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Ecosystem services associated with a mosaic of alternative states in a Mediterranean wetland: case study of the Doñana marsh (southwestern Spain)

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Abstract Aquatic systems can flip from clear water to turbid water states. Previous research in shallow wetlands from the northern temperate zone identify clear water states as the most socially desirable based on their enhanced capacity to host biodiversity and deliver ecosystem services. However, the degree to which this model stands for Mediterranean shallow wetlands remains largely unexplored. We analyse ecosystem services associated with alternative stable states in the Doñana marsh (southwestern Spain). First, clear and turbid water states of the marsh are identified. Then, four critical ecosystem services are characterized together with the key species, and ecosystem functions on which they depend. Ecosystem service performance under the alternative stable states is assessed combining qualitative and quantitative analysis of biophysical indicators. Our results describe a patchy mosaic in which clear water and turbid water states co-exist in the marsh. All ecosystem services analysed performed better in macrophyte-dominated clear water states.

Key words alternative stable states; regime shifts; ecosystem functions; ecosystem services; submerged macrophytes; marshes; Doñana Natural Area

Services écosystémiques associés à une mosaïque d'états alternatifs dans une zone humide méditerranéenne : étude de cas du marais de Doñana (sud-ouest de l'Espagne)
Résumé Les systèmes aquatiques peuvent basculer d'états d'eau claire à eau turbide. Des recherches antérieures sur les zones humides peu profondes de la zone nord tempérée identifient les états d'eau claire comme les états les plus souhaitables socialement, en se basant sur leur capacité accrue à héberger la biodiversité et à fournir des services écosystémiques. La pertinence de ce modèle pour les zones humides méditerranéennes peu profondes reste cependant largement inexplorée. Nous analysons les services écosystémiques associés à différents états stables dans le marais de Doñana (sud-ouest de l'Espagne). D'abord, les états d'eau claire et d'eau turbide du marais sont identifiés. Ensuite, quatre services ecosystémiques critiques sont caractérisés par leurs espèces caractéristiques, et les fonctions ecosystémiques desquelles ils dépendent. La performance des services écosystémiques pour différents états stables est évaluée en combinant des analyses qualitative et quantitative des indicateurs biophysiques. Nos résultats décrivent une mosaïque inégale dans laquelle les états d'eau claire et d'eau turbide coexistent au sein du marais. Tous les services écosystémiques analysés ont une meilleure performance dans les états d'eau claire dominés par les macrophytes.

Mots clefs états stables alternatifs; changements de régime; fonctions écosystémiques; services écosystémiques; macrophytes immergés; marais; Zone Naturelle de Doñana

INTRODUCTION

Marshes, floodplains and other shallow aquatic systems play an important ecological and economic function by providing habitat for biodiversity and by delivering diverse ecosystem services for humans, including food production, water purification, protection against floods, and various recreational and spiritual benefits (Postel and Carpenter 1997, Mitsch and Gosselink 2000, MEA 2005, de Groot *et al.* 2006, TEEB 2010). During the last 50 years, drivers of change such as increased

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urbanization, sewage disposal, regulation of water courses, conversion of land for agricultural purposes and more intensive farming practices, have altered hydrological cycles and increased the nutrient loading to aquatic systems worldwide, affecting their structure and functioning (Carpenter and Cottingham 2002). A consequence of these changes that is attracting growing attention among scientists and conservation planners is the way human-induced disturbance can trigger abrupt changes (flips) towards alternative, often less-desired, stable states in various aquatic systems (Carpenter *et al.* 2001, Folke *et al.* 2004). Concern about ecological flips has been reinforced by growing evidence that aquatic systems such as shallow lakes show patterns of hysteresis, meaning that recovering the environmental conditions that prevailed before the flip is not sufficient to induce a switch back to the previous state (Scheffer *et al.* 2001). This phenomenon poses great challenges for wetland restoration efforts (Meijer *et al.* 1989, Suding *et al*. 2004, Søndergaard *et al.* 2007, Scheffer 2009).

Alternative equilibria in shallow aquatic systems were first described in the 1990s (Blindow *et al.* 1993, Scheffer *et al.* 1993), and models depicting shifts have thereafter been largely explored in shallow lakes of the Northern Hemisphere at temperate locations (Blindow *et al.* 2002, Jackson 2003, Kisand and Noges 2003, Hargeby *et al.* 2004, Schröder *et al*. 2005, Rip *et al.* 2006, Hansson *et al.* 2010). As a result of this accumulated empirical research, shallow lakes have become the archetypical example of ecosystems with alternative stable states (Scheffer and van Nes 2007). The original model used in the alternative stable states theory has been developed on observations that beyond critical levels of nutrient loading, shallow lakes can change rather abruptly from a situation characterized by abundant submerged vegetation and transparent waters (*clear water state*) to another situation characterized by turbid conditions with absence of vegetation and dominance of phytoplankton (*turbid water state*) (Scheffer *et al.* 1993).

Processes that could drive shallow lakes to shift between alternative states operate on a variety of time scales, and assumed mechanisms leading to change can be separated into internal and external drivers. Drivers operating at a large scale are related to regional climate and regional homogeneity of a watershed, while those which are internal and operate at the local scale are mostly related to nutrient cycling. Although the shift between alternative states in shallow lakes may be part of the intrinsic lake dynamics, humans can exert a strong influence on the thresholds that separate these states. The main causes behind the destruction of submerged vegetation include anthropogenic actions such as direct mechanical damage, increased nutrient load from fertilizers, alteration of the hydrological cycle, and illegal water extractions (Blindow *et al.* 1998, Fernández-Aláez *et al.* 1999, Coops *at al.* 2003), pollution from biocides and other chemical compounds (Vandergaag, 1992, Angeler *et al.* 2007).

The present paper focuses on the ecological and socio-economic implications of regime shifts in shallow aquatic systems resulting from changes in the capacity to deliver ecosystem services. A growing body of literature has aimed at comparing desired and non-desired states in aquatic systems in order to provide guidance for ecosystem management and restoration policies (e.g. Carpenter *et al.* 2001, Folke *et al.* 2004). Early theory of alternative stable states in shallow lakes emphasized the potential negative effects of flips in terms of impoverished biodiversity and lower performance of ecosystem functioning (e.g. Mitchell 1989, Duarte *et al.* 1990, Scheffer *et al.* 1993, Hargeby *et al.* 1994). In the last decade, with the move towards more anthropocentric conservation strategies (McCauley 2006), and with exponential growth of ecosystem service research (Fisher *et al.* 2008), the literature has increasingly highlighted the potential negative effects that regime shifts may have in terms of ecosystem service decline (Engelhardt and Ritchie 2001, Folke *et al.* 2004, Hansson *et al.* 2010). The general model resulting from this research differentiates desired from less desired stable states according to their ecological and socio-economic performance (Folke *et al.* 2004). Clear water states are typically characterized by the presence of extensive beds of macrophytes that stabilize sediments and reduce recycling of phosphorus to phytoplankton (Jeppesen *et al.* 1997), which allows for enhanced habitat provision and capacity to provide ecosystem services such as recreation and water supply for irrigation or human consumption. In contrast, turbid water states dominated by phytoplankton generally host lower levels of biodiversity and provide fewer ecosystem services because of the presence of abundant toxic cyanobacteria and anoxic conditions (Smith 1998). In accordance with this scheme, research in temperate shallow wetlands typically identifies clear water states as socially desirable, because of their enhanced capacity to host biodiversity and deliver ecosystem services, as compared to turbid water states (e.g. Carpenter *et al.* 2001, Hansson *et al.* 2010) (Fig. 1).

The model illustrated in Fig. 1 builds on a large body of literature that has led to major advances in

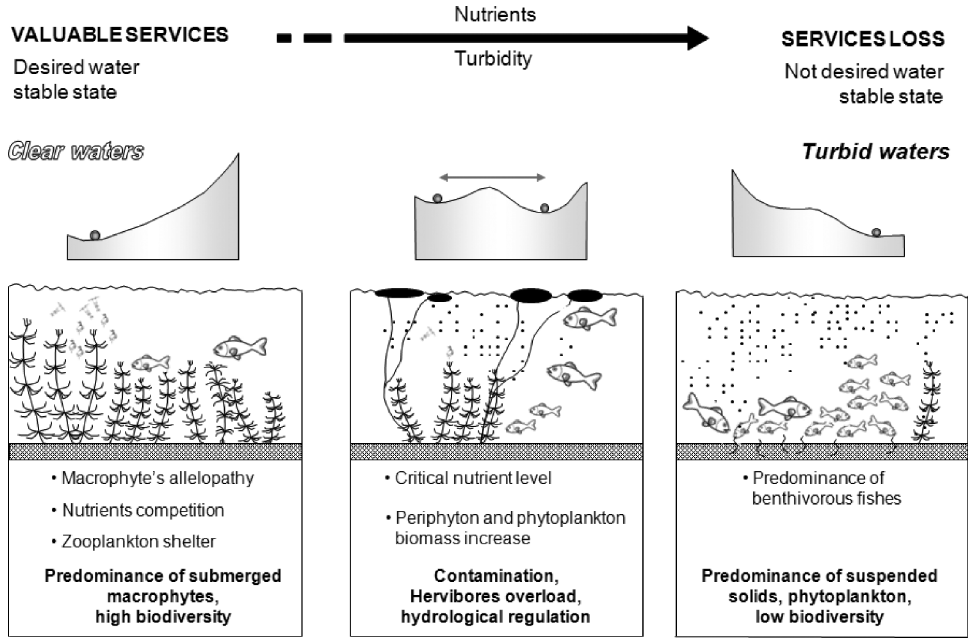

Fig. 1 Model describing regime shifts in shallow aquatic systems. The flip from a macrophyte-dominated clear water state to a turbid water state with little or no vegetation involves biodiversity loss and ecosystem service decline. Modified from various sources.

understanding the ecological functioning of northern temperate shallow lakes (Scheffer *et al.* 1993, Jeppesen *et al.* 1998, Moss 2007). However, despite growing efforts in the last two decades (Duarte *et al.* 1990, Grillas *et al.* 1993, Romo *et al.* 2005, Beklioglu *et al.* 2006), the availability of comparable information for understanding regime shifts and their implications for humans in Mediterranean shallow wetlands is still very limited (Trobajo *et al*. 2002, Beklioglu *et al.* 2007). This paper aims to reduce this knowledge gap by analysing the performance of ecosystem services associated with a mosaic of alternative stable states in the marsh of the Doñana Natural Site, in southwestern Spain. More specifically, the present research has two main objectives: to provide a model showing the co-existence of alternative states in the Doñana marsh, and to assess the performance of ecosystem services associated with such alternative states. Our working hypothesis is that the ecological functioning of Doñana is based on its mosaic-like, patchy structure in which alternative states co-exist and influence each other, changing, on a local scale (i.e. ranging from several tens to hundreds of metres), according to the influence of several driving factors, be they endogenous, such as herbivore pressure, or exogenous, such as changes in water quality due to anthropogenic pressures.

The paper proceeds as follows. First, alternative states are categorized using quantitative data from biological, chemical and physical features at different sites of the marsh; then, four key ecosystem services provided by the marsh are characterized, together with the key species, ecological components and ecosystem functions responsible for their delivery. Finally, the performance of each ecosystem service under alternative states of the marsh is assessed through indicators based on proxy measures. The validity of the model describing desired *versus* non-desired states in shallow lakes is discussed in the context of Mediterranean shallow wetlands, and particularities resulting from Mediterranean climate characteristics are highlighted and discussed.

METHODS AND APPROACH

Study area

The Doñana marsh is a silty-clayey, calcareous and saline floodplain located in the lower Guadalquivir River basin and extending along the coastal plain of the Gulf of Cadiz (371°N, 61°W), in southwestern Spain. The non-converted area of the marsh covers 27 000 ha and falls within the limits of the Doñana National Park (53 835 ha), which was designated as a Ramsar Site in 1982 and as World Heritage Site by UNESCO in 1994. Despite vast conversion for agricultural purposes that led to the loss of more than two thirds of the original flooding area (González-Arteaga

1993), the Doñana marsh is nowadays the largest wetland in Spain, and one of the largest and most studied wetlands in Europe, because of its wide range of well-preserved and highly diverse habitats (Santamaría and Amézaga 1999, Fernández-Delgado 2005, García-Novo and Marín-Cabrera 2005, García-Novo *et al.* 2007). The marshland is seasonally flooded by freshwater supplied by direct rainfall, two streams (El Partido stream and La Rocina brook) and groundwater flows (Serrano *et al.* 2006). The average annual rainfall in the region is approximately 600 mm and real evapotranspiration is estimated at between 400 and 500 mm/year. The water level may vary by several centimetres, as wind force and intensity change, although the prevailing winds are from the west (Bayán 2005). The marsh follows a marked annual cycle. It fills up in October–November, reaching an average depth of 20 cm, and remains flooded until March or April. Afterwards, net water losses through evapotranspiration gradually dry out the marsh. By the end of the summer, only the deepest depressions retain some highly saline waters (shallow ponds, gullies and some channel stretches) (Montes *et al.* 1993, Bayán 2005, Geertz-Hansen *et al*. 2011).

Data sampling

Primary data were gathered throughout a two-year study (2007–2008) at 27 sampling sites in the marsh. Site selection was based on a fieldwork campaign performed during spring 2006, in a period when the macrophyte beds were expected to be properly developed, with the aim of representing the variety of conditions occurring in a highly heterogeneous system. During the flood period, a monthly record was conducted in order to measure significant limnological variables linked to the theory of alternative stable states, including turbidity, soluble reactive phosphorus (SRP), total phosphorus (Total-P) in water and sediments, organic matter in sediments, chlorophyll *a*, and macrophyte and helophyte coverage and richness. In addition, some other basic limnological descriptors were measured *in situ* using a WTW Multi350i multiprobe, including electrical conductivity, dissolved oxygen, pH and water temperature. Turbidity was measured using a HANNA HI91703 turbidity meter. Water samples for the estimation of SRP (μg/L) were obtained following APHA protocols, filtered with a Whatman GF/C filter (1.2 μm nominal pore size), stored in dark glass bottles, and refrigerated until processed. Samples for Total-P were stored in dark glass bottles and kept refrigerated until processed using APHA methodology (ascorbic acid method after persulfate digestion) (Clesceri *et al.* 1999). Sediment samples of the upper 3-cm layer were obtained using a cut-down syringe (3 cm in diameter). The content of Total-P in sediments was estimated using the ignition method (Andersen 1976). The organic matter content of the sediments (measured as loss of ignition, LOI) was determined by combustion of samples in porcelain crucibles at 550°C for 12 h in a muffle furnace. The final product of the combustion was expressed as the ash content of the sediment (Clesceri *et al.* 1999). Clorophyll *a* (μg/L) was analysed after acetone extraction (90% v/v). Samples were filtered *in situ* (GF/C filter (1.2 μm pore size) and kept dark and refrigerated until laboratory processing (Jeffrey and Humphrey 1975). Macrophyte and helophyte amounts were estimated as the percentage of plant cover observed in three sampling quadrats (50 cm^2) randomly placed at each site following Prodon (1988) methodology. Macrophyte richness was simultaneously recorded in all sampling quadrats.

Data analysis

We performed an ordination by principal component analysis (PCA) of the samples (site × date) using variables directly related to the *clear–turbid* model as descriptors: turbidity, SRP, total phosphorus in sediment, and chlorophyll *a* concentration in the water column (Total-P in water was discarded due to high redundancy with SRP). Other included variables were pH, organic matter content in sediments, and helophyte coverage. Normality of variables was examined and appropriate transformations (log(x), log(x) +1 or arcsine(x)) were used as necessary to meet the assumptions of parametric tests (Zar 1999). Next, we estimated the ordination "place" of each site in both periods studied (2007, 2008) by averaging sample scores in the eight components of the PCA, with the aim of testing the co-existence of *clear* and *turbid* states due to the patchy structure of the wetland. For each site and sampling period, seasonal variability was computed as the mean Euclidean distance between samples. Finally, the obtained disposition of points was compared with their geographical coordinates to assess whether spatially close sites have similar limnological features (i.e. are closer in the PCA space) using a Mantel test (10 000 randomizations).

Assessment of ecosystem services

We used a function analysis approach (de Groot *et al.* 2002) for the assessment of ecosystem functions and services. Adopting an anthropocentric perspective, this approach portrays ecosystem functions as ecological processes and components involved in the delivery of ecosystem services. In turn, ecosystem services are defined as the benefits humans derive from ecosystem functions, thus implying that functions generate services only if they are used or enjoyed by beneficiaries (Gómez-Baggethun and de Groot 2010). Given the biophysical approach of this research, no distinction was made between ecosystem services and benefits, as suggested by recent ecosystem service research for economic valuation purposes (e.g. Fisher *et al.* 2008, Pascual *et al.* 2010).

Four ecosystem services were assessed: water purification, soil retention, flood control and recreation. Ecosystem services were selected from a previous classification of the ecosystem services provided by the Doñana wetlands commissioned by the European Environmental Agency (Haines-Young *et al.* 2010, Gómez-Baggethun 2010) for a pilot case study of the international initiative *The Economics of Ecosystems and Biodiversity* (TEEB, 2010). The original list was narrowed down to a sample of four ecosystem services using criteria of: *specificity*, i.e. marshland ecosystem (see MEA 2005, de Groot *et al.* 2006), *relevance* for this research (services likely to be affected by regime shifts), and *policy context*, i.e. since the marsh is managed for conservation purposes, regulating services are the most widely represented in the sample. Capacity to generate services under alternative stable states was assessed through a three-step qualitative scale ranging from low performance to high performance. Three of the four ecosystem services—water purification, soil retention and flood control—were assessed through proxy quantitative measures from our primary data. Recreation (bird watching), for which quantitative primary data were not available, was inferred from secondary data and findings of previous research on the Doñana marsh or other shallow wetlands.

RESULTS

Alternative stable states

As would be expected in an extensive and flat wetland like the marsh of Doñana, all sampled sites are shallow (<45 cm), with clayey sediments and basic pH (Table 1). In accordance with previous research (Duarte *et al.* 1990), salinity, measured as conductivity, follows an increasing gradient from north to south and from west to east, following the main discharge flows along the floodplain.

The first two principal components of the PCA explain nearly 50% of the overall variance. Sampling sites do not split into discrete groups, but spread evenly as a cloud of points (Fig. 2(a)). According to the plot of the variable vectors (Fig. 2(b)), rather than bimodality of two states, our results suggest a trend line running from a macrophyte-rich condition, i.e. clear water state, in the lower right corner to a highly turbid state in the upper left one. Nearly uncorrelated there is another trend line moving from sites rich in phosphorous load (in both the sediments and the water column), phytoplankton (estimated as chlorophyll *a*), and organic matter content in the sediment. The ordination space of each site on both sampling periods, estimated as the average of sample scores in all principal components, is represented in Fig. 3. No significant correlation between the PCA scores matrix and the geographical coordinates of the sites was found (Mantel test $p = 0.895$ for 2007, $p = 0.9951$ for 2008), reinforcing the idea that this heterogeneous aquatic system does behave in a patchy way.

Our results do not show a clear discrete pattern of clear and turbid water alternative states in the marsh. On the contrary, the transition between alternative states seems to be gradual, more like a gradient with several intermediate states between clear and turbid patches, as shown in the ordination along the first PCA axis (Fig. 2(a), Table 2). The PC-I is explained mainly by turbidity and submerged macrophyte and, to a lesser extent, helophyte cover in the opposite corner, while other variables that should *a priori* be expected to be more related to the shift between states (chlorophyll *a*, nutrient and organic matter content), have no relationship with the ordination pattern found (Fig. 2(b)). Further, one would expect geographically close patches to share similar limnological features and, for instance, the same state, but the distribution of the different patches seems to be independent of their location.

Thus, the dynamics of each type of patch is neither constant in time nor uniform in space, but subject to seasonal and inter-annual variability (Fig. 3). Patterns obtained after analysing a series of patches for different dates (2007 and 2008) suggest that there are multiple responses of the sites independently of their geographical location (Figs 2 and 3). Some patches changed inter-annually from a clear to

Table 1 Location and selected physical and chemical characteristics of 27 sampling sites in the Doñana marsh, southwestern Spain: average and ranges of values calculated for all the sampling dates ($n = 8$, 4 in 2007 and 4 in 2008).

Site	Location (geodesic coordinates)		Water depth, Z (cm)			O_2 (mg/L)			pH mean	Conductivity (μS/cm)		
	Latitude N	Longitude W	Mean	Range		Mean	Range			Mean	Range	
M1	37° 01′ 48.04″	6°24′ 00.54″	16.0	38.9	6.5	10.6	11.4	10.0	9.4	3251.2	10690.0	1111.0
M2	37° 01′ 52.44″	6°24′ 09.22″	26.3	36.8	17	11.5	17.0	8.1	8.9	1825.9	4400.0	762.0
M3	36° 02′ 8.47″	6°25′ 44.46″	11.1	12	10.1	15.1	19.2	11.1	9.0	1733.0	2360.0	1106.0
M4	36° 58′ 45.58″	6°24′ 29.79″	14.2	27	4.2	11.4	12.9	8.0	8.4	4442.7	8670.0	1376.0
M5	36° 58′ 49.17″	6°24′ 17.62″	13.3	27	5.3	17.7	20.4	13.2	9.1	3229.8	5910.0	1250.0
M6	36° 58′ 40.23″	6°24′ 27.16″	14.6	24	5.5	13.5	22.8	6.1	8.6	4114.7	7600.0	1246.0
M7	37° 06′ 28.64″	6°27′ 57.09″	17.3	21.6	13.5	6.7	12.5	0.6	7.5	804.3	1124.0	399.0
M8	37° 02′ 9.24″	6°25′ 31.50″	21.3	32	14	9.9	13.2	5.8	8.3	1466.6	2160.0	664.0
M9	36° 57′ 57.96″	6°26′ 02.39″	25.8	37.6	12	12.4	18.4	3.4	9.0	11145.1	18170.0	1291.0
M10	36° 58′ 19.74″	6°25′ 49.91″	23.1	38.9	10.5	10.5	20.4	3.2	9.2	10171.3	17560.0	2430.0
M11	37° 04′ 18.01″	6°17′ 13.68″				13.3	13.3	13.3	9.2	4560.0	4560.0	4560.0
M12	37° 01′ 40.47″	6°24′ 04.58″	13.5	24.5	2	10.8	15.0	4.2	9.1	2411.3	6280.0	799.0
M13	37° 01′ 46.51″	6°24′ 23.04″	23.9	38.6	13	12.0	14.9	6.9	9.1	1773.8	3830.0	803.0
M14	37° 06′ 8.88″	6°27′ 44.46″	45.7	61	32	7.8	22.6	2.2	7.8	717.7	1111.0	405.0
M15	36° 58′ 0.41″	6°25′ 53.00″	26.8	32	16	11.2	18.1	6.2	8.9	12433.3	17690.0	8030.0
M16	36° 57′38.8″	6°26′ 11.96″	24.1	34.5	12.5	8.0	10.9	4.4	8.8	11113.3	15910.0	6360.0
M17	37° 01′ 45.57″	6°26′ 11.59″	30.6	41	16	8.3	12.5	5.6	7.9	824.8	1810.0	182.0
M18	37° 01′29.56″	6°26′ 03.48″	21.0	29	8.4	5.8	7.8	2.5	7.7	1814.0	2610.0	1196.0
M19	36° 58′ 40.12″	6°24′ 11.84″	20.6	25.5	12	9.9	12.2	5.3	8.4	4419.3	5800.0	2300.0
M20	37° 00′ 32.64″	6°17′ 21.59″	36.0	43	29	6.1	9.3	2.8	8.1	10135.0	12310.0	7960.0
M21	36° 59′ 58.42″	6°17′ 32.61″	11.8	18.5	5	13.3	15.4	11.2	9.1	19135.0	31900.0	6370.0
M22	37° 00′ 51.55″	6°17′ 17.38″	15.0	23.5	6.5	11.3	13.4	9.3	8.7	24240.0	41700.0	6780.0
M23	37° 01′ 17.54″	6°17′ 12.45″	20.5	29.2	11.7	12.3	13.7	10.9	9.6	13665.0	20800.0	6530.0
M24	37° 01′ 33.69″	6°18′ 38.91″	15.8	27	4.5	13.3	14.9	11.7	9.6	11990.0	18950.0	5030.0
M25	37° 01′ 45.02″	6°19′ 54.78″	17.9	28	7.8	12.7	16.2	9.2	9.1	12170.0	18520.0	5820.0
M26	37° 01′ 41.51″	6°19′ 56.43″	20.8	29	12.5	14.9	15.3	14.6	9.4	8425.0	12060.0	4790.0
M27	37° 01′ 8.33″	6°18′ 42.15″	21.1	30	12.1	12.9	17.4	8.4	9.3	8330.0	11980.0	4680.0

a turbid water state, as shown by sites M06, M08, M15 and M16, while others remained in different parts of the turbid space described by the PCA (sites M14 and M17). Also, there are other sites that seem to change in the opposite direction, from a turbid to a clear water state (M12, M18 and M19, Fig. 3, Table 1).

Performance of ecosystem services

Key species and functional groups, ecological processes and components, and ecosystem functions involved in the delivery of ecosystem services were identified and characterized (Table 3). A description of the ecosystem services and results regarding their performance under alternative stable states, is provided below.

Water purification The role of shallow wetlands in water purification has been widely acknowledged in the literature (MEA 2005, de Groot *et al.* 2006). The Doñana marsh acts as a sink for agricultural runoff enriched with nutrients and pesticides. Research findings suggest that the purifying capacity of shallow wetlands is intimately related to the communities of macrophytes that remove excess nutrients from the water column through filtering and sediment stabilization (Engelhardt and Ritchie 2001, Greenway 2003, Veraart *et al.* 2004). Several studies, specifically conducted in the Doñana marsh have emphasized the critical role played by aquatic macrophytes, in particular submerged plants, in the recycling of nutrients and other potentially water pollutant elements (Duarte *et al.* 1990, Santamaría 1995). There is evidence of releases of heavy metals (Zn, Cu, Pb) from metalliferous mines to the Guadiamar River (Arambarri *et al.* 1984, Cabrera *et al.* 1994, Albaiges *et al.* 1987), but isolation of this stream from the marsh after the catastrophic mine spill in Aznalcóllar in 1998 (Prat *et al*. 1999) left El Partido and La Rocina streams as the only water flows entering the marsh. Since El Partido stream brings runoff from urban waste and agriculture (Arambarri *et al.* 1996), pollution problems in the

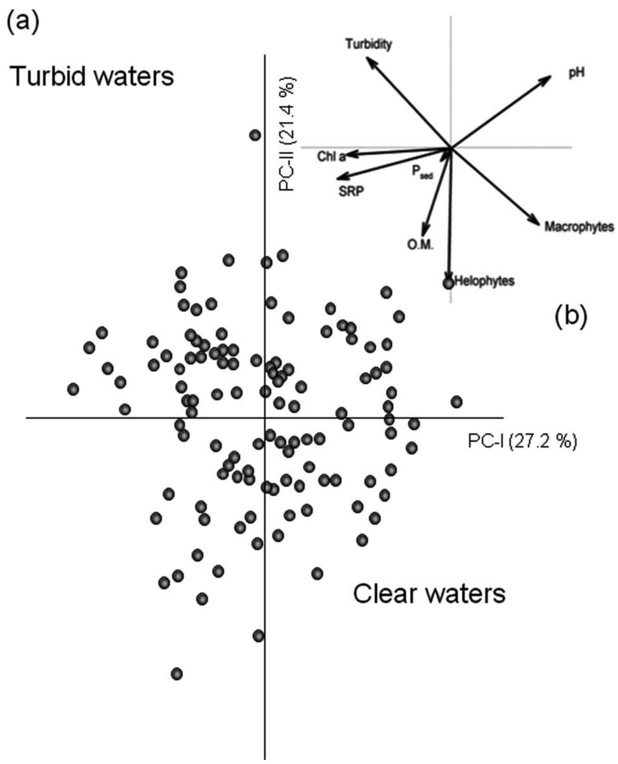

Fig. 2 (a) PCA sample scores (site × date), and (b) variable vectors.

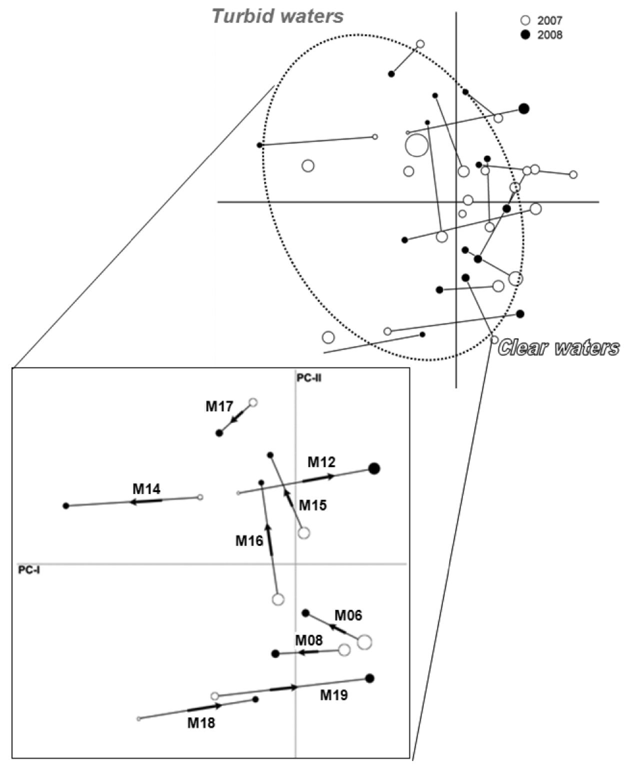

Fig. 3 Representation of the average sample scores of the ordination of Fig. 2 in all principal components. Lower left: representation of selected sites showing their tendency to change between the variation dimensions that characterize the turbid and clear water states between both studied hydro-periods (open circles represent 2007 samples, closed circles – 2008 samples; a line links sites that were sampled on both cycles). Point size is proportional to seasonal variability.

marsh are related to P and N concentrations (Reina *et al*. 2006). Because no data on N concentration were sampled for this study, we followed previous research on the ability of wetlands to retain nutrients (Mitsch *et al.* 1995, Engelhardt and Ritchie 2001) and used P measures (Total-P sediment and SRP) as proxy indicators for water purification performance. Whereas Total-P sediment was only slightly higher in the clear water state (4.178 μg/L, compared to 4.348 μg/L in the turbid water state), the clear water state showed far lower average values of SRP (62.12 μg/L, against 128.57 μg/L in the turbid water state). Our results thus suggest higher performance of water purification through P uptake in the clear water state.

Soil retention Since the mid-20th century, the Doñana Marsh has experienced an accelerated colmatation process, as a result of dramatic increases of the sediment load to the marsh due to loss of vegetation cover, land cover change towards agriculture, and modification of river streams (Rodríguez-Ramirez *et al.* 2003, García-Novo *et al.* 2007). According to Rodríguez-Ramirez *et al.* (2005), human-induced impacts have increased sedimentation filling rates from less than 1 mm/year during the last 2500 years, to 3–6 mm/year over the last 50 years, leading to substantial reduction in water storage capacity, modification of the hydrological dynamic, and affecting several plant (e.g. *Scirpus lacustris* and *Scirpus maritimus*) and bird species (*Oxyura leucocephal* and *Aythya nyroca*) (Castroviejo 1993). Macrophyte abundance, measured as submerged macrophyte and helophyte coverage, was used as an indicator for soil-retention capacity. This choice is based on evidence that aquatic plant communities (especially helophytes and submerged macrophytes) play a critical role in stabilizing soil in the marsh (Duarte *et al*. 1990, García-Murillo *et al*. 2006) and protecting it against erosion by wind and rainfall (Bayán 2005). Our results suggest higher performance by the clear water state: mean submerged macrophyte coverage of 52% (against 29% in the turbid water state) and mean helophyte coverage of 19% (against 5% in the turbid water state).

Table 2 Descriptive statistics of variables describing most contrasting alternative states of the patchy mosaic in the Doñana marsh (NTU: nephelometric turbidity units; SRP: soluble reactive phosphorus).

State	Variable	Average	Std dev.	Range
Clear water	Turbidity (NTU)	28.32	31.99	1.0–14.33
	Total-P sediment (μg/L)	4177.55	1608.80	1838.07–8402.01
	SRP (μg/L)	62.12	58.79	0–240.33
	Total chlorophyll *a* (μg/L)	20.02	27.81	0.44–130.26
	Submerged macrophyte coverage (%)	52	35	0–90
	Helophyte coverage (%)	19	20	0–75
Turbid water	Turbidity (NTU)	85.62	107.87	2.58–575.33
	Total-P sediment (μg/L)	4347.62	2922.82	307.31–12973.71
	SRP (μg/L)	128.57	162.29	0–665.62
	Total chlorophyll *a* (μg/L)	20.54	22.37	0–138.84
	Submerged macrophyte coverage (%)	29	36	0–90
	Helophyte coverage (%)	5	15	0–85
Mixed character	Turbidity (NTU)	24.05	17.46	4.58–52.33
	Total-P sediment (μg/L)	4696.25	2835.76	2245.26–10069.42
	SRP (μg/L)	82.68	89.35	23.40–252.83
	Total chlorophyll *a* (μg/L)	44.96	56.37	8.5–155.76
	Submerged macrophyte coverage (%)	23	16	10–50
	Helophyte coverage (%)	22	16	5–50

Table 3 Characterization of key species, functional groups, ecological elements and processes, and ecosystem functions underlying ecosystem services provided by the Doñana marsh.

Ecosystem service	Key species	Biological communities / functional groups	Structural features / ecological processes	Ecosystem function
Water purification	*Ruppia drepanensis, Zannichellia obtustifolia, Potamogenon pectinatus, Chara galioides, C. connivens, Tolypella hispanica, Nitella hyalina*	Macrophytes / Submerged plants	Macrophyte beds / Filtering and removal of potentially pollutant components	Nutrient uptake and retention
Soil retention	*Ruppia* spp, *Zannichellia obtustifolia, Chara spp., Nitella hyalina Ranunculus, R. ophioglossifolius, R. tripartitus, Callitriche* spp., *Lemna gibba, Juncus* spp., *Scirpus* spp.	Submerged plants, floating plants, helophytes	Root systems / sediment retention and stabilization / physical wind break	Soil stabilization / wind buffering
Flood control	*Typha* spp., *Phragmites australis, Juncus* spp., *Scirpus* spp., *Arthrocnemum* spp., *Tamarix* spp.	Helophytes	Vegetative structure / water storage	Physical buffering by rooted plants
Recreation	*Anser anser, Tadorna* spp., *Anas* spp., *Marmaronetta angustirostris, Aythya farina, Fulica atra, Phoenicopterus ruber roseus, Platalea leucorodia, Sterna nilotica, Plegadis falcinellus, Himanthopus himantopus, Recurvirostris avosetta, Charadrius dubius, Limosa limosa, Tringa totanus, Actitis hypoleucos*	Water fowl and other wetland migratory species	Pasture growth for waterfowl breeding	Breeding and refuge of waterfowl

Flood buffering Historically, major flood events in the Doñana marsh involved human casualties and loss of cattle (González-Arteaga 1993), but at present floods are regulated through artificial walls and gates (Ojeda-Rivera and Moral-Ituarte 2004, García-Novo and Marín-Cabrera 2005). The two branches of the Guadalquivir River that formerly flooded the marsh were closed and diverged, and an artificial clay wall at the southern limit inhibits the original channels of riverine water circulation (Santamaría 1995). The original capacity of the marsh to dampen floods has been significantly reduced, firstly because more than two thirds of the marsh have been reclaimed and converted for agricultural purposes (González-Arteaga 1993), and secondly, because siltation of the marsh as a result of anthropogenic pressures has led to a reduction of water storage capacity, estimated at 26 hm^3 in the last 50 years (Rodríguez-Ramírez *et al.* 2005, p. 44). Still, the remaining vegetative structure contributes to buffering floods by providing a physical barrier (de Groot *et al.* 2002). Studies conducted specifically in the Doñana marsh noted that communities of *Artrocnemum* spp. provide protection against waves in the shallower parts of the marsh (Duarte *et al.* 1990, Espinar 2004). We used the abundance of emergent rooted aquatic vegetation (helophytes), measured as percentage coverage, as a proxy measure for flood buffering capacity. Our results suggest higher performance by the clear water state as compared to the turbid water state (19% against 5%).

Recreation The Doñana marsh attracts about 1 150 000 visitors per year, yielding an economic value of €37 million per year (Martín-López *et al.* 2009). With an estimated 40 000 geese and 150 000–200 000 waterfowl overwintering regularly in the marsh (Aguilar *et al.* 1986), bird watching is the main recreational activity. The abundance of waterfowl was therefore used as an assessment criterion. Previous research related waterfowl in the marsh to high primary production of the submerged vegetation (Duarte *et al.* 1990), and subsequent high secondary production of invertebrates (Montes *et al.* 1982) and fish (Hernando 1978), suggesting higher presence of these species in macrophyte-dominated clear water states. This parallels research findings for northern European shallow lakes. For example, Hansson *et al.* (2010) found a strong correlation between macrophyte cover and abundance of waterfowl for all analysed functional groups (herbivores, invertebrate feeders, and fish-feeding waterfowl), except for omnivorous species. Extrapolation of these findings, however, is not straightforward. For instance, Duarte *et al.* (1990) observed that the flag species for bird watching *Phoenicopterus ruber roseus*, was most abundant in turbid waters. Secondary data, and findings from other areas of the Doñana marsh (Rodríguez-Pérez *et al* 2007), support the idea of higher waterfowl abundance at the clear water state, but further empirical research is needed to confirm this hypothesis.

In summary, our results suggest that the patches of marsh with a clear water state dominated by submerged macrophyte beds are significantly more productive in terms of their capacity to generate ecosystem services (Table 4).

DISCUSSION

Our results on the stable states and associated services in the Doñana marsh are generally consistent with the broad pattern described by the theory of alternative stable states in shallow lakes from the north temperate zone. However, beyond this general pattern, our data also suggest a number of significant particularities that do not seem to be captured by the archetypical model (Fig. 1). The Doñana marsh exhibits an ecological functioning in which patches in a clear water state dominated by macrophytes coexist with patches in a turbid water state with little or no vegetation. This parallels previous findings by Santamaría *et al.* (1996), who observerd, in specific areas of the marsh, that local increase in *Ruppia dreppanansis* was coupled with a decrease in turbidity. Afterwards, with the disappearance of plant biomass by waterfowl grazing, turbidity increased again (Rodríguez-Pérez *et al.* 2007). In accordance with the shallow lakes theory, our results suggest that macrophytes (in particular, submerged plants) play a critical role in the performance of ecosystem functions on underlying ecosystem services supply.

Table 4 Performance of ecosystem services under alternative stable states of the marsh.

Ecosystem service	Assessment criteria	Proxy measure / indicator	Performance clear water	Performance turbid water
Water purification	Nutrient uptake and retention	Total-P sediment (μg/L) and SRP (μg/L)	●●●	●
Soil retention	Abundance of submerged macrophytes and helophytes	Submerged macrophytes and helophyte coverage (%)	●●	●
Flood buffering	Abundance of emergent rooted macrophytes (helophytes)	Helophyte coverage (%)	●●	●
Recreation	Quantity of waterfowl available for bird-watching	Abundance of waterfowl	●●●	●●

●: Low performance; ●●: medium performance; ●●●: high performance.

Consequently, in accordance with previous research on the ecological functioning of the marsh (Duarte *et al.* 1990, Grillas *et al.* 1993), our results suggest that ecosystem service performance was higher in the macrophyte-dominated clear water state, as compared to the turbid water state.

We highlight two particularities and advance hypotheses of possible explaining factors. The first particularity concerns the factors governing critical turbidity levels, and "flips" towards the turbid water state. Theories generally points to eutrophication by nutrient load as a determinant of the critical turbidity levels triggering shifts. However, in the Doñana marsh, turbidity levels did not respond primarily to nutrient load (Total-P). In fact, clear water states with abundant vegetation were found over a wide range of nutrient concentrations. Whereas this pattern differs from that described in many studies in shallow lakes, other studies found that clear water states can persist over a range of nutrient concentrations well beyond those observed in Doñana (see e.g. Beklioglu and Moss 1996, Ibelings *et al.* 2007). This result may be related, among other factors, to the depth, as in shallower waters the light reaches the bottom more easily and facilitates vegetation development, even with high nutrient concentrations and periphyton. As put forward by Scheffer and van Nes (2007), plants are less affected by turbidity at shallower sites. This is also consistent with findings by van Nes *et al.* (2002), who suggest that the range of nutrient values is narrower in deeper water systems. We hypothesize that inorganic suspended particles stirred up by livestock and waterfowl may play a more decisive role than nutrient load in promoting turbidity levels that trigger shifts in the marsh. A number of studies in Doñana (Duarte *et al.* 1990, Montes *et al.* 1993, Santamaría 1995, Santamaría *et al.* 1996, González 1999) have already suggested that intense grazing and trampling of macrophytes by animals such as cows, horses, sheep, deer, waterfowl (e.g. *Phoenicopterus rubber*), benthivorous fish (e.g. *Cyprinus carpio*), and the invasive crayfish (*Procambarus clarkia*), combined with suspended solids from mechanical disturbance, play a critical role in triggering shifts. Other studies have also stressed the impact of waterfowl on germination and growth of submerged macrophytes in the Doñana marsh (Grillas *et al*. 1993, Figuerola and Green 2004). Our descriptions are consistent with previous work that emphasizes the importance of consumers in explaining the dynamics of self-organized patchiness in ecosystems where there is a resource concentration through consumer–resource feedback (Hargeby *et al.* 2004, Rietkerk *et al*. 2004).

The second particularity relates to the observation that the pattern of alternative stable states arising in the marsh is apparently more complex than the image of just two contrasting states (i.e. clear waters and turbid waters) described in most shallow lake studies. Rather than showing bimodality, the pattern observed in the marsh is better described by a patchy mosaic in which turbid water states, clear water states, and intermediate states with mixed characteristics co-exist in a dynamic fashion. Rather than abrupt shifts taking place in the marsh as a whole, flips occur locally and asynchronously at the patch scale. Arguably, this behaviour relates to the highly heterogeneous character of the marsh, in which patches do not share the same properties at a given point in time. In other words, in a smooth environmental gradient, the response of the overall system tends to be gradual, and hysteresis becomes reduced if dispersion is strong. Hysteresis is mainly confined to the initial phases, in which none of the patches have shifted to the alternative state yet. As soon as the first patch shifts, a domino effect occurs, pushing over the neighbouring patches. The behaviour observed in the Doñana marsh is coherent with previous findings, suggesting that spatial heterogeneity tends to reduce the likelihood of abrupt large-scale shifts (Van Nes and Scheffer 2005, Scheffer and van Nes 2007). Moreover, patches did not show unambiguous characteristics of either clear water states or turbid water states. Indeed, as hinted by van Nes and Scheffer (2005) for relatively heterogeneous aquatic systems with a moderate dispersion of matter or organisms, a patchy pattern of co-existing alternative states occurs in the marshland of Doñana. The composition and structure of different patches of germinated hydrophytes depend on the interaction of the seed bank with features of each hydro-period (i.e. duration, quantity), and on the microtopology of the sediment surface (Geertz-Hansen *et al.* 2011). This latter feature is also modulated by pressure from the activity of several types of herbivores, e.g. mammals such as cattle and deer, waterfowl such as flamingo (*Phoenicopterus rubber*), benthivorous fish (*Cyprinus carpio*), and crayfish (*Procambarus clarkii*), and the relative contribution of each type needs to be assessed in future studies. In addition, the trampling effect of mammals in the marsh has a strong negative impact on the seed germination of macrophytes (Duarte *et al.* 1990, Montes *et al.* 1993, Grillas *et al.* 1993, González 1999, Geertz-Hansen *et al.* 2011).

Two possible alternative explanations of this patchy pattern may be advanced. The first concerns the possibility that areas presenting mixed characteristics represent transitional states between clear and turbid water. However, the fact that some variables in these patches do not show intermediate values, even if this could be explained in principle by hysteresis in the system, challenges this hypothesis. A second potential explanation concerns the possibility that more than two stable states co-exist in the marsh. Scheffer and van Nes (2007) argue that shallow lakes may be in more than just two stable states, and several additional alternative states have been described in the literature for shallow lakes dominated alternately by different types of primary producers such as charophytes (van Nes *et al.* 2002), submerged angiosperms, free-floating plants (Meerhoff *et al.* 2003, Scheffer *et al.* 2003), green algae or cyanobacteria (Scheffer and van Nes 2007). Beds of floating *Rannunculus baudotii* and *Lemna gibba* dominating particular patches of the Doñana marsh point towards the possibility of a floating plant-dominated state, but more research will be needed to confirm that these patches can be classified as an alternative stable state.

In synthesis, whereas our results are consistent with the broad pattern described by the theory of shallow lakes from northern temperate zones, factors such as heterogeneity, climate variability, marked shallowness and non-equilibrium dynamics suggest that extrapolation of management implications to Mediterranean shallow wetlands should, at best, be taken with care. Even if our study suggests higher performance of ecosystem services and higher biodiversity levels in the clear water state, the "desired *versus* non-desired state" scheme does not seem to be readily applicable for guiding wetland management and restoration in the Mediterranean context. In the Doñana marsh, the co-existence of turbid and clear waters in dynamic patchy mosaics seems to be part of the intrinsic functioning of the marsh and, thus, a precondition for the maintenance of its ecological functions and related services. Notwithstanding the need to address anthropogenic pressures affecting the function and regime-shift frequencies, the stability of ecosystem services in the long run may be enhanced by letting the hydrological cycle of the marsh function with its natural rhythm of flooding pulses and ecological shifts, rather than controlling them for short-term optimization of particular ecosystem services. Existing management plans in the marsh aim to maintain artificial flooding during the drought season to guarantee habitat provision for waterfowl and water supply for wildlife (mainly mammals) and domestic livestock (García-Novo and Marín 2005). Whereas this command-and-control approach is likely to increase ecosystem services in the short term, its interference with the natural processes and seasonal dynamics of the marsh may negatively affect siltation and euthrophication processes that are likely to affect the sustained long-term capacity to deliver ecosystem services.

However, our understanding of the links between alternative states and ecosystem service supply in the Doñana marsh is still limited, and it is clear that more research will be needed to develop sound models that describe alternative stable states in Mediterranean shallow wetlands and the implications of regime shifts for biodiversity and human well-being.

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