Multiple global-change drivers and cascading effects in Mediterranean ecosystems: Lessons from an iconic national park

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Abstract

Historically, Mediterranean systems, particularly the Mediterranean Basin, have been substantially impacted by multiple regional-scale disturbances resulting from complex interactive effects of global-change drivers. However, such effects are typically studied on isolated groups of organisms, often disregarding how ecological processes such as biotic interactions affect ecosystem responses to global change. We use the Doñana Protected Area, one of the most important wetlands and shrublands in Europe, as a well-documented case study to highlight how regional anthropogenic pressures simultaneously affect various interacting species, creating cascading impacts across trophic webs on different ecosystems. Using two examples representing the role of key habitat-structuring species on ecosystem processes, the cork oak (*Quercus suber*) and European rabbit (*Oryctolagus cuniculus*), we show how abundance decreases of such key species due to interlinked direct and indirect anthropogenic pressures can alter multitrophic communities – but not always negatively, as other species can adapt to the loss of key species. We also use two examples of species that have flourished under human pressures, the native wild boar (*Sus scrofa*) and invasive red swamp crayfish (*Procambarus clarkii*), and how their abundance increases have had complex impacts on ecosystems. We then discuss, based on the outcomes of actual conservation actions, how management targeted at single species or taxa is ineffective for ecosystem functioning, as it ignores complex interlinks with other components of the system. Instead, the ecosystem-wide impacts of gain and losses of interacting species serves as an excellent empirical example for the need for conservation management and research agenda that account for the complexity of global change in the Mediterranean.

1. Impacts of interacting global-change drivers in the Mediterranean Basin

Ecosystems in the Mediterranean Basin have been shaped by human activities for millenia (Blondel 2006; Valladares et al. 2014, Peñuelas et al. 2017), and much of the current biodiversity is the result, at least in part, of human land use and exploitation (Pausas et al. 2008). Biodiversity is, however, increasingly threatened by global change drivers such as land-use change, climate change, invasive species, pollution, and overexploitation of natural resources (Brook et al. 2008)

(IPBES 2018) (Fig. 1). For instance, over the past two decades, the intensification of agriculture and expansion of urban areas (Miranda et al., 2018) has led to habitat loss and fragmentation, excessive withdrawal of groundwater, high levels of pollution of coastal ecosystems and altered fire regimes (PBES, 2018; Bourlion and Ferrer, 2018; Jaureguiberry et al. 2022). Thus, land-use change has been proven the strongest driver of global biodiversity loss (Jaureguiberry et al. 2022), whose effects are moreover exacerbated by climate change. In the Mediterranean region, annual mean temperatures are already 1.5 ºC above their preindustrial averages and are expected to increase by up to 5.6 ºC by 2100 under the most pessimistic representative concentration pathway of emissions (RCP 8.5; MedECC et al. 2020); while winter precipitation has decreased by 25-40 % over the past two decades (Tuel & Eltahir 2020). The severe changes in climate put further stress on altered or exploited natural communities (Díaz et al. 2019), such that Mediterranean biomes affected by a changing climate are projected to see a 30% reduction in species richness in human-modified landscapes compared to natural habitats (Newbold et al. 2020). This makes the Mediterranean, along with the tropics, the most sensitive biomes to biodiversity loss (Newbold et al. 2020).

Both land-use and climate change in the Mediterranean are modulating other threats on biodiversity, such as the impacts of biological invasions or environmental pollution (Stachowicz et al. 2002; Green et al. 2017; Taylor et al. 2021; Gallardo et al. 2024). For instance, human infrastructure has facilitated biological invasions, and the western Mediterranean Basin is already among the regions with the highest invasion threats (Early et al. 2016). The levels of environmental contaminants or their toxicity can also increase under predicted rises in extreme events such as fires, droughts and floods (Souza et al. 2016; Nunes et al. 2018; MedECC, 2020). These interactions can then facilitate the spread of invasive species (Crooks et al. 2011). These examples highlight the complex ways in which regional pressures from interacting global-change drivers affect natural ecosystems in the Mediterranean Basin. However, past and current research has typically assessed the effects of a single global-change driver on a limited number of species or overlooked non-additive effects of multiple drivers and their impacts across the ecosystem (Peñuelas et al. 2004; Giannakopoulos et al. 2009). Here, we use one of the most well-studied examples of threatened Mediterranean ecosystems, the Doñana Protected Area (hereafter Doñana) in Southern Spain, to first highlight how several, simultaneously acting, regional pressures from global-change drivers affect multiple species across trophic levels. Using evidence from the numerous studies about Doñana, we then show how these complex global-change effects can produce cascading impacts, from populations to communities up to whole ecosystems, and discuss the need for a shift in the management paradigm towards conservation that recognizes and integrates such complex impacts.

2. Doñana as a hotspot for Mediterranean biodiversity and effects of global-change drivers

The Doñana area is located in southwestern Spain, around the Guadalquivir estuary. It originally included a marshland in the left bank of the river which has now been totally lost (Fig.1). Doñana's ecological value has been recognised for centuries, but it was only in 1963 when the first hectares of land were protected. The Doñana National Park was created in 1969, and it was classified as a UNESCO Biosphere Reserve in 1980 and as a UNESCO World Heritage Site in 1994. The Doñana Natural Area, which corresponds to the Biosphere Reserve, includes the National Park, the Natural Park, formed by some peripheral areas of different habitats surrounding the National Park, and areas with lower level of protection in contact with agricultural areas (Fig. 1). It is considered a Mediterranean-climate region with a subhumid climate characterized by variable rainy seasons historically centred in autumn and spring but shifting towards winter over the last decades, and hot and dry summers (Pérez-Ramos et al. 2017; Paniw et al. 2023). Doñana integrates a large variety of terrestrial and aquatic ecosystems, including pine and cork oak forests, shrublands, grasslands, sand dunes, and marshlands with different levels of salinity. This mosaic of habitats is the main reason for its great biodiversity. Over 1,300 species of plants, including 170 endemisms, have been identified, 400 of which are associated with wetlands (Díaz-Delgado et al. 2024; Díaz-Paniagua et al. 2010). The diversity of terrestrial vertebrates is also remarkable, with 50 species of mammals, over 300 species of birds, and 25 species of reptiles, including emblematic species such as the Spanish imperial eagle (*Aquila adalberti*) and the Iberian lynx (*Lynx pardinus*) (Green et al. 2016). The aquatic fauna is also highly diverse, with rich communities of continental fishes (27 species) and amphibians (11 species), as well as macro- and micro-invertebrates occurring mostly in a complex network of temporary and permanent ponds. In addition, Doñana hosts numerous endemic terrestrial invertebrate species (Cárdenas et al. 2024; Serediuk et al. 2024; Wood et al. 2022).

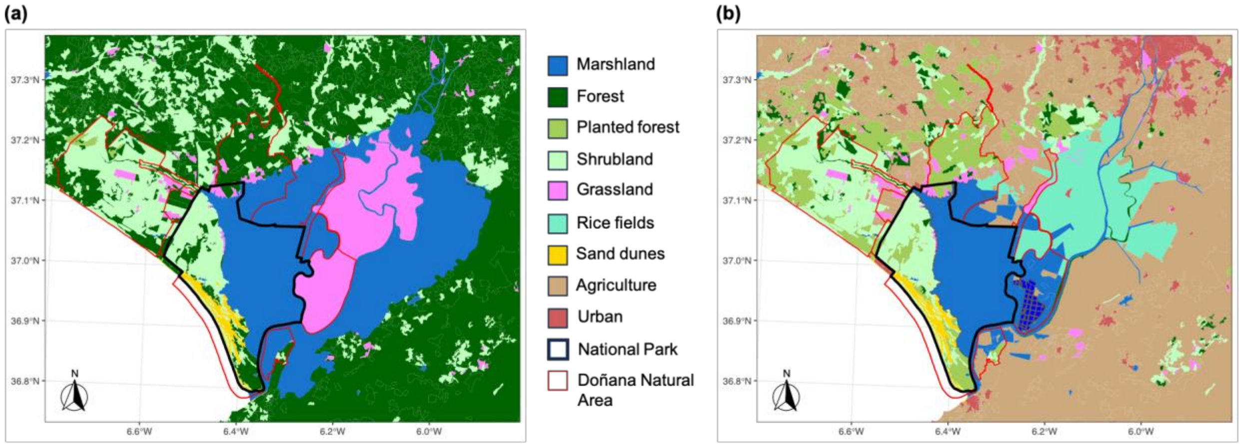

Figure 1: Representation of the historical (a) and present (b) landscape of the Doñana National Park, the Doñana Natural Area, and the surrounding influence zone. The historical representation is a recreation of the landscape before the major anthropogenic alterations started (i.e. ca. 17th century) based on topographical criteria and historical information (for the marshland), and with an arbitrary mosaic of native habitats. The present landscape is based on a reclassification of Corine Land Cover data.

Doñana cannot be fully understood without considering its long history of anthropogenic pressures (Martín-López et al. 2011; Santamaría & Martin-Ortega 2023) (Figs. 1 & 2). Before the creation of the National Park in 1969, it was mostly a hunting reserve. But centuries of deforestation dramatically modified the landscape. In the 17th century, the climax forest dominated by cork oak (*Quercus suber*) started being heavily exploited for the extraction of firewood and charcoal (Corona et al. 1988). In the 18th century, official documents already report extensive plantations of pine trees in some areas, which were progressively extended until the 20th century. Over the last century, most of the remaining native forest was replaced (Fig. 2) (Granados Corona 1987): first, by extensive plantations of non-native *Eucalyptus* sp. (1940-1990), and then, in an attempt to eradicate the eucalypt and alleviate the damages these tree produce in terrestrial ecosystems, by plantations of native pine species, i.e., *Pinus pinea* (reviewed in Román Sancho 2009).

The history of direct and indirect human pressures on Doñana has led to major landscape transformations. More than 80% of the original marsh surface area has been transformed, representing one of the largest losses of marshes in Europe (Ruiz et al. 2015) (Fig. 1). Between 1956 and 2007, urbanized areas in the surroundings of the protected area increased by 590% and irrigated fields by 126%, whereas scrubland area diminished by 44%, wetlands by 40%, and grasslands by 20% (Palomo et al. 2014). Road density (mainly unpaved) has doubled since 1956, currently covering approximately 4% of the protected area and causing habitat fragmentation (Román et al., 2010). Although the hydrological alterations in Doñana's ecosystems slowed down after the creation of the National Park (Zorrilla-Miras et al. 2014), an open conflict over water use emerged since the 1980s, causing a persistent tension between economic development, including urbanization (Fig. 1), and conservation efforts for expanding the protected area, which increased to more than 100,000 ha (Gómez-Baggethun et al. 2012) (Fig. 1).

The profound land transformation not only destroyed natural habitats but has also led to increased pollution pressures (Fig. 1) (Paredes et al. 2021). In addition, a tailing dam collapsed at the mine of Aznalcóllar in 1998 (60 km north of Doñana), leaking away six million m^3 of acidic water and mud enriched in heavy metals into the Guadiamar river, which used to feed part of the Doñana marshes (Grimalt et al. 1999). This pollution event affected 2,754 ha within Doñana Natural and National Parks and led to a mass die-off of fishes and aquatic invertebrates, whereas many terrestrial species suffered long-lasting health effects and habitat loss (Meharg et al. 2002; Baos et al. 2006; Sánchez-Chardi et al. 2009).

Currently, excessive and unsustainable groundwater extraction, up to 20 m in the deep aquifer, is the biggest threat to Doñana's ecosystems (de Felipe et al. 2023, Green et al. 2024). This is mostly due to intensive agriculture and urbanization (Fig. 1) in adjacent areas that heavily exploit the aquifer that feeds Doñana (Serrano & Serrano 1996; Blade et al. 2010) (Sousa et al. 2007), but climate change is aggravating the water-deficit problem (Guardiola-Albert & Jackson 2011) (Fig. 1). Temperatures have been increasing in the last three decades, while precipitation has decreased in the last decade; and these trends are projected to continue into the future (Fig. 2; Supporting Material S1). This conjunction of pressures is resulting, among others, in lower recharges to the aquifer, lower water inputs into ponds and marshes, poorer water quality owing to greater salinity and pollutant concentrations, and lower soil moisture (Silva Junior et al. 2010; Guardiola-Albert & Jackson 2011; Fernández-Delgado 2017; Paredes et al. 2021). Consequently, multiple impacts to temporary ponds and marshes, as well as to terrestrial vegetation, are already evident (Green et al. 2024). For example, numerous temporary ponds (59.2%) have not flooded since 2013, and many are expected to disappear (de Felipe et al. 2023). In July 2024, for the first time since we have records, the biggest permanent lagoon in Doñana totally dried up for the third consecutive summer.

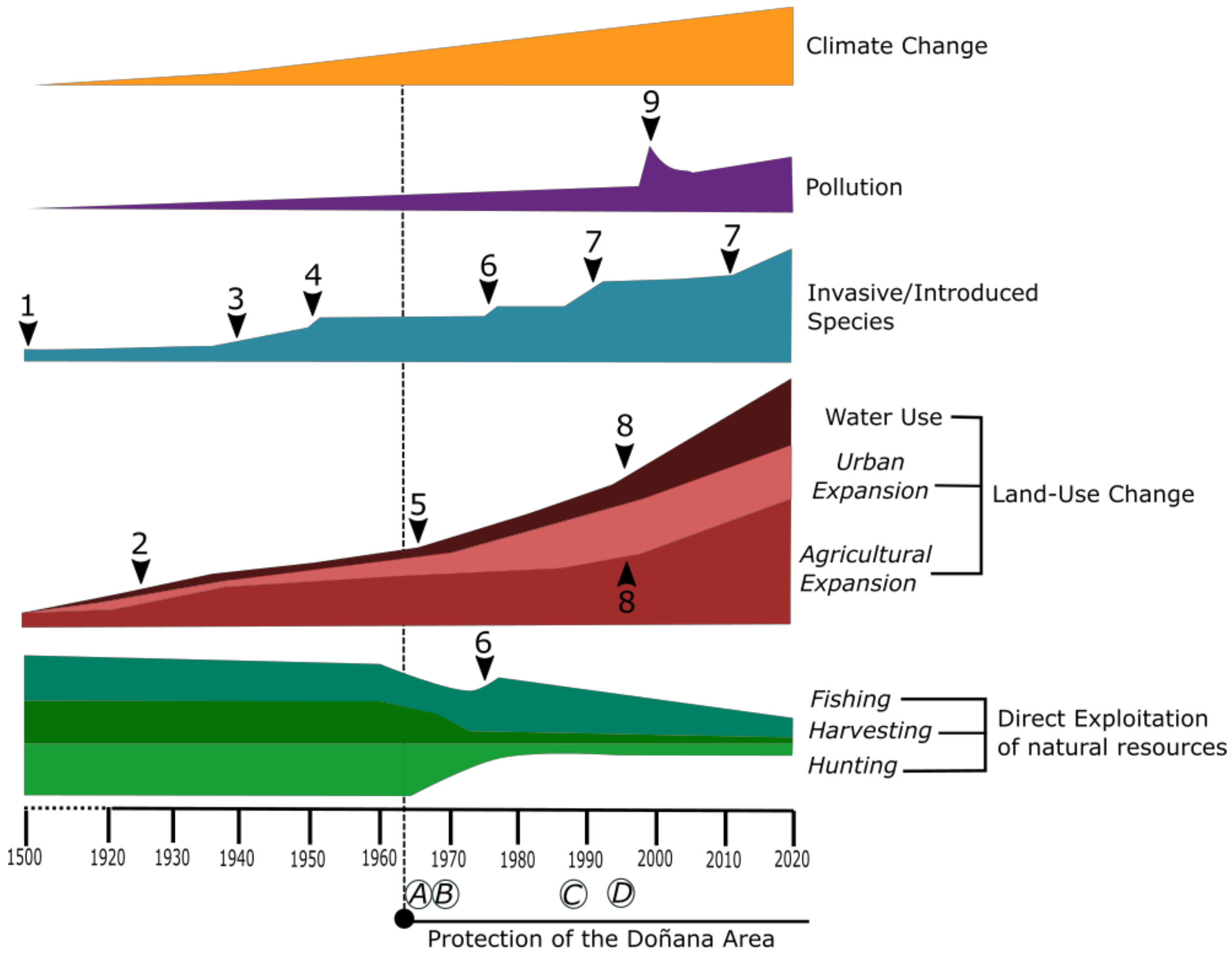

Figure 2: Conceptual representation of the relative intensity of the different drivers impacting Doñana over time. Note that the width (i.e., intensity) cannot be compared between drivers. The vertical dashed line marks the beginning of the protection of the area in the mid-60s: A. Protection of the first hectares of land (1963) B. Creation of the Doñana National Park (1969); C. Classification as a UNESCO Biosphere Reserve (1980); D. Designation as UNESCO World

Heritage Site (1994). Numbers represent notable events (see the main text for a more detailed description): (1) Beginning of international trading in which the Guadalquivir estuary served as the "gateway to the Indies/Americas"; (2) Large scale conversion of natural land to rice fields and other irrigated crops; (3) Increased spread of non-native vegetation (*Eucalyptus* sp.); (4) Arrival of Myxomatosis; (5) tourism and urban expansion; (6) Introduction of the red swamp crayfish; (7) Arrival of the Rabbit Hemorrhagic Fever; (8) Large scale conversion of land for berry production; (9) Aznalcóllar mine spill.

Biological invasions represent another strong stressor in Doñana and exacerbate the combined challenges of land-use and climate change (Fig. 2). Multiple invasions have occurred in both aquatic (e.g., marshes and ponds) and terrestrial (e.g., shrubland, grassland) ecosystems, with a range of examples from viruses to vertebrates (see Supporting Material S2). In aquatic ecosystems, shorter wetland hydroperiods, resulting from aquifer extraction and reduced rainfall, have facilitated the establishment of tolerant and fast-growing aquatic species, such as the water boatman *Trichocorixa verticalis* (Céspedes et al. 2019); and increased phosphorus loading has facilitated the introduction of the invasive aquatic fern *Azolla filiculoides* (García-Murillo et al. 2007; Espinar et al. 2015), producing cascading trophic negative impacts on macrophytes and amphibians (Pinero-Rodríguez et al. 2021). Warmer temperatures have benefited other aquatic invasive species with wide physiological tolerances over native biodiversity (Lejeusne et al. 2014; Espinar et al. 2015). Moreover, fish communities in the Doñana marshes are now almost entirely composed of invasive species (Moreno-Valcárcel et al. 2013). Intended introductions, such as those of red swamp crayfish *Procambarus clarkii* for aquaculture (Oficialdegui et al. 2020, see below), and unregulated activities, such as intensive hunting and poaching of wild ungulates and native predators (Revilla et al. 2001; López et al. 2014), are also promoting invasive species establishment. In terrestrial ecosystems, pollution and human-mediated dispersal have facilitated the spread of invertebrate invaders, such as the Argentine ant (*Linepithema humile*) (Carpintero et al. 2005), and generalist, stress-tolerant invasive vegetation from areas surrounding Doñana (the number of catalogued non-native plant species is at least 99; Valdés 2015). Of serious concern is also the arrival of pathogenic organisms, such as the invasive oomycetes *Phytophthora cinnamomi* and *Pythium spiculum* that infect and cause defoliation and root necrosis in cork oaks (see below) (Vita et al. 2013; González et al. 2020).

The above-described regional pressures exerted by interacting global-change drivers have impacted Doñana' biodiversity. The hydrological alterations and increased aridity have led to substantial decreases in primary production (Alcaraz-Segura et al. 2009, Green et al. 2024), as well as to decreased food quality and quantity for herbivores and frugivores that affect animal phenology (e.g., Campo-Celada et al. 2022) and fitness components (Millán et al. 2021; Giralt-Rueda & Santamaria 2021; Lloret et al. 2016; Pérez-Ramos et al. 2017; Paniw et al. 2021b). Also, climate change has been linked to the local extinction of some common species, such as the Eurasian hobby (*Falco subbuteo*) (Sergio et al. 2021) and to a higher prevalence of some disease vectors (Roiz et al. 2014). On the other hand, species more tolerant to salinity, heat, and/or concentration of nutrients have increased (Rouco et al. 2011; Espinar et al. 2015; Green et al. 2017; González-Ortegón et al. 2020). In what follows, we describe how the plethora of stressors and their interactions have affected four key species in Doñana (Fig. 3) that led to cascading effects across taxa, trophic webs, and ecosystems.

3. Cascading impacts of global-change drivers on biodiversity: four case studies in Doñana

Doñana is an intensively studied natural area. The effects of direct or indirect human pressures on its ecosystems have been described in 395 peer-reviewed articles (ca. 40% of all scientific publications about Doñana on the Web of Science until the end of 2024). This makes Doñana an ideal system to describe the impacts of global-change drivers on populations and communities of interacting species, and how these in turn affect ecosystem processes and services.

To highlight the importance of understanding the complex interactions of abiotic and biotic factors on Mediterranean ecosystems, we focus on four well-documented case studies in which the available scientific literature identifies both trophic and co-extinction cascading effects in Doñana (Fig. 3). The selected species, i.e., cork oak, European rabbit, wild boar, and red swamp crayfish are important elements in different ecosystems (from aquatic to terrestrial), play a variety of ecological roles within the ecosystems (predator, prey, host, structuring agents of the physical and biotic characteristics of habitats) and reflect different responses to global-change drivers (negative or positive) across different timescales (centuries to decades; see abundance trends of these species in Fig. 3). We rely on a wide scientific literature to identify major impacts on these species and infer cascading effects through biotic interactions with other species, including different trophic levels. Such cascading effects have substantial impacts across food webs, causing for example the collapse of top predator species, and transforming the ecosystems and even the landscape.

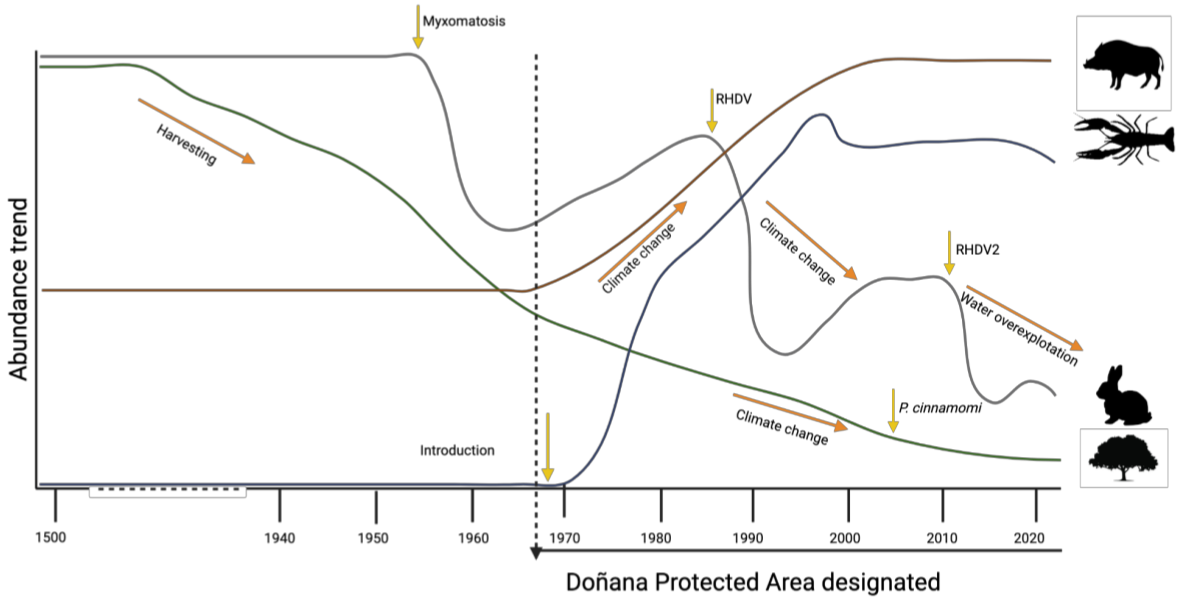

Figure 3: Conceptual timeline of the impacts of the drivers on the relative abundance trends of the four case study species. Note that line slopes and levels cannot be compared between species. Some of the most relevant impacts for each species are represented with arrows. The cork oak (*Quercus suber*) and the European rabbit (*Oryctolagus cuniculus*) show negative trends, whereas the wild boar (*Sus scrofa*) and the red swamp crayfish (*Procambarus clarkii*) overall show positive trends.

3.1 Habitat-structuring species negatively affected by global change: the case of cork oaks and European rabbits

The cork oak is an emblematic long-lived evergreen tree of the Mediterranean Basin that provides valuable economic and cultural services to humans, such as cork and high-quality fodder for domestic animals (Aronson et al. 2012). It also provides food, shelter, and nesting support for many species (Valverde 1967). After centuries of logging, cork oak populations have decreased in Doñana from approximately 16,000 individuals in 1600 to a few hundred isolated centenary trees at present (Corona et al. 1988; Castroviejo 1993) (Fig. 3). The remaining individuals are vulnerable to emerging local threats such as unsustainable seed predation, seedling browsing, or trampling by wild and domestic ungulates (Venero Gonzalez 1984; Herrera 1995), which have become more abundant under land-use change (including the wild boar *Sus scrofa*, see below) (Fig 4A). These local pressures can also directly collapse the natural regeneration of cork oak (Herrera 1995). The regional effects of land-use change are interacting with effects of climate change, especially prolonged droughts (Corcobado et al. 2014; González et al. 2020), and invasive pathogens that negatively affect cork oak stands (Robin et al. 2001; Homet et al. 2019). In particular, the invasive pathogen cinnamon fungus *Phytophthora cinnamomi* has affected several cork oak populations in Doñana (Vita et al. 2013) and across the Iberian Peninsula (Brasier 1992; Gómez-Aparicio et al. 2012; Moricca et al. 2016) (Fig. 4A). The remaining Doñana's cork oaks have been home, until few years ago, to large colonies of waterbirds whose droppings alter the chemistry and microbial community of the soil, ultimately resulting in higher cork oak mortality (García et al. 2011; Domínguez et al. 2017). Although we do not have a documented history of impacts caused by the loss of cork oak forest, several historical accounts, including Valverde (1967), support the conclusion that the loss of cork oaks meant the destruction of an entire biome once dominating the terrestrial landscape of Doñana. The different life stages of a cork oak tree once provided habitat and shelter for reptiles, birds, and mammals, including iconic species that are nowadays very scarce in Doñana, such as the Iberian lynx, the Spanish imperial eagle and many other bird species (see cascading effects on top predators and waterbirds in Fig. 4A). More than half a dozen species were observed to breed at the same time in a single cork oak tree (Valverde 1967). This highly diverse biome is not observed in the (currently) dominating pine forest (Valverde 1967; Rogers & Myers 1980), which suggests the magnitude of biodiversity depletion following the cork oak forest loss. Other ecosystem services, such as carbon sequestration, water quality regulation, and protection from erosion, have been also arguably severely affected by the decline of this foundation species (Marañón et al. 2012).

Just like cork oaks, the European rabbit (*Oryctolagus cuniculus*) plays a key ecological role in southwestern Mediterranean areas, including Doñana (Delibes-Mateos et al. 2008). Rabbits alter chemical and physical soil properties through their latrines and their digging activities (Willott et al. 2000; Eldridge & Simpson 2002), and disperse seeds of numerous plant species (Delibes-Mateos et al. 2007). They are also an important prey for >30 species, including the threatened Spanish imperial eagle and Iberian lynx (Veiga & Hiraldo 1990; Delibes-Mateos et al. 2008). Once extremely widespread in Doñana, rabbit populations have declined by > 90% since the early 2000s (Moreno et al. 2007; Delibes-Mateos et al. 2009). This decline can only be understood in light of complex regional manifestations of interacting global-change drivers, including habitat loss and introduced diseases (Fig. 4B). Rabbits have suffered mass mortality events due to diseases since the 1950s, first myxomatosis and then, aggravating the population declines under myxomatosis, rabbit hemorrhagic disease virus (RHDV in 1988 and RHDV2 in 2012; Moreno et al. 2007; Delibes-Mateos et al. 2009, 2014). RHDV caused mortality rates of 55-75% (Villafuerte et al. 1995; Tablado et al. 2012), whereas RHDV2 was linked to a decrease in abundance of > 80% in 2013 in Doñana (Delibes-Mateos et al. 2014; Monterroso et al. 2016). Rabbit populations have been slow to recover from these population declines (Calvete 2006). Climate change may further compromise population recovery, since decreasing rainfall in southwestern Spain is leading to shorter and less successful breeding seasons (Tablado et al. 2009; Tablado & Revilla 2012). Another important factor precluding the recovery of rabbit populations is that suitable habitats (i.e., mixture of pasture for feeding and shrublands for sheltering) are increasingly being lost in Doñana due to a higher frequency of drought under climate change, high herbivory pressure (including introduced and domestic species), and land use change causing groundwater overexploitation (Moreno & Villafuerte 1995; Cabezas & Moreno 2007; de Felipe et al. 2023; Paniw et al. 2023). Past declines in rabbit populations have had severe negative effects on specialist predator populations, and these effects are projected to continue (Fordham et al. 2013) (Fig. 4B). Declines in rabbit populations by 60–70% have been associated with decreases of 65.7% in Iberian lynx and 45.5% in imperial eagle fecundities (Monterroso et al. 2016). The population declines of these highly specialized apex predators favor mesopredator release (Fig. 4B) (Palomares et al. 1995; Jiménez et al. 2019), which, in the absence of rabbits, may increase predation pressures on other species (Delibes-Mateos et al. 2007). Furthermore, the cascading effects of rabbit declines on decreasing nutrient availability, which affect plant community composition and landscape structure, are well documented in Doñana (Delibes-Mateos et al., 2008). Furthermore, since rabbit pellets importantly affect the levels and distribution of soil nutrients and fertility (Delibes-Mateos et al. 2008), rabbits declines in Doñana are likely to have negative cascading effects in plant community composition and landscape structure.

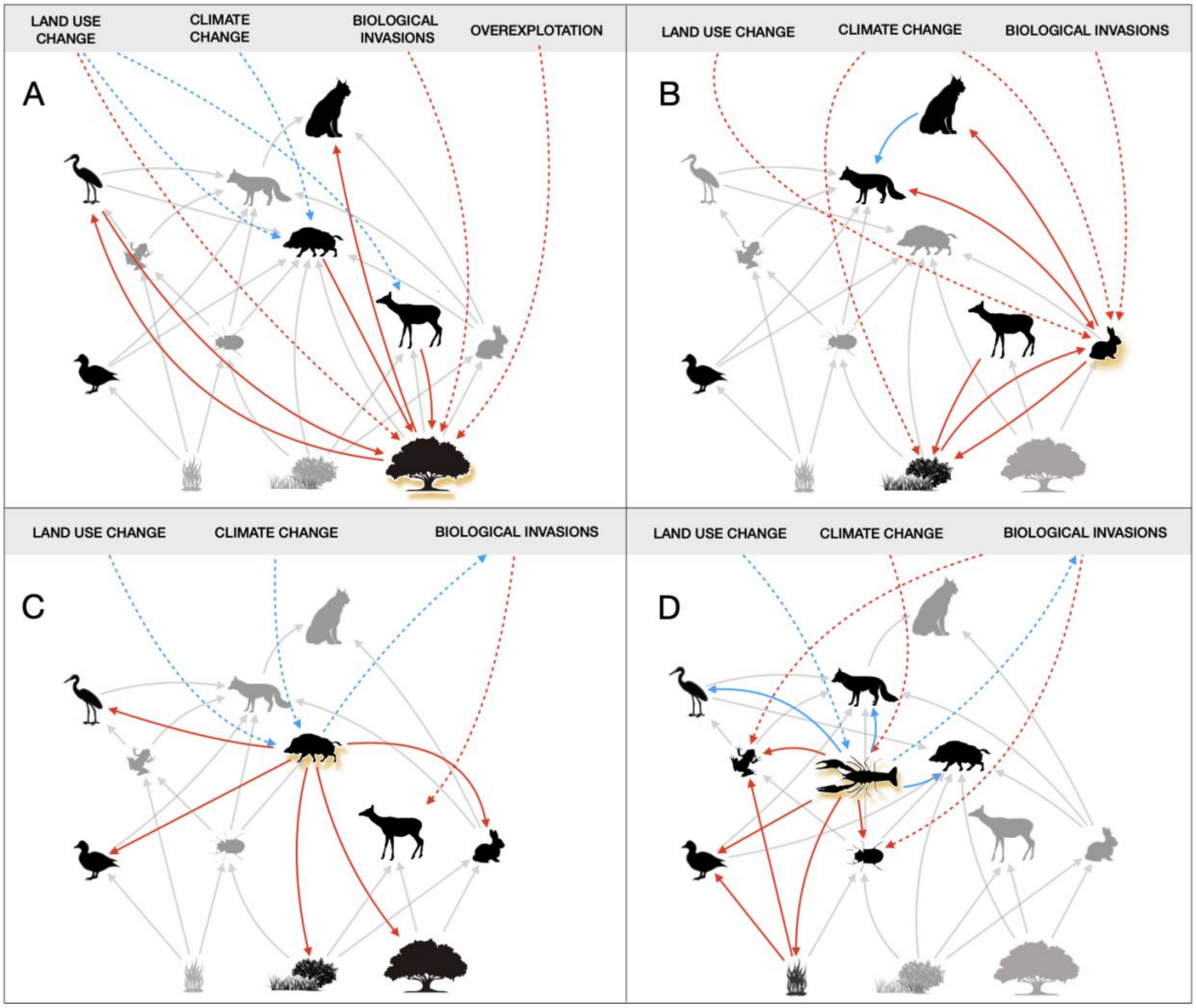

Figure 4: Summary of the impacts of global-change drivers on the four case study species and associated cascading effects. Each panel builds on a simplified trophic web of Doñana that illustrate several hierarchical trophic levels, while additional biotic interactions are also shown, such as nesting or interference interactions. Icons represent different functional groups, including predators, omnivores, herbivores, and primary producers (see Fig. S3.1 for details). Arrows indicate the impacts of global-change drivers (dotted lines) and biotic interactions (solid lines) affecting the case study species (highlighted with an orange border) and cascading effects on species interacting directly with the focal species. Arrow color denotes effect direction: blue for positive and red for negative effects on or from the focal species. The figure highlights the

complexity of how global-change drivers and ecological interactions jointly propagate disturbances throughout the ecosystem, as discussed in detail in the main text. This representation should not be interpreted as a typical trophic web but as a representation of the evidence-based interconnections among global-change drivers and species/functional groups discussed in the text.

3.2 Habitat-structuring species positively affected by global change: the case of wild boars and red swamp crayfish

The wild boar can substantially affect ecosystems both positively and negatively depending on population densities. Wild boar behaviors such as uprooting, digging, and trampling can change soil structure and thus decomposition and nutrient cycling (Macci et al. 2012; Wirthner et al. 2012), as well as facilitation of seed recruitment for some species, which can ultimately affect plant species composition (Lowe et al. 2000; Barrios-Garcia & Ballari 2012). As in other European countries, wild boar populations have been increasing since the 60's in Spain (Sáez-Royuela & Tellería 1986; Valente et al. 2020) due to the interplay between human activities and climate change (Melis et al. 2006; Acevedo et al. 2011). The overabundance of feeding resources derived from anthropogenic activities (Castillo-Contreras et al. 2021; Markov et al. 2022) is often accompanied by rising temperatures and milder winters, favoring a higher reproductive success especially in Central and Northern Europe (Melis et al. 2006; Vetter et al. 2015). The disappearance of its main natural predator, the wolf *Canis lupus*, across many regions (including Doñana; Clavero et al. 2023) since the beginning of the 20th century probably also promoted increased wild boar abundance (Melis et al. 2006; Rodriguez-Recio et al. 2022).

In Doñana, wild boars have always been widely distributed (Valverde 1967; Venero Gonzalez 1984) and actively hunted by landowners and poachers (Acosta Naranjo 2004). The local populations likely increased after the establishment of the protected area and the reduction of both hunting and poaching activities (Mulero Mendigorri 1986; Castroviejo 1993). More recently, since the end of the 20th century, this species has been regularly culled in order to control bovine tuberculosis (Gortázar et al. 2008; Barroso et al. 2020), which caused its local populations to remain stable from 2005 to 2021 (ICTS-RBD, 2022). Climate change will likely increase the risk of transmitting diseases to other wild and domestic ungulates because the number of watering holes is projected to decrease, thus bringing wild boars into contact with other species more frequently

(Barasona et al. 2014; Magallanes et al. 2023). At the same time, the management of wild boar populations in Doñana does not seem suitable to mitigate the negative effects that increasing densities had over the years on several species locally threatened by multiple global-change drivers (Fig. 4C). For instance, high densities of wild boars contributed to severely reducing recruitment of cork oaks due to the consumption of acorns (Herrera 1995). Rooting behavior has also resulted in a reduction of 9% of the total herbaceous production of Doñana (Fernández-Llario, 1996), and now this overgrazing, together with groundwater overexploitation (de Felipe et al. 2023) and climate change (Paniw et al. 2023), are drastically threatening local plant communities and animal populations relying on them (Giralt-Rueda & Santamaria 2021). Additionally, wild boars act as opportunistic predators of ground-nesting birds and their clutches and nestlings in Doñana (Santoro et al. 2010), but also amphibians (Díaz-Paniagua et al. 2007) and young rabbits (Venero Gonzáles 1982). This predation has even been suggested to negatively affect rabbit abundances and recovery (Virgós et al. 2011) (Fig. 4C). Overall, wild boars have a negative effect on individual species, which, together with the local actions of global change drivers, impact the entire ecosystems of Doñana.

The red swamp crayfish *Procambarus clarkii* is one of the most studied and controversial invasive species worldwide (e.g., Souty-Grosset et al. 2016: Guareschi et al. 2024). Native to North America, it currently represents a common species in Doñana since the intended introduction into nearby rice fields in 1974 (Delibes & Adrián 1987; Oficialdegui et al. 2020). This species has spread across various freshwater environments in Doñana (Cruz & Rebelo 2007; Garcia-Murillo et al. 2025), though water shortages and hydroperiod alterations significantly impact its seasonal distribution (Arribas et al. 2014), highlighting the need for further research in the context of climate change. The red swamp crayfish affects native communities through direct consumption of macrophytes and consequent increase in water turbidity (Garcia-Murillo et al. 2025), which cascades to upper trophic levels, for example by decreasing food availability for herbivorous waterbirds (Rodríguez et al. 2005) (Fig. 4D). This omnivore-polytrophic species also consumes microbial and plant detritus, invertebrates (Gherardi 2006; Loureiro et al. 2015), small fish (Gutiérrez-Yurrita et al. 1998; Alcorlo et al. 2004) and amphibians (Cruz et al. 2008; Arribas et al. 2014), which can substantially decrease the local viability of the latter group (e.g., Cruz et al. 2008). Importantly, this species is also a major vector and reservoir of invasive pathogens, such as the fungi *Aphanomyces astaci* and *Batrachochytrium dendrobatidis*, which exacerbate the devastating effects on amphibians (Oficialdegui et al. 2019) (Fig. 4D). On the other hand, positive feedback loops have emerged, as some native species in Doñana have benefited from the introduction of the invasive crayfish (Fig. 4D). For instance, over 60% of native generalist predators, mostly piscivorous waterbirds but also raptors (Tablado et al. 2010) and some mammal species, e.g., European otter *Lutra lutra* and wild boar (Delibes & Adrián 1987), have adapted their diet to prey on this abundant invader, increasing, in some cases, their local abundance (Tablado et al. 2010; but also see Ramo et al. 2013). Therefore, this invasive species has had far-reaching impacts spanning both aquatic and terrestrial ecosystems, with parallel economic consequences, and addressing its multiple implications would benefit from a multidisciplinary approach.

4. A way forward for the conservation of Mediterranean ecosystems

Global change drivers are becoming more severe and interact synergistically (e.g., Northrup et al. 2019; Giejsztowt et al. 2020), and, as illustrated above in the case of the Doñana Protected Area, many species such as the cork oak or the European rabbit are succumbing to the new conditions (section 3.1), while others such as the wild boar or the red swamp crayfish may thrive in these altered environments (section 3.2). At the population level, impacts of global change are manifested primarily by decreasing or increasing individual fitness, leading in turn to population reduction and even local extinction (Paniw et al. 2021a). When scaling up to communities and ecosystems, the direct and indirect interactions between species may be affected by these population changes and result in impacts beyond single species. This is particularly relevant for species that are considered ecosystem engineers, such as our four case studies. Ecosystem engineers may directly affect just a few ecological processes or species. Yet, because of their location within the food web they may have myriads of indirect effects on many other species, and alterations in their abundances can have ecosystem-wide cascading impacts (Loreau & de Mazancourt 2013).

Doñana is a living laboratory and an excellent example for the wider Mediterranean on how the intensity of the multiple interacting human pressures, and their cascading effects on ecosystems, can influence future conservation practices. The conservation of Doñana transcends its regional value due to the role it plays in global conservation (Navedo et al. 2022; de Felipe et al. 2024), holding a great diversity of Mediterranean ecosystems and endemic species and being a key migratory hotspot for birds (Valverde 1967; Camacho et al. 2022). Our case studies, documenting the impacts of global change from single species to the ecosystem level, illustrate the importance of implementing an ecosystem-based conservation approach focused on ecological processes and restoration of habitats and the functionality of interactions. As discussed below, many conservation interventions in Doñana targeting specific species have not been successful, highlighting the need for more ambitious and holistic approaches. Doñana also emphasizes that in the Mediterranean, where humans have dominated landscapes for millennia, such approaches must include the co-design of strategies with multiple stakeholders to increase the chances of success of ecosystem-based conservation approaches (Perino et al. 2022; Fisher et al. 2023). With the following discussion we intend to highlight some critical elements to be considered in future conservation and land management planning that are often overlooked when targeting single species or taxa or omitting the human dimension.

4.1 Conservation challenges and solutions

A simplified, single-species focus in conservation, decoupled from wider ecosystem processes, may decrease the resilience of Mediterranean systems to ongoing global change (Verissimo et al. 2011). In the case of species such as the cork oak, where only small fragments of previous ecosystems remain and many species have adapted to the loss of the once dominant species (Fedriani et al. 2017), an important conservation dilemma is: should we restore what once was the climax (forested) community, or make sure that species that have replaced cork oaks and their habitat remain resilient to climate change? As another example, the conservation of the Iberian lynx and Spanish imperial eagle has relied on reinforcing rabbit populations. Yet, rabbit restockings have had a limited effect on the recovery of their predators (Carro et al. 2019). This is in part due to the ongoing pressures from global-change drivers on rabbit populations, which limit rabbit densities hence jeopardising efforts to increase the population densities of their predators (Ferrer & Negro 2004). A more integrative landscape management approach to conservation may put more emphasis on restoring the habitat suitability for the rabbit populations, for instance through the restoration of the natural hydrology of the area, including the temporary ponds that once provided feeding pastures to rabbits well into the summer and stricter active management of (semi)domestic ungulates and wild boars to prevent overgrazing. Such actions would improve the resilience of multiple species to future pressures (Cabezas & Moreno 2007; D'Amico et al. 2014). In Doñana, like in other Mediterranean ecosystems, the many decades of interactive global-change drivers may be leading natural systems towards ecological thresholds beyond which the resilience of the ecosystem is irreversibly damaged (e.g., Leadley et al. 2014; Rocha et al. 2015). Recently, appeals have been made for more integrated research and conservation strategies, specifically aimed to avoid reaching these thresholds (Green et al. 2017). Such strategies increasingly focus on ecosystem integrity, as well as on the integration of the social and economic dimensions of biodiversity conservation. The preservation and restoration of ecosystem integrity, resilience and connectivity is the first goal of the Kunming-Montreal Global Biodiversity Framework (CBD 2022). Conservation approaches that allow the achievement of this goal, may contemplate the metacommunity framework (Chase et al. 2020; Gawecka & Bascompte 2023) in order to link global change with impacts on ecological processes and biodiversity. The operationalization of those frameworks to manage and restore ecological processes is challenging but could lead to a more complete, integrative and effective conservation strategy (Ladd et al. 2018; Villalva et al. 2025). For example, although the current active management (culling) of ungulates in Doñana is arguably needed to ensure healthy habitats, that might not be a sustainable strategy in the long term. Rather, natural predation may be a more sustainable long-term management strategy (Nores et al. 2008; Tanner et al. 2019). This would require managing ecosystem dynamics, including ambitious connectivity planning, that would allow wolves to recolonize the area from the North. Yet, wolf recolonization would likely also cause social conflicts, which would need to be addressed through environmental education.

Finally, the anthropogenic origin of the multiple pressures affecting the biodiversity of the iconic Doñana Protected Area and, more generally, the entire Mediterranean region, together with the deep traditional human uses of natural land, highlights the importance of considering the human dimension of conservation. Broad stakeholder engagement is essential to limit conflict and maximize both social and ecological outcomes (Fisher et al. 2023). In the case of Doñana, this has already happened successfully in the past. For example, stripping the eucalypt plantations, as well as two restoration actions that recovered 15% of the current Doñana marshland area, involved the active collaboration of political, economic, and conservation parties. Currently, efforts should reconcile mainstreaming biodiversity conservation with the agricultural and tourism sectors by informing and communicating on the services that a healthy ecosystem provides to the region. A striking example is the overexploitation of the Doñana's aquifer, that is leading Doñana to higher levels of aridity (Green et al. 2024). This is not good news for any of the interested parties, but only the convergence of conservation, political, and local stakeholders (in the agricultural and touristic sectors) interests could lead to a long-term sustainable use of the Doñana aquifer. At the same time, preserving the aquifer can only be an effective conservation strategy if pollution and nitrification spillover from agricultural areas surrounding the Protected Area are also heavily restricted – highlighting the need to holistically manage different global-change drivers in Doñana. Such efforts should also be accompanied by higher collaborations of the administrations playing a role in the area, stronger governance and prosecution of illegal activities, as well as more integration of expert technical advice in the management plans (Fernández-Delgado 2017).

4.2 Knowledge gaps and a future research agenda

All of the authors of this work are researchers working on different systems in Doñana. We chose Doñana as a case study for global-change impacts in the Mediterranean due to the rich literature about ecological impacts of various global-change drivers. A detailed quantitative review of how global change drivers have been quantified in Doñana is in process to be published elsewhere. Overall though, an increasing number of papers about direct or indirect human pressures addresses two or more global-change drivers simultaneously (35 papers since 2010, compared with only 13 from 1977-2010); and, in most cases, the impacts of land-use change have been investigated in combination with one or two other drivers, particularly climate change and pollution (e.g., Fernández-Delgado 2017; Ramírez et al. 2018; Paredes et al. 2019; Rodríguez-Rodríguez et al. 2021). However, the remaining literature still focuses on individual drivers, particularly on pollution and invasive species. Similarly, although global-change effects on multiple species (e.g., Fordham et al. 2013; Paniw et al. 2023) and ecosystem processes (e.g. Huertas et al. 2017) are increasingly being studied in this Mediterranean hotspot, we still need to better quantify complex interactions of global-change drivers and complex impacts across species and ecosystems. Doñana is a reference for long-term monitoring of populations and communities across numerous ecosystems. Yet, a stronger integration of the data generated from these long-term monitoring datasets is essential to understand the consequences of interactions between global change drivers and their impacts on populations, communities and ecosystems (Zipkin et al. 2021).

Supporting Material S1 Weather trends and climate change in Doñana

Supporting Material S2 Biological invasions in Doñana

Supporting Material S3 Food web summary of Doñana

Supporting Material S4 Detailed author contributions

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Supplementary Material S1

Long-term trends of climatic change of Doñana National Park

Methodology

Climatic observational data from Doñana Biological Station have been extracted from the manual station placed at the Palace of Doñana National Park (35.988856, -6.443619), which are publicy available at the ICTS-RBD website. Those data appear in the form of individual Excel spreadsheets, separated by variables. Data have been compiled in a unique spreadsheet, including maximum, minimum and mean temperature. Original data cover since 1979 to 2025. However, the series of the first years is not complete, so we have included meteorological information from 1985 to 2024, i.e., belonging to 39 hydrological years. A hydrological year in Doñana, as in the rest of ecosystems of the Mediterranean Basin, is defined from September to August, corresponding to the start of the rainy season. Analyses were done using hydrological (and not natural) years for the precipitation data. Selected variables were accumulated precipitation and maximum temperature, as they showed the highest rate of change over time.

The signficance of the trends was analysed with a Mann-Kendall test.

Precipitation

We analyzed inter-decadal trend of change of precipitation in Doñana, including the accumulated precipitation all over the year as well as the winter precipitation (defined as the rainfall accumulated from October to April.

Total rainfall

Some years were exceptionally dry in Doñana (Table S1.1), whereas others were exceptionally wet for the region (Table S1.2), according to the first and the third quartile.

Table S1.1. Driest years of Doñana (with less than 375 mm of total precipitation, equivalent to the first quartile of the data series

year	prec
1980	316.300
1981	274.300
1983	276.200
1987	351.600

year	prec
1993	373.500
1995	253.400
1999	252.701
2005	173.000
2012	330.400
2014	359.000
2022	282.500
2023	330.400

Table S1.2. Wettest years of Doñana (with more than 700 mm of total precipitation, equivalent to the third quartile of the data series

year	prec
1988	946.30
1990	963.50
1996	1032.30
1997	885.30
1998	721.81
2004	774.90
2007	716.90
2010	784.20
2011	712.51

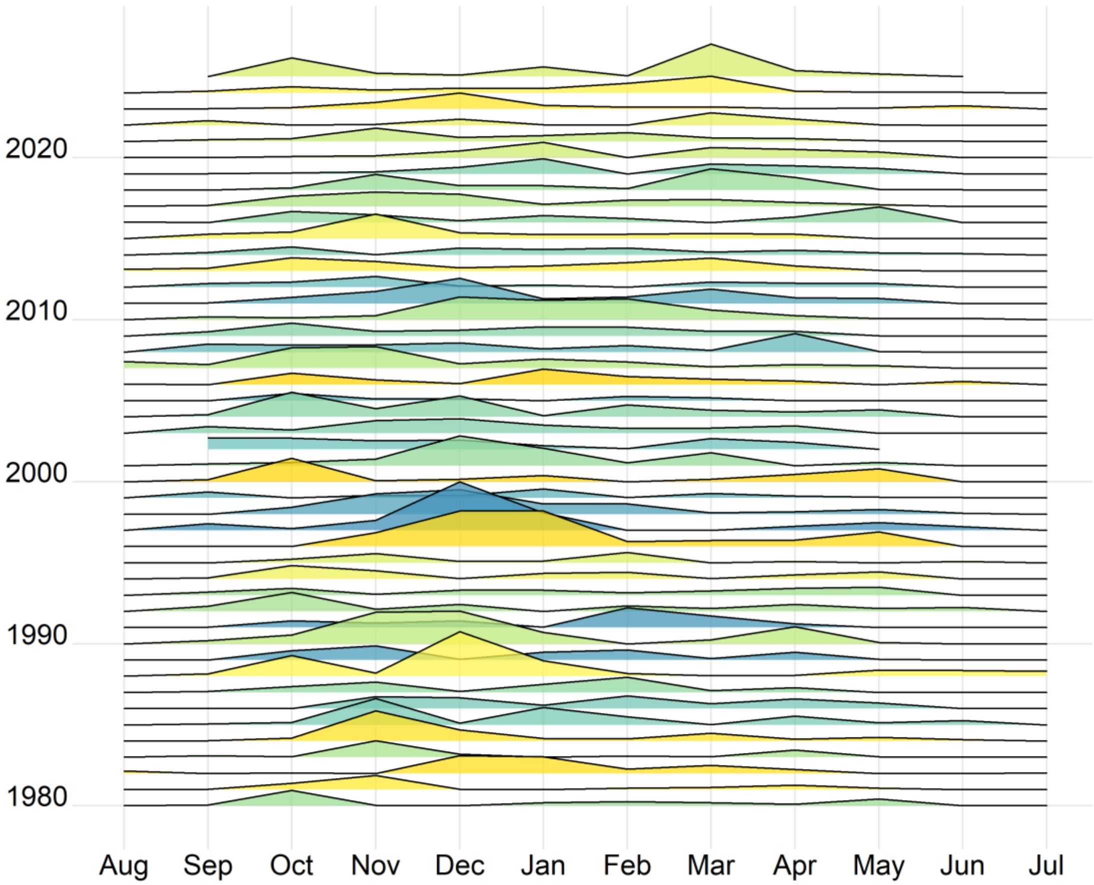

Figure S1.1.*Ridgeline graph for annual precipitation in Doñana National Park*

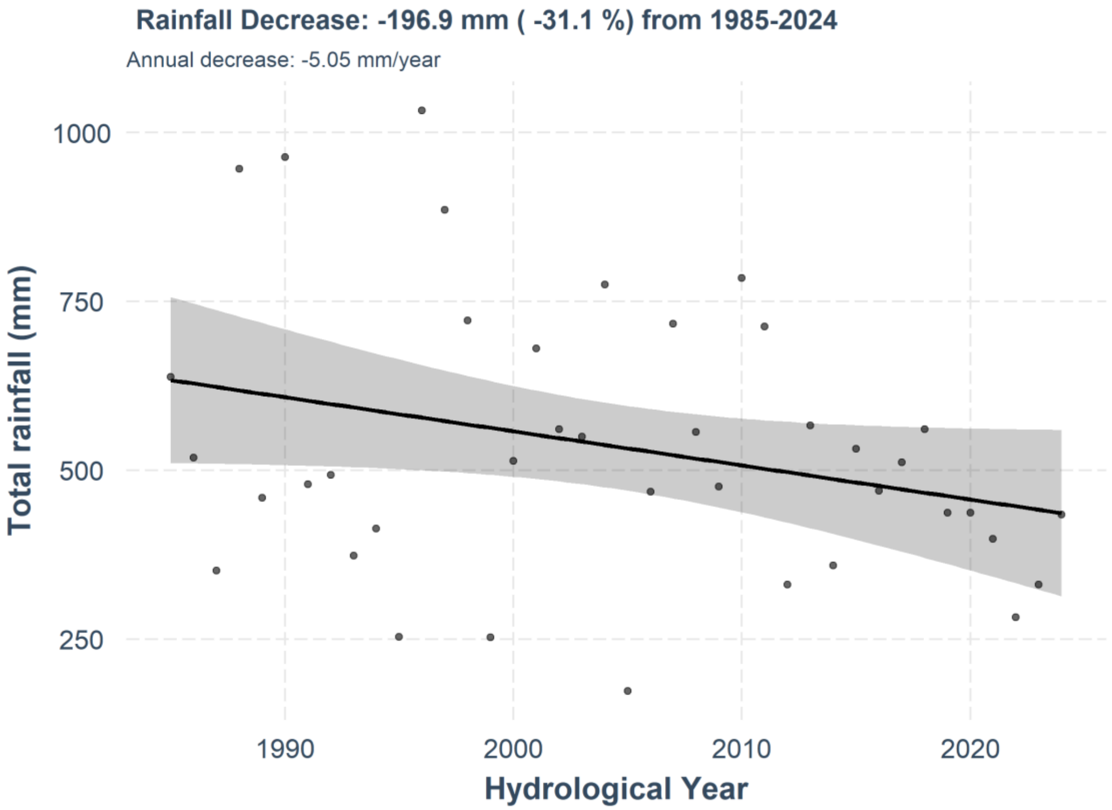

Figure S1.2. *Temporal trend of change in total rainfall in Doñana National Park.*

Total rainfall has a large inter-annual variability in Doñana, as it is the typical case of Mediterranean climates (see Fig. S1.1). However, in the region, the overall trend is showing a decrease in the total precipitation (data from 1985), although the trend is not significant (Mann-Kendall test, *tau* = -0.0708, 2-sided *p-value* = 0.49965). With a simple linear model, we can estimate a decrease in the total precipitation of 168 mm (a 27% less over 40 years, Fig. S1.2).

Winter precipitation (since 1985)

The same patterns than for the total rainfall appear for the winter precipitation (from October to April, Fig. S1.3). The general trend is to decrease over time, although again the relationship is not significant (*tau* = -0.143, 2-sided *p-value* = 0.19258). The estimated winter rainfall decrease from 1985 to 2025 is -137.21 mm (which represents a 25.14 % less).

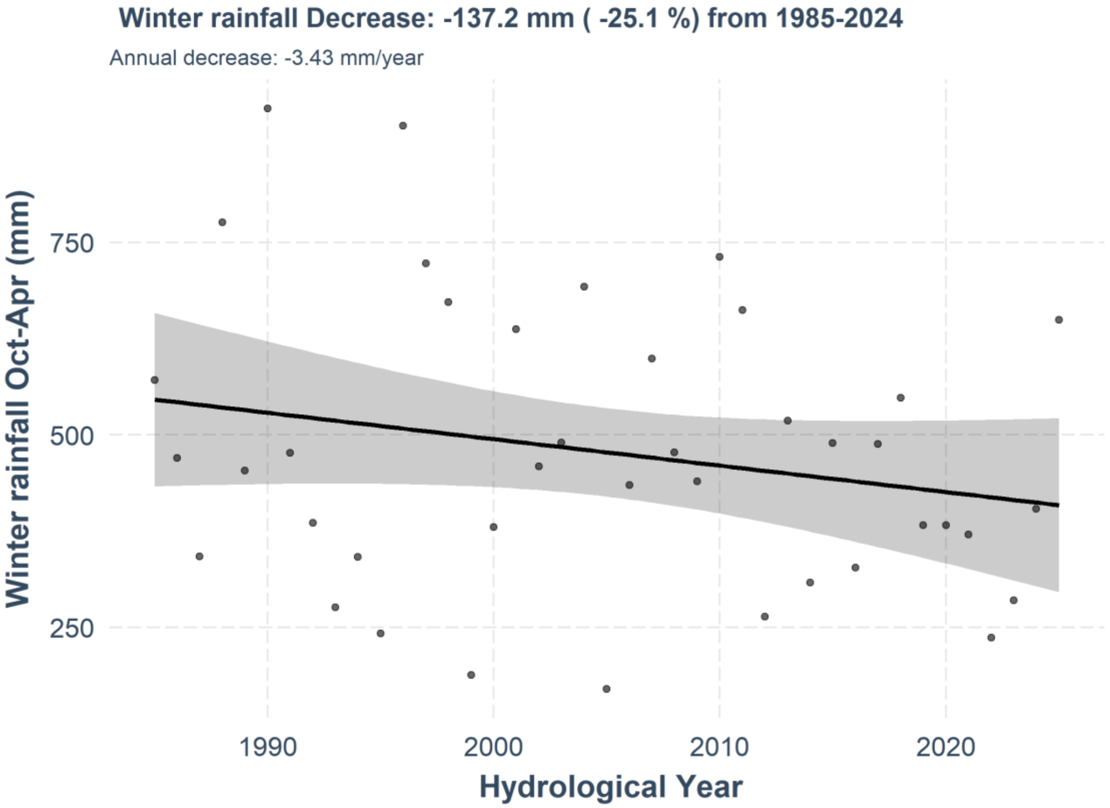

Figure S1.3. *Temporal trend of change in winter rainfall (October-April) in Doñana National Park*

Temperature

Maximum temperature (since 1985)

By contrast, the maximum temperature shows the opposite pattern than rainfall, with an increasing trend over the last 40 years (Fig. S1.4). This time the relationship is highly significant (*tau* = 0.424, 2-sided *p-value* < 0.001). The estimated increase in maximum temperature is 1.96 ºC (which represents a 8.44 % increase). The rate of change is of 0.049 ºC/year (0.009 % ºC/year).

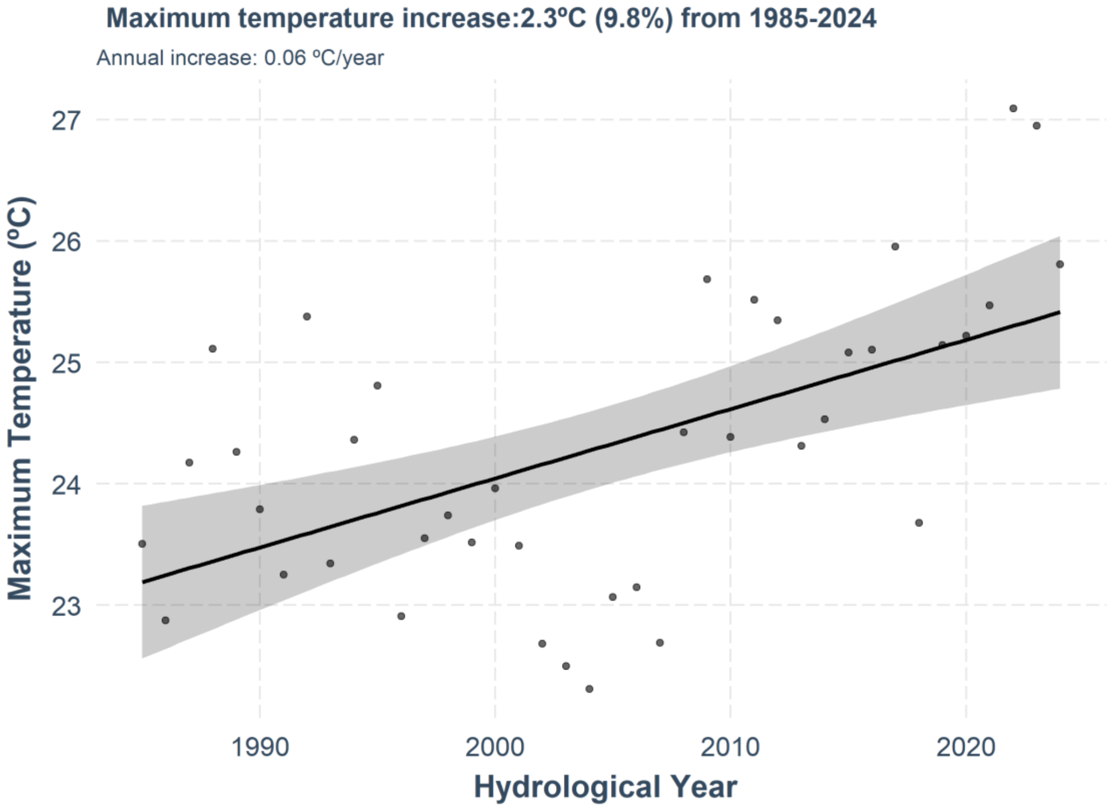

Figure S1.4.*Temporal trend of change maximum temperature in Doñana National Park*

Summer maximum temperature

The same pattern than for the mean maximum temperature repeats for the summer temperature (June-August), with a significant trend of increase over time (*tau* = 0.377, 2-sided *p-value* = 0.0006) although in this case, the values were even more extreme (Fig. S1.5), with an estimated summer maximum temperature increase from 1985 to 2024 of 2.33 ºC (7.6 %). This corresponds to an annual change of 0.06 ºC/year (0.009 %/year).

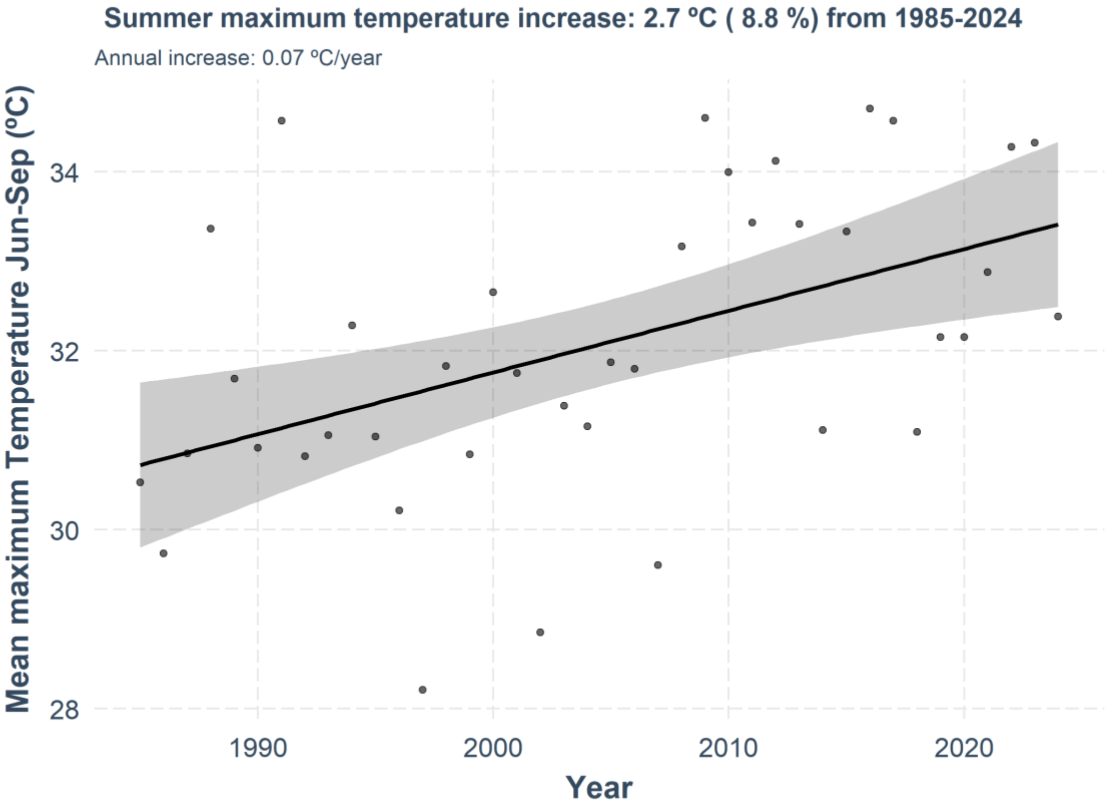

Figure S1.5. *Temporal trend of the change in summer maximum temperature in Doñana NP*

Projections of temperature increase over time

We have used the prediction models of climate change from the website AdapteCCa, a Spanish Portal of Climate Change developed by the Spanish Ministry of Science and the Spanish Meteorological Agency (AEMET). In particular, we have downloaded the data from the municipality of Almonte (date of download: 14/06/2025), to which it belongs Doñana, and selected the projections of two scenarios of climate change: middle emissions ((SSP2-4.5) and high emissions (SSP5-8.5). This models are specially suitable for temperatures, and they present a range of variables. In particular, we have selected the increase of the maximum temperature estimated for the whole year and the summer period (June-July-August).

Projections of change of the maximum temperature (all over the year)

The two projected scenarios of emissions (4.5 and 8.5) predict an overall increase of maximum temperature in Doñana.

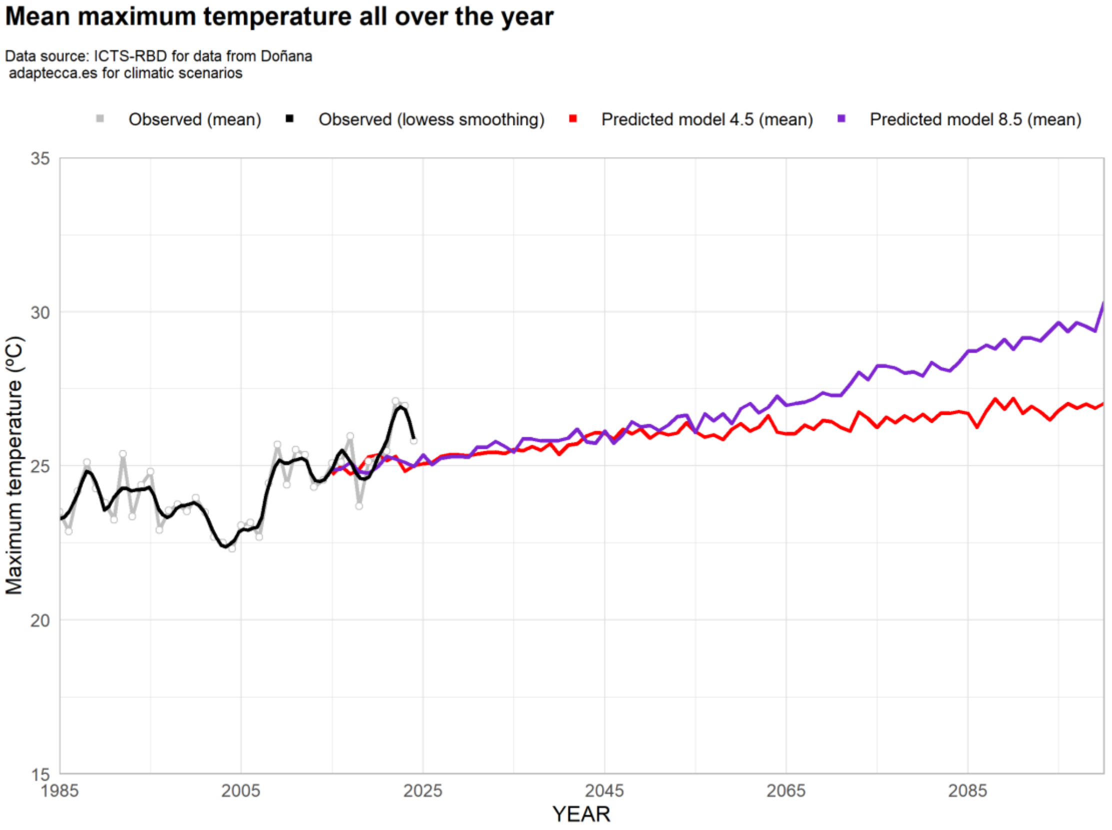

Figure S1.6. *Predicted change in maximum temperature according to two scenarios of emissions*

Maximum temperature in summer

Summer temperature is expected to increase over time for both emissions scenarios. However, the predicted values for the common period (2015-2025) are lower for Doñana than the observed ones, so it is likely that the models are undestimating summer variation.

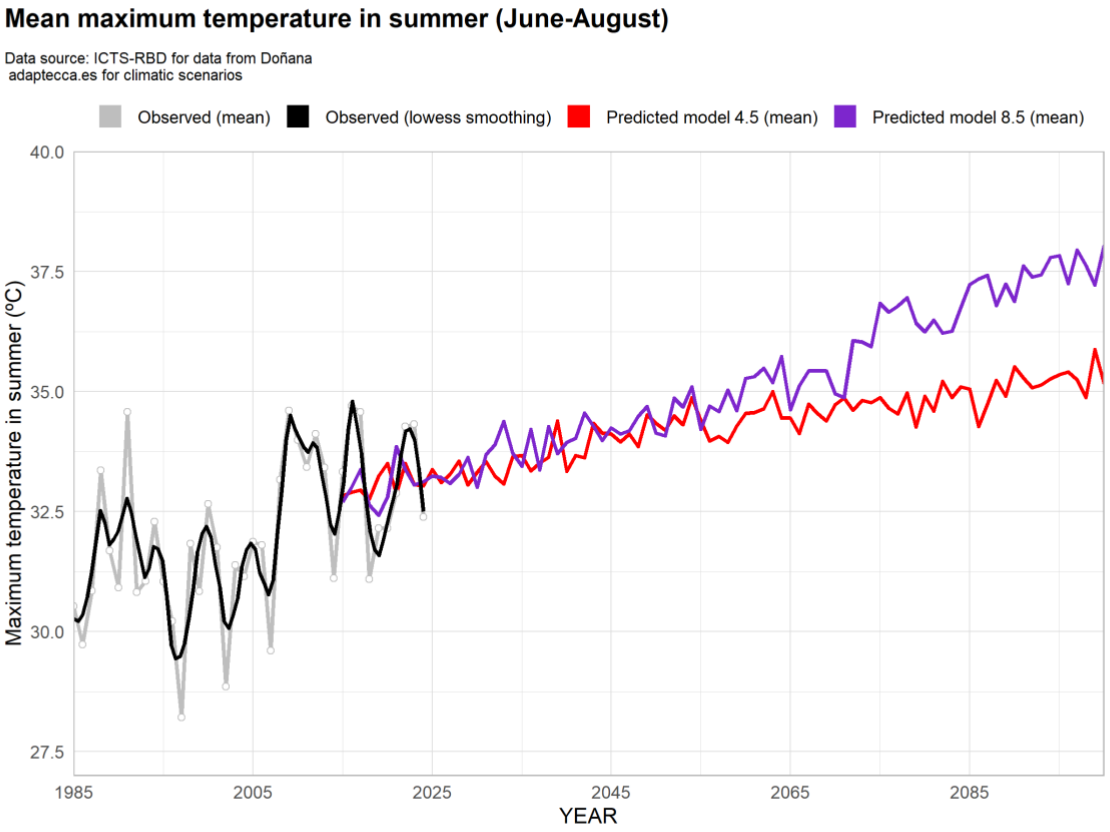

Figure S1.7. *Predicted change in summer maximum temperature according to two scenarios of emissions*

Supporting Material S2

Table S2.1. Representative examples of prominent non-native taxa recorded in the Doñana Natural Area and Guadalquivir Estuary. Information about taxonomic order, native range and specific references are also provided.

Taxa	Order	Native range	Reference
Pathogens			
Phytophthora cinnamomic	Pythiales	Asia	Burgess et al., 2017
Pythium speculum[a]	Pythiales	unknown (located in Spain, France and Portugal)	Paul et al., 2006
Myxoma virus	Chitovirales	America	Villafuerte et al., 1997
Rabbit hemorrhagic disease virus	Calicivirus	China	Moreno et al., 2007
Sindbis Virus Genotype I	Alphavirus	Africa and Northern Europe	Gutiérrez-López et al., 2025
Invertebrates			
Procambarus clarkii	Decapoda	North America	Oficialdegui et al., 2019
Callinectes sapidus	Decapoda	North America	Izquierdo-Gómez, 2022
Palaemon macrodactylus	Decapoda	China, Japan, Korea	Lejeusne et al., 2014
Rhithropanopeus harrisii	Decapoda	North America	Walton et al., 2015
Synidotea laticauda	Isopoda	East Asia	Ruiz-Delgado et al., 2019
Pseudodiaptomus marinus	Calanoida	NW Pacific region	Reyes-Martínez et al., 2019
Potamopyrgus antipodarum	Littorinimorpha	New-Zealand	Rodríguez-Pérez & Green, 2012
Stenopelmus rufinasus	Coleoptera	North-America	Florencio et al., 2015
Trichocorixa verticalis	Hemiptera	North America	Rodríguez-Pérez et al., 2009
Linepithema humile	Hymenoptera	South-America	Castro-Cobo et al., 2019
Aedes albopictus	Diptera	Asia	Martínez-de la Puente et al., 2024
Vertebrates			
Fish			
Fundulus heteroclitus	Cyprinodontiformes	North-America	Fernández-Delgado, 1989
Gambusia holbrooki	Cyprinodontiformes	North-America	Moreno-Valcárcel et al., 2013
Cyprinus carpio	Cyprinodontiformes	Eastern Europe/ Central Asia	Moreno-Valcárcel et al., 2013
Carassius spp	Cyprinodontiformes	Eastern Europe and Asia	Moreno-Valcárcel et al., 2013
Micropterus salmoides	Perciformes	Eastern North America	Moreno-Valcárcel et al., 2013
Lepomis gibbosus	Perciformes	Eastern North America	Moreno-Valcárcel et al., 2013
Ameiurus melas	Siluriformes	North-America	Sáez-Gómez & Prenda, 2019
Reptiles			
Trachemys scripta elegans	Testudines	North-America	Hidalgo-Vila et al., 2020
Mammals			
Dama dama[c]	Artiodactyla	East Europe-Asia	Ascensão et al., 2021
Genetta genetta[c]	Carnivora	Africa	Ascensão et al., 2021

Procyon lotor[b]	Carnivora	North and Central America	Fernández-Aguilar et al., 2012
Birds			
Ploceus melanocephalus	Passeriformes	Sub-Saharan Africa	Royal Decree 630/2013
Euplectes afer	Passeriformes	Sub-Saharan Africa	Royal Decree 630/2013
Estrilda astrild	Passeriformes	Sub-Saharan Africa	Ascensão et al., 2021
Anser indicus	Anseriformes	Asia	Ascensão et al., 2021
Vegetation			
Carpobrotus edulis	Caryophyllales	South Africa	Valdes, 2015[c]
Spartina densiflora	Cyperales	South America	Walton et al., 2015
Azolla filliculoides	Salviniales	South America	Espinar et al., 2015
Acacia spp. (A. saligna, A. dealbata)	Fabales	Australia	Royal Decree 630/2013
Nicotiana glauca	Solanales	South America	Valdes et al., 2011
Eucalyptus spp. (E. globulus)	Solanales	Australia	Trick & Custodio, 2000
Arundo donax	Poales	Asia	Gutiérrez-Cánovas et al. 2020

Notes. [a] unclear origin; [b] not-confirmed established population (single individual); [c]historical introduction in Iberian Peninsula; [d] complete review for the introduced vegetation of the area;

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Supporting Materials S3. Biotic Interaction Complexity in Doñana

The environmental heterogeneity of Doñana supports a rich diversity of species and a complex network of biotic interactions, making it an ideal case for exploring the effects of global-change drivers. **Figure 4** in the main text is a conceptual synthesis that aims to distill this complexity into a simplified trophic web, while simultaneously encompassing other biotic interactions such as nesting interactions or interferences via habitat alteration. Rather than attempting to capture the full spectrum of biotic interactions in Doñana, **Figure 4 presents a heuristic model centered on four focal species to showcase the impact of global-change drivers on these species and the propagation of ecological effects through immediate biotic interactions.** This schematic is not intended as a quantitative path analysis but rather as a qualitative visualization to contextualize the focal species and illustrate how ecosystem-level impacts may arise through interconnected interactions.

The foundation for Figure 4 is a schematic trophic structure derived from the Eltonian pyramid of the Doñana ecosystem (Fig. S3.1). This structure integrates ecological data from the literature, supported by expert knowledge on trophic interactions. We organized the system into broadly defined trophic levels, each comprising functional groups selected for their relevance to the four focal species. Figure 4 is structured according to these hierarchical levels:

1. **Primary Producers:** Include aquatic macrophytes (e.g., algae and submerged aquatic plants), terrestrial herbs and shrubs, and tree strata, represented by the focal species cork oak (*Quercus suber*)
2. **Herbivores:** Comprise aquatic herbivorous birds (e.g., *Mareca penelope*), herbivorous invertebrates (e.g., *Scarabeus spp*), large terrestrial herbivores such as ungulates (represented by *Cervus elaphus)*, and small terrestrial herbivores—represented by the focal species European rabbit (*Oryctolagus cuniculus*).
3. **Omnivores:** Include amphibians (e.g., *Rana sp*.), omnivore ungulates —represented by the focal species *Sus scrofa*, and mesopredators (e.g., *Vulpes vulpes*).
4. **Carnivores:** Include aquatic carnivorous birds (represented by *Ardea sp.*) and the apex predator (represented by *Lynx pardinus*).

Note that the focal species *red swamp crayfish* that is shown in Figure 4 is not included in the diagram. This species is not part of the natural trophic web in Doñana, but included in Figure 4 as an example of a biological invasion into the system.

This conceptual framework underscores the importance of considering ecological complexity when assessing the vulnerability of species and ecosystems to global change.

Interpretation of the interactions illustrated for the four focal species in Figure 4.

(A) **Cork oak (Quercus suber).** Cork oak populations are negatively impacted by overexploitation (e.g., historical logging), biological invasions (notably *Phytophthora cinnamomi*), and land-use change (e.g., conversion to agriculture). Climate change and land-use change both positively influence wild boar while large herbivore populations (e.g. domestic herbivores) are affected by land use change, which in turn suppress oak recruitment through grazing and disturbance. Aquatic birds also exert negative effects on oaks by nesting in them and altering soil biochemistry. Conversely, the decline of oak populations reduces suitable nesting habitat for these bird species.

(B) **European rabbit (*Oryctolagus cuniculus*).** Rabbit populations are negatively affected by biological invasions (e.g., RHDV, RHDV2), climate change, and habitat loss through land-use change. Climate change influences vegetation, which constitutes the primary food source for rabbits. High grazing pressure from large herbivores further depletes vegetation. Rabbit decline, in turn, impacts mesocarnivores and especially top predators (especially the specialist *Lynx pardinus*), which leads to a mesocarnivore release and a subsequent increase in mesocarnivore populations (note the double pointed arrow in mesocarnivores coming). Rabbits also play a role in plant community dynamics by grazing and dispersing seeds of different plant species, suggesting cascading effects on plant composition and structure.

(C) **Wild boar (*Sus scrofa*).** Wild boar benefit from both climate and land-use change thriving in human modified landscapes, which promote their expansion. They are disease vectors (e.g. *Mycobacterium bovis* or *Brucella suis*), contributing to biological invasions that negatively affect other large herbivores (e.g. ungulates). Wild boars also act as active predators, preying on ground-nesting birds and rabbits. Their foraging behavior (e.g. digging, trampling, rooting) modifies herbaceous plant communities and the species negatively affects oaks by impeding recruitment through acorn consumption.

(D) **Red swamp crayfish (*Procambarus clarkii*).** This invasive species is favored by land-use change, particularly those altering water regimes for agriculture (e.g., rice cultivation). They degrade macrophyte communities and increase water turbidity. This, in turn, affects upper trophic levels such as herbivorous waterbirds (dependent on macrophytes) and diving carnivorous waterfowl (dependent on aquatic invertebrates). Besides being considered an invasive species itself, it acts as a reservoir for multiple pathogens, contributing to biological invasions that indirectly affect amphibians. They also serve as a prey item for various predator species, including carnivorous birds, wild boar, and mesocarnivores, thus promoting population increases in these groups.

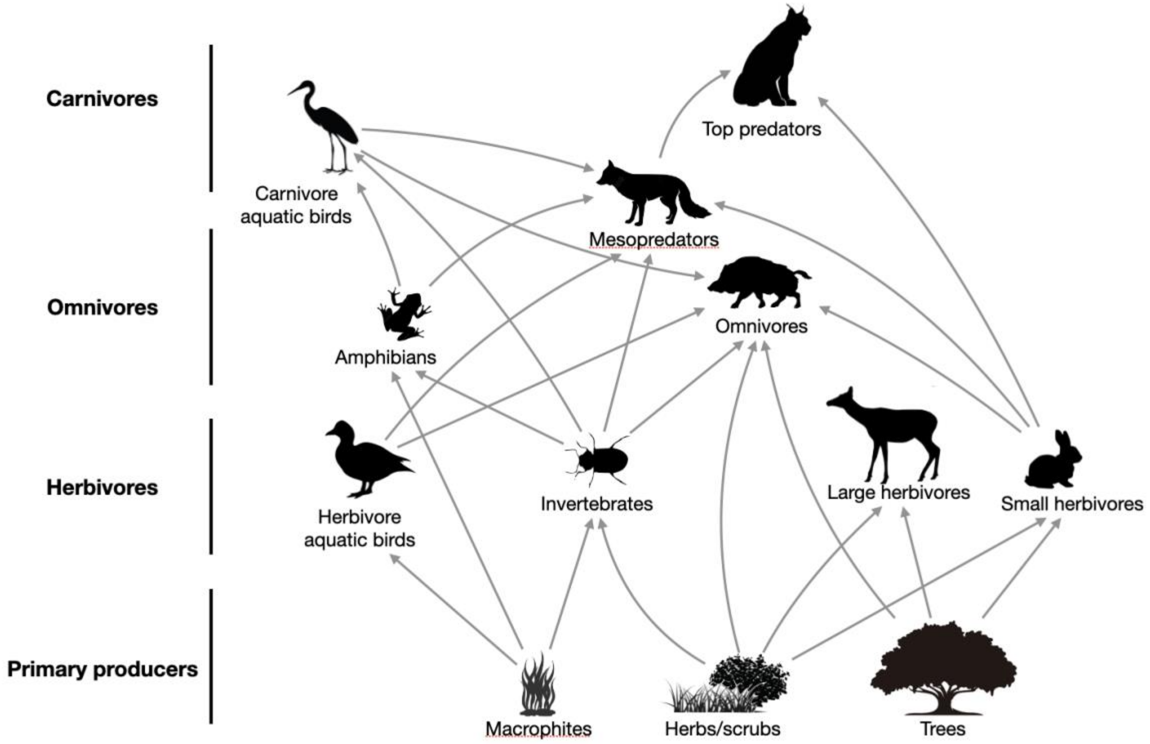

Figure S3.1. Conceptual synthesis of a trophic web in Doñana. This figure illustrates key trophic interactions among species and functional groups highlighted in the literature review, offering a simplified representation of Doñana's food web. It serves as a foundation for visualizing the four focal case studies and their interconnections. The relative position of different species corresponds to their average trophic level (i.e The trophic level of a species is the average level of their prey plus one, Levine 1980). Arrows represent energy transfers; upward direction reflects an increase in the trophic level. Note that Figure 4 in the main text (unlike Fig S4.1 above) also includes non-trophic interactions, such as anthropogenic drivers and abiotic effects mediated by species.

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Supporting Material S4 – Extended Contributions

Table S4.1 Extended task contribution by each author in this manuscript

Author	Conceptualize ms	Main text lead writing	Part 1	Part 2	Part 3	Part 4	Figures	revisions	SI 1	SI 2	SI 3
MP	x	x	C	C	R	CC		x			
DSV	x	x		x	CO	x	x	x			
SdF				x		KG					
CLC	x		P	P	CF		x	x			
IM	x		C	C		KG	x	x	x		
LMN	x		L			CC, KG	x	x			
SG	x		I	I	CF			x		x	
MJRL	x				R, W		x	x			
JP	x		C	C	CO			x	x		
VD-G	x					KG	x	x			
EV-A	x		L	L		KG		x			
EM	x				CO	CC	4	x			x

CC	x		I,P	I,P				x			
AGR	x		I,O	I,O	R			x			
ETe	x		O	O	CO	KG		x			
PH	x			I	CO	KG		x			
JMR-G	x		L	L	CF, W			x			
ZT	x			C	R, CF	CC		x	x		
NV	x				W	KG, R, WB, CC		x			
PV	x				W	CC	4	x			x
MD	x		L	L	x	CC	1	x			
ETo	x		L		CO			x			
JBL	x				CO			x			
IDA			I,P,L	I,P,L							

L - land-use change; C - climate change; I - invasion; P - pollution; O - overexploitation; CO - cork oak; R - rabbits; W - wild boars; CF - crayfish; CC - conservation challenges; KG - knowledge gaps; SI - Supporting Material.