



From stationary to directional transition: a case study in Doñana

José Carlos Muñoz-Reinoso 

Received: 29 January 2023 / Accepted: 16 September 2023 / Published online: 24 October 2023
© The Author(s) 2023

Abstract

Context Doñana’s landscape is a mosaic of different types of transitions at different spatial and temporal scales. Among them, stationary transitions are relatively stable over time, while directional transitions involve the unidirectional movement of boundaries. The fiftieth anniversary of the Doñana National Park (SW Spain) provided a framework to test the transformation of a biotic transition from stationary to directional.

Objectives This study aimed to examine landscape changes along a stationary groundwater-dependent transition, the processes responsible for them, and the consequences for the biotic transition.

Methods Through detailed photointerpretation, nine land use/land cover categories were mapped at four dates (1971, 1984, 2002, 2019) on a ca. 2 square km plot, and then changes analysed at three levels (interval, category, and transition) using Intensity Analysis. Potential causes including precipitation, groundwater levels, local management and changes in the surroundings were examined to understand the changes.

Results Juniper woodland, spontaneous pines and mixed shrub categories showed the greatest gains and were most active. In the third interval (2002–19) largest transitions from pond-grassland to several

terrestrial categories and the dead of heathlands indicate the encroachment of xeric communities into hygrophytic ones. Observed changes seem to be due to succession, forestry management and extrinsic drivers such groundwater overexploitation in the surroundings of the protected area.

Conclusions The long-term study of this stationary transition shows the weakening of the factors that controlled its establishment, the loss of its constituent habitats due to groundwater withdrawal, and its conversion into a directional transition.

Keywords Directional transition · Groundwater withdrawal · Analysis · Landscape dynamics · Long-term study · Stationary transition

Introduction

Landscape ecology studies the structure (spatial relationships among the landscape elements), function (flows of energy, materials, and species among landscape elements), and dynamics (temporal change in structure and function) of landscapes (Forman and Godron 1986) of different kinds, including natural, seminatural, agricultural, and urban landscapes (Wu 2013). Change is an inherent characteristic of landscapes (Bürgi et al. 2004), and landscape dynamics involve the study of temporal changes in the structure

J. C. Muñoz-Reinoso (✉)
Departamento de Biología Vegetal y Ecología,
Universidad de Sevilla, Seville, Spain
e-mail: reinoso@us.es

and function of a landscape, and their ecological causes and consequences (Wiens 1999).

The spatial configuration of landscapes is a result of natural and socioeconomic processes (Naveh and Lieberman 1984; Forman and Godron 1986; Turner 1987, 1990). The interaction between natural and modified elements creates complex landscape patterns because driving forces operate at different spatial and temporal scales (Dunn et al. 1990). According to Peters et al. (2006), landscape dynamics depend on the mosaic of types of transitions contained within the landscape. Thus, determining the type of transition for each boundary within a landscape is a critical step in predicting the response of the landscape to environmental drivers.

In 2006, Peters et al., using the theory of patch dynamics, proposed a conceptual framework to describe and understand the structural properties of biotic transitions, and to predict changes in boundaries through time and across space. Biotic transitions are understood as consisting of a hierarchy of dynamic patches with different properties, spatial arrangements, and connectivity with other patches that determine the response of the transition zone to a range of environmental conditions (Peters et al. 2006). Those biotic transitions are understood as including the boundary and the neighbouring areas (the end states, the two states on either side of the boundary). Finally, three types of transitions were proposed (directional, stationary, and shifting) differentiated by their patch and boundary characteristics and dynamics as well as the key drivers and constraints influencing their dynamics.

Directional transitions involve the movement or invasion by patches from one end state into another end state. Thus, the location of the boundary between the two states moves unidirectionally through time, although the rate may be variable. Directional transitions are strongly influenced by abiotic drivers and biotic and abiotic feedback mechanisms, and initially, a strong abiotic constraint that weakens with time. Landscapes consisting primarily of directional transitions will respond to favourable land use or climatic conditions, and this expansion will be maintained through time even if the environmental conditions become unfavourable (Peters et al. 2006). However, stationary transitions are relatively stable over scales of decades with little movement by patches from one end state into

another end state. These environmental boundaries are controlled by inherent abiotic constraints that are reinforced through time by strong biotic feedbacks. Stationary transitions are most common along abrupt elevational or geomorphic gradients. Landscape consisting primarily of stationary transitions will be relatively stable through time regardless of changes in environmental drivers. The third type of transitions, shifting transitions, involve no net change in the location of a boundary over relatively long periods of time (Peters et al. 2006). Temporary changes in abiotic drivers mean that end states can move forward or backward along the boundary.

The stabilized sand dunes of Doñana Biological Reserve (DBR) constitute a wide transition between the recharge and discharge areas of the Almonte-Marismas aquifer (Fig. 1; Muñoz-Reinoso and García Novo 2005), where environmental or natural boundaries are produced by differences in groundwater availability, which is related to topographic gradients. Those gradients are determined by the West–East slope of the territory, the superimposition of several dune generations, and the rolling topography of the stabilized sand dunes constituting the Doñana landscape. The analysis of the spatial patterns of vegetation along those topographic gradients showed the existence of boundaries at several spatial scales (Muñoz-Reinoso and García Novo 2005). Those boundaries were discussed in the framework of boundaries and ecotones (van Leeuwen 1966; van der Maarel 1976, 1990; Margalef 1982, 1997) and characterized according to Peters et al. (2006) by Muñoz-Reinoso (2009). Therefore, landscapes at the Doñana's stabilized sands consist of a mosaic of different types of transitions at different spatial scales where geomorphology, through groundwater availability and dynamics, exerts a multiscale control on plant communities' composition and boundaries (Muñoz-Reinoso 2009).

Small scale boundaries, occurring along dune slopes, are established on transitory gradients linked to local exchanges (Margalef 1997), constituting a shifting transition with strong abiotic drivers. Temporal variation in small scale boundaries happens as a response to groundwater fluctuation (Zunzunegui et al. 1998) due to variation in annual and interannual precipitation (Muñoz-Reinoso and de Castro 2005).

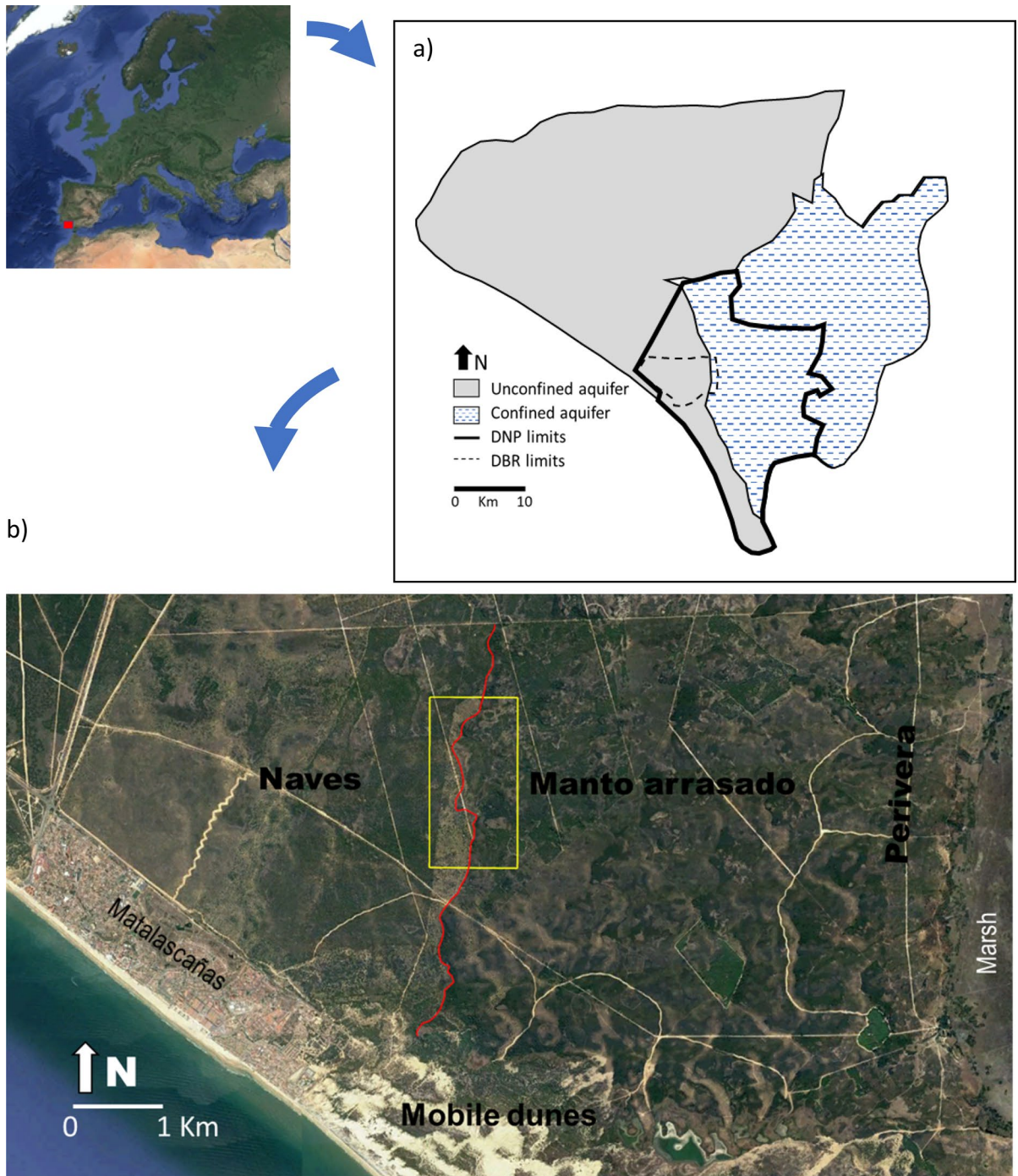


Fig. 1 Location map **a** Almonte-Marismas aquifer showing the limits of Doñana National Park (DNP), Doñana Biological Reserve (DBR), and the confined and unconfined aquifer;

b DBR showing the transition Naves-Manto Arrasado and the location of the studied plot Images from GoogleEarth

Intermediate scale boundaries take place between the dune generations distinguished in the Doñana stabilized sands. Within the DBR, three different old dune-building events have been recognized and traditionally called Naves, Manto Arrasado, and Perivera (Muñoz-Reinoso 2009), aeolian dune systems III, II and I by Rodríguez-Ramírez et al. (1996), and Dry High, Humid High, and Lower aeolian sand sheets by Borja and Díaz del Olmo (1996). The transitions between different dune generations show steep topographic slopes where groundwater discharges take place creating small ponds and dense heathlands. Mature serial stage of those dune generations was Phoenician juniper, cork-oak, and ash woodlands respectively, where structure and function are similar in the ecosystems on both sides of the boundaries (Muñoz-Reinoso 2009). The abrupt boundaries which separate plant communities in the same serial stage without clear trophic relationships between them are symmetric interfaces (Margalef 1982) and show the characteristics of the stationary transitions (Peters et al. 2006), being very stable over time.

Large scale boundary occurs nearby the discontinuity between sands (dunes) and silt and clays (marshes). Although this transition internally is very dynamic, is also very stable in a long term, working as a stationary transition (Peters et al. 2006), with strong inherent abiotic constraints (regional groundwater discharges) reinforced by strong biotic feedbacks (intense herbivory).

Here, I focus on intermediate boundaries, specifically in the boundary between the Naves and the Manto Arrasado (Fig. 1b). This intermediate boundary is particularly relevant because it is formed by three priority habitats of European interest (Habitats Directive 92/43/EEC) such as 2150 “Atlantic decalcified dunes”, 3170 “Mediterranean temporary ponds”, and 4020 “Temperate Atlantic wet heaths with *Erica ciliaris*”, two of them (3170, 4020) seriously threatened in the Mediterranean context due to anthropogenic activities and climate change (Ruíz 2008; Sousa et al. 2013). These habitats are highly groundwater-dependent, and it was hypothesized that due to groundwater decline, that intermediate scale boundary may be becoming a directional transition (Muñoz-Reinoso 2009) because some evidence such as ponds desiccation and effects on hygrophytic

species were reported (Serrano and Serrano 1996; Muñoz-Reinoso 2001).

Lindenmayer et al. (2022) have pointed out that large-scale, long-term monitoring is essential for documenting the response of biodiversity and key ecological processes to environmental change. Long-term studies are also needed to document boundaries dynamics and changes in boundary location and composition over time (Peters et al. 2006; Álvarez-Martínez et al. 2014). The fiftieth anniversary of the creation of the National Park (1969–2019) provided a framework to test the hypothesis of the transformation of that biotic transition from stationary to directional. Thus, this study aimed to (1) analyse the spatio-temporal changes of land use/land cover units in the transition Naves-Manto Arrasado from 1969 to 2019, so the analysis of boundary dynamics will be carried out by studying changes in its constituent habitats, (2) ascertain the drivers of the processes that take place in the transition, and (3) understand the consequences for the biotic transition.

Methods

Study area

The Doñana Biological Reserve (DBR) is the core area of the Doñana National Park (SW Spain; Fig. 1) and has the highest level of protection in the park. Within the DBR limits there is a representation of the characteristic ecosystems of the protected area such as stabilized sands, mobile dunes, temporary and permanent ponds, and inland saltmarshes (Fig. 1). Present vegetation is dominated by Mediterranean type shrublands, with remnants of Phoenician juniper and cork oak woodlands, stone pine afforestations, and grasslands. Groundwater is a key component for the functioning of these ecosystems.

Doñana National Park (DNP) lies on the SE of the Almonte-Marismas aquifer system (3400 km², Fig. 1a). That aquifer is considered as a multilayer alluvial aquifer constituted of silts, sands, and gravels of fluvial-deltaic and marine origin (Salvany and Custodio 1995). Seventy-five percent of the aquifer surface corresponds to an unconfined aquifer (sands) and the rest is confined below the clayey sediments of the marshlands. Groundwater recharge is produced by rainfall infiltration in the unconfined aquifer;

then groundwater flows mainly eastwards, toward the marshes (ITGE 1992), with several flow systems crossing the DBR stabilized sands (Muñoz-Reinoso and García Novo 2005). Since the 1980s, several studies have warned about the effects of groundwater withdrawal on the groundwater-dependent wetlands and terrestrial vegetation of Doñana (Rodríguez Arévalo and Llamas 1986; Llamas 1987; Suso and Llamas 1993). Since then, the peridune string of temporary and permanent ponds has attracted a considerable amount of research (Serrano and Zunzunegui 2008; Díaz-Paniagua and Aragonés 2015; Dimitriou et al. 2017; Fernández-Ayuso et al. 2018) due to its proximity to the pumping area of the neighbouring Matalascañas tourist resort and its effects on the conservation of these unique habitats.

Doñana has a Mediterranean climate with Atlantic influences. The annual rainfall is about 560 mm, with large annual and interannual variations that condition groundwater recharge. Eighty percent of precipitation falls between October and March, with scarce or no rainfall in summer. The mean annual temperature is 17° C, with the highest mean temperatures in July and August, and the coldest in December and January.

Doñana stabilized sands are composed of several Holocene dune generations originated by west winds. The younger and higher dune generation (locally called the *Naves*) partially extend over an older and lower system (the *Manto arrasado*), producing a marked unevenness (ca. 10 m). To the East, bordering the saltmarshes, is the oldest and lowest dune system, the Perivera (Muñoz-Reinoso 2009). Within the DBR, the transition between the Naves (NN) and the Manto Arrasado (MA) is ca. 6 km long, from the Charco del Toro pond in the south, to the limits with the Mogeia property, in the north. The transition is formed by a string of small ponds (Charco del Toro, Brezo, El Pino, Acebuche de Matalascañas, Ojillo, Navazo del Toro, Acebuche de las Palomas, El Moral and some smaller unnamed ones) and a wide, dense band of heathland, with stands of *Erica ciliaris* heaths, associated to peat bogs, all showing the importance of groundwater discharges in the transition.

With the aim of studying the changes that took place in this boundary a plot, 1 km wide and 1.95 km long, was laid out along the NN-MA transition, avoiding the southern area because of its proximity to the mobile dunes transition and the effects of the Matalascañas tourist resort pumping area (Dimitriou

et al. 2017) (Fig. 1b). The northern area was also avoided because it is entirely covered by a pine plantation (that is, the end states on both sides of the transition are the same and a result of human activity). The plot includes, from south to north, ponds such as Ojillo, Navazo del Toro, Acebuche de las Palomas and El Moral.

Landuse/landcover types

Nine land use/land cover (LULC) types have been chosen in accordance with previous work (Allier et al. 1974; Díaz Barradas et al. 1999; Muñoz-Reinoso 2001, 2009), which represent the most widespread vegetation types in the study area, reduce the error in photointerpretation, and due to their composition and previous knowledge allow the hypothesis to be tested. Although the chosen LULC types reduce the error in the detailed photointerpretation performed, a conservative approach has been chosen in determining the LULC type. For example, the early stages of succession in the juniper or pine forest have been classified as the corresponding shrubland type on which juniper or pine was establishing. In the 2016 images, areas of dead heathland were observed, but during fieldwork it was observed that these areas were beginning to be colonised by other species, especially Phoenician juniper, so it was decided to include dead heathland (MNM) as a new category, instead of considering it as juniper woodland. Table 1 shows the characteristics and plant composition of these LULC types.

Landuse/landcover changes

The study of LULCs changes was accomplished by comparing four sets of orthorectified aerial photographs. The availability of black and white, 1:10,000 scale, aerial photographs of the DBR made it possible to establish the starting point of the study in 1971, shortly after the creation of the national park. Considering the availability and quality of aerial images from the Institute of Statistics and Cartography (IECA, Junta de Andalucía), and a series of key dates in the protection and management of the National Park and its surroundings, such as the Doñana National Park Law (Law 91/1978), the implementation of the “Lynx Plan” (1986), the coming into force of the POTAD (Plan de Ordenación del Territorio del

Table 1 Description of land use/land cover categories

Land use/land cover	Abb	Description	Height (m)	Plant composition	WTDW (m)
Phoenicean juniper woodland	SAB	Mature ecosystem of xeric series. Open forest. 2250 “Coastal dunes with <i>Juniperus</i> spp.”	> 2	<i>Juniperus phoenicea</i> , <i>Osyris lanceolata</i> , <i>Cladonia mediterranea</i>	> 3
Xerophytic shrub	MB	Serial sclerophyllous shrub of juniper woodland, composed by seeder pyrophytic species	< 1.5	<i>Cistus libanotis</i> , <i>Halimium calycinum</i> , <i>Lavandula stoechas</i> , <i>Salvia rosmarinus</i> , <i>Stauracanthus genistoides</i>	> 3
Mixed shrub	MI	Shifting transition between MB and MN	< 1.5	<i>Ulex australis</i> , <i>H. halimifolium</i>	2–3
Hygrophytic shrub	MN	Heathland. 2150 “Atlantic decalcified dunes” and 4020 “Temperate Atlantic wet heaths with <i>Erica ciliaris</i> ”. Includes serial species of Cork-oak woodland	> 2	<i>Erica scoparia</i> , <i>E. ciliaris</i> , <i>Calluna vulgaris</i> , <i>Ulex minor</i> , <i>Genista anglica</i> , <i>Quercus suber</i> , <i>Myrtus communis</i>	Flooded-1,5
Pond-grasslands	LP	Seasonal ponds covered by grass during summer. 3170 “Mediterranean temporary ponds”		<i>Mentha pulegium</i> , <i>Cynodon dactylon</i> , <i>Juncus</i> spp., <i>Holoschoenus scirpioides</i>	Flooded-1
Pine afforestation	PR	<i>Pinus pinea</i> plantations realized in the 1950s. High densities	1–3	<i>Pinus pinea</i>	1-> 3
Sub-spontaneous pines	PS	Pine trees coming from the plantations and invading the shrubs	> 2	<i>Pinus pinea</i> , xeric shrubs	1-> 3
Firebreak	CF	strip of open space			
Dead hygrophytic shrub	MNM	Drought-dead heathland. 2150 “Atlantic decalcified dunes”	2	<i>Erica scoparia</i>	

Priority habitats of European interest constituent of the transition are included

WTDW water table depth in winter (according to Allier et al. 1974), Abb abbreviations

Ámbito de Doñana=Land Management Plan for the Doñana region) and the 50th anniversary of its creation (2019), three sets of aerial images were chosen (1984, 2002 and 2016). Law 91/1978, of 28 December, on the Doñana National Park increased the size of the protected area, created new buffer protection zones, and forbade traditional uses such as prescribed burning. The Lynx Management Plan (1986) was the first global plan established in the National Park and affected the food web of the protected area with the aim of increasing net primary productivity and channelling the energy through the rabbit to the Iberian lynx. It established old age shrubland clearing, thinning of recent (1950s) stone pine afforestations, sowing of herbaceous plants, exclosures for passive vegetation protection, reforestation with native species, wild rabbit restocking, construction of artificial warrens, control of wild ungulates, removal of foxes,

captive breeding of the Iberian lynx, and monitoring and research support activities. Finally, the purpose of the POTAD (2003) was to establish the legal framework for the land use planning and sustainable development of the Doñana area to guarantee and make compatible the preservation of environmental and territorial resources with socio-economic progress, and the improvement of the living conditions of its citizens. It established three general objectives and 17 lines of action.

Fieldwork was carried out in 2019 to assess the photointerpretation of the last set of images. Through photointerpretation, a LULC map for each date was delineated. The maps were manually digitized into 0.0625 ha pixels (25 m×25 m), assigning to each pixel an integer representing a LULC category (Table 1) which had more surface (Legg 1980). Digitized data were transformed into raster using the

raster package (Hijmans and van Etten 2019) in R (R Core Team 2022). The analysis of LULC time series was performed with R software using the *OpenLand* package (Exavier and Zeilhofer 2020). *OpenLand* implements a complete Intensity Analysis (Aldwaik and Pontius 2012). Intensity Analysis (IA) is a quantitative method to analyse LULC maps at several time steps, using cross-tabulation matrices, where each matrix summarizes the LULC change at each time interval. IA tests at three levels for stationarity of patterns of change across time intervals. Here, stationary means that the pattern of change in one time interval is the same as the pattern of change in a different time interval. First, the interval level examines how the size and rate of change varies across time intervals (slow vs. fast intervals). Second, the category level examines how the size and intensity of gross losses and gross gains in each category vary across categories for each time interval (dormant vs. active categories). Third, the transition level examines how the size and intensity of a category's transitions vary across the other categories that are available for that transition (avoided vs. targeted categories). To perform the intensity analysis at the transition level *OpenLand* requires that two categories, n and m , are predefined; the first n is a target category which experienced relevant gains and m a category with important losses. In the present study, two analyses have been carried out at the transition level using PS and SAB as “winners” and LP and MN as “losers” categories respectively (see Table 1 for abbreviations of categories), the former characteristics of the “end states” and the latter of the NN-MA boundary.

Groundwater levels

In boundary analysis is needed to understand the factors that control the establishment and demise of boundary structure (Cadenasso et al. 2003). Given that transitions between different dune generations at DBR are produced by groundwater discharges (Muñoz-Reinoso and García Novo 2005; Muñoz-Reinoso 2009), measurements of water table levels may show differences in groundwater availability over time in the transition. The oldest recordings of water table levels in DBR are from the Corral Largo (1974), a dune slack in the mobile dune system, 4.3 km SE

from the Ojillo pond (Muñoz-Reinoso and de Castro 2005).

Since 1989 there are monthly measurements of water table levels in shallow PVC piezometers (2.5 m depth) located in the bed of several ponds of the boundary (Muñoz Reinoso 1996; Serrano and Zunzunegui 2008). Since 1995, Confederación Hidrográfica del Guadalquivir (CHG) installed an important network of deep piezometers (14–17 m) to monitor the characteristics and levels of the groundwater in the DNP. Every year CHG publishes a report on the state of the aquifer containing data on groundwater levels in different areas of Doñana and their surroundings (<https://www.chguadalquivir.es/estudios-tecnicos>; CHG 2020) report. One of these points is Ojillo, within the boundary, where there also was a shallow piezometer in the deepest point of the pond with recordings from 1990 to 1999.

Precipitation

Because of the recharge of the aquifer is produced by infiltration of precipitation on the unconfined aquifer (Suso and Llamas 1993), precipitation variability affects to groundwater flows of different scale (Muñoz-Reinoso and García Novo 2005) and water availability. Thus, precipitation data of hydrological years (from October to September) have been compiled for the period 1969–2019. Data for the year 1969/70 come from the Los Bodegones meteorological station, located to the North, about 12 km away from the study area. Data for the period 1970/71–1980/81 was provided by the DNP staff, while the data for the period 1981–2019 come from the DBR meteorological station.

Management

Several management activities within the protected area may condition changes in the LUCs considered in this study. Article 13 of Law 8/1999, of 27 October, on the Doñana Natural Area, states that the functions of the Management Team are to draw up the Annual Report on Activities and Results and submit it to the Participation Council for approval for its knowledge and report. These documents, available since 2000, show the basic information, activities, and results of the management of the natural area (<https://www.juntadeandalucia.es/medioambiente/portal/>

home). Previous activity reports of the National Park (1985–1999) by its technical staff are kept in the offices of the DBR. For previous years, management information is much scarcer, and without special attention to the study area. Consultation of these reports makes it possible to analyse the effects that the management of the protected area may have on the LULCs and their changes.

Changes in the surroundings

The increase in urban areas and irrigated agriculture around the protected area may affect its wetlands and the most sensitive plant communities to water availability (see Muñoz-Reinoso 2001; Serrano and Zunzngui 2008; Dimitrou et al. 2017). The direct study of the changes that have occurred in the surroundings of the national park and that may affect water availability for the LULCs considered in this work (Table 1) is beyond the scope of this paper. However, several papers dealing with these topics (WWF 2009; Prados et al. 2014; Izquierdo Cubero et al. 2020) have been revised to understand the possible effects on the dynamics of landscape change.

Results

Spatio-temporal changes

The study area was clearly dominated by the *Pinus pinea* afforestation (PR, Table 2), which experienced a fire during the first interval (1971–84), remaining stable until the end of the study period. However,

Table 2 Percentage of landuse/landcover (LULC) for each date in the Ojillo area

Category #	LULC category	1971	1984	2002	2019
1.	SAB	7.56	9.97	12.34	18.97
2.	MB	18.97	18.53	15.29	12.56
3.	MI	4.94	4.90	5.61	6.35
4.	MN	16.89	19.13	18.27	10.64
5.	LP	5.58	4.71	4.46	1.67
6.	PR	44.58	40.13	40.32	39.62
7.	PS	0.06	1.19	2.21	4.55
8.	CF	1.41	1.44	1.51	1.41
9.	MNM	0.00	0.00	0.00	4.23

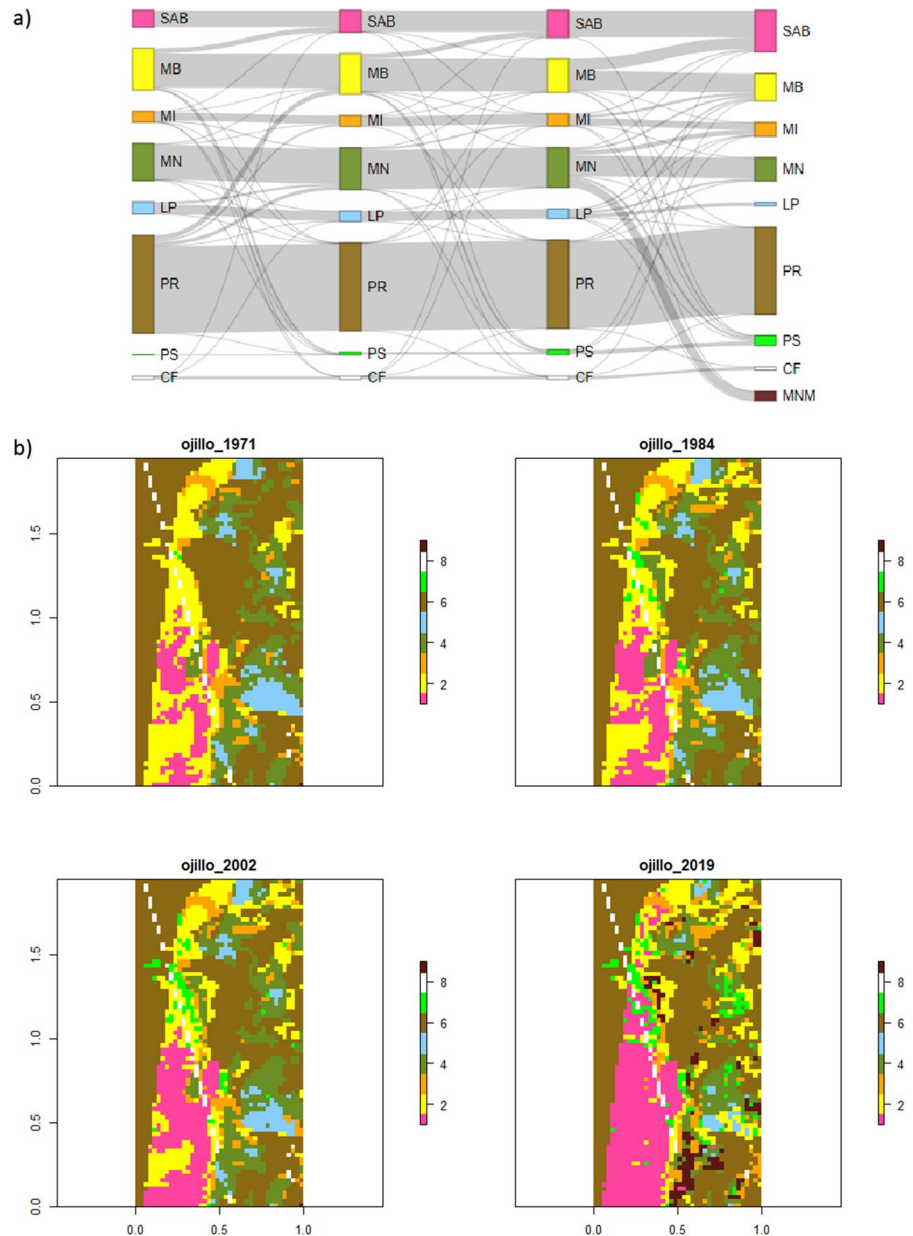
Phoenician juniper woodland (SAB) and sub-spontaneous pines (PS) increased, and dead heathland (MNM) appeared in the last interval (2002–2019). The categories that decreased in extent were xerophytic scrub (MB), heathland (MN) and pond-grassland (LP), the rest of the categories remaining without relevant changes. Figure 2a shows the complexity and magnitude of the changes among the different LULC categories and between the four dates, and Fig. 2b the raster maps for each date. The increasing trend in SAB and PS as well as the decreasing trend in MB, MN and LP can be easily visualised.

Intensity Analysis (IA) at the interval level (Fig. 3) shows that the size of the change (left side of plot) during the second time interval was lower than in the first and third intervals. It also shows that the annual rate of changes (right side) in the first and third period were faster. That is, the rate of change was not stationary at the interval level.

At the category level, Fig. 4a shows that different categories had different gains during the three intervals (left side), with SAB, MI and PS showing more gains, and being categories more active in the changes (right side). Also remarkable in the third interval are the gains and rates of change of MB and MNM. The sizes and rates of loss (Fig. 4b) also varied among categories and intervals. LP had significant losses throughout the study period, which slowed down during the second interval, but increased in intensity in the third one. Losses in MN were very stable during the first two intervals but increased considerably in size and intensity during the third interval. Also important were the size of the losses and their rates for MB and MI which, although slowed down during the second interval, increased again in the third one.

At the transition level, I investigate the transition to LP and MN to other categories (PS and SAB respectively, see Table 1 for abbreviations) although the results show the transition to the rest of categories. Figure 5a presents the annual rate and the transition intensity to which LP loses; it shows that during the first two intervals, when LP loses, the largest transitions were towards MN, while in the third interval the transitions include other categories (PS, MN, MI, MB) indicating the colonization of the dry pond beds by vegetation. Figure 5b shows that MN losses, although small in extent in the first two intervals, were intense towards PS and MI. However, during

Fig. 2 **a** Sankey Diagram showing the multistep transition between categories (1971–1984–2002–2019, from left to right). Abbreviations according to Table 1; **b** Raster maps for the four dates. Colours for LULCs according to Sankey diagram



the third interval the losses were more extensive and intense towards PS and MI, but the largest and intense transitions were towards MNM, that is, they were caused by heathland death. SAB and PS gains were similar (plots not shown), with a target on MB and MI, especially on the former. However, it is remarkable that during the second interval SAB was also a target for PS, and that during the third interval LP and MN were also targets for PS.

Precipitation

The mean precipitation in the study area for the complete period (1969/70–2018/19) was 554.7 mm, with wet and dry periods of irregular duration (Fig. 6). The first (1969/70–1983/84) and third (2002/03–2018/19) periods showed similar rainfall (530.1 mm and 525.0 mm respectively). However, while the first period showed two wet and two dry cycles (the second of which was very dry), the third

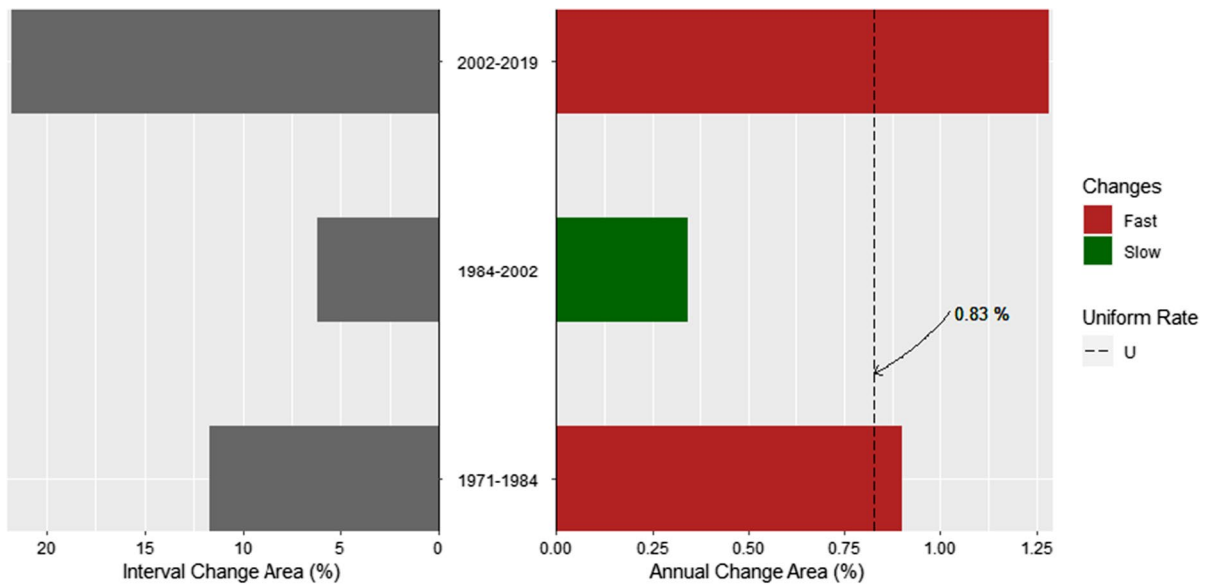


Fig. 3 Intensity Analysis at interval level. On the left, percentage of area that change in each interval. On the right, intensity on the change in each interval. Uniform rate (U, vertical dashed line) is the rate which would exist if the pattern of

change were perfectly stationary (the same among intervals) in terms of rate of overall change. It distinguishes between slow and fast change intervals

period showed a first phase of alternating wet and dry years and a second phase with years predominantly below average rainfall. In contrast, the second period (1984/85–2001/02) showed a mean precipitation of 603.2 mm, above the 50-year average, and was characterised by the two wettest periods of the series as well as the longest dry period (1990/91–1994/95).

Water table levels

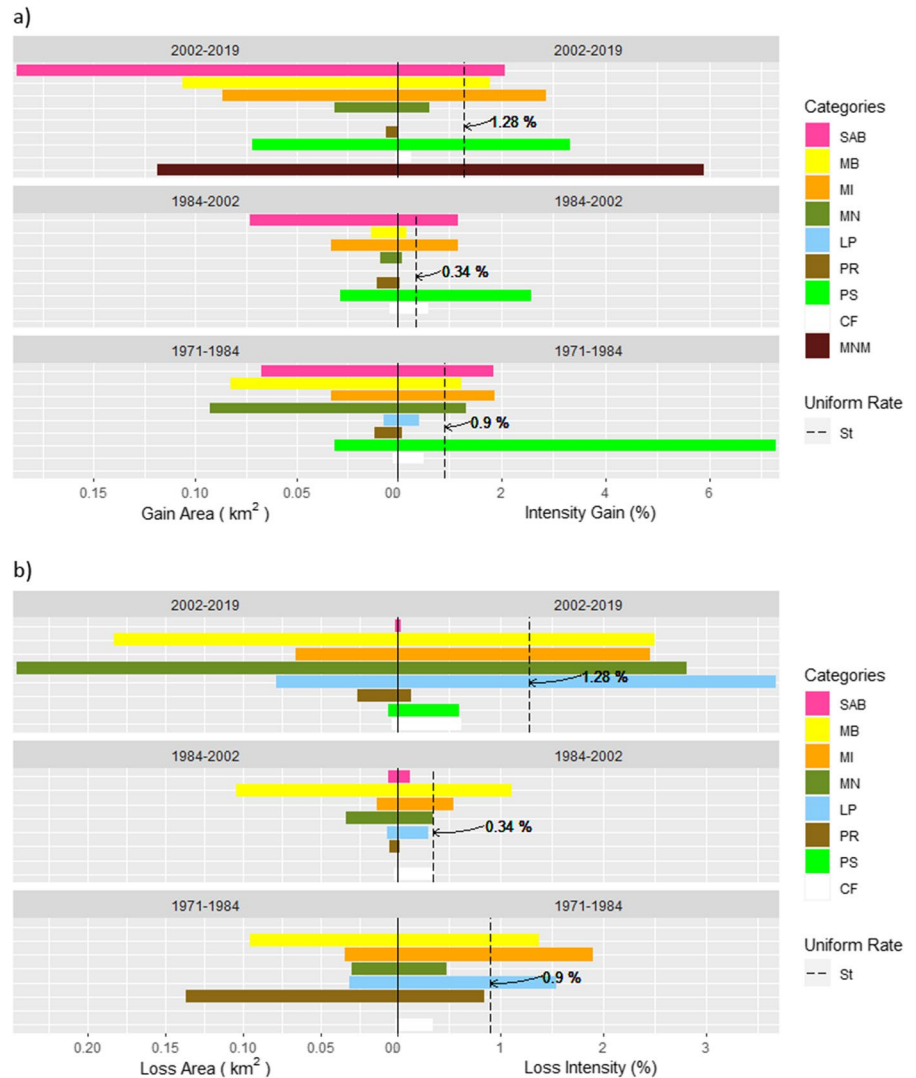
The evolution of the water table levels in both piezometers of Ojillo shows the 91/92–94/95 drought, at the end of which the lowest levels of recordings were reached (Fig. 7). Subsequently, heavy rainfall in the period 95/96–97/98 caused the pond to flood again. In the deep piezometer, the water table shows annual fluctuations in response to precipitation and reflect the discharges in the transition zone. However, from the 2004/05 drought onwards the maximum (shallower) values were not reached again despite precipitations (Fig. 6), and since then the levels showed a downward trend, most markedly since 2011/12, although the deepest levels of 1994/95 were not reached, as pointed out by the CHG (2020).

Management

The most relevant management activities carried out in the protected area for the LULCs present in the study area (Table 1) were the activities on recent *Pinus pinea* plantations and on old age, senescent shrublands. These activities were included in the Lynx Management Plan (actions shared with a later Imperial Eagle Management Plan), the prevention of forest fires, and the subsequent plans that would replace the first one (Restoration of potential habitats of threatened predators occupied by recently *Pinus pinea* afforestations in the Doñana National Park, etc.).

The thinning of the pine afforestation basically consisted of reducing the densities of the trees (which could exceed 10,000 individuals/ha, with pines over 35 years old and between 1 and 3 m in height) in proportions varying between 60 and 80%, with different strategies depending on the topographical location of the pines. The latter allowed the pines to be maintained in the lower areas, with shallower water table, on the edge of heathlands and ponds, where they had a higher growth rate. Treatments included

Fig. 4 Intensity Analysis at category level showing **a** the gains of each category at each time interval, and **b** the losses of each category at each time interval, in area (left) and intensity (right). Vertical dashed line is the uniform rate, *St* Stationary for the categories within each interval



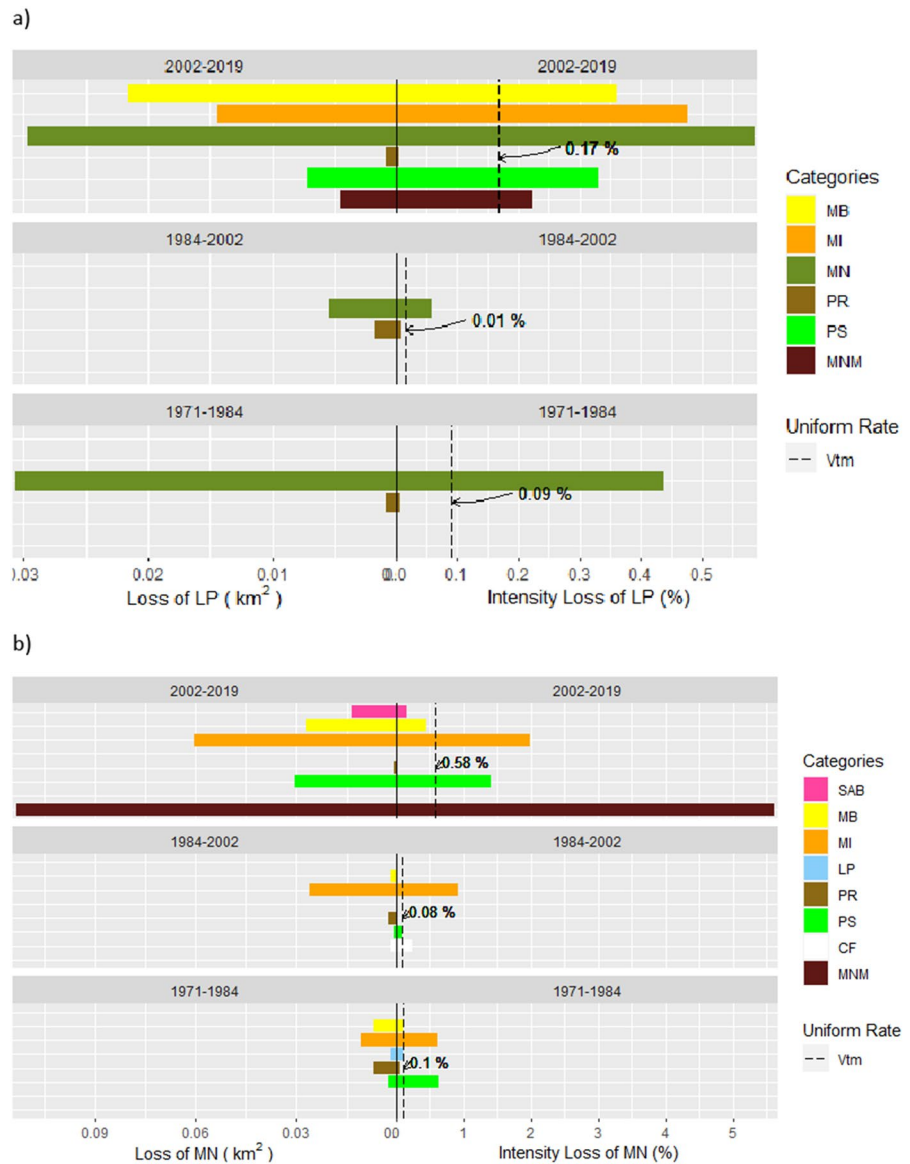
thinning, pruning and removal of biomass from the felled trees (see Annual Reports of Activities).

The treatment of old age, senescent shrublands was intended to restore a lost patchiness and productivity traditionally maintained by prescribed fires. This traditional practice maintained grasslands in lower, more productive areas, for the feeding of wild and domestic herbivores. That practice was forbidden with the entry into force of Law 91/1978. After years of trials, the practice of clearing the shrublands was carried out with a tractor with a chain cutting saw and established in strings of small plots (0.5 ha) linked by corridors, on a total area of ca. 25 ha/year. However, this new treatment was carried out in topographically intermediate areas, between the MN and the MB, that

is, on the MI (Table 1). Over time and in successive projects, shrub treatment has included plowing, clearing, and burning.

Both practices, pine thinning and shrub clearance, do not promote a change in the affected LULCs (PR, MB, MI, MN), in the sense that these units remain as the same after the treatment within a few years. Nor do they directly affect LULCs other than themselves, although they may do so indirectly. On the other hand, the implementation of these practices can give us information on previous changes in the plant communities. Thus, the thinning and pruning of pine trees can be seen in the images from 2002 and 2016, and the treatment of the shrublands can also be seen in the latter date. It is worth noting two aspects that

Fig. 5 Intensity Analysis at transition level showing the transitions: **a** from pond-grassland (LP) and **b** from heathlands (MN) categories to other categories at each time interval, in area (left) and intensity (right). V_{tm} value of uniform intensity of transition from category m to all non- m categories



will be considered later: i) the growth of the pine trees and its potential consequences, and ii) the treatment of heathlands (MN), dead or weakened at the time of the treatment.

Changes in the surrounding areas of DNP

In 2009, WWF-Spain carried out a study that aimed to identify and quantify the surface of the crops under plastic in the region of Doñana (7 municipalities in the recharge area of the aquifer) between 2003 (approval of POTAD) and 2009 (WWF 2009). The

conclusions showed that the total area transformed into plots covered by plastic at the time of the approval of POTAD was 9118 ha, and the surface transformed into intensive crops under plastic during the studied period were 1688 ha (representing an increase of 18.5%). On the other hand, the study reports that the loss of public forest land during the process of agricultural intensification was 2436 ha. These transformations do not only affect the recharge of the aquifer and the availability of water resources, but also aspects related to the connectivity of the protected area. Later, a paper by Bea et al. (2014)

Fig. 6 Precipitation of the studied period showed for the three time-intervals. Average and moving average are also shown

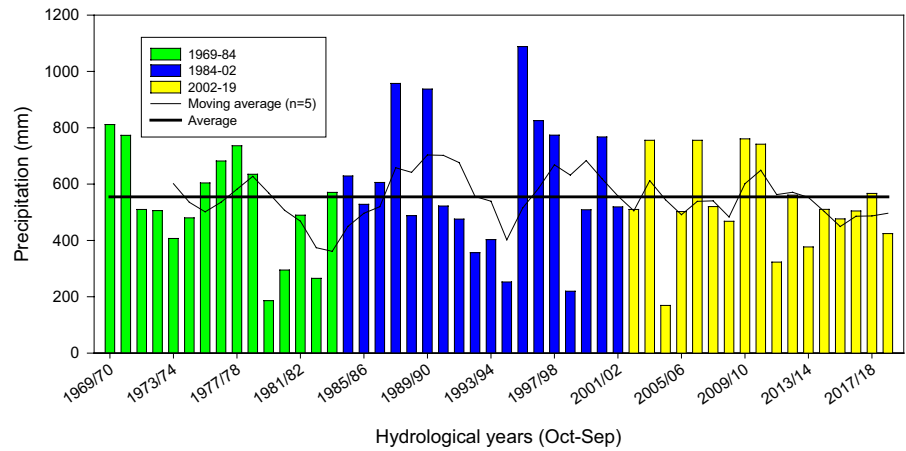
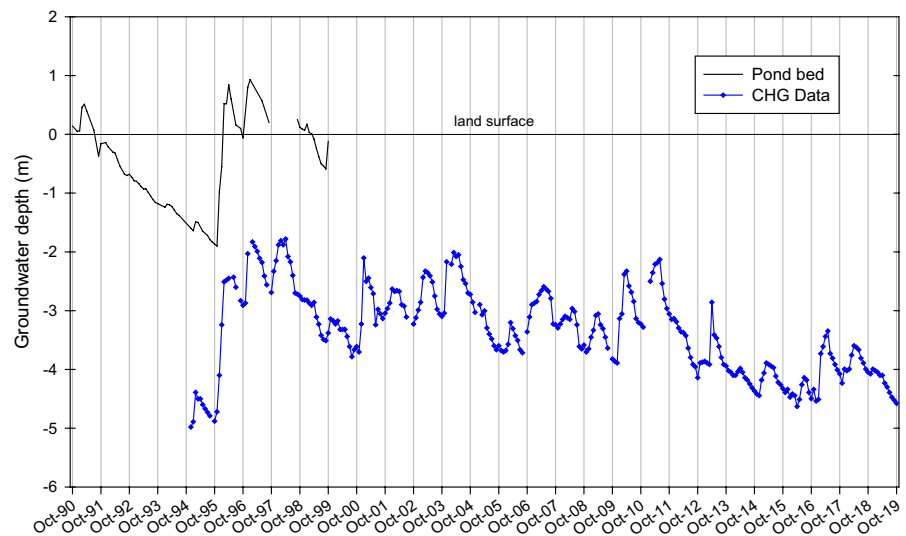


Fig. 7 Groundwater dynamics in shallow (located in pond bed) and deep (out of the pond) piezometers located at Ojillo. Deep recordings modified from CHG (2020)



delves into social, economic, legal and, especially, technological aspects in the analysis of these changes, as an example of how to use it to achieve water governance.

Prados et al. (2014) studied the changes in land uses in the socioeconomic areas of influence of Doñana for the period 1990–2006 using 13 adapted classes from Corine-Land Cover. The study was restricted to the four municipalities with an area inside the national park, DNP representing this a 20% of the total area. Results showed that, during the fifteen-year time span concerned, changes affected 17% of the fringe area of the national park and all Corine classes surveyed. Changes in the surroundings of the DNP tend to concentrate in the west of the protected area, with losses in the natural component

(forests) and gains in urban and agricultural (crops on permanently irrigated land) uses.

Izquierdo Cubero et al. (2020) analysed the processes of artificialisation and naturalisation in the Comarca of Doñana (2900 km², 14 municipalities) during the period 1956–2018 using the Map of Uses and Cover of Andalusia (Junta de Andalucía), Corine-Land Cover and other sources of information. The authors evaluate the evolution of the transformation of both, land from natural to agricultural and from agricultural to urban (and vice versa) and make a comparative chronology for different phases of the period studied between the processes of land use, the legal framework, and singular moments in the development of Doñana. According to their maps, after a long initial period (1956–77), the largest

transformations from natural to agricultural land in the western area of the national park took place in the periods 1984–99, 1999–2003 and 2003–07. These changes involved the development of intensive, irrigated agriculture.

Discussion

Landscape dynamics

The current analysis has shown complex patterns of change, varying over time in size and rate, and affecting different LULC categories in different ways (Fig. 2) because natural and anthropogenic driving forces operate at different spatial and temporal scales (Dunn et al. 1990). In heterogeneous and changing landscapes, the detection of temporal changes is subject to uncertainties associated with misclassification of units and the spatio-temporal variability of change patterns (Álvarez-Martínez et al. 2011). It is necessary to know whether errors in the data could explain the differences observed over time between categories (Aldwaik and Pontius 2013). Despite the lack of a numerical assessment of uncertainties and errors, the chosen LULCs reduce photo-interpretation errors and show observable trends of increasing organisation (juniper succession, pines encroachment) and desiccation (loss of ponds and heathland reduction). Throughout the study period the area occupied by hygrophytic communities (MN, LP) underwent a significant decrease, dying ca. 25% of the heathlands. Desiccation of the heathland and its treatment also contributed to its transformation into mixed shrub (Table 2). During the first interval (1971–1984), a fire affecting PR favoured an initial increase in MN, as well as other shrub types (MB, MI, Fig. 4a) although the latter were suffering more intense losses towards SAB and PS (Fig. 4b). In their study on the expansion of Phoenician juniper (SAB) in the DBR between 1956 and 2005, García et al. (2014) showed that the population growth was smaller at low elevation areas occupied by heathlands. Muñoz-Reinoso (1997) showed that, until at least the 1990s, neither junipers nor pines colonised heathlands due to regular flooding by rising water table during wet periods. However, in the third interval of the present study (2002–19), junipers, which previously remained on the heathland edges,

were colonising dead heathland (MNM) and low elevation areas. Throughout the study period, PS also showed a continuous and significant process of growth on heathlands (MN), especially in the third period (Fig. 5b). In addition to death and colonisation by pine trees, in this third period heathland also decreased due to the colonisation of intermediate shrubland species (MI).

In Doñana, the decline of ponds and grasslands (LP) does not seem to be recent. Fernández Alés et al. (1992) already noted it in the period 1956–1984 in the centre of the DBR, although they related it to changes in management practices (prescribed fires). After the creation of the national park, practices such as thinning and burning of low elevation areas and heathlands were prohibited. According to successional processes, heather colonises grasslands (Allier et al. 1974; García Novo and Merino 1997), a process that is observed in the first two intervals of the present study (Fig. 5a); however, between 2002–19 these areas were not only colonised by heather (MN), but also by MB, MI, PS and even heather, that had previously established in the pond basin, dies out (Fig. 5a). These results show a clear trend towards desiccation even though groundwater did not reach the levels of the drought 1994/95 (Fig. 7) as the CHG (2020) report states. That is, the plant communities that constitute the transition are not directly dependent on deep groundwater levels.

Mediterranean temporary ponds have a great importance for biodiversity conservation. However, they are in a regressive trend due to a lack of recognition of its values and functions because of its ephemeral nature and small size (Ruíz 2008). In Doñana the loss of ponds has been observed for more than 20 years (Muñoz-Reinoso 2001; Serrano and Zunzunegui 2008; Díaz-Paniagua and Aragonés 2015). The decline of the NN-MA transition's constituent ponds has been constant throughout the study period, accelerating in the last interval (Table 2), in which the ponds appear to be invaded by shrublands and pine trees (Fig. 5a).

These changes in aquatic and terrestrial groundwater-dependent ecosystems coincide with changes in the immediate surroundings of the national park (WWF 2009; Prados et al. 2014; Izquierdo Cubero et al. 2020). Although this process has been very continuous over time, the most significant changes have occurred during the last time

interval, which coincides with the entry into force of the POTAD (2003) and the irregularity of rainfall (Fig. 6). Recently, Rodríguez-Rodríguez et al. (2021) have shown that the reduction in the flooded area of peridunal ponds during the period 1994–2015 cannot be explained only by a reduction in precipitation, which is consistent with the continued reduction in the surface area of the ponds shown in the present study (Fig. 4b).

Processes and drivers

During the study period, the main processes observed in this biotic transition were succession in the juniper woodland, pine expansion, drying out of the temporary ponds and the death of heathlands. According to Bürgi et al. (2004), to explain those changes the distinction between intrinsic and extrinsic driving forces is helpful.

Phoenician juniper succession is a typical process of inherent dynamic (Bürgi et al. 2004) in the drier areas of Doñana (Allier et al. 1974). Recently, García et al. (2014) have shown an overall demographic expansion of the juniper woodland between 1956 and 2005, with significant spatio-temporal variation in population trends. Protection of the area and the control of fires must have benefited the encroachment of this endozoochorous species characteristic of the drier areas of Doñana, and which may have secondarily benefited from a generalised drying out of the territory.

The case of pine trees expansion, although more limited in the study area, follows a different process. At the time of the creation of the DBR (1964), approximately 2000 ha of its 6794 ha were covered by high-density pine plantations. Several fires in the early 1980s reduced this area to about 1249 ha, which have been treated since the mid-1980s to prevent fires and within the Lynx Plan to create suitable habitats for rabbits and their predators (see Annual Reports of Activities). Although there are still no studies on the expansion of the pine trees in the DBR stabilised sands, the initial high planting densities must not have allowed for adequate growth and fruiting of the pines. Subsequent thinning and pruning must be responsible for the continued and significant expansion of the pines (Fig. 4) by favouring their growth and reproduction. In addition, the criterion of keeping the pines in low elevation areas, at the edge

of heathlands and ponds, must have contributed to the desiccation and colonisation of those, which was lower in the second, wetter, interval (Fig. 5). Negative effects of pine trees on groundwater have been also shown by Tölgyesi et al. (2020) in sandy dry lands. They stated that individual trees as well as forests and tree plantations may contribute to decreases of water balance at the regional scale. Thus, intrinsic political drivers (*sensu* Bürgi et al. 2004) responsible for this kind of management do not seem to have understood the functional keys of the Doñana groundwater dependent ecosystems.

Many studies have pointed to pumping for urban water supply and irrigated agriculture as responsible for the decline in groundwater discharges, the lowering of groundwater table, the decrease in hygrophytic vegetation and the drying up of Doñana ponds (Muñoz-Reinoso 2001; Serrano and Zunzunegui 2008; Díaz-Paniagua and Aragonés 2015; Dimitrou et al. 2017; Naranjo-Fernández et al. 2020). Since the warnings issued in the mid-1980s about the potential effects of water abstractions (Rodríguez Arévalo and Llamas 1986; Llamas 1987) on the groundwater dependent ecosystems of Doñana, numerous studies have been carried out on the aquifer, its structure and functioning (Manzano et al. 2013; Kohfahl et al. 2019 and included references). However, this research effort has not translated into an improvement in the state of Doñana's wetlands. Extrinsic driving factors of socioeconomic, political, and technological type (irrigation agriculture, urban water supply) that promoted groundwater withdrawal seem to be responsible for landscape and boundary changes within the protected area (WWF 2009; Prados et al. 2014; Izquierdo Cubero et al. 2020). Other extrinsic (protection laws) and intrinsic (management) political factors have not been able to counteract the negative effects of the above (Izquierdo Cubero et al. 2020).

Boundary dynamics

In the Doñana landscape, the NN-MA transition is an abrupt boundary, where species from adjacent communities meet their distribution limits (Clements 1905, in Hansen et al. 1988), juniper woodland from the Naves and cork oak woodland from the Manto Arrasado (Muñoz-Reinoso and García Novo 2005). Along this

structural discontinuity (different dune generations), groundwater discharges occur that established and control this stationary transition. This strong abiotic constraint (groundwater discharges) has been weakening in recent decades, because deep groundwater abstractions have produced a flow from shallow to deep groundwater levels (Muñoz-Reinoso 2001), reducing discharges to the point of disappearing. For this reason, although the deep levels of Ojillo have not reached the values of the 91/92–94/95 drought (Fig. 7), the ponds of this transition (Ojillo, Navazo del Toro, Acebuche de las Palomas, El Moral) have dried up and the heathlands are dying (Table 2, Fig. 5).

According to Peters et al. (2006), landscape dominated by stationary transitions will be relatively stable through time regardless of changes in environmental drivers. However, the study by Tölgyesi et al. (2016) on the dynamics of grassland ecotones in Central Hungarian inland dunes contradicts this conceptualization; they stated that, under certain circumstances, these landscapes can also show changes in the spatial pattern. In our case, the transition has been invaded by species from the drier end state (SAB, PS, MB, MI), moving the location of the boundary unidirectionally, indicating that the boundary is transforming into a directional transition, making this ancient stationary transition disappear.

It has been postulated that boundaries or ecotones are very sensitive areas to environmental change (Gosz and Sharpe 1989). However, as pointed out by Delcourt and Delcourt (1992), ecotone dynamics are conditioned by the rate and magnitude of environmental change, by the tolerance thresholds of dominant species, and by the geographic proximity, competitive abilities, and dispersal capabilities of invading species. These changes seem to have been taking place in the NN-MA transition for several decades now, but favourable periods (heavy rainfalls, Fig. 6) may have masked long-term trends in those communities and habitats already established at the boundaries (Fig. 5). It seems that the magnitude of the present environmental change is not fully understood, and human activities are replacing natural agents of change as the primary determinants of landscape structure and dynamics in protected areas such as Doñana.

Conclusions

Long-term studies are needed to document boundaries dynamics and changes in boundary location and composition over time (Peters et al. 2006). This study, with a time span of *ca.* 50 years divided into three intervals, has addressed the analysis of the dynamics of a stationary transition through landscape changes by means of intensity analysis (Aldwaik and Pontius 2012). The studied transition (Fig. 1) is produced by a structural discontinuity (different dune generations) where intermediate groundwater flows discharge (Muñoz-Reinoso and García Novo 2005; Muñoz-Reinoso 2009), and is formed by priority habitats of European interest such as 2150 “Atlantic decalcified dunes”, 3170 “Mediterranean temporary ponds”, and 4020 “Temperate Atlantic wet heaths with *Erica ciliaris*” (Habitats Directive 92/43/EEC). Documented changes show the transformation of this biotic transition from stationary to directional, where xeric communities encroach into hygrophytic ones. Those changes are caused by multiple interacting factors originating from different levels of organization of the coupled human–environment systems (Lambin et al. 2003), although the main cause seems to be groundwater withdrawal for irrigated agriculture and urban supply. This is leading to the disappearance of these habitats of European interest, as well as their constituent species.

The root of this problem is a lack of a land-use planning policy in the 1960s that allowed contradictory and conflict generating situations (the National Park, Almonte-Marismas Agricultural Transformation Project, Matalascañas Tourist Centre of National Interest) that has not been resolved. It is urgent to address the restoration of Doñana’s groundwater dependent ecosystems from a broader perspective, such as that provided by Landscape Ecology, considering pattern and processes that take place at several spatial and temporal scales.

Acknowledgements My thanks to Guyonne Jaans for her help in consulting the Annual Activity Reports of the National Park, and to Dr Exavier for his help with OpenLand. I am grateful to two anonymous reviewers for their comments and suggestions that considerably improved the manuscript.

Author contributions M.R. wrote the manuscript, prepared all the figures and reviewed the text.

Funding Funding for open access publishing: Universidad de Sevilla/CBUA. No funds, grants, or other support were received.

Declarations

Conflict of interest The author declares that no funds, grants, or other support were received during the preparation of this manuscript. The author has no relevant financial or non-financial interests to disclose. The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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/>.

References

- Aldwaik SZ, Pontius RG Jr (2012) Intensity analysis to unify measurements of size and stationarity of land changes by interval, category, and transition. *Landsc Urban Plan* 106:103–114
- Aldwaik SZ, Pontius RG Jr (2013) Map errors that could account for deviations from a uniform intensity of land change. *Int J Geogr Inf Sci* 27(9):1717–1739.
- Allier CF, González Bernáldez F, Ramírez Díaz L (1974) Mapa Ecológico de la Reserva Biológica de Doñana. División de Ciencias del C.S.I.C. Estación Biológica de Doñana, Sevilla
- Álvarez-Martínez JM, Suárez-Seoane S, de Luís CE (2011) Modelling the risk of land cover change from environmental and socio-economic drivers in heterogeneous and changing landscapes: The role of uncertainty. *Landsc Urban Plan* 101:108–119.
- Álvarez-Martínez JM, Suárez-Seoane S, Stoorvogel JJ, de Luís CE (2014) Influence of land use and climate on recent forest expansion: a case study in the Eurosiberian-Mediterranean limit of north-west Spain. *J Ecology* 102:905–919
- Bea M, Gómez-Gun E, Vay del Caño L (2014) Forensic water governance? Analyzing land and water use changes in North-Western Doñana (Spain). *International Journal of Water Governance* 2:133–152.
- Borja F, Díaz del Olmo F (1996) Manto eólico litoral (MEL) del Abalario (Huelva, España): Episodios morfogenéticos posteriores al 22,000 BP. In: Pérez Alberti A, Martini P, Chesworth W and Martínez Cortizas A (eds) *Dinámica y Evolución de Medios Cuaternarios*. Xunta de Galicia, Santiago de Compostela: 375–390
- Bürgi M, Hersperger AM, Schneeberger N (2004) Driving forces of landscape change – current and new directions. *Landsc Ecol* 19:857–868
- Cadenasso ML, Pickett STA, Weathers KC, Bell SS, Benning TL, Carreiro MM, Dawson TE (2003) An interdisciplinary and synthetic approach to ecological boundaries. *Bioscience* 53:717–722
- CHG (2020) Informe de estado de los acuíferos del entorno de Doñana. Año 2018–19. Confederación Hidrográfica del Guadalquivir, Min Transición Ecológica, 19 pp + annexes
- Delcourt PA, Delcourt HR (1992) Ecotone dynamics in space and time. In: Hansen AJ, di Castri F (eds) *Landscape Boundaries*. Ecological Studies, vol 92. Springer, New York
- Díaz Barradas MC, Zunzunegui M, Ain-Lhout FZ, Tirado R, García Novo F (1999) Plant functional types and ecosystem function in Mediterranean scrub. *J Veg Sci* 10:709–716
- Díaz-Paniagua C, Aragonés D (2015) Permanent and temporary ponds in Doñana National Park (SW Spain) are threatened by desiccation. *Limnética* 34:407–424
- Dimitriou E, Moussoulis E, Díaz-Paniagua C, Serrano L (2017) Hydrodynamic numerical modelling of the water level decline in four temporary ponds of the Doñana National Park (SW Spain). *J Arid Environ* 147:90–102
- Dunn CP, Sharpe DM, Guntenspergen GR, Stearns F, Yang Z (1990) Methods for analyzing temporal changes in landscape pattern. In: Turner MG, Gardner RH (eds) *Quantitative methods in Landscape Ecology*. Ecological Studies, vol 82. Springer, New York, pp 173–198
- Exavier R, Zeilhofer P (2020) OpenLand: Software for quantitative analysis and visualization of land use and cover change. *The R Journal* 12:359–371
- Fernández Alés R, Martín Vicente A, Ortega F, Alés EE (1992) Recent changes in landscape structure and function in a Mediterranean region of SW Spain (1950–1984). *Landsc Ecol* 7:3–18
- Fernández-Ayuso A, Rodríguez-Rodríguez M, Benavente J (2018) Assessment of the hydrological status of Doñana dune ponds: a natural World Heritage Site under threat. *Hydrol Sci J* 63:2048–2059.
- Forman RTT, Godron M (1986) *Landscape ecology*. Wiley, New York, USA
- García C, Moracho E, Díaz-Delgado R, Jordano P (2014) Long-term expansion of juniper populations in managed landscapes: patterns in space and time. *J Ecology* 102:1562–1571
- García Novo F, Merino J (1997) Pattern and process in the dune system of the Doñana National Park, Southwestern Spain. In: van der Maarel E (ed) *Dry Coastal Ecosystems, General aspects*. (Ecosystems of the World 2C). Elsevier, Amsterdam, The Netherlands, pp 453–468
- Gosz JR, Sharpe PJH (1989) Broad-scale concepts for interactions of climate, topography, and biota at biome transitions. *Landsc Ecol* 3:229–243
- Hansen AJ, di Castri F, Naiman RJ (1988) Ecotones: what and why? In: di Castri F, Hansen AJ, Holland MM (eds) *A new look at ecotones: emerging international projects on*

- landscape boundaries. *Biology International*, New York, pp 9–46
- Hijmans RJ, van Etten J (2019) raster: Geographic data analysis and modelling (R package). <https://CRAN.R-project.org/package=raster>
- ITGE (1992) Hidrogeología del Parque Nacional de Doñana y su Entorno. Inst. Tecnológico GeoMínero, Serv. Publ. Min. Industria y Energía, Madrid, p 64
- Izquierdo Cubero J, Górgolas Martín P, Pico Valimaña R (2020) Relaciones simbióticas del proceso de urbanización: una historia socio-ecosistémica del diseño del territorio en el entorno de Doñana (1969–2019). IV Congreso Internacional ISUF-H Barcelona. VOL. 1. A1. Territorios sensibles. Geografías y paisajes en transformación. P 41–54. <https://isuf-h-congreso-barcelona-2020.com/actas>
- Kohfahl C, Molano-Leno L, Guardiola C, Manzano M, Ruiz F, Naranjo-Fernández N, Rebollo A, Martínez D, Martínez A, Heredia J, Custodio E, Vanderlinden K, Higuera JH, Giráldez V (2019) Monitoring and current research of groundwater resources and recharge in the Doñana Natural area (SE Spain). *Bol Geol Min* 130:661–690.
- Lambin EF, Geist HJ, Lepers E (2003) Dynamics of land-use and land-cover change in tropical regions. *Annu Rev Environ Resour* 28:205–241
- Legg CJ (1980) A Markovian approach to the study of heath vegetation dynamics. *Bull Ecol* 11:393–404
- Lindenmayer DB, Lavery T, Scheele BC (2022) Why we need to invest in large-scale, long-term monitoring programs in landscape ecology and conservation biology. *Curr Lands Ecol Rep*. <https://doi.org/10.1007/s40823-022-00079-2>
- Llamas MR (1987) Impact of groundwater exploitation on two wetlands in Spain. *Abst. 20th Intern. Congress I.A.H. Roma*
- Manzano M, Custodio E, Lozano E, Higuera H (2013) Relationships between wetlands and the Doñana coastal aquifer (SW Spain). In: Ribeiro L, Stigter TY, Cambel A, Condeso de Melo MT, Monteiro JP, Medeiros A (eds) *Groundwater and ecosystems. Selected papers on Hydrology*. CRC Press, Florida, pp 169–182
- Margalef R (1982) *Ecología Segunda edición*. Omega, Barcelona
- Margalef R (1997) *Our biosphere. Excellence in ecology 10*. Ecology Institute, Oldendorf/luhe
- Muñoz Reinoso JC (1996) Tipología de las descargas sobre arenas de la Reserva Biológica de Doñana. *Limnetica* 12:51–61
- Muñoz-Reinoso JC (2001) Vegetation changes and groundwater abstraction in SW Doñana, Spain. *J Hydrology* 242:197–209.
- Muñoz-Reinoso JC (2009) (2009) Boundaries and scales in shrublands of the Doñana Biological Reserve, southwest Spain. *Landscape Ecol* 24:509–518.
- Muñoz-Reinoso JC, de Castro F (2005) Application of a statistical water-table model reveals connections between dunes and vegetation at Doñana. *J Arid Environ* 60:663–679.
- Muñoz-Reinoso JC, García Novo F (2005) Multiscale control of vegetation patterns: the case of Doñana (SW Spain). *Landscape Ecol* 20:51–61.
- Muñoz-Reinoso JC (1997) Patrón espacio-temporal del matorral de la Reserva Biológica de Doñana y sus relaciones con el acuífero Almonte-Marismas. Thesis. Universidad de Sevilla
- Naranjo-Fernández N, Guardiola-Albert C, Aguilera H, Serrano-Hidalgo C, Montero-González E (2020) Clustering groundwater level time series of the exploited Almonte-Marismas Aquifer in Southwest Spain. *Water* 12:1063.
- Naveh Z, Lieberman AS (1984) *Landscape ecology, theory and application*. Springer-Verlag, New York, USA, p 356
- Peters DPC, Gosz JR, Pockman WT, Small EE, Parmenter RR, Collins SL, Muldavin E (2006) Integrating patch and boundary dynamics to understand and predict biotic transitions at multiple scales. *Landscape Ecol* 21:19–33.
- Prados MJ, Barral MA, Hurtado C, Lourenço JM (2014) On the fringe: tracking and evaluating changes in land use in the areas surrounding three national parks in Spain and Portugal. *Int Symp on Sustainable Rural Development in peripheral regions*, 18 p
- R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>
- Rodríguez Arévalo J, Llamas MR (1986) Groundwater development and water table variation in the Doñana National Park (Spain). *Mem. Int. Assoc. Hydrogeol.*, XIX: 203–211
- Rodríguez-Ramírez A, Rodríguez Vidal J, Cáceres L, Clemente L, Belluomini G, Manfre L, Improta S, de Andrés JR (1996) Recent coastal evolution of the Doñana National Park (SW Spain). *Quatern Sci Rev* 15:803–809
- Rodríguez-Rodríguez M, Aguilera H, Guardiola-Albert C, Fernández-Ayuso A (2021) Climate influence vs. local drivers in surface water-groundwater interactions in eight ponds of Doñana National Park (Southern Spain). *Wetlands* 41:25.
- Ruiz E. (2008) Management of Natura 2000 habitats. 3170 *Mediterranean temporary ponds. European Commission
- Salvany JM, Custodio E (1995) Características litoestratigráficas de los depósitos plio-cuaternarios del bajo Guadalquivir en el área de Doñana: implicaciones hidrogeológicas. *Rev Soc Geol España* 8:21–31
- Serrano L, Serrano L (1996) Influence of groundwater exploitation for urban water supply on temporary ponds from the Doñana National Park (SW Spain). *J Environ Mng* 46:229–238
- Serrano L, Zunzunegui M (2008) The relevance of preserving temporary ponds during drought: hydrological and vegetation changes over a 16-year period in the Doñana National Park (south-west Spain). *Aquat Conserv Mar Freshwat Ecosyst* 18:261–279
- Sousa A, Morales J, García-Barrón L, García-Murillo P (2013) Changes in the *Erica ciliaris* Loeffl. Ex L. peat bogs of southwestern Europe from the 17th to the 20th centuries AD. *The Holocene* 23:255–269
- Suso J, Llamas MR (1993) Influence of groundwater development on the Doñana National Park ecosystems (Spain). *J Hydrol* 141(1–4):239–269.
- Tölgyesi C, Zalatnai M, Erdős L, Bátori Z, Hupp NR, Körmöczy L (2016) Unexpected ecotone dynamics of a sand dune vegetation complex following water table decline. *J Plant Ecol* 9:40–50
- Tölgyesi C, Török P, Hábcenzys AA, Bátori Z, Valkó O, Deák B, Tóthmérész B, Erdős L, Kelemen A (2020)

- Underground deserts below fertility islands? Woody species desiccate lower soil layers in sandy drylands. *Ecography* 43:1–20
- Turner MG (1987) Spatial simulation of landscape changes in Georgia: a comparison of 3 transition models. *Landscape Ecol* 1:29–36
- Turner MG (1990) Landscape changes in nine rural counties in Georgia. *Photogram Engin and Remote Sensing* 56:379–386
- van der Maarel E (1976) On the establishment of plant community boundaries. *Ber Dtsch Bot Ges* 89:415–433
- van der Maarel E (1990) Ecotones and ecoclines are different. *J Veg Sci* 1:135–138.
- van Leeuwen CG (1966) A relation theoretical approach to pattern and process in vegetation. *Wentia* 15:25–46
- Wiens JA (1999) Toward a unified landscape ecology. In: Wiens JA, Moss MR (eds) *Issues in landscape ecology*. International Association for Landscape Ecology, Snowmass Village, pp 148–151
- Wu J (2013) Landscape Ecology. In: Leemans R (ed) *Ecological Systems*. Springer, pp 179–200
- WWF (2009) Changes in land use in the region of Doñana from POTAD to 2009. http://awsassets.wwf.es/downloads/changes_landuse_donana_wwf_1.pdf
- Zunzunegui M, Díaz Barradas MC, García Novo F (1998) Vegetation fluctuation in Mediterranean dune ponds in relation to rainfall variation and water extraction. *Appl Veg Sci* 1:151–160.

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