

Perennial plant recovery after the removal of invasive *Pinus halepensis* in coastal habitats in Cádiz, southern Spain

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DOI: <https://doi.org/10.52201/CEJ20/USEK6519>

SUMMARY

Aleppo pine *Pinus halepensis* is a tree native to the Mediterranean basin. Even within its native range, *P. halepensis* may behave as an invasive species when planted beyond the original forest areas. Despite its potentially negative effects on the receiving ecosystems, little is known about the response of native plant communities following removal of *P. halepensis*. In southern Spain, *P. halepensis* plantings are outcompeting native shrubland communities (*Juniperus* spp.), which are home to several endangered and protected species. We present the results of an intervention to control the spread of *P. halepensis* in an area of coastal dunes at the La Breña y Marismas del Barbate Natural Park, Cádiz, southern Spain in 2016. An area of 22.4 ha of *P. halepensis* cover was removed using portable chainsaws and a forwarder. We analysed the species richness and composition of native perennial plant species recorded three and six years after the removal of *P. halepensis* in treated, invaded and uninvaded areas. Removal of *P. halepensis* increased the cover of perennial grasses and woody shrubs typical of sun-exposed areas, such as esparto grass *Stipa tenacissima*, rosemary *Rosmarinus officinalis*, turbit *Globularia alypum*, white-leaved rock-rose *Cistus albidus* and the shrub *Anthyllis citisoides*. We conclude that *P. halepensis* removal promotes coastal shrub recovery. We recommend periodic rounds of manual, selective control every three to five years to avoid reinvasion.

BACKGROUND

Aleppo pine *Pinus halepensis* is a drought-tolerant tree native to the Mediterranean basin (Barbéro *et al.* 1998, Quézel 2000). It is a pioneer species that colonises bare, sun-exposed habitats due to the production of numerous relatively small, wind-dispersed seeds and a fast-growing, extensive, branched root system (Puértolas *et al.* 2012). In southern Spain, pine trees *Pinus* spp. were extensively planted to stabilise 'non-productive' coastal sand dunes, harvesting pine nuts, and for timber production (Cueto 1998, Martínez & Montero 2004). *P. halepensis* is considered one of the most invasive pine species outside its native region, where it has spread from planted areas (Richardson & Higgins 1998). Even within its native range, *P. halepensis* may behave as an invasive species when planted beyond the original forest areas, causing negative effects on other plant species (Maestre & Cortina 2004, Pasta *et al.* 2012; Hernandez-Tecles *et al.* 2015, Lavi *et al.* 2005). The effects on the receiving ecosystems are highly dependent on the planting technique employed and tree density (Bellot *et al.* 2004).

Woody species have often been used for dune fixation (Martínez & Psuty 2004, Pye *et al.* 2014). However, dune stabilisation disrupts environmental heterogeneity, biodiversity and natural disturbance (Avis 1995, Wouters *et al.* 2012). In coastal dune areas,

pine plantations reduce sand mobility and salt spray deposition, the main factors causing vegetation zonation, thus outcompeting species adapted to mobile sands and salt laden winds. Moreover, pinewoods shade and reduce wind flow, impairing the growth and pollination of sun-tolerant and wind-pollinated species, such as large-fruited juniper *Juniperus macrocarpa*, which is protected in Andalusia (Muñoz-Reinoso 2021). Despite its potential impacts, reported control actions of *P. halepensis*, i.e. those aimed at restoring the invaded habitats, are surprisingly scarce (Miles 2009, Cuevas & Zalba 2010).

In the La Breña y Marismas del Barbate Natural Park, *P. halepensis* plantations date back to 1930-1950 (Cueto 1998, 2001) and used seeds and seedlings from central Spain (CMA 1997), i.e., outside the original forest areas. These plantations partially replaced the *Juniperus* spp. and shrubland typical of coastal dunes (Ceballos & Martín-Bolaños 1930), which are home to several endangered, protected species, such as large-fruited juniper *Juniperus macrocarpa*, Phoenician juniper *Juniperus phoenicea* var. *turbinata*, ironwort species *Sideritis arborescens*, Portuguese crowberry *Corema album*, *Odontites foliosus*, etc. Since the 1990s, campaigns to reduce the density of the main species planted (*P. pinea*), were initiated to restore the original *Juniperus* spp. forest; however, expanding *P.*

halepensis plantations remained unmanaged. Initially, clearcutting of *P. pinea* followed forestry standards, leaving maximum densities of 150 trees/ha (CAGPDS 2020). Since 2002, the treatments were focused on the removal of pines that surrounded coastal junipers, whilst retaining scrub species typical of the juniper habitat such as *Juniperus phoenicea* subsp. *turbinata*, *Pistacia lentiscus*, *Chamaerops humilis* (CMA 2010). These actions were developed within the framework of a regional "Conservation Program of Maritime Juniper Woodlands" (Muñoz-Reinoso *et al.* 2013). Nowadays, both coastal dunes with *Juniperus* spp. and dunes with forests of *P. pinea* are considered habitats of priority interest in the European Union; thus, current conservation efforts are aimed at their restoration. In other areas, restoration actions involving removal of *P. halepensis* are scarce (Agra *et al.* 2020). To our knowledge, only a pilot trial of *P. halepensis* removal has been developed in Pampean inland grasslands (Cuevas & Zalba 2013). In this case, the invasive pine forests were younger (ca. 20 years) than those reported in the present study and were carried out on plots of 312 m². We report on the effectiveness of a novel action to control *P. halepensis* in a coastal Special Area of Conservation in Cádiz, Spain.

ACTION

Study Area: Removal of *P. halepensis* was carried out in the Special Area of Conservation La Breña y Marismas del Barbate Natural Park, Cádiz (southern Spain, 36.19° N, 6.001° W, altitude = 90-120 m.a.s.l.) (Figure 1). Soil type is a mixture of sand dunes and calcarenites on coastal cliffs. The climate is Mediterranean, with hot, dry summers and mild, wet winters (Peel *et al.*, 2007). Based on comparison of aerial photographs, the area covered by dense stands of *P. halepensis* has doubled between 1978 (11 ha) and 2013 (22.1 ha - there are isolated *P. halepensis* trees scattered over a larger area) (Figure 1).

Removal of *Pinus halepensis*: In February – October 2016, all *P. halepensis* trees (ca. 2,700) were removed from a 22.4 ha area using portable petrol chainsaws. Trees were cut as close to ground level as possible whilst retaining the understorey vegetation. All the logs and branches were removed with a forwarder to prevent seedling recruitment from the breakdown of the cones in the slash (Prévosto & Ripert 2008). To avoid widespread impacts on the soil surface, the forwarder used existing tracks and fire-breakers, going over the same tracks whenever possible. Protected species present in the treated plots were marked beforehand with white/red tape to avoid damage during felling and forwarding.

Experimental design: In June 2019 (three years after *P. halepensis* removal) and October 2022 (six years after removal), plant composition was analysed

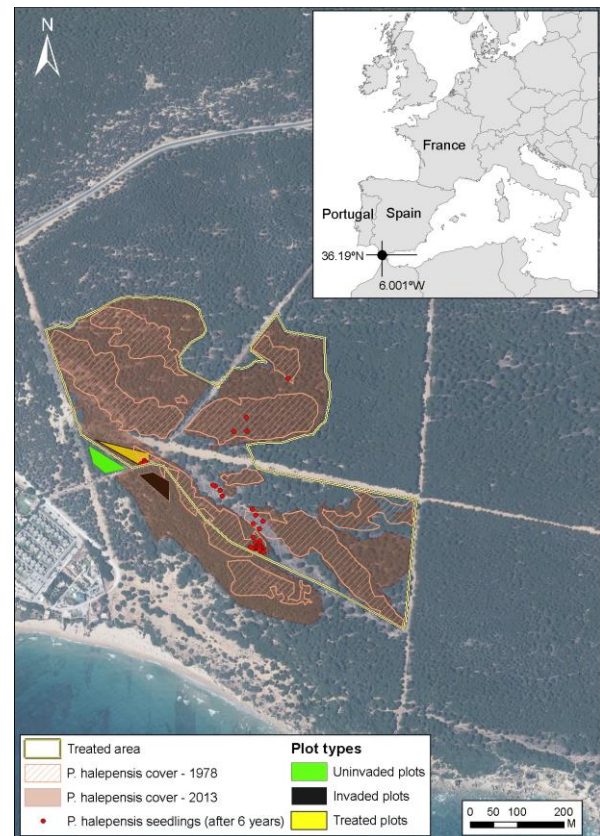


Figure 1. Area of study. Plots used to compare the response of native vegetation after *P. halepensis* removal are close to each other in order to keep similar slope, orientation and substrate.

in three plot types: invaded (untreated) (*P. halepensis* cover = 100%), treated and uninvaded (*P. halepensis* cover = 0%). Given the spatial heterogeneity throughout the study area, a stratified random sampling method was developed. We selected plots with similar slopes, orientation and soil type. A single plot (ca. 2,000 m²) of each type was selected. Within each plot, the presence/absence of plant species was recorded in 50 quadrats (1 x 1 m) distributed in different sections and orientations within the plot in order to best sample the existing vegetation. In summary, we analysed vegetation changes in 50 quadrats for the three plot types and two different years (2019 and 2022). To minimise intragroup variability, the quadrats were set along the same transects each year, by georeferencing the initial and final points of the transect with the OruxMaps® mobile app and casting a cord between these points as a guide.

Uninvaded plots showed a high *Pinus pinea* cover (64-82%) (Figure 2). Uninvaded plot was initially chosen as a reference of well-preserved vegetation. However, *P. pinea* and *P. halepensis* differ in their needle length (*P. pinea*: 9-18 cm *P. halepensis*: 6-13 cm), needle thickness (*P. pinea*: 1.5-2, *P. halepensis*:

0.5-0.8 mm) (Valdés *et al.* 1987) and crown shape (*P. pinea*: umbrella, *P. halepensis*: oval). This way, comparisons between invaded and uninvaded plots highlight the effect of the two *Pinus* species on the understorey (see below). The same plots (one treated, one invaded and one uninvaded) were sampled after three and six years.

treated plot (ca. 2,000 m²) used for assessing perennial plant recovery, seedling density analysis was extended throughout the entire treated area (22.4 ha) by a systematic search. Quadrats (1 x 1 m) were placed along twenty 250 m-long linear transects (i.e., 250 quadrats per transect), that were distributed across the treated area (total sampling effort = 5,000



Figure 2. Pictures of the three plot types analysed: Invaded with *Pinus halepensis*, treated (three years after pine removal) and uninvaded.

Plot comparison: The comparison of invaded and uninvaded plots provided a potential assessment of the impact of *P. halepensis* on native plant assemblages. The comparison of treated and invaded plots provided information on the causal assessment of impact, whereas the comparison of treated and uninvaded plots offered information on the native community recovery after the removal of the invader (Díaz *et al.* 2003). Given the absence of data before trees were cut, we inferred plant recovery by comparing changes in plant composition for the different plots 3 and 6 years after the treatment. Further explanation of the inference of each paired comparison is included in Table 1.

Plant recovery: Perennial species were recorded in each quadrat to make data independent of the sampling season. Bulbous species, such as *Drimeia maritima* and the parasitic *Orobancha* spp., were excluded from analysis because they remain undetected for part of the year. From presence/absence data, we calculated species richness in each quadrat and applied multivariate analysis to compare species composition. We hypothesise that removal of *P. halepensis* led to an increase in species richness compared to invaded (untreated) plots.

Reinvasion analysis: Seedling density of *P. halepensis* was evaluated six years after felling within the treated areas in order to assess the magnitude of reinvasion, as a basis for planning follow-up treatments. Given the relatively small size of the

quadrats). Transects were spaced approximately 20-30 meters apart. To ensure a homogeneous sampling within the closed heath areas, georeferenced tracks were recorded using the OruxMaps[®] mobile app.

Statistical analysis: As data were not normally distributed, we used a non-parametric Mann-Witney U test for pairwise comparisons of species richness between the different plot types. Species composition was compared using pairwise Similarity Percentage (SIMPER) and one-way Analysis of Similarities (ANOSIM) multivariate tests (Clarke & Warwick 2001). SIMPER calculations used the Bray-Curtis coefficient, whereas ANOSIM calculations used the Jaccard similarity coefficient calculated from presence-absence data, according to Legendre *et al.* (2005), with 9,999 permutations. All analyses were carried out using Past 4.02 software (Hammer 2001). Differences were considered significant for Bonferroni-corrected p-values < 0.05.

Table 1. Pairwise comparisons of species richness between the different plot types.
 * Indicates significant differences ($p < 0.05$, Mann-Whitney U test).

Site (plot) comparison	Explanation	Inference	p-value	Mann-Whitney U
Uninvaded (3 vs 6 years)	Changes in uninvaded plot in year 3 vs uninvaded plot in year 6	Infers whether the magnitude of change of treated plots is higher or lower than other plot types for the same period	0.0748	1000.5
Treated (3 vs 6 years)	Changes in treated plot in year 3 vs treated plot in year 6		0.0001*	459.5
Invaded (3 vs 6 years)	Changes in invaded plot in year 3 vs invaded plot in year 6		0.278	1118.5
Treated vs Uninvaded (3 years)	Difference between treated and uninvaded plot after three years	Infers the vegetation recovery after <i>P. halepensis</i> removal. Also infers the role of <i>Pinus pinea</i> (present in uninvaded plot) in vegetation.	0.2371	1083.5
Treated vs Uninvaded (6 years)	Difference between treated and uninvaded plot after six years		0.0001*	536.5
Treated vs Invaded (3 years)	Difference between treated and invaded plot after three years	Infers the causal assessment of the impact induced by <i>P. halepensis</i>	0.0374*	915.5
Treated vs Invaded (6 years)	Difference between treated and invaded plot after six years		0.0033*	843
Uninvaded vs Invaded (3 years)	Difference between uninvaded and invaded plot after three years	Compares the effect of <i>P. halepensis</i> (invaded) and <i>P. pinea</i> (uninvaded) in vegetation	0.0011*	752.5
Uninvaded vs Invaded (6 years)	Difference between uninvaded and invaded plot after six years		0.0336*	935.5

Table 2. Analysis of similarity (ANOSIM) and similarity percentage (SIMPER) of the three plot types. The Simper analysis assesses which taxa are primarily responsible for an observed difference between groups (plot types or sites); whereas the Anosim analysis assesses the overall significance of the difference by reporting significance (p) and R values. R values close to 1 indicate high dissimilarity, while values close to 0 indicate no difference in community composition between sites.

Site (plot) comparison	ANOSIM		SIMPER
	R statistic	Bonferroni-corrected p value	Dissimilarity %
Uninvaded (3 vs 6 years)	0.05	0.042	67
Treated (3 vs 6 years)	0.06	0.012	65
Invaded (3 vs 6 years)	0.06	0.016	52
Treated vs Uninvaded (3 years)	0.35	0.0015	82
Treated vs Uninvaded (6 years)	0.57	0.0015	81
Treated vs Invaded (3 years)	0.45	0.0015	78
Treated vs Invaded (6 years)	0.65	0.0015	79
Uninvaded vs Invaded (3 years)	0.64	0.0015	87
Uninvaded vs Invaded (6 years)	0.71	0.0015	83

CONSEQUENCES

Landscape change: The removal of *P. halepensis* led to a drastic change in the landscape, from a closed forest up to 7-10 m high to a sun-exposed, medium-sized shrubland (height ca. 1.5-2 m) (Figure 3).



Figure 3. Comparative pictures of the managed area, before (October 2016) and after (October 2022) *Pinus halepensis* removal. Before treatment, *P. halepensis* stands completely obscured the stone pines behind. Note the position of the same strawberry tree *Arbutus unedo* in both pictures (white arrow).

Species richness: The removal of *P. halepensis* significantly increased species richness ($p = 0.0001$, $U = 459$) in treated plots after six years (median $S = 5.0$; first quartile $Q_1 = 4.0$; third quartile $Q_3 = 5.0$) compared to data obtained after three years (median $S = 3.0$; $Q_1 = 2.0$; $Q_3 = 4.0$). There was no significant change in species richness for invaded plots (3 vs 6 years) or uninvaded plots (3 vs 6 years). However, when comparing invaded vs uninvaded plots, species richness was significantly higher ($p = 0.0011$, $U = 752$ after three years; $p = 0.0336$, $U = 935$ after six years) in invaded plots (median $S = 4.0$; $Q_1 = 3.0$; $Q_3 = 4.0$ after three years; median $S = 4.0$; $Q_1 = 3.0$; $Q_3 = 5.0$ after six years) than in uninvaded plots (median $S = 3.0$; $Q_1 = 2.0$; $Q_3 = 4.0$ after three years; median $S = 3.0$; $Q_1 = 3.0$; $Q_3 = 4.0$ after six years) (Table 1). Despite invaded plots having a full cover of *P. halepensis*, the understorey showed a well-developed scrub, dominated by *Pistacia lentiscus*, *Rhamnus oleoides*, *Rosmarinus officinalis*, *Quercus coccifera* and *Phyllirea angustifolia* (Table 2).

Plant composition changes: Treated plots after six years showed an increase of woody shrubs and grasses typical of sun-exposed areas such as *Cistus albidus*, *Globularia alypum*, *Anthyllis citisoides*, *Phagnalon* sp., *Stipa tenacissima*, and *Coronilla juncea* compared to treated plots after three years. These species showed minor cover ($\leq 6\%$) in both invaded plots and uninvaded plots after six years (full SIMPER analysis available on request). Treated plots showed the highest proportion of species with net cover changes (i.e., cover after six years minus cover after three years) greater than 10% (seven of 25 species, with respect to four of 24 species in uninvaded plots and four of 19 species in invaded plots).

Plot comparisons: We found high dissimilarities between all plot pairs (79-83%, SIMPER test) as well as significant differences (ANOSIM test) after six years (Table 2). Pairwise comparisons including treated plots showed the highest change in R statistic (ANOSIM test) after six years compared to data obtained after three years. R values close to 1 indicate high dissimilarity, while values close to 0 indicate no difference in community composition between sites (Clarke & Warwick 2001). Treated and uninvaded plots increased the R statistic from 0.35 to 0.57, after three and six years, respectively. Similarly, treated and invaded plots increased the R statistic from 0.45 to 0.65, after three and six years, respectively. This result reveals an increasing difference in plant composition of treated plots compared to uninvaded or invaded plots. In contrast, the comparison between uninvaded and invaded plots showed virtually no change (Table 2).

Seedling reinvasion: Six years after treatment, reinvasion in treated plots was negligible. We found 36 seedlings in 5,000 quadrats (mean \pm SD = 0.007 ± 0.098 seedling/m²) (Figure 4). Seedlings were highly aggregated east of the treated area (Figure 1). Felled trees showed no resprouting or regeneration.



Figure 4. Seedlings of *Pinus halepensis* that appeared in treated plots.

COSTS

The action had a total cost of €84,600 (ca. £75,000). Costs for personnel (project staff and practitioners) who coordinated, designed and monitored the action, and felled the trees were €45,360. Forwarding required

€28,600. Costs for other auxiliary materials used (vehicles, fuel, chainsaw renting, and personal protective equipment) were ca. €10,640.

DISCUSSION

In the present study, the high dissimilarity between all plot pairs suggests that despite showing similar slope, orientation and soil type, plant assemblages of the different plot types analysed are clearly different. Since the vegetation analysis only included perennial (long-lived) woody species, the data obtained after three years suggest that differences between uninvaded and invaded plots and between treated and invaded may have existed before treatment. However, comparison of data obtained after six years with those obtained after three years provides evidence of vegetation recovery after the elimination of *P. halepensis*. Firstly, treated plots showed a significant increase in species richness not observed in uninvaded and invaded plots. Secondly, treated plots showed the highest proportion of species showing a net cover change higher than 10%. Thirdly, comparison including treated plots showed the highest change in R statistic, that reveals an increasing difference in plant composition of treated plots with respect to uninvaded or invaded plots. The increase of perennial species richness in treated compared to invaded sites suggests a negative impact of *P. halepensis* on coastal shrublands, as was recorded in other reports (Maestre & Cortina 2004; Mohammed & Mohamed 2020). Surprisingly, species richness in invaded plots was significantly higher than uninvaded plots both after three and six years (Table 1). The low species richness in uninvaded plots was likely due to the high cover of *P. pinea*. These plots were chosen as a reference of 'wooded dunes with *Pinus pinea*', a priority habitat according to Council Directive 92/43/CEE. However, our results show that the presence of dense *P. pinea* forests may compromise the development of a rich, diverse plant community. In fact, thinning campaigns are carried out periodically in dense *P. pinea* stands that outcompete the native vegetation (Arduini & Ercoli 2012, García-de-Lomas *et al.* 2019). Both *P. halepensis* and *P. pinea* have been reported to negatively affect species richness when planted at high densities (Bonari *et al.* 2017, Tecimen *et al.* 2017). Needle features and crown shape produce higher shading in *P. pinea* stands than in *P. halepensis* (Ganatsas & Thanasis 2010). Therefore, the consideration of wooded dunes with *P. pinea* as the ideal reference state in the study area should be reconsidered in the future.

The effects of removing conifer species on the understorey by using different logging methods or harvest intensities have been widely reported but restoration actions involving removal of *P. halepensis* are scarce (Agra *et al.* 2020). Our results support those

of Cuevas & Zalba (2010), who reported a significant increase in native plant cover and species richness two years after *P. halepensis* removal in Argentinian grasslands. Similarly, our results also align with those of Heinrichs & Schmidt (2009), after clearcutting Norway spruce *Picea abies* stands in German temperate forests. These authors showed an increase of species richness of understorey vegetation (including shrubs and herbaceous species) compared to invaded plots. Even actions aimed at opening canopy gaps (such as glades and firebreaks) in *Pinus nigra* plantations showed positive effects for open dune habitats and their typical plant species (Hunt *et al.* 2019). Similarly, gaps created after removal of conifer species (*Picea glauca*, *Abies balsamea* and *Thuja occidentalis*) in a Canadian boreal forest resulted in an increase of species richness, diversity, and total cover, including an increase of *Aralia nudicaulis*, *Aster macrophyllus*, *Clintonia borealis* in gaps of mature stands and *Rubus idaeus* and *Geranium bicknellii* in gaps within old-growth stands (Grandpré *et al.* 2011). In Italian coastal habitats, removal of stone pine *Pinus pinea* led to a significant increase of plant cover and species richness compared to invaded plots (Arduini & Ercoli 2012). In contrast, removal of dense *P. pinea* stands in stabilised dunes in southern Spain showed a poor recovery of the drought-tolerant plant community, even lower than open areas that underwent a deep disturbance by the forwarder (García-de-Lomas *et al.* 2019). Such long-lasting effects were likely due to the absence of a developed understorey before treatment and to the habitat alteration produced by *P. pinea* stands (Muñoz-Reinoso 2021).

In conclusion, *P. halepensis* removal promoted coastal shrub recovery, by increasing both species richness and the cover of perennial grasses and woody shrubs typical of sun-exposed areas. The low number of seedlings and the fact that *P. halepensis* reproduction begins at the age of five years (Richardson 1998, Shmida *et al.* 2000, Ne'eman *et al.* 2011) indicates that periodic rounds of manual, selective control are needed to avoid reinvasion of treated areas, e.g., one review every three or five years.

ACKNOWLEDGEMENTS

We thank Carmen Rodríguez-Hiraldó, Raquel Checa, Laura Fernández-Carrillo and Manuel Cabaco for their support and coordination effort. This project has been financed with the Life Conhabit Andalucía Project (LIFE13/NAT/ES/000586), coordinated by the Regional Ministry for the Environment and Land Planning of the Regional Government of Andalusia, and is 60% co-financed via the Life+ programme, an EU financial instrument for the environment.

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