



RESEARCH

Open Access



Fire shifts the structure and dynamics of woody plant communities in a Mediterranean coastal dune ecosystem

André F. Mira^{1*}, Nagore G. Medina^{2,3}, Sergio Chozas⁴, Raquel Divieso⁵, Juan Castro-Rivadeneira¹, Mari Cruz Díaz-Barradas^{6†} and Joaquín Hortal^{1,4†}

Abstract

Background Coastal dune ecosystems are fragile habitats where vegetation interacts with harsh abiotic conditions, making them highly vulnerable to climate-driven disturbances such as wildfire. In 2017, a large fire in Doñana Natural Park (SW Spain) provided an opportunity to assess how fire affects woody plant community composition, structure, and interactions across a natural coastal–inland gradient. We compared a burnt area (Cuesta Maneli) with an adjacent unburnt area (Laguna del Jaral) by applying non-metric multidimensional scaling (NMDS), Mantel tests, and analyses of co-occurrence and spatial aggregation.

Results Species composition in the unburnt area was strongly linked to soil variables and showed clear spatial differentiation along the coastal–inland gradient, reflecting strong abiotic filtering and structured negative interactions. In contrast, the burnt area exhibited homogenized community composition across the gradient, with increased species abundance but no significant relationship between soil and species composition, suggesting that fire weakened environmental filters. Species co-occurrence patterns also differed: neutral associations dominated in the burnt area, whereas negative associations and spatial clustering prevailed in the unburnt area. These results suggest that fire reduced competition and increased resource availability, producing a more homogeneous and opportunistic community structure. The findings highlight that post-fire community dynamics cannot be explained solely by deterministic filters but also by neutral dynamics that shape community organization and successional pathways.

Conclusion Fire disturbance reshapes Mediterranean coastal dune plant communities by weakening environmental filtering, reducing competitive structuring, and promoting more neutral patterns of species co-occurrence, ultimately leading to a more homogeneous community across environmental gradients. Recognizing these shifts advances our understanding of woody plant community reorganization after a fire and provides a framework to inform conservation and restoration in fire-prone Mediterranean dune systems.

Keywords Filtering processes, Mediterranean shrub, Community ecology, Species co-occurrence, Spatial organization

[†]Mari Cruz Díaz-Barradas and Joaquín Hortal contributed equally to/were joint senior authors for this work.

The publisher did not copyedit the Portuguese-language abstract.

*Correspondence:

André F. Mira
andrefmira94@gmail.com

Full list of author information is available at the end of the article

© The Author(s) 2026. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

Resumen

Antecedentes Los ecosistemas dunares costeros son hábitats frágiles cuya vegetación soporta condiciones abióticas severas, haciéndolos vulnerables a las perturbaciones producidas por condiciones climáticas adversas, como los incendios. En 2017, un gran incendio en el Parque Natural de Doñana (suroeste de España) proporcionó una oportunidad para estudiar los efectos del fuego sobre la composición, estructura e interacciones de una comunidad de plantas leñosas a lo largo del gradiente natural entre la costa y el interior del sistema dunar. Se compararon un área quemada (Cuesta Maneli) y un área adyacente no quemada (Laguna del Jaral) mediante la aplicación de un Escalamiento Multidimensional No Métrico (NMDS), tests de Mantel, y análisis de co-ocurrencia y agregación espacial.

Resultados La composición de especies en el área no quemada está fuertemente asociada a variables edáficas y mostró una clara diferenciación espacial a lo largo del gradiente de la costa hacia el interior, reflejando un fuerte filtro abiótico e interacciones negativas espacialmente estructuradas. En contraste, las comunidades en el área quemada mostraron una composición más homogénea a lo largo de este gradiente, con un incremento en la abundancia de especies, aunque sin relaciones significativas entre las condiciones edáficas y la composición de especies, sugiriendo que el fuego debilitó el efecto de los filtros ambientales. Los patrones de co-ocurrencia de especies también difirieron: asociaciones neutrales predominan en el área quemada, mientras que en el área no quemada prevalecen asociaciones negativas y agrupamientos de especies en el espacio. Estos resultados sugieren que el fuego redujo la competición e incrementó la disponibilidad de recursos, produciendo una estructura de la comunidad más homogénea y oportunista. Los resultados subrayan que la dinámica de la comunidad después del fuego no se asocia tan sólo a filtros determinísticos, sino también a dinámicas neutras que moldean la organización de la comunidad y las trayectorias de la sucesión.

Conclusiones El fuego modifica las comunidades costeras mediterráneas mediante un debilitamiento de los filtros ambientales, reduciendo la estructura competitiva, y promoviendo patrones más neutros de co-ocurrencia de especies, favoreciendo una comunidad más homogénea a lo largo de los gradientes ambientales. El reconocimiento de estos cambios constituye un avance en la comprensión acerca de cómo se reorganizan las comunidades de leñosas después de un incendio, y proporciona un marco de referencia para la conservación y restauración de ecosistemas mediterráneos dunares costeros proclives al fuego.

Resumo

Antecedentes Os ecossistemas dunares costeiros são habitats frágeis, nos quais a vegetação está exposta a condições abióticas severas, tornando-a vulnerável a perturbações provocadas por condições climáticas adversas, como é o caso dos incêndios. Em 2017, um grande incêndio no Parque Natural de Doñana (sudoeste de Espanha) proporcionou uma oportunidade para examinar como a composição, a estrutura e as interações de uma comunidade de plantas lenhosas são afetadas pelo fogo ao longo de um gradiente natural (costa-interior) neste parque. Comparou-se uma área afetada pelo fogo (Cuesta Maneli) com uma área adjacente não afetada (Laguna del Jaral), através da utilização de Escalonamento Multidimensional Não Métrico (NMDS), testes de Mantel e análises de co-ocorrência e agregação espacial.

Resultados A composição de espécies na área não afetada pelo incêndio estava fortemente associada às variáveis edáficas e apresentou uma clara diferenciação espacial ao longo do gradiente costa-interior. Esta comunidade exibiu também uma forte influência dos fatores abióticos e associações bióticas predominantemente negativas entre as plantas. Por outro lado, a área queimada apresentou uma comunidade com uma composição mais homogénea ao longo deste gradiente e um aumento significativo da abundância das espécies. No entanto, não foi identificada uma relação significativa entre a composição das espécies e as condições edáficas, sugerindo que o fogo reduz a influência dos filtros ambientais.

Conclusões O fogo modifica as comunidades mediterrânicas através da redução da influência dos filtros ambientais, o que, por sua vez, diminui a frequência de associações negativas e promove padrões de co-ocorrência mais neutros entre as espécies, originando uma comunidade mais homogénea ao longo do gradiente estudado. O reconhecimento destas alterações constitui um avanço no entendimento de como as comunidades de plantas lenhosas se reorganizam após um incêndio e proporciona um quadro de referência para apoiar a conservação e a restauração de ecossistemas dunares costeiros mediterrânicos vulneráveis ao fogo.

Background

Coastal dune ecosystems are unique transitional belts between terrestrial and marine environments (Carboni et al. 2009; Malavasi et al. 2018). These systems are characterized by a distinctive combination of environmental constraints, such as high temperature variability, low soil fertility, limited water availability, high light intensity, varied geomorphology, sand movement, strong winds, and salt spray (McLachlan 1991; Miller et al. 2010; Marchante et al. 2011). Together, these factors create a highly dynamic and spatially heterogeneous habitat, forming a pronounced coastal–inland gradient. As a result, coastal dune vegetation is shaped not only by harsh abiotic conditions but also by the fine-scale spatial variability in the distribution of these stressors (Conti et al. 2017).

In addition to these abiotic constraints, vegetation and environmental conditions interact reciprocally to shape community composition and structure. As plants establish, they modify the surrounding environment by trapping sand, stabilizing substrates, and altering micro environmental conditions (Stallins and Parker 2003; Miller et al. 2010). These changes can alter the local conditions in ways that either facilitate or inhibit the establishment of other species from the regional pool (Miller et al. 2010). As a result, the interplay between environmental filters and vegetation can generate spatially heterogeneous mosaics with distinct plant assemblages (Stallins 2005; Chozas et al. 2015). Therefore, understanding community structure in coastal dunes requires considering both the abiotic filters acting along successional gradients and the biotic interactions that provide feedback on species assembly.

While these unique characteristics shape coastal dune communities, they also make them fragile ecosystems, highly vulnerable to biodiversity loss (Brown and McLachlan 2002; Defeo et al. 2009; Shine et al. 2000). Mediterranean coastal dunes present many unique habitats of international conservation interest that host highly specialized flora and fauna (Janssen et al. 2016; Malavasi et al. 2018). Among the disturbances that can affect these systems, fire represents a major threat (Keeley et al. 2012). Fire can severely change the structure, composition, and functioning of ecosystems (Marcos et al. 2023), directly affecting plant growth, survival, and reproduction as well as seed and seedling dynamics (Bond and van Wilgen 1996b). Mediterranean ecosystems are naturally fire-prone landscapes characterized by recurrent fire regimes (Pausas and Fernández-Muñoz 2012; Turco et al. 2018). As a result, Mediterranean shrub ecosystems are considered to be fire resilient, which is defined as the capacity of a system to return to a pre-fire-like state (Halpern 1988). This resilience largely reflects the adaptations of their characteristic woody vegetation (Abella and Fornwalt

2015; Chozas et al. 2025). In particular, Mediterranean shrubs exhibit two main post-fire regeneration strategies, including species capable of vegetative resprouting from stems or roots (resprouters) and species whose persistence depends on seeds stored in the soil or canopy seed bank (seeders, Bond and van Wilgen 1996b; Keeley 2012; Parra and Moreno 2017). Such strategies allow these ecosystems to recover after fire disturbances, maintaining relatively similar structure and composition. However, not all members of plant communities are able to recover after fire. Hence, post-fire recovery trajectories can be highly variable, depending on both species-specific traits and environmental conditions such as fire intensity, and the amount and timing of pre- and post-fire precipitation (Keeley et al. 2012). In recent decades, the increase in fire frequency and burnt area in Mediterranean coastal dune ecosystems, together with the emergence of highly destructive megafires, has further intensified disturbance and reduced the capacity of species to recover (Moreno et al. 2023). As a result, communities may follow alternative successional pathways, with some shrub species failing to regenerate and being replaced by others, ultimately reshaping community composition (Ojeda et al. 1996; Fernández-Guisuraga et al. 2023; Salesa et al. 2024; Trotta et al. 2024).

The recovery of plant communities after fire has important implications for biodiversity, ecosystem functioning, and the provision of ecosystem services (Pausas and Keeley 2009; Keeley et al. 2012; Doblas-Miranda et al. 2017). Hence, understanding the factors and mechanisms that shape vegetation recovery, particularly how species interact along the coastal–inland gradient, can help improve restoration strategies in burnt ecosystems (Padilla and Pugnaire 2006; Bashirzadeh et al. 2024). Although several studies have examined species interactions in dune vegetation, much less is known about how these interactions vary spatially along the coastal–inland gradient. This knowledge gap is even larger when considering how fire-driven changes may alter interactions within plant communities and, ultimately, affect their composition and structure. Therefore, examining post-fire recovery dynamics can provide important insights into the mechanisms driving community reassembly after a disturbance.

The objective of this work is to investigate how fire disturbance changes Mediterranean coastal shrub communities by comparing the composition and structure of woody plants 5 years after the fire event in two adjacent coastal dune areas of southwestern Spain. The two localities were very similar in structure and community composition until 2017, when one experienced a fire event and the other remained unburnt. By burning biomass, fire releases nutrients into the soil which can lower competition, further enhancing opportunities for plant establishment

and growth. Hence, following the colonization–nutrient competition hypothesis (Tilman 1990), we anticipate that the burnt area will harbor a higher abundance and diversity of opportunistic and fire-adapted species, as the fire-induced vegetation gaps and nutrient increases are likely to facilitate colonization, seed germination, and/or resprouting (Poorter et al. 2024). Furthermore, for this area we also hypothesize that (i) post-disturbance conditions will homogenize species composition along the coastal–inland gradient; (ii) species associations will be more randomly distributed, reflecting an early successional stage dominated by opportunistic species where interactions are weaker and community assembly is primarily driven by environmental filtering and stochastic colonization (Poorter et al. 2024); and (iii) the community will be less spatially structured, in contrast to the unburnt area, where well-established species interactions maintain a more predictable and organized pattern of species distribution across the landscape.

Methods

Study region

The study areas are located within the same coastal dune system of the Doñana Natural Park, southwest Iberian Peninsula (Fig. 1), whose extensive area encompasses various geomorphological features such as embryonic dunes, fossil dunes, and eolian sand sheets, extending along approximately 30 km of the Atlantic coast with 1 km width (Díaz-Barradas et al. 2023; Chozas et al. 2025). The vegetation of this region was composed of an extensive pinewood of *Pinus pinea* L. (especially the more interior sections, resulting from afforestation efforts in the 1950s) and some shrub species (Díaz Barradas et al. 1999; Zunzunegui et al. 2006; Díaz-Barradas et al. 2023; Chozas et al. 2025). However, the 2017 fire affected the western portion of the coastal dune system, burning over 10,000 ha (more precisely, approximately 8486 ha of woodland and shrubland) and causing severe impacts on vegetation (Consejería de Medio Ambiente y Ordenación



Fig. 1 Study area location and sampling design. **A** Location of the study area within the Iberian Peninsula. **B** Zoomed view of the area outlined in **A**; the dashed line indicates the boundaries of Doñana Natural Park, as defined in Consejería de Medio Ambiente y Ordenación del Territorio (2016). The orange point marks the burnt area (Cuesta Maneli), and the green point marks the unburnt area (Laguna del Jaral). **C** Satellite image showing the location of the sampled zones in the burnt area. **D** Satellite image showing the location of the sampled zones in the unburnt area. Satellite imagery from 2021 was obtained from Google Earth (Google LLC 2026) and processed using QGIS (QGIS Development Team 2025).

del Territorio 2017). Notably, it led to the near-complete removal of *Pinus pinea* and *Juniperus phoenicea* L. from this part of the landscape.

Following the fire, spring rains in 2018 significantly enhanced the establishment of pyrophytic seeder species. In particular, *Cistus halimifolius* L., *Cistus salviifolius* L., and various herbaceous annuals proliferated during this period, thereby contributing to the early development of the plant community. Likewise, resprouter shrub species such as *Corema album* (L.) D. Don and *Osyris lanceolata* Hochst. and Steud. recolonized the landscape through their regenerative growth capacity. Over time, this sequence of colonization led to the emergence of a distinct vegetation structure in the burnt western area, while the eastern area remains unaffected by recent fire.

Sampling methodology

Sampling was conducted in two sites within Doñana's Natural Park coastal dune system: Cuesta Maneli in the west, affected by the fire (herein referred to as the "burnt area"), and Laguna del Jaral in the east, which remained unaffected (the "unburnt area" herein) (Fig. 1). These areas are located 6.5 km apart, share the same climatic exposure and sand supply, and had similar community composition prior to the fire (see Fig. S1 for photographs of the plant community in both areas prior to the fire, and Fig. S2 for orthophotographs comparing the areas before and after the fire).

In each study area, three 200 m transects were drawn along a coastal–inland gradient characterizing three zones: a coastal zone 200 m from the shoreline, an intermediate zone 500 m inland, and an interior zone 850 m from the shore. Since the burnt area is characterized by the noticeable absence of *Pinus pinea*, to avoid an excessive overrepresentation of this species, plots in the unburnt area were established (whenever possible) in portions of the transect that did not contain dense pine woodland (i.e., more open areas). Altogether, 36 sampling plots were established (six per transect). Plot size (2 m × 2 m) was selected as an appropriate sampling scale for Mediterranean dune vegetation given the small size of scrub species in these habitats, where woody seedlings and small shrubs occur at relatively fine spatial scales. Each plot was subdivided into sixteen (0.5 m × 0.5 m) subplots to facilitate accurate counting of individuals and to record their spatial positions within the plot. This subdivision also enabled analyses of species co-occurrence and spatial aggregation at a fine spatial scale. Within each sampling plot, composite soil samples were collected from the four corners and the center of the plot for soil element analysis. The burnt area was sampled in January 2022 and the unburnt area in January 2023. As this study

focuses on the succession of woody plants after fire and given that Mediterranean shrubs can persist and endure across several seasons (Keeley 1977; Bond and van Wilgen 1996a; Bond and Midgley 2001), the one-year difference in sampling was not expected to affect community structure. Moreover, the unburnt area did not experience any major disturbance that could have altered its composition. Previous studies have shown that, in the absence of major disturbances, community composition remains relatively stable between years in similar ecosystems (Chozas et al. 2015). Therefore, we sampled the burnt area first and surveyed the unburnt area in the following year, during the same season. This approach allowed us to distribute the sampling effort while maintaining comparability between the study areas.

Soil analyses

The collected composite soil samples were air-dried and passed through a 2 mm sieve before laboratory analysis. For each sample, we tested: (a) *pH*: measured using water (pH H₂O) and potassium chloride (pH KCl) extraction; (b) *Organic Matter*: Quantified as a percentage of the total sample; (c) *Nitrogen Content*: Total nitrogen measured using the Kjeldahl method; (d) *Available Phosphorus and Potassium*: Analyzed to determine the concentrations accessible to plants; (e) *Exchangeable Potassium, Calcium, and Magnesium*: Measured to assess the nutrient availability; (f) *Carbonates (Bernard Method)*: Carbonate content was determined; (g) *Soil Texture (Hydrometer Method)*: Analyzed using a densimeter; (h) *Active Lime*: Determined to assess the presence of active calcium carbonate; (i) *Nitrate and Ammonium*: Extracted using KCl and analyzed; (j) *Total Nutrients and Micronutrients*: Assessed using ICP-OES and ICP-MS for a broad spectrum of elements; (k) *Available Micronutrients (EDTA Extraction)*: Analyzed using ICP-OES; (l) Electrical Conductivity (EC). All the above analyses were performed at the Institute of Natural Resources and Agrobiology of Seville (IRNAS)

Data analyses

Woody plant species community composition

To study the effect of spatial distance and soil variables on the composition of woody species, we used a Multivariate Mantel test (Mantel 1967; Legendre 2000), using the "mantel" function of the "vegan" R package (Oksanen et al. 2022). Three data matrices were created for each sampling area: (1) Abundance Matrix: containing Bray–Curtis dissimilarity indices computed for woody plant abundance within plots (Bray and Curtis 1957; De Caceres et al. 2013); (2) Geographical Matrix: plot coordinates (longitude and latitude measured at the center of each plot) were converted into distance matrices

using the Haversine formula (Sinnott 1984); and (3) Soil Matrix: in which Euclidean distances were calculated from scaled soil variables (Gauch Jr 1973). To explore the relationships among the measured soil variables, a Principal Component Analysis (PCA) was performed on the standardized (mean-centered and scaled to unit variance) soil variables (Dray et al. 2012). For more information on the PCA results, see Table S1 and Fig. S3. The PCA was conducted using the “rda” function of the “vegan” R package (Oksanen et al. 2022).

Additionally, a Non-Metric Multidimensional Scaling (NMDS) analysis was performed to explore the patterns in woody plant species composition across the sampling plots (McCune and Grace 2002). The analysis was conducted using the “MetaMDS” function from the “vegan” R package. To assess the relationship between community composition and environmental conditions, the soil PCA axes (summarizing variation in soil variables), as well as area and zone, were fitted onto the NMDS ordination using the “envfit” function with 1000 permutations. Lastly, to identify the species associated with an area or zone an indicator species analysis was conducted using the “multipatt” function from the “indicspecies” package in R (De Cáceres and Legendre 2009).

To assess the effects of fire and zone on woody individual abundance and species richness, we fitted generalized linear models (from the “stat” package in R) using area (burnt vs. unburnt) and zone as explanatory variables. Zone was included as a numerical predictor because it represents an ordered coastal–inland gradient (coastal, intermediate, interior). Both response variables correspond to count data; therefore, generalized linear models were fitted using a Poisson error distribution with a log link function. Model adequacy was assessed through residual diagnostics, which indicated an appropriate fit and no evident violations of model assumptions. The significance of the explanatory variables was assessed using likelihood ratio tests based on the analysis of deviance.

Spatial structure of woody plant community

To study the spatial organization of the woody plant community, we built a presence-absence “area x species” matrix, and analyzed species co-occurrence using the “EcoSim” package (Gotelli et al. 2015). We applied the SIM9 randomization algorithm (Gotelli 2000), which preserves both species frequencies and area richness, to compare the observed C-score checkerboard index with those from 30,000 randomized matrices. A C-score significantly higher than expected under the null model implies that species co-occur less often than expected by chance, suggesting spatial segregation potentially driven by negative interactions such as competition (but see Blanchet et al. 2020; Keil et al. 2021). While a C-score

significantly lower than expected implies that species co-occur more often than random, suggesting positive associations between species. Lastly, a C-score that does not differ from the simulated one suggests that species co-occur by chance.

To better understand the spatial structure of the studied communities, a co-occurrence network was developed to analyze the organization of woody plant species across different zones. This was done by applying the ratio index of adjacency (using the “get_network” function from the “asnipe” R package; Farine 2013), which gauges the strength of association between species pairs. Afterwards, based on the co-occurrence network, we applied the Louvain algorithm (Blondel et al. 2008) to identify modules of interacting species and assess the strength of the community structure. This process was repeated for each area to understand how fire affected community structure. The co-occurrence networks were created using the “igraph” package in R (Csardi et al. 2026).

All statistical analyses were performed using R 4.3.1 (R Core Team 2023).

Results

Drivers of community composition

The Mantel test identified the main relationships between woody species turnover (i.e., compositional dissimilarity), geographic location, and soil variables across sampling areas (Fig. 2). In the burnt area, compositional dissimilarity showed a significant positive correlation with geographic distance (Mantel's $R=0.26$, $p=0.006$), while no significant correlation with the variation in soil conditions was observed (Mantel's $R=0.03$, $p=0.39$). In contrast, in the unburnt area, dissimilarity was strongly and positively correlated with both geographic distance (Mantel's $R=0.50$, $p=0.0002$) and soil variables (Mantel's $R=0.35$, $p=0.004$).

The main variation in species composition was captured by the first axis of the NMDS ordination (Fig. 3), identifying a gradient of soil development that discriminates between plots with higher organic matter content and finer soil particle sizes (positive values) and those characterized by lower organic matter content and coarser soil particles (negative values). Interestingly, plots in the burnt area were grouped around the central area of the NMDS plot, without any clear distinction among them, albeit presenting a higher dominance of *Cistus calycinus* and *Corema album* in the coastal zone plots. On the other hand, the unburnt area plots present a more prominent division along the gradient, with coastal and intermediate zone plots presenting poor soils dominated by *C. album* and *Stauracanthus genistoides*, while the interior zone plots present richer soils dominated

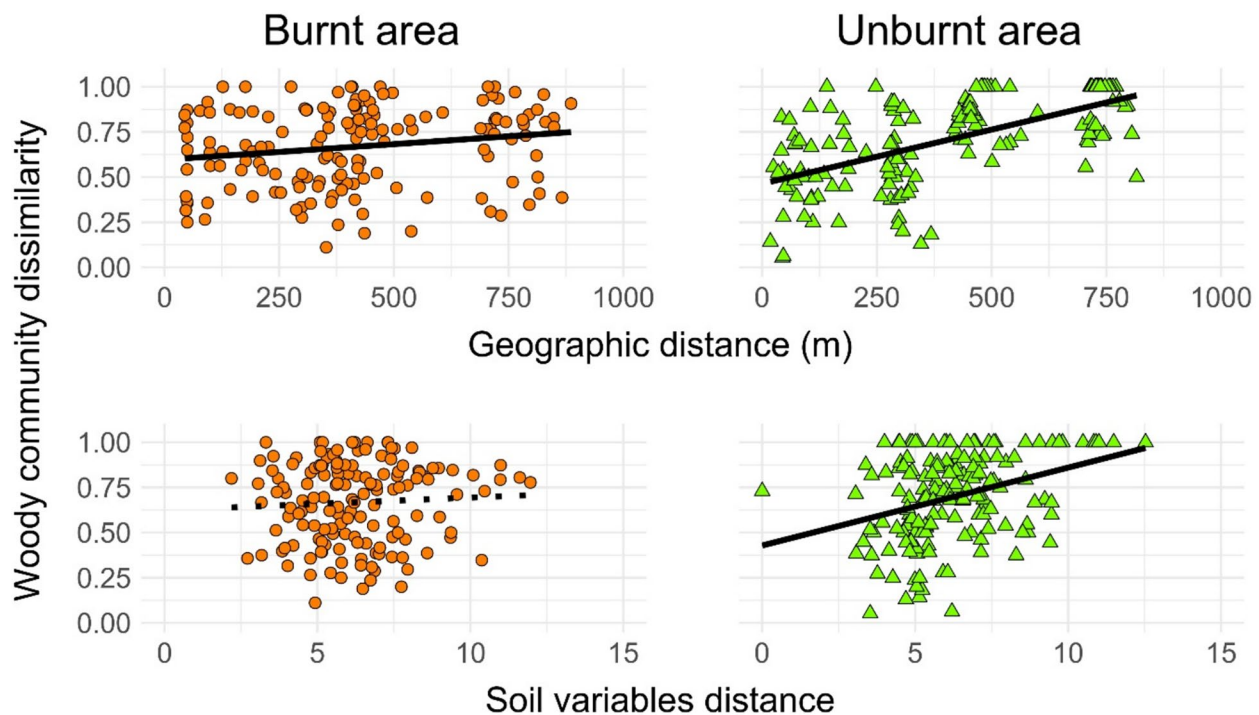


Fig. 2 The figure presents the relationship between woody species turnover (i.e., compositional dissimilarity) and the two studied factors: geographic distance (top row) and variation in soil composition (bottom row) across the two sampling areas, in the burnt area (left column and in orange circles) and in the unburnt area (right column and in green triangles)

by *Daphne gnidium*, *Lavandula stoechas* and *Salvia rosmarinus*. Three groups of species can be discriminated along Axis 1: *Corema album* and *Stauracanthus genistoides* dominate the coastal plots of both sampling areas, as well as the intermediate plots of the unburnt area; *C. calycinus*, *Cistus salviifolius* and *Cistus halimifolius* form a transitional group located near the center of the first NMDS axis; and the remaining seven species (*Osyris lanceolata*, *Salvia rosmarinus*, *Cytisus grandiflorus*, *D. gnidium*, *L. stoechas*, *Pinus pinea*, and *Juniperus phoenicea*) form a third group, primarily corresponding to more mature communities located in unburnt interior plots with more developed soils.

These community responses are corroborated by the indicator species analysis (Table S2). When grouped by area, *C. halimifolius* was strongly associated with the burnt area (IndVal=0.898, p -value=0.001). Additionally, *L. stoechas* was also significantly associated with the unburnt area (IndVal=0.527; p -value of 0.046). In the analysis grouped by zone, *L. stoechas* also demonstrated a significant association with the interior zone (IndVal=0.563, p -value=0.024).

The generalized linear models revealed a significant effect of area on woody individual abundance, with higher abundances recorded in the burnt area compared to the unburnt area (Table 1). Zone also had a significant

effect on abundance, indicating variation in woody individual density along the coastal–inland gradient. The interaction between area and zone was not statistically significant, although it showed a marginal trend, suggesting that the effect of zone may differ slightly between burnt and unburnt areas. In contrast, the general linear model assessing woody species richness did not detect significant effects of area, zone, or their interaction (Table 2). However, zone showed a marginal trend, indicating a possible increase in species richness toward intermediate or interior zones.

Spatial structure of species co-occurrence

The observed C-score at the burnt area (6.54) fell within the 95% confidence interval of the simulated scores (mean=6.34, 95% CI=5.86 to 7.04, SES=0.64), suggesting random co-occurrence patterns among woody species. In contrast, in the unburnt area, the observed C-score (9.83) exceeded both the mean simulated score (0.07) and the upper 95% confidence interval (8.71 to 9.56, SES=3.56), indicating non-random co-occurrence with repulsion being the dominant pattern among species (check Fig. S4).

The modularity analysis with the 11 woody species sampled in the burnt and unburnt areas revealed notable differences in plant community structure (Fig. 4). The

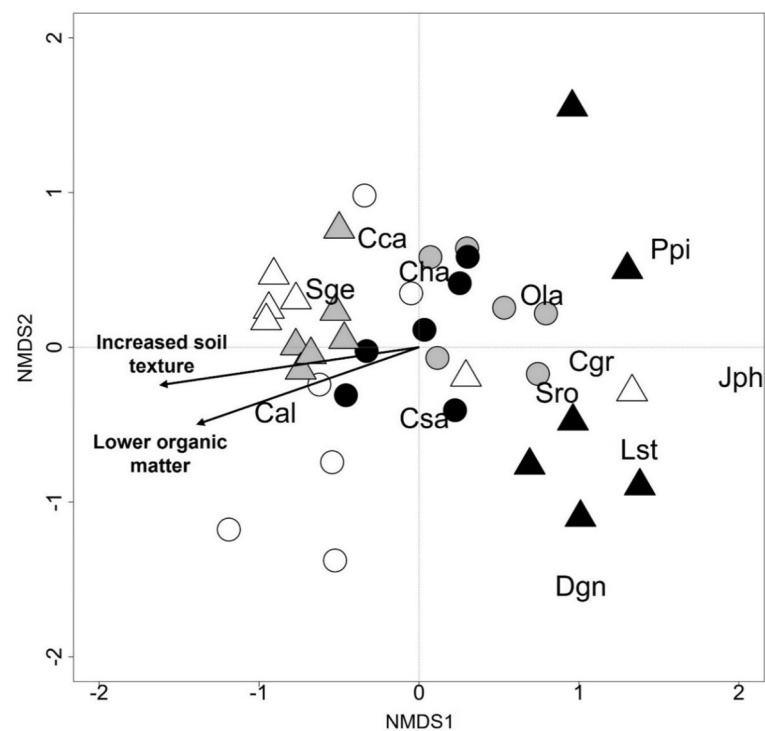


Fig. 3 Axes 1 and 2 of the two-dimensional Non-Metric Multidimensional Scaling (NMDS) of sampling plots based on plant species cover (final stress 16.5%). Circles represent plots in burnt areas and triangles represent plots in unburnt areas. Colours reflect location: white for coastal zone plots, grey for intermediate zone plots, and black for interior plots. Arrows indicate the main environmental gradients identified through correlation analysis. Species codes are as follows: Cal—*Corema album*; Cca—*Cistus calycinus*; Cgr—*Cytisus grandifloras*; Cha—*Cistus halimifolius*; Csa—*Cistus salviifolius*; Dgn—*Daphne gnidium*; Jph—*Juniperus phoenicea*; Lst—*Lavandula stoechas*; Ola—*Osyris lanceolata*; Ppi—*Pinus pinea*; Sge—*Stauracanthus genistoides*; and Sro—*Salvia Rosmarinus*

Table 1 Analysis of deviance results assessing the effects of area, zone, and their interaction on woody individual abundance

Factor	Df	Deviance	Residual Df	Residual Dev	Pr(> Chi)	Sig
Area	1	151.33	34	286.76	<0.001	***
Zone	1	31.40	33	155.37	<0.001	***
Area:zone	1	3.30	32	252.07	0.07	

Table 2 Analysis of deviance results assessing the effects of area, zone, and their interaction on woody species richness

Factor	Df	Deviance	Residual Df	Residual Dev	Pr(> Chi)	Sig
Area	1	0.85	34	23.72	0.36	
Zone	1	3.41	33	20.31	0.06	
Area:zone	1	0.47	32	19.84	0.49	

results of this analysis were consistent for each sampling area throughout the three zones. For instance, in the burnt area, all co-occurrence networks indicate the absence of internal species clustering, and present modularity values

of 0 (or near 0, in the case of the intermediate zone). However, in the unburnt area, all networks present higher levels of modularity, suggesting a more defined community structure.

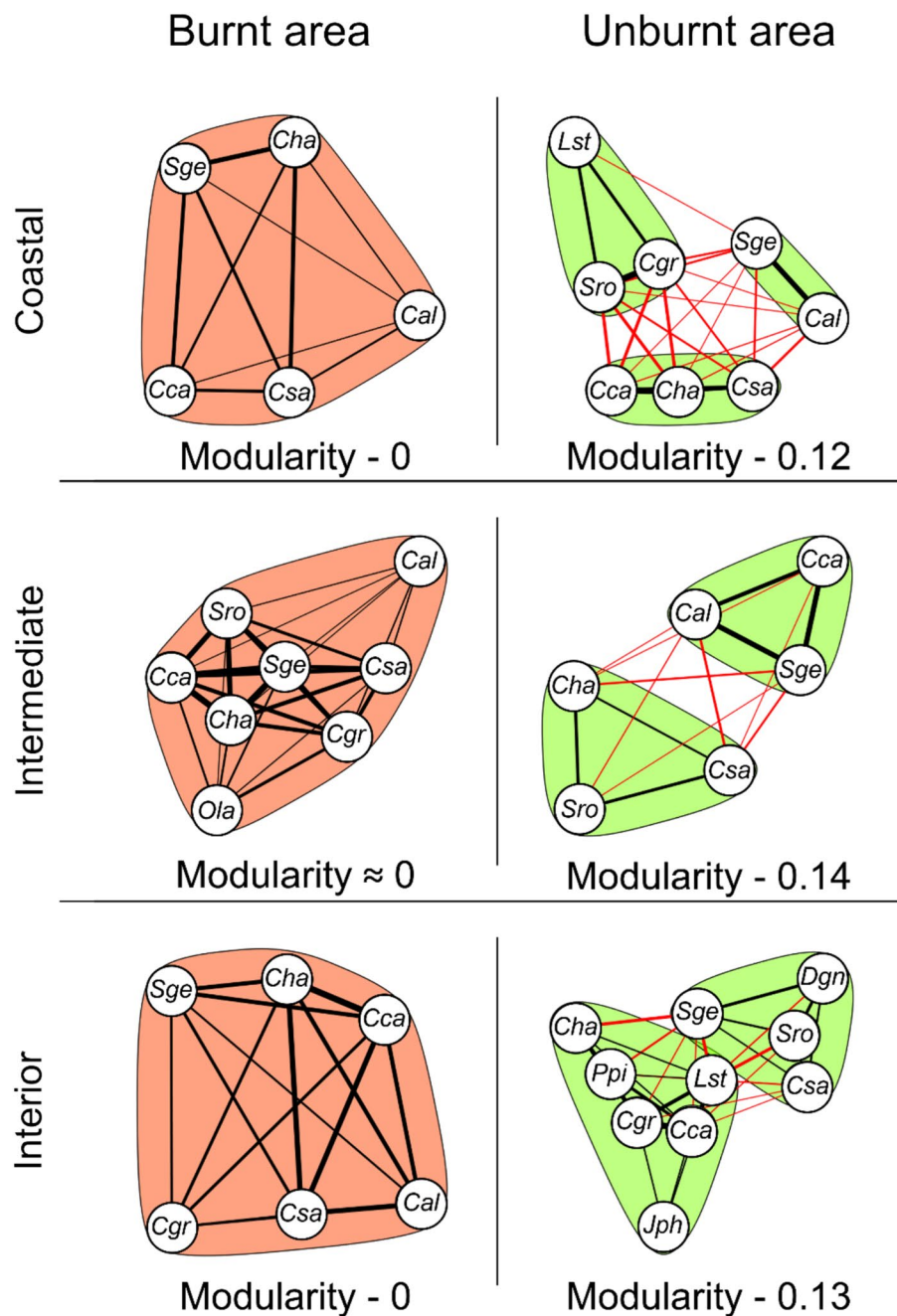


Fig. 4 Co-occurrence networks of the woody plant communities across the three sampling zones in the burnt area (orange) and the unburnt area (green). The network diagrams include nodes (which represent species) connected by lines which represent their co-occurrence (i.e., probability of being present in the same plot). The thickness of the lines indicates the frequency of co-occurrence and the arrangement of species within each outlined colored section illustrates their modular grouping as determined by the Louvain method. Species codes as in Fig. 3

Discussion

Our results reveal how fire disturbance affects the core dynamics of a community of dune woody plants. In the unburnt area (Laguna del Jaral), species composition is

strongly influenced by the coast-to-inland gradient and soil variables, with well-structured communities shaped by deterministic. In contrast, the burnt area (Cuesta Maneli) exhibits more homogeneous species composition across the gradient,

with greater overall abundance and no differences in species' richness. Species in the burnt area co-occur randomly, suggesting that neutral interactions are more common there, while unburnt areas display structured patterns dominated by negative spatial associations, suggesting a stronger effect of competition. This supports the idea that fire reduces competitive pressures, creating conditions that favor neutral interactions during early successional stages (Verdú et al. 2009).

Community composition and abundance following the fire

One of the most evident effects of the fire was the widespread disappearance of *Pinus pinea* and *Juniperus phoenicea* (MCD-B, personal observations). However, it is important to note that the absence of *P. pinea* was not captured in our dataset because the transects were deliberately established in more open dune areas, consequently their fire-induced loss falls outside the scope of our sampling design. Furthermore, the lack of natural recruitment of *Juniperus* in the burnt area may reflect its vulnerability to fire and reduced reproductive capacity following a fire disturbance (Alcahud et al. 1997; Camarero et al. 2022), potentially explaining its low representation in our sampling.

Beyond these species, fire appears to have altered community composition along the coastal–inland gradient, reflecting fire-induced changes in soil conditions. In the unburnt area, significant spatial turnover indicates a structured community across this gradient. This pattern is likely generated by local environmental variation, as evidenced by the correlation between soil dissimilarity and species composition. Such relationship is consistent with the well-established role of environmental gradients in driving zonation patterns in coastal plant communities (Alvarez-Cansino et al. 2012; Chozas et al. 2015, 2017; Díaz-Borrego et al. 2024; Jené et al. 2024). In contrast, fire appears to have reduced soil heterogeneity in the burnt area, likely through the homogenization of nutrients and alterations to microtopography, thereby weakening soil-driven environmental gradients (Giovannini et al. 2001; Sankey et al. 2012; Pereira et al. 2018). This interpretation is supported by the absence of a correlation between soil dissimilarity and species composition in the burnt area (a pattern also reported in previous studies, e.g., Sankey et al. 2012; Fernández-García et al. 2021) as well as by the lack of clear separation among zones along gradients of soil texture and organic matter.

The apparent lack of separation between zones in the burnt area may also be explained by the effects of fire on species abundance. Beyond its homogenizing influence, fire can enrich soil nutrient content through the production of ash, leading to increases in soil organic matter, pH, electrical conductivity, and several elements essential for plant growth, such as carbon, calcium, magnesium, sodium, and

nitrogen (Pereira et al. 2018). Under these conditions, and given the space created by fire, negative interactions do not appear to be a primary driver of community composition, thereby reducing species turnover. Rather, the species that are able to establish under the existing abiotic conditions may even benefit from positive interactions such as facilitation (Chozas et al. 2025). This pattern is consistent with the strong association of *Cistus halimifolium* with the burnt area, likely driven by the massive post-fire germination of *Cistus* species (including *C. halimifolium* and *C. salvifolius*) following the fire. In contrast, the weaker association of *Lavandula stoechas* with the unburnt area may reflect greater environmental heterogeneity, suggesting a more variable community composition.

The observed patterns are consistent with established frameworks of post-disturbance community assembly. For instance, Egler's Initial Floristic Composition hypothesis (Egler 1954) proposes that post-fire community recovery may be largely driven by the species present immediately after disturbance, with their initial establishment exerting a lasting influence on community organization. This aligns with priority effects, whereby the order of arrival (rather than strong ongoing interactions) determines community composition through the availability of resources and space (Fukami 2015). Alternatively, stochastic colonization and dispersal limitation may play a dominant role in early succession, where community assembly reflects chance arrival events rather than deterministic environmental filtering.

Spatial organization of the shrub community

Fire appears to have reduced the structural complexity of the shrub community in the burnt area by disrupting the coastal–inland gradient, redistributing nutrients, and creating vacant ecological space (further amplified by the absence of *P. pinea*). Such changes likely weakened environmental constraints and relaxed competitive pressures, enabling existing woody species to expand into spaces that previously limited their occurrence. For instance, seeder species (particularly those of the genus *Cistus*) rapidly exploited these newly available resources and space, having their recruitment further enhanced by heat-triggered germination of hard-coated seeds (Santana et al. 2012).

Consequently, community organization at this stage may be more strongly influenced by neutral processes, such as stochastic dispersal or environmental variability that affect species in similar ways. This pattern is reflected in the absence of internal clustering among woody species in the burnt area, indicating a diffuse community structure with weak or absent species associations, which is typical of Mediterranean vegetation during early stages of post-fire recovery (<15 years, Santana et al. 2012; Ortega et al. 2025). In contrast, the

unburnt area shows stronger spatial and environmental structuring. Pronounced environmental gradients likely reinforce niche differentiation, promoting competitive interactions that are reflected in co-occurrence patterns dominated by species segregation. These contrasting patterns support the view that fire can act as a resetting disturbance, temporarily reducing competitive pressures and allowing species to co-occur more readily (Bond and van Wilgen 1996b; Pausas and Keeley 2009). What makes this finding particularly compelling is that the burnt and unburnt areas share largely the same woody species pool. Therefore, the observed shift (from negative spatial associations in the unburnt area to random patterns in the burnt area) represents a change in the nature of interactions among the same species, rather than a consequence of species turnover (also suggesting that the community may be in an early transitional stage, see also Chozas et al. 2025). Fire, in this context, does not merely alter community composition; it reconfigures the ecological rules by which coexisting species interact, shifting the balance from competition-driven assembly toward more neutral dynamics. This context-dependent flexibility of species interactions is an underexplored dimension of post-fire succession and offers a novel perspective on how disturbance mediates community assembly.

Conclusion

Our results show that fire can significantly alter woody plant communities in coastal dune ecosystems by homogenizing species composition and shifting community assembly processes. The burnt community appears to be in an early transitional stage, where neutral processes may temporarily dominate before competitive dynamics become more influential over time. Notably, the same species that form a spatially structured community characterized by repulsive interactions in the unburnt area instead form a diffuse community with no evidence of negative associations after fire. The reorganization of woody plant communities following fire is likely shaped by several factors, including species-specific traits such as dispersal ability, survival strategies, and regeneration modes.

From a management and conservation perspective, the absence of *Pinus pinea* has created open space that may facilitate the recovery of native dune vegetation. However, as fire disturbances generate windows of opportunity for plant establishment, they may also promote the uncontrolled proliferation of certain species or even enable the establishment of species previously absent from the community. Hence, monitoring post-fire recovery is essential to detect shifts in vegetation composition and structure, particularly during the

early stages of succession when colonization processes are most active, to prevent excessive dominance and to reduce the risk of future fires.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-026-00520-5>.

Supplementary Material 1.

Acknowledgements

We thank Doñana Biological Station (EBD-CSIC) and Doñana National Park for granting permissions and facilitating our work in the study area.

Authors' contributions

AFM, NGM, MCDB and JH conceived the ideas and designed methodology; AFM, RD, JCR, MCDB and JH collected the data; AFM, NGM, SC, MCDB and JH analyzed the data; AFM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Funding

Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. This research has been supported by projects SCE-NIC, PID2019-106840 GB-C21, and NICED, PID2022-140985NB-C21 and PID2022-140985NB-C22, Ministerio de Ciencia, Innovación y Universidades (Spain).

Data availability

The dataset supporting the conclusions of this article is available in the Zenodo repository [<https://doi.org/10.5281/zenodo.17623475>, <https://zenodo.org/records/17623476>].

Declarations

Competing interests

The authors declare no competing interests.

Author details

¹Department of Biogeography and Global Change, Museo Nacional de Ciencias Naturales (MNCN-CSIC), Madrid, Spain. ²Departamento de Botánica, Universidad Autónoma de Madrid, Madrid, Spain. ³Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, Madrid, Spain. ⁴CE3C - Centre for Ecology, Evolution and Environmental Changes & CHANGE - Global Change and Sustainability Institute, Faculdade de Ciências da Universidade de Lisboa, Lisboa, Portugal. ⁵Department of Biodiversity and Conservation at Real Jardín Botánico (RJB), CSIC, Madrid, Spain. ⁶Departamento de Biología Vegetal y Ecología, Universidad de Sevilla, Sevilla, Spain.

Received: 7 January 2026 Accepted: 14 May 2026

Published online: 15 June 2026

References

- Abella, S. R., and P. J. Fornwalt. 2015. Ten years of vegetation assembly after a North American mega fire. *Global Change Biology* 21:789–802. <https://doi.org/10.1111/gcb.12722>.
- Alcahud M., J.J. Martínez, and E. Orozco. 1997. Influencia de los incendios forestales sobre la regeneración y distribución de la sabina negral (*Juniperus phoenicea* L.) en las provincias de Albacete y Murcia. In: Actas del II Congreso Forestal Español. SECF Pamplona, Spain, pp 27–29.
- Alvarez-Cansino, L., M.C.D. Barradas, M. Zunzunegui, et al. 2012. Gender-specific variation in physiology in the dioecious shrub *Corema album* throughout its distributional range. *Functional Plant Biology* 39: 968–978. <https://doi.org/10.1071/FP12131>.

- Bashirzadeh, M., M. Abedi, and M. Farzam. 2024. Plant-plant interactions influence post-fire recovery depending on fire history and nurse growth form. *Fire Ecology* 20: 9. <https://doi.org/10.1186/s42408-024-00246-2>.
- Blanchet, F.G., K. Cazelles, and D. Gravel. 2020. Co-occurrence is not evidence of ecological interactions. *Ecology Letters* 23: 1050–1063. <https://doi.org/10.1111/ele.13525>.
- Blondel, V. D., J. L. Guillaume, R. Lambiotte, and E. Lefebvre. 2008. Fast unfolding of communities in large networks. *Journal of Statistical Mechanics: Theory and Experiment*. <https://doi.org/10.1088/1742-5468/2008/10/P10008>.
- Bond, W.J., and J.J. Midgley. 2001. Ecology of sprouting in woody plants: The persistence niche. *Trends in Ecology & Evolution* 16: 45–51. [https://doi.org/10.1016/S0169-5347\(00\)02033-4](https://doi.org/10.1016/S0169-5347(00)02033-4).
- Bond, W. J., and B. W. van Wilgen. 1996a. Fire and plants. *Chapman and Hall, London, UK*. <https://doi.org/10.1007/978-94-009-1499-5>.
- Bond, W.J., and B.W. van Wilgen. 1996b. Surviving fires—vegetative and reproductive responses. In *Fire and plants*, 34–51. London, UK: Chapman and Hall. <https://doi.org/10.1007/978-94-009-1499-5>.
- Bray, J.R., and J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 326–349. <https://doi.org/10.2307/1942268>.
- Brown, A.C., and A. McLachlan. 2002. Sandy shore ecosystems and the threats facing them: Some predictions for the year 2025. *Environmental Conservation* 29: 62–77. <https://doi.org/10.1017/S037689290200005X>.
- Camarero, J.J., R. Díaz-Delgado, M. Colangelo, et al. 2022. Differential post-fire recovery of tree and shrub growth and water-use efficiency in a Mediterranean coastal dune system. *Fire* 5: 135. <https://doi.org/10.3390/fire5050135>.
- Carboni, M., M. L. Carranza, and A. Acosta. 2009. Assessing conservation status on coastal dunes: a multiscale approach. *Landscape and Urban Planning* 91:17–25. <https://doi.org/10.1016/j.landurbplan.2008.11.004>.
- Chozas, S., O. Correia, M. Porto, and J. Hortal. 2015. Local and regional-scale factors drive xerophytic shrub community dynamics on Mediterranean stabilized dunes. *Plant and Soil* 391: 413–426. <https://doi.org/10.1007/s11104-015-2439-z>.
- Chozas, S., O. Correia, A.M.C. Santos, and J. Hortal. 2017. Trait dynamics of Mediterranean xerophytic shrub communities growing on stabilised inland dunes respond to nutrient and aridity gradients. *Plant Ecology & Diversity* 10: 115–126. <https://doi.org/10.1080/17550874.2017.1345997>.
- Chozas, S., A.F. Mira, M. Serrano, et al. 2025. Dynamics of post fire plant community assembly in Doñana coastal dunes. *Scientific Reports* 15: 1–13. <https://doi.org/10.1038/s41598-025-04400-x>.
- Consejería de Medio Ambiente y Ordenación del Territorio. 2016. *Plan de ordenación de los recursos naturales del espacio natural Doñana. Decreto 142/2016*. Sevilla: Junta de Andalucía.
- Consejería de Medio Ambiente y Ordenación del Territorio. 2017. *Informe de medio ambiente en Andalucía 2017*. Sevilla: Junta de Andalucía.
- Conti, L., F. de Bello, J. Lepš, et al. 2017. Environmental gradients and micro-heterogeneity shape fine-scale plant community assembly on coastal dunes. *Journal of Vegetation Science* 28: 762–773. <https://doi.org/10.1111/jvs.12533>.
- Csárdi, G., T. Nepusz, V. Traag, Horvát Sz, F. Zanini, D. Noom, and K. Müller. 2026. igraph: network analysis and visualization in R. *R Package Version* 1 (5): 1. <https://doi.org/10.5281/zenodo.7682609>.
- De Cáceres, M., and P. Legendre. 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology* 90:3566–3574. <https://doi.org/10.1890/08-1823.1>.
- De Cáceres, M., P. Legendre, and F. He. 2013. Dissimilarity measurements and the size structure of ecological communities. *Methods in Ecology and Evolution* 4: 1167–1177. <https://doi.org/10.1111/2041-210X.12116>.
- Defeo, O., A. McLachlan, D.S. Schoeman, et al. 2009. Threats to sandy beach ecosystems: A review. *Estuarine, Coastal and Shelf Science* 81: 1–12. <https://doi.org/10.1016/j.ecss.2008.09.022>.
- Díaz-Barradas, M.C., M. Zunzunegui, R. Tirado, et al. 1999. Plant functional types and ecosystem function in Mediterranean shrubland. *Journal of Vegetation Science* 10: 709–716. <https://doi.org/10.2307/3237085>.
- Díaz-Barradas, M.C., J. Valera, M.P. Esquivias, and M. Zunzunegui. 2023. The hemiparasitic shrub *Osyris lanceolata* (Santalaceae) does not disturb the ecophysiology of its hosts. *Flora* 303: 152277. <https://doi.org/10.1016/j.flora.2023.152277>.
- Díaz-Borrego, R., M.Á. Pérez-Navarro, L. Jaime, et al. 2024. Climatic disequilibrium of recruit communities across a drought-induced die-off gradient in Mediterranean shrubland. *Oikos* 2024: 1–11. <https://doi.org/10.1111/oik.10465>.
- Doblas-Miranda, E., R. Alonso, X. Arnan, et al. 2017. A review of the combination among global change factors in forests, shrublands and pastures of the Mediterranean Region: Beyond drought effects. *Global and Planetary Change* 148: 42–54. <https://doi.org/10.1016/j.gloplacha.2016.11.012>.
- Dray, S., R. Pélissier, P. Couteron, et al. 2012. Community ecology in the age of multivariate multiscale spatial analysis. *Ecological Monographs* 82: 257–275. <https://doi.org/10.1890/11-1183.1>.
- Egler, F. E. 1954. Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development with 2 figs. *Vegetatio* 4: 412–417. <https://doi.org/10.1007/BF00275587>.
- Farine, D.R. 2013. Animal social network inference and permutations for ecologists in R using *asnipe*. *Methods in Ecology and Evolution* 4: 1187–1194. <https://doi.org/10.1111/2041-210X.12121>.
- Fernández-García, V., E. Marcos, S. Huerta, and L. Calvo. 2021. Soil-vegetation relationships in Mediterranean forests after fire. *For Ecosyst* 8:18. <https://doi.org/10.1186/s40663-021-00295-y>.
- Fernández-Guisuraga, J. M., P. M. Fernandes, R. Tárrega, et al. 2023. Vegetation Recovery Drivers at Short-Term after Fire Are Plant Community-Dependent in Mediterranean Burned Landscapes. *Forest Ecology and Management* 539: 121034. <https://doi.org/10.1016/j.foreco.2023.121034>.
- Fukami, T. 2015. Historical contingency in community assembly: Integrating niches, species pools, and priority effects. *Annual Review of Ecology Evolution and Systematics* 46: 1–23. <https://doi.org/10.1146/annurev-ecolsys-110411-160340>.
- Gauch Jr., H.G. 1973. The relationship between sample similarity and ecological distance. *Ecology* 54: 618–622. <https://doi.org/10.2307/1935348>.
- Giovannini, G., R. Vallejo, S. Lucchesi, et al. 2001. Effects of land use and eventual fire on soil erodibility in dry Mediterranean conditions. *Forest Ecology and Management* 147:15–23. [https://doi.org/10.1016/S0378-1127\(00\)00437-0](https://doi.org/10.1016/S0378-1127(00)00437-0).
- Google LLC. 2026. Google Earth (Version 10.107.73.2 Multi-threaded). Available at: <https://earth.google.com/>
- Gotelli, N.J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81: 2606–2621. [https://doi.org/10.1890/0012-9658\(2000\)081\[2606:NMAOSC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[2606:NMAOSC]2.0.CO;2).
- Gotelli N.J., E. M. Hart, and A.M. Ellison. 2015. *EcoSimR: null model analysis for ecological data*. R package version 0.1.0. <https://doi.org/10.5281/zenodo.16522>.
- Halpern, C.B. 1988. Early successional pathways and the resistance and resilience of forest communities. *Ecology* 69: 1703–1715. <https://doi.org/10.2307/1941148>.
- Janssen, J. A. M., J. S. Rodwell, M. García Criado, et al. 2016. *European red list of habitats. Part 2: Terrestrial and freshwater habitats*. Brussels: European Commission. <https://doi.org/10.2779/091372>.
- Jené, L., M. Massó-Rodríguez, and S. Munné-Bosch. 2024. Interactive effects of *Orobanchelatisquama* parasitism and drought stress in *Salvia rosmarinus* plants growing under Mediterranean field conditions. *Physiologia Plantarum* 176:1–15. <https://doi.org/10.1111/ppl.14652>.
- Keeley, J.E. 1977. Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparral shrubs. *Ecology* 58: 820–829. <https://doi.org/10.2307/1936217>.
- Keeley, J.E. 2012. Fire in Mediterranean climate ecosystems—A comparative overview. *Israel Journal of Ecology & Evolution* 58: 123–135. <https://doi.org/10.1560/IJEE.58.2-3.123>.
- Keeley, J.E., W.J. Bond, R.A. Bradstock, J.G. Pausas, and P.W. Rundel. 2012. *Fire in Mediterranean ecosystems: ecology, evolution and management*. Cambridge: Cambridge University Press. <https://doi.org/10.1017/CBO9781139033091>.
- Keil, P., T. Wiegand, A.B. Tóth, et al. 2021. Measurement and analysis of interspecific spatial associations as a facet of biodiversity. *Ecological Monographs* 91: 1–22. <https://doi.org/10.1002/ecm.1452>.
- Legendre, P. 2000. Comparison of permutation methods for the partial correlation and partial Mantel tests. *Journal of Statistical Computation and Simulation* 67: 37–73. <https://doi.org/10.1080/00949650008812035>.
- Malavasi, M., V. Bartak, M.L. Carranza, et al. 2018. Landscape pattern and plant biodiversity in Mediterranean coastal dune ecosystems: Do habitat loss and fragmentation really matter? *Journal of Biogeography* 45: 1367–1377. <https://doi.org/10.1111/jbi.13215>.
- Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27:209–220. [https://doi.org/10.1016/S0140-6736\(54\)90013-6](https://doi.org/10.1016/S0140-6736(54)90013-6).

- Marchante, H., H. Freitas, and J. H. Hoffmann. 2011. The potential role of seed banks in the recovery of dune ecosystems after removal of invasive plant species. *Applied Vegetation Science* 14:107–119. <https://doi.org/10.1111/j.1654-109X.2010.01099.x>.
- Marcos, B., J. Gonçalves, D. Alcaraz-Segura, et al. 2023. Assessing the resilience of ecosystem functioning to wildfires using satellite-derived metrics of post-fire trajectories. *Remote Sensing of Environment* 286: 113441. <https://doi.org/10.1016/j.rse.2022.113441>.
- McCune, B., and J.B. Grace. 2002. *Analysis of ecological communities*. Gleneden Beach, USA: MjM Software Design.
- McLachlan, A. 1991. Ecology of coastal dune fauna. *Journal of Arid Environments* 21: 229–243. [https://doi.org/10.1016/s0140-1963\(18\)30684-0](https://doi.org/10.1016/s0140-1963(18)30684-0).
- Miller, T.E., E.S. Gornish, and H.L. Buckley. 2010. Climate and coastal dune vegetation: Disturbance, recovery, and succession. *Plant Ecology* 206: 97–104. <https://doi.org/10.1007/s11258-009-9626-z>.
- Moreno, M., C. Bertolin, D. Arlanzón, et al. 2023. Climate change, large fires, and cultural landscapes in the Mediterranean Basin: An analysis in Southern Spain. *Heliyon* 9: 1–19. <https://doi.org/10.1016/j.heliyon.2023.e16941>.
- Ojeda, F., T. Marañón, and J. Arroyo. 1996. Postfire Regeneration of a Mediterranean Heathland in Southern Spain. *International Journal of Wildland Fire* 6 (4): 191–98. <https://doi.org/10.1071/WF9960191>.
- Oksanen, J., Simpson GL, Blanchet FG, et al. 2022. *vegan: community ecology package*. R package version 2.6–4. <https://CRAN.R-project.org/package=vegan>.
- Ortega, M., Á. Lora, L. Yocom, et al. 2025. Effects of fire recurrence and severity on Mediterranean vegetation dynamics: Implications for structure and composition in Southern Spain. *Science of the Total Environment* 961: 178392. <https://doi.org/10.1016/j.scitotenv.2025.178392>.
- Padilla, F.M., and F.I. Pugnaire. 2006. The role of nurse plants in the restoration of degraded environments. *Frontiers in Ecology and the Environment* 4: 196–202. [https://doi.org/10.1890/1540-9295\(2006\)004\[0196:TRONPI\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2006)004[0196:TRONPI]2.0.CO;2).
- Parra, A., and J.M. Moreno. 2017. Post-fire environments are favourable for plant functioning of seeder and resprouter Mediterranean shrubs, even under drought. *New Phytologist* 214: 1118–1131. <https://doi.org/10.1111/nph.14454>.
- Pausas, J. G., and S. Fernández-Muñoz. 2012. Fire regime changes in the Western Mediterranean Basin: from fuel-limited to drought-driven fire regime. *Climatic Change* 110:215–226. <https://doi.org/10.1007/s10584-011-0060-6>.
- Pausas, J. G., and J. E. Keeley. 2009. A burning story: the role of fire in the history of life. *BioScience* 59:593–601. <https://doi.org/10.1525/bio.2009.59.7.10>.
- Pereira, P., M. Francos, E.C. Brevik, et al. 2018. Post-fire soil management. *Current Opinion in Environmental Science & Health* 5: 26–32. <https://doi.org/10.1016/j.coesh.2018.04.002>.
- Poorter, L., M.T. van der Sande, L. Amissah, et al. 2024. A comprehensive framework for vegetation succession. *Ecosphere* 15: 1–25. <https://doi.org/10.1002/ecs2.4794>.
- QGIS Development Team. 2025. QGIS Geographic Information System (Version 3.40.9-Bratislava). Open Source Geospatial Foundation Project. Available at: <https://qgis.org/>.
- RStudio Team. 2023. *RStudio: integrated development for R*. Boston, USA: RStudio, PBC.
- Salesa, D., M. J. Baeza, and V. M. Santana. 2024. Fire Severity and Prolonged Drought Do Not Interact to Reduce Plant Regeneration Capacity but Alter Community Composition in a Mediterranean Shrubland. *Fire Ecology* 20 (1): 61. <https://doi.org/10.1186/s42408-024-00292-w>.
- Sankey, J.B., S. Ravi, C.S.A. Wallace, et al. 2012. Quantifying soil surface change in degraded drylands: Shrub encroachment and effects of fire and vegetation removal in a desert grassland. *Journal of Geophysical Research: Biogeosciences* 117: 1–11. <https://doi.org/10.1029/2012JG002002>.
- Santana, V. M., M. J. Baeza, and F. T. Maestre. 2012. Seedling establishment along post-fire succession in Mediterranean shrublands dominated by obligate seeders. *Acta Oecologica* 39:51–60. <https://doi.org/10.1016/j.actao.2011.12.001>.
- Shine, C., N. Williams, and L. Gündling. 2000. *A guide to designing legal and institutional frameworks on alien invasive species*. Gland and Cambridge, UK: IUCN.
- Sinnott, R. W. 1984. Virtues of the Haversine. *Sky and Telescope* 68:158.
- Stallins, J. A. 2005. Stability domains in barrier island dune systems. *Ecological Complexity* 2:410–430. <https://doi.org/10.1016/j.ecocom.2005.04.011>.
- Stallins, J.A., and A.J. Parker. 2003. The influence of complex systems interactions on barrier island dune vegetation pattern and process. *Annals of the Association of American Geographers* 93: 13–29. <https://doi.org/10.1111/1467-8306.93102>.
- Tilman, D. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos* 58:3–15. <https://doi.org/10.2307/3565355>.
- Trotta, G., L. Cadez, F. Boscutti, et al. 2024. Interpreting the Shifts in Forest Structure, Plant Community Composition, Diversity, and Functional Identity by Using Remote Sensing-Derived Wildfire Severity. *Fire Ecology* 20 (1): 94. <https://doi.org/10.1186/s42408-024-00330-7>.
- Turco, M., J.J. Rosa-Cánovas, J. Bedia, et al. 2018. Exacerbated fires in Mediterranean Europe due to anthropogenic warming projected with non-stationary climate-fire models. *Nature Communications* 9: 3821. <https://doi.org/10.1038/s41467-018-06358-z>.
- Verdú, M., P.J. Rey, J.M. Alcántara, et al. 2009. Phylogenetic signatures of facilitation and competition in successional communities. *Journal of Ecology* 97: 1171–1180. <https://doi.org/10.1111/j.1365-2745.2009.01565.x>.
- Zunzunegui, M., M.C. Díaz Barradas, A. Clavijo, et al. 2006. Ecophysiology, growth timing and reproductive effort of three sexual forms of *Corema album* (Empetraceae). *Plant Ecology* 183: 35–46. <https://doi.org/10.1007/s11258-005-9004-4>.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.