plots A, B and C have no meaning.

2.3. Soil analysis

In the laboratory, soil samples were dried at +30 °C, manually sieved with a metal-free 2 mm sieve and then homogenized by quartering and mechanical pulverization. Soil pH_(H₂O) and electrical conductivity (EC) were measured on the <2 mm fraction of soil samples in a 1:2.5 (weight/volume) soil:water mixture applying the methods III.1 and IV.1 defined in the Italian Ministerial Decree “Official Methods for Soil Chemical Analysis” (September 13th, 1999).

The carbonate content, expressed as calcium carbonate percentage (% CaCO₃), was determined on the pulverized soil samples by calcimetry using De Astis calcimeter. Loss on ignition was used to determine the content of organic matter in soil samples (SOM). An aliquot of about 0.5 g of pulverized soil was oven-dried at +105 °C for 16 h, cooled in a desiccator and weighed; then it was

combusted at +375 °C for 16 h in a muffle furnace. After combustion, the sample was cooled in a desiccator and weighed again. Soil organic matter content(% SOM) was calculated as [(oven-dry soil weight – soil weight after combustion) / oven-dry soil weight] × 100.

To determine the particlesize distribution, about 200 g of soil sample was placed in a sieve stackconsisting of sieves with the mesh sizes of 2, 1, 0.4, 0.25, 0.1 and 0.063 mm. After stirring for 10 min, the fraction in each sieve was collected and weighed.

2.4. Data analysis

We considered individual sites as independent observations (with F and NFplots) in data analysis. Vascular plant cover and soil data were averaged, and mite data were pooled within each plot. The mite pooled data were square-root transformed to prevent overwhelming effect of few dominant species on the analysis. We computed a matrix of Bray-Curtis dissimilarities in community composition between all pairs of sites. First, we computed a principal coordinate analysis (PCoA) based on this matrix to display the fencing-induced changes within the context of the major community composition gradients. Then, we used a partial redundancy analysis (RDA) to test the effects of fencing on soil properties and a partial distance-based redundancy analyses (db-RDA) to test the effect of fencing on plant and mite community composition. Site identity was used as a covariate in these analyses. The significance of the effect of fencing was assessed by permutation of F and NF plots within sites. Congruence between plant and mite community composition in response to fencing was tested by a series of (partial)Mantel tests. Bray-Curtis dissimilarity matrices of plant and mite communities and a Euclidean distance matrix based on the binary fencing variable (fencing matrix) were used as an input for the Mantel tests. We quantified Pearson correlations between fencing and community composition as well as partial correlations with the community dissimilarity matrix of the other organism group used as a covariate. The resulting correlations were used to partition the effect of fencing into three components: congruent response of the plant and mite community compositions and an independent response of each of these two communities. In

addition, we tested overall congruence between plant and mite communities by comparing the two community dissimilarity matrices (both with and without the fencing matrix as a covariate) using the Mantel test. The significance of all effects in multivariate analyses was assessed by permutation tests, with blocks defined by site identity and plot permutation within blocks. All permutation tests used 127 permutations, which was the maximal number of possible combinations with the data available; therefore the minimal achievable type I error probability was $P = 0.008$. The effect of fencing on plant and mite diversity (measured as species richness and Shannon index) and total mite abundance were tested by linear mixed-effect models with the respective diversity parameter as a response, site identity as random effect and fencing as fixed effect predictor. Data for species richness and total mite abundance were log-transformed. The analyses were conducted in the R packages *vegan* (Oksanen et al., 2018) and *nlme* (Pinheiro et al., 2017).

3. Results

Soils sampled in the F and NF plots were sandy with a prevalence of the medium and fine sand fractions, and they had a low electrical conductivity (EC=107-717 $\mu\text{S}/\text{cm}$; Table 1). Analytical data suggested that pH was very variable ranging from 4.5 to 8.2, though most soil samples were neutral to moderately alkaline ($n=29$; pH ranged from 6.6 to 8.2) and slightly to very strongly acidic ($n=134$; pH ranged from 6.5 to 4.5). Moreover, pH values <7 characterized non-calcareous to slightly calcareous soils with low carbonate contents (1-5% CaCO_3), while moderately to very calcareous soils (6-23.8% CaCO_3) showed the highest pH levels up to 8.2. Soil organic matter (SOM) content was very variable from 3 to 86.5 % but frequently $<15\%$.

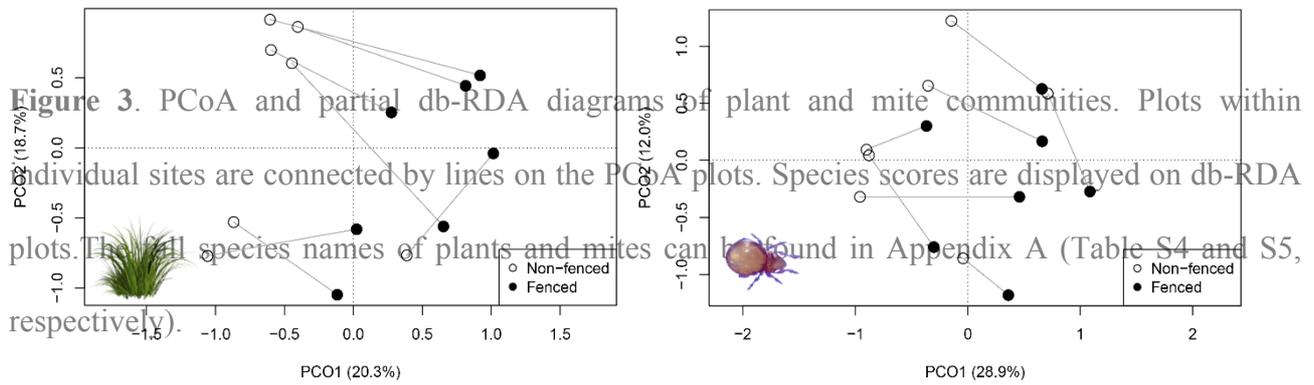
No statistically significant difference was found in properties of soil samples between F and NF sites (see Table 1 for comparison).

Table 1. Descriptive statistics of properties of soil samples including mean and standard deviation (SD), maximum (Max) and minimum (Min) values for fenced (F) and non-fenced (NF) sites.

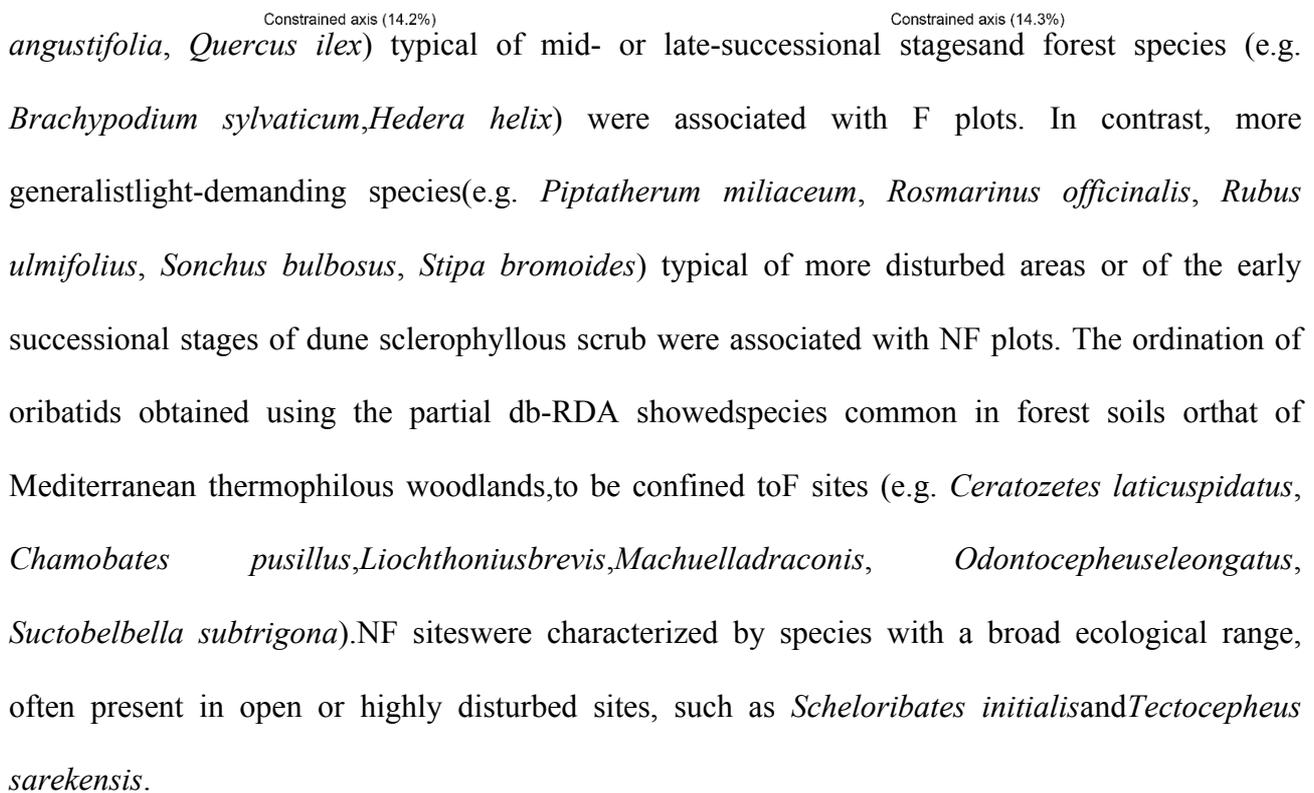
Soil properties	F				NF			
	mean	SD	min	max	mean	SD	min	max
pH	7.0	1.2	4.7	8.1	6.7	1.2	4.5	8.2
Electrical conductivity ($\mu\text{S}/\text{cm}$)	358	156	127	717	337	143	107	685
Carbonate content (% CaCO_3)	6.9	6.3	1.0	23.8	5.2	3.0	1.0	10.9
Soil organic matter (% SOM)	9.0	8.6	3.5	44.4	15.9	21.8	3.0	86.5
Particle size distribution (%)								
2-1 mm (very coarse sand)	1.1	0.9	0.1	3.5	1.1	1.2	0.1	4.9
1-0.4 mm (coarse sand)	18.0	16.6	2.3	60.5	18.6	18.2	1.4	53.4
0.4-0.25 mm (medium sand)	43.4	15.4	17.0	75.3	39.9	15.7	12.4	66.7
0.25-0.1 mm (fine sand)	33.7	18.8	7.9	69.7	35.8	14.3	16.2	66.8
0.1-0.063 mm (very fine sand)	2.2	1.1	0.5	4.3	3.0	2.7	0.6	9.3
<0.063 mm (silt + clay)	1.7	0.9	0.4	3.7	1.6	0.7	0.4	2.9

Species matrix of plants is provided as supplementary materials in [Appendix A \(Table S2\)](#). In the seven surveyed sites, 975 unique species-site records were obtained for 191 vascular plant species. The average number of species per site was 50 ± 11 (mean \pm SD), the minimum was 38 and the maximum was 71. More species-site records were from NF plots (567 occurrences) than from F plots (408 occurrences). The dominant *Pinus pinea* was present at all sites and at all treatments. Otherwise, the most frequent species were *Smilax aspera*, *Quercus ilex* (all sites, but not at all treatments), followed by *Asparagus acutifolius*, *Carex flacca*, *Dactylis glomerata*, *Hedera helix*, *Myrtus communis*, and *Rubia peregrina*.

Species matrix of mites is provided as supplementary materials in [Appendix A \(Tables S3\)](#). We recorded 16,502 individuals of 153 oribatid species across the seven surveyed sites. The average number of individuals per site was 1179 ± 899 (mean \pm SD), the minimum was 157 and the maximum was 3056. The average number of species per site was 41 ± 12 (mean \pm SD), the minimum was 23 and the maximum was 59. Overall, higher total abundance was recorded in NF plots (11061 individuals) than in F plots (5441 individuals). The most abundant species were the cosmopolitan species *Micropoppia minus*, *Oppiella nova* and *Sphaerochthonius splendidus* (2054, 1989 and 1255 individuals, respectively). Most of the mites were widespread species with Holarctic, Palearctic or cosmopolitan distributions (see also [Appendix A, Table S5](#)).



Principal coordinate analyses of vascular plant and oribatid community compositions show a difference between communities in F and NF plots (Fig. 3; permutation tests of significance of the constrained axis: $F_{1,6} = 2.80$, $P = 0.016$ for plants; $F_{1,6} = 3.28$, $P = 0.016$ for oribatids; 127 permutations), which was also reflected by significant effects of fencing on community composition. In plant communities, woody sclerophyllous species (e.g. *Erica arborea*, *Phillyrea angustifolia*, *Quercus ilex*) typical of mid- or late-successional stages and forest species (e.g. *Brachypodium sylvaticum*, *Hedera helix*) were associated with F plots. In contrast, more generalist light-demanding species (e.g. *Piptatherum miliaceum*, *Rosmarinus officinalis*, *Rubus ulmifolius*, *Sonchus bulbosus*, *Stipa bromoides*) typical of more disturbed areas or of the early successional stages of dune sclerophyllous scrub were associated with NF plots. The ordination of oribatids obtained using the partial db-RDA showed species common in forest soils or that of Mediterranean thermophilous woodlands, to be confined to F sites (e.g. *Ceratozetes laticuspidatus*, *Chamobates pusillus*, *Liochthonius brevis*, *Machuella draconis*, *Odontocephuseleongatus*, *Suctobelbella subtrigona*). NF sites were characterized by species with a broad ecological range, often present in open or highly disturbed sites, such as *Scheloribates initialis* and *Tectocephus sarekensis*.



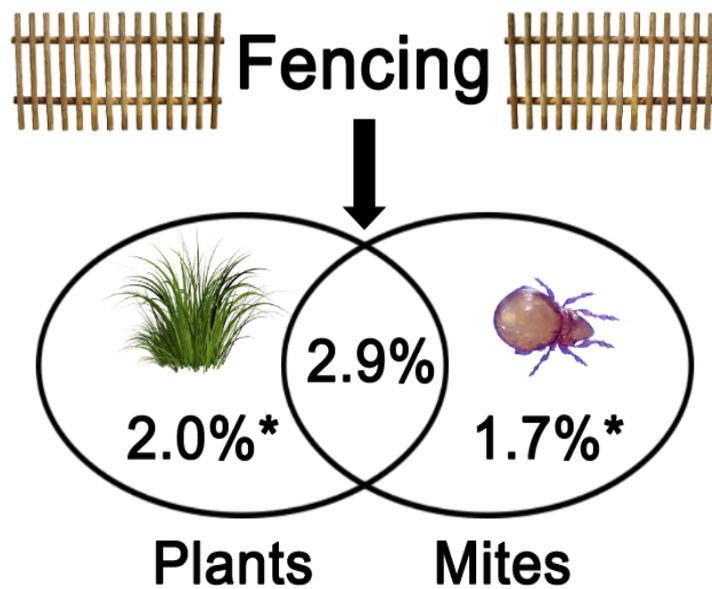


Figure 4. Variation partitioning of the effect of fencing on species composition of plant and mite communities. Partial effects on the two community types as well as the shared effect between them are displayed. Percentages are derived from the R^2 based on partial Mantel tests (127 permutations). Note that the effect of fencing on the shared component of community composition was not tested.

Results of variation partitioning of the effect of fencing on plant and oribatid communities showed a similar effect for plant and mite communities (Fig. 4). The partial effect of fencing accounted for 2.0% ($P = 0.023$) in plant communities and 1.7% ($P = 0.016$) for oribatid communities. The shared effect accounted for 2.9% (not tested). There was a significant congruence between plant and oribatid community composition (Mantel test: $R^2 = 0.21$; $P = 0.008$; Mantel test when fencing was set as a covariable: $R^2 = 0.021$; $P = 0.008$; 127 permutations).

There was a significant negative effect of fencing on plant species richness (mixed-effect model, $F_{1,6} = 16.9$, $P = 0.007$) and no effect on oribatid species richness. We did not find any significant effect of fencing on the Shannon diversity index of plant and oribatid community.

4. Discussion SONO QUI

Our study demonstrates that fencing affects biota in the Mediterranean coastal pine forests. Both vascular plant and oribatid mite species composition responded to fencing, while no difference between fenced and non-fenced plots was found for the measured soil properties. Species richness of plants was lower in fenced plots, while that of oribatids was not. We will separately discuss the effect of fencing on plant and oribatid community composition and soil properties, and species richness. Then, we will attempt to synthesise our findings and provide conservation management recommendations.

4.1. Responses of community composition and soil properties to fencing

Direct comparisons of different taxa sampled in the same sets of plots are often used to obtain deeper insight into the effects of various factors and processes on communities (e.g. [Lososová et al., 2011](#); [Chytrý et al., 2012](#); [Sitzia et al., 2017](#); [Burrascano et al., 2018](#)). In this study, we found a common response to fencing at the community level for vascular plants and oribatids in Mediterranean coastal pine forests. This supports the results of our previous local-scale study in that community patterns of plants and oribatids in this habitat showed a high degree of congruence ([Bonari et al., 2017c](#)). Moreover, we confirmed the results of a former study that mite community composition changes in response to the management of plant communities ([Gormsen et al., 2006](#)). We also found that soil properties were not affected by fencing, implying that the differences in community composition between fenced and non-fenced treatments were not caused by soil factors. Nevertheless, field observations revealed that litter cover was much higher in fenced plots (litter provides shelter and food resources to oribatids), but SOM did not significantly differ between fenced and non-fenced plots. Soils from fenced plots had, on average, pH and carbonate content lower than soils from the non-fenced plots. All these findings were consistent with the more abundant vegetation, including thicker pine needles layer (but no quantification of the removed

material was achieved in the field), responsible of higher soil organic matter contents that lower pH levels, also for a minor role of carbonate buffering in fenced plots. This would suggest that litter has not been incorporated into mineral soil so far, probably due to arid climatic conditions of the Mediterranean area, which slow down decomposition. However, soil factors were found to be of minor importance (at least for mites) also in other studies, both in agricultural and forest ecosystems (Bonari et al., 2017c; Liu et al., 2018).

Plant composition changed due to fencing in coastal pine forests. This result is relevant since plant species assemblages are recommended to be taken into account for a correct management of pine coastal woodlands (Bonari et al. 2017a). This outcome also suggests that, within fenced areas, unaffected by any silvicultural treatments or trampling by humans, vegetation succession on old inland dunes is ongoing. In stabilized coastal sand dunes, the climax is represented by holm oak forests. Nevertheless, when pines are present, the light-demanding *Quercus ilex* rarely becomes dominant, usually occurring in the lower tree layer only. It can become dominant when pines die or are not present at all, but such situations are relatively rare along the coasts of the Italian Peninsula. The most widespread stage of the succession in fenced plots coincides instead with the presence of tall shrub species in the shrub layer. This physiognomy suggests that coastal pine forests dominated by *Pinus pinea* are closely interconnected with Mediterranean macchia, representing a transitional, though very common, successional stage. This also implies that fenced plots, with generally more closed canopy than in the non-fenced areas, tend to develop towards the climax, with a decrease of annual species and rapid increase of perennial, including woody, species (Bonet, 2004).

Non-fenced areas were subjected to silvicultural treatments which interfere with vegetation dynamics by preventing the establishment of the Mediterranean macchia and then of the holm oak forest. However, these treatments also favour the formation of grassland patches by creating physically empty space within pine woodland understories. Moreover, non-fenced plots host typical

species of coastal habitats, although subjected to more frequent and more intensive disturbance, e.g. cutting of macchia shrubs in the pine forest understorey, trampling, harvesting of pine cones and camping (Leone & Lovreglio, 2004). Such disturbances also influence the plant community composition by supporting, e.g. ruderal species. However, a large part of the disturbance is to be attributed to the massive touristic use, where off-trail trampling by vacationers, aiming to reach the sea, is relatively common (see also Ciccarelli, 2014, for the effects on foredune communities). Remarkable is the fact that disturbance in this habitat type, when too intense, decreases the presence (and sometimes the survival) of plant communities, mostly that of shrubs and herbs. Under such condition, an impoverished aspect of the pine woodland without any shrub species and abundance of generalist herbs prevails.

In our study, oribatids differed substantially between the fenced and non-fenced plots. Oribatid communities, as most of the biological ones, have the ability to regenerate after disturbance, and this could have partially masked the magnitude of the effect of the forestry management-related disturbance, such as those generated by e.g. thinning operations. Rather, we found a clear response of the soil biota. We primarily link the difference in oribatid communities found to forest management, which plays a relevant role, apparently not only for plants. This result suggests that the effects of forest dynamics, mainly altered by forest management decisions in our study, are preponderant (Salmon, 2018). As mentioned, the impact of human-related disturbance in this habitat type is heavy. Though, the effects of logging on oribatids can be detected even after 15 years (Kokořová & Starý, 2017). Regrettably, a detailed chronological record of the silvicultural treatments applied in our plots is lacking. Yet, our results have shown a differentiation of oribatid assemblages between fenced and non-fenced plots, the habitat of the latter being changed in relation to forestry-related operations. These differences, that are those between fenced and non-fenced plots, imply that changes in soil biota are present also after (at least) 30 years, latest date of enclosing of our fenced plots. In the areas subjected to enclosure, changes do directly affect important characteristics of the

soil environment, such as moisture and temperature levels, the dynamics and the composition and thickness of the organic layer and light. Still, important disturbance to soil biota can also directly derive from soil animals such as earthworms (Maraun & Scheu, 2000). However, these differences can be also attributable to changes in assemblages due to different evolution in various geographical districts of our study area (Mediterranean versus temperate macro-bioclimate), or to non-measured environmental variables (Gergócs & Hufnagel, 2017), or simply to stochastic factors (Caruso et al., 2012). Differently to plants, oribatids have generally a low rate of dispersal (cit.). Nevertheless, since they can combine different dispersal mechanisms (Lehmitz et al., 2012), they may have had time to differentiate their assemblages, contributing to explain this contrasting pattern of oribatids communities.

4.2. Species richness in fenced and non-fenced areas

Our study confirms that fencing influences species richness of plants. Lower plant species richness in fenced than in non-fenced plots means that species richness markedly decreased with increasing successional age and under lower disturbance level, in agreement with the Intermediate Disturbance Hypothesis of Huston (1979). Our result is also consistent with what was found in other types of Mediterranean forests (Amici et al., 2013) or other habitat types where disturbance resulted in increased species richness (Chytrý et al., 2001). Our data show that in forest ecosystems the influence of disturbance on understorey plant diversity varies with stand development (Bartels & Chen, 2010). The plant successional stages in coastal stone pine forests relate to species richness. The first is the successional most advanced vegetation which is represented by pure holm oak forests with scarce shrubs and few understorey species, including shade-tolerant plants of evergreen oak forest, typical of the natural vegetation of inner dunes and dune slacks (Acosta et al., 2003; Bonari et al., 2017a). The second is an intermediate successional stage with abundance of shrubs, typical sclerophyllous species of the Mediterranean macchia, both (medium-)tall (e.g. *Erica* spp.,

Phillyrea spp., *Rhamnus* spp.) and low (*Cistus* spp.). In addition, there is also another vegetation aspect, quite common, linked to the heavy disturbance due to considerable thinning, clearcutting or trampling: it is represented by an impoverished stage without any shrub species and abundance of generalist herbs. Therefore, late-successional stages of dune woodlands lead to the holm oak forest, which is a dark sclerophyllous forest type of low species richness. In contrast, more heterogeneous environment of non-fenced plots, lead to a higher species richness (see also the paragraph 4.1). However, contrasting levels of plant species richness could also be considered natural in stone pine dune woodlands, rather than as a result of management, given the long-lasting human impact context in which Mediterranean forests evolved (Blondel et al., 2010).

Unlike for plants, we did not find a difference in species richness of oribatids between fenced and non-fenced plots. Small-scale heterogeneity in soils is known to increase species richness of intermediate-sized soil fauna (Nielsen et al., 2010). In our study, the sampling design tried to minimize the soil heterogeneity by selecting sites as homogenous as possible, thus highlighting the net effect of non-intervention management measure on oribatid diversity, which did not differ between disturbance regimes. Therefore, this would suggest that species richness of oribatids in sandy soil is driven by other factors than forest management (Farská et al., 2014; Kokořová & Starý, 2017). We also advocate that not recorded changes in oribatid species richness may be linked to not measured environmental drivers acting at different spatial scales from those under investigation (Lindo & Winchester, 2009). Although oribatids are considered prevalently generalist, they have also been termed as ‘choosy generalists’ (Schneider & Maraun, 2005). This could imply that trophic resources for these animals were probably not sufficiently different under dissimilar disturbance regimes to lead to a detectable variation in species richness.

5. Conclusions and outlook for conservation

We studied whether fencing affects biological components of coastal pine forests such as vascular plants and oribatid mites. Our findings support the appropriateness of the current mosaic-like management with fencing of smaller areas within larger non-fenced areas. It seems to be a suitable choice for nature conservation purposes because it simultaneously supports different communities of vascular plant and soil fauna (oribatids in our case) and increases plant beta diversity of plants. Therefore, we can claim that current diversity of dune woodlands seems to be partly kept by different practices of logging. Still, it can be enhanced by the implementation of physical barriers (such as fences) which have the chiefly function to attenuate, in small areas, the heavy effect of trampling by vacationers. This non-intervention management will allow maintaining zones with a low degree of disturbance and to create heterogeneity promoting biodiversity.

To summarise, conservation authorities should keep fenced and non-fenced areas within protected areas of coastal pine forest – and create such a mosaic where it does not exist – as an effective and relatively cheap nature conservation measure. Direct application of this recommendation means that practitioners should consider to apply a patchy management of dune woodlands with a periodical cutting of the understorey to balance the most evolved stages of the plant succession, while abandonment of other parts will turn in vegetation development towards the climax. These choices will positively contribute to the maintenance of biodiversity in the stone pine habitat in coastal areas.

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Author contributions

G.B., with contributions of M.C., J.T., C.A. and M.M., conceived the study. G.B. did the field sampling and identified plants. M.M. identified mites. F.N. did the soil analyses. J.T. performed the statistical analyses. G.B. led the writing of the paper, with contributions of M.C., C.A., M.M., J.T., G.P., F.N. All the authors commented on the manuscript before submission.

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