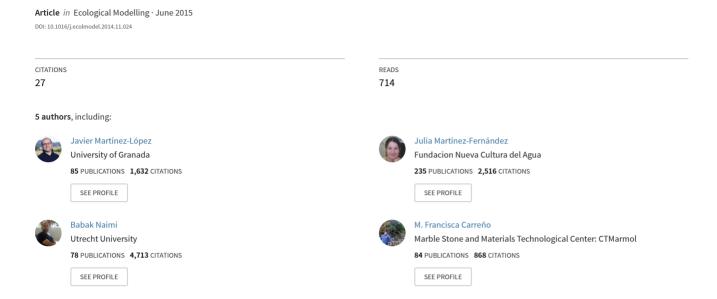
# An open-source spatio-dynamic wetland model of plant community responses to hydrological pressures

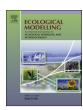


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## An open-source spatio-dynamic wetland model of plant community responses to hydrological pressures



Javier Martínez-López<sup>a,\*</sup>, Julia Martínez-Fernández<sup>b,c</sup>, Babak Naimi<sup>d,e</sup>, María F. Carreño<sup>a</sup>, Miguel A. Esteve<sup>a</sup>

- <sup>a</sup> Ecology and Hydrology Department, University of Murcia, Campus de Espinardo, E-30100 Murcia, Spain
- <sup>b</sup> Applied Biology, University Miguel Hernandez de Elche, Edificio Torreblanca, Av. de la Universidad s/n, E-03202 Elche, Alicante, Spain
- <sup>c</sup> Sustainability Observatory of Murcia Region, Institute for Water and Environment, University of Murcia, Edificio D. Tercera Planta, Campus de Espinardo, E-30100 Murcia, Spain
- d InBio/CIBIO, University of Eivora, Largo dos Colegiais, 7000 Eivora, Portugal
- e Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot SL5 7PY, Berks, United Kingdom

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#### ABSTRACT

Semiarid Mediterranean saline wetlands are semi-terrestrial ecosystems, which yearly undergo dry periods of several months, and shelter a rich, endemic and sensitive biota. In the last decades, the expansion of agricultural irrigated areas in semiarid Mediterranean catchments has led to altered inputs of water and nutrients to lowland wetlands. Hydrological alterations have affected characteristic plant communities, resulting in the replacement of valuable halophilic salt marsh and salt steppe plant communities by more generalist and opportunistic taxa, such as Phragmites australis (reed beds). A spatio-dynamic model and library were developed that aimed to explain the spatial distribution of three characteristic wetland plant communities in a semiarid Mediterranean wetland site in response to hydrological pressures from the catchment. Wetland plant communities and watershed irrigated agricultural areas were mapped by means of remote sensing at several dates between 1984 and 2008 and were partly used as forcing inputs and validation data. A dynamic model was initially developed using Stella software and then converted into R language by means of the StellaR software. Spatial dimension was added including neighbourhood and spatial flow algorithms representing the dispersion of plant communities. The conversion between plant communities was caused by the increase in water inflows from the watershed, mediated by spatial parameters, such as the distance to ephemeral rivers and the flow accumulation map within the wetland site. Results of the model were in agreement with remote sensing data, showing that in 2008 salt steppe had lost a half of its original area, whereas salt marsh and reed beds expanded extensively. The model developed in this study is available online as an R library, including all necessary input data sets and maps and documentation to run it. The model library offers a flexible tool that suits the needs of both advanced modellers and neophytes. Free and open source software and online code sharing repositories are proposed as modelling tools for future research.

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#### 1. Introduction

Semiarid Mediterranean saline wetlands are unique and endangered ecosystems which shelter high biodiversity. These are highly complex ecosystems in which the distribution of plant communities is mainly determined by spatial environmental gradients of

E-mail addresses: javier.martinez@um.es (J. Martínez-López), juliamf@um.es (J. Martínez-Fernández), naimi.b@gmail.com (B. Naimi), mariafra@um.es (M.F. Carreño), maesteve@um.es (M.A. Esteve).

water availability and salinity (Álvarez Rogel et al., 2001, 2006). During the last decades, land use changes in Murcia province and the associated hydrological changes at watershed scale have caused a rise in water tables of aquifers and have increased the levels of groundwater, flooding periods and soil water content in the wetlands (Álvarez Rogel et al., 2007). Characteristic plant communities, especially salt steppe, are negatively affected by these pressures to the wetland, while opportunistic invasive species, such as *Phragmites australis* (reed beds), are favoured (Chambers et al., 1999; Burdick and Konisky, 2003; Maheu-giroux and Blois, 2005). These changes are relevant from a biodiversity and conservation perspective since salt steppe is considered to be of priority interest

<sup>\*</sup> Corresponding author. Tel.: +39 (0) 332 789197.

according to the European Habitat Directive (Council of Europe, 1992).

A proper management of protected areas, such as wetlands, should aim at decreasing the influences on them from external anthropogenic pressures (Chape et al., 2005; Martínez-Fernández et al., 2014a). However, the failure to perceive that wetlands are not standalone elements in the landscape and to understand or express the complexity of spatial relationships among hydrology and wetland vegetation, has led to an extensive loss of the most characteristic wetland habitats during the last decades (Turner et al., 2000; Cools et al., 2013; Martínez-López et al., 2014a). In this regard, tools are needed to design effective management actions and evaluate potential scenarios. To this end, modelling the physical environment of wetlands is essential for assessing the relationships among pressures and species responses in these threatened ecosystems (Zhou et al., 2008).

Spatial modelling has become an important tool for plant ecology and biodiversity studies (Turner et al., 1995; Moloney and Jeltsch, 2008; Gardner and Engelhardt, 2008). In particular, spatio-dynamic modelling has served as a tool to assess the effects of land use changes on wetland ecosystems and to substantiate and improve wetland restoration measures (Fitz et al., 1996; Hattermann et al., 2006; Fagherazzi et al., 2012). When linked with remote sensing and field studies, spatio-dynamic modelling can help in overcoming some typical limitations of ecological studies, such as the lack of historical data or the difficulty of studying species interactions and their relationships with environmental variables and pressures both in space and time (Damgaard, 2003; Perry and Millington, 2008; Chen et al., 2011). In the last decades there have been important advances in spatio-dynamic modelling, leading to a diversity of models and modelling environments, such as SLAMM (Sea Level Affecting Marshes Model; Park et al., 1986), CELSS (Coastal Ecological Landscape Spatial Simulation model; Costanza et al., 1990), SME (Spatial Modelling Environment; Maxwell and Costanza, 1997), BTELSS (Barataria-Terrebonne Ecological Landscape Spatial Simulation model; Reves et al., 2000), MOHID (Braunschweig et al., 2004), Simile (Muetzelfeldt and Massheder, 2003), SimuMap (Pullar, 2004), Tarsier (Watson and Rahman, 2004) and TerraME (de Senna Carneiro et al., 2013). However, some of these remain unavailable for the research community and others represent commercial non-open source solutions, which limits their use and development. Furthermore, some key issues still remain open, such as the compatibility between models, the lack of model reusability and transparency and the nature of the targeted end-users or developers communities (Argent et al., 2006; Jørgensen, 2008). To propose a solution, we identified several requirements for modelling tools, as follows: (1) they should allow interoperability between models; (2) they should represent adequately documented software tools that can be useful for non-programmers, and (3) they should be flexible enough that advanced users can fully understand the role of each component and adapt them to case-specific requirements. The challenge is to develop modelling tools which are as general and flexible as possible to suit the needs of both advanced and less skilled modellers (Voinov et al., 2004; Jakeman et al., 2006). Trying to address these challenges, we have used R (R Core Team, 2013) as a modelling environment which meets the above-identified needs with an application for spatio-dynamic ecological modelling of semiarid Mediterranean saline wetlands.

R is an advanced statistical computing system that is freely available for most computing platforms and can be used for modelling. Among other advantages, R offers dynamic modelling, GIS and advanced graphics capabilities by means of multiple libraries (Petzoldt and Rinke, 2007; Pebesma, 2012; Hijmans et al., 2013). R offers the possibility of developing new functions and can easily connect to other free and open source GIS, such as GRASS GIS

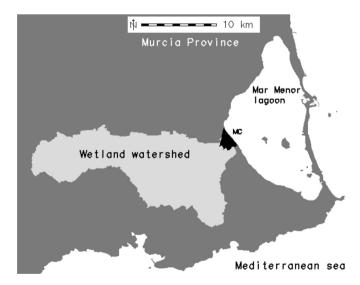
(GRASS Development Team, 2008), SAGA GIS (Development Team, 2010) or Quantum GIS (Development Team, 2009). Besides, R is used extensively in elementary teaching, for student projects and by researchers including those in companies and it is supported by a worldwide community of users (Ripley, 2001). Modellers need to be aware of the best practices and modelling techniques to improve their own approaches. It is essential that researchers make their models available and adopt common modelling tools and methodologies based on free and open source software tools (FOSS), which are freely accessible and can be iteratively improved by their community of users (Turner et al., 1995; Argent, 2004; Augusiak et al., 2014).

The model developed in this study addresses three plant communities in the Marina del Carmolí wetland in terms of spatio-dynamic interactions and responses to agricultural hydrological pressures from the catchment area over a 24-year period. The specific aims of the study were: (1) to develop an ecological model of a semiarid Mediterranean wetland site; (2) to build a user-friendly, online and documented version of a spatio-dynamic modelling library using R and (3) to test the wetland model by means of empirical and remote sensing data for the period 1984–2008.

#### 2. Background information

Murcia province (SE Spain: 37° N, 1° W) has a semiarid Mediterranean climate with a mean annual temperature of 16°C and a mean annual rainfall of 339 mm (Esteve et al., 2006). A semiarid Mediterranean saline coastal wetland was studied, which comprises 314 ha (Fig. 1). The Marina del Carmolí wetland is located in a lowland coastal plain, adjacent to the internal shore of the Mar Menor coastal lagoon, which comprises 12,700 ha (Conesa, 1990; Conesa and Jiménez-Cárceles, 2007). The lagoon and its adjacent wetlands are all RAMSAR sites, containing 18 Habitats of Community Interest according to the European Habitat Directive (Council of Europe, 1992). This site is also a Special Protection Area for Birds, a Site of Community Importance and a Special Protection Area for the Mediterranean.

The wetland mainly comprises salt steppe, salt marsh and reed bed areas, which are distributed according to the availability of water and salinity. Salt steppe is located in areas with low water availability and high salinities; reed beds (*P. australis*) are in areas



**Fig. 1.** Location map of the Marina del Carmolí wetland (MC) and its watershed area in Murcia province (SE Spain).

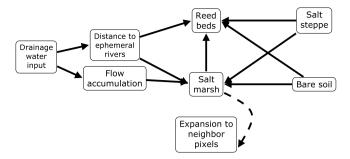


Fig. 2. Conceptual representation of the model.

with high water content and low salinity, whereas salt marsh occupies areas with intermediate water content and higher salinity (Álvarez Rogel et al., 2006, 2007; MARM, 2009). Salt steppe is considered of priority interest according to the European Habitat Directive (Council of Europe, 1992), salt marsh is of community interest and reed beds are not included in the Directive.

#### 3. Model description

#### 3.1. State variables and model assumptions

The three above-mentioned plant community types (i.e. salt steppe, salt marsh and reed beds) and the bare soil were the state variables of the model and were represented as four continuous raster maps, according to the initial maps of salt steppe, salt marsh and bare soil in the wetland that were established by means of remote sensing in year 1984, originally resampled to a pixel size of  $25 \text{ m} \times 25 \text{ m}$  (Carreño et al., 2008). The maximum total abundance of plant communities and bare soil in each pixel was limited to 25 units. Conversion among plant communities was caused by the drainage water input to the wetland and mediated by spatial environmental variables influencing water availability and growth. The model assumes only increasing or no water inputs, thus accounting only for the conversion of drier and more saline plant communities to more humid or less saline ones, i.e. salt steppe and bare soil (initially present) into salt marsh, and for the conversion of all of them into reed beds. In this regard, the model only accounts for the growth and expansion of the reed beds and salt marsh communities, considering the decrease of salt steppe and bare soil as a side effect of the growth of salt marsh and reed beds. Model variables and parameters were established using a deterministic approach based on the knowledge of the ecological tolerance of the plant communities and environmental variables (Martínez-López et al., 2014a).

Since reed bed stands were not dense enough to be mapped by remote sensors at that early stage, we did not know their initial location in the wetland and therefore they were assumed to be potentially present in all wetland pixels with an initial value of one unit in each pixel. As an invasive and clonal species which spreads rapidly by extending its rhizomes in all directions, this seemed an ecologically meaningful assumption (Bart and Hartman, 2003; Engloner, 2009). On the other hand, spatial neighbourhood algorithms were developed and included in the model in order to allow the salt marsh community to disperse to the surrounding pixels. Since this is the most typical plant community present under wet conditions, we considered this as a reasonable assumption. Since only increasing changes in water inputs were considered in the model, the dispersion of salt marsh was limited to neighbouring pixels containing bare soil or salt steppe, which are negatively affected by these pressures. Fig. 2 shows the conceptual diagram of the model.

#### 3.2. Driving force and environmental variables

In order to assess the agricultural hydrological pressures coming from the watershed over time, first the watershed area draining to the wetland was delineated from a raster DEM ( $10\,\mathrm{m}\times10\,\mathrm{m}$ ) using GRASS GIS 6.4 (GRASS Development Team, 2008; Martínez-López et al., 2013a). Historical watershed land cover maps for years 1987, 1996, 2000 and 2008 were obtained by means of remote sensing techniques (Carreño et al., 2011; Martínez-López et al., 2013a). The percentage of irrigated agricultural areas in the watershed was then calculated and converted into a Wetland Area Relative Percentage index (WARP; Martínez-López et al., 2014a,b), which was included in the model as a forcing input representing the agricultural hydrological pressure on the wetland over time ( $ILA_{WARP}$ ).  $ILA_{WARP}$  values for intermediate years were obtained by means of linear interpolation (Fig. 3).

The environmental factors considered in the model at wetland scale were: (1) the distance to two ephemeral rivers crossing the wetland and (2) the potential surface flow accumulation over the wetland area, as a proxy of waterlogging. Maps of distance of each pixel to the ephemeral rivers crossing the wetland were produced by means of map algebra operations using a digitized river network. The surface flow accumulation map over the wetland area was derived from a DEM by means of a watershed modelling operation using GRASS GIS. The resulting maps of flow accumulation and distance to ephemeral rivers were scaled to a 0–1 range.

#### 3.3. Potential growth rate and water availability

Potential growth rates for reed beds  $(pgr_{rb}=0.005)$  and salt marsh  $(pgr_{sm}=0.2)$  communities were estimated according to their degree of adaptation to the saline environment of the wetland. The water availability and growth of reed beds was influenced by the proximity to the ephemeral rivers  $(eph_1 \text{ and } eph_2)$ , whereas the salt marsh community was influenced by the potential flow accumulation (fa) in combination with the average distance to both ephemeral rivers (fa ave ephs; Pennings and Callaway, 1992; Alvarez Rogel et al., 2001, 2006, 2007; Carreño et al., 2008; Moffett et al., 2010), which ranges from 0 to 2 and is shown in Eq. (1). According to the best of our knowledge of the ecological tolerances for each plant community, potential water availability parameters <math>(pwa) for the expansion of the reed beds  $(pwa_{rb})$  and salt marsh  $(pwa_{sm})$  communities in each pixel were then computed using Eqs. (2) and (3), respectively:

$$fa\_ave\_ephs = fa + \left(1 - \frac{eph_1 + eph_2}{2}\right) \tag{1}$$

$$pwa_{rb} = eph_1^5 + eph_2^5 \tag{2}$$

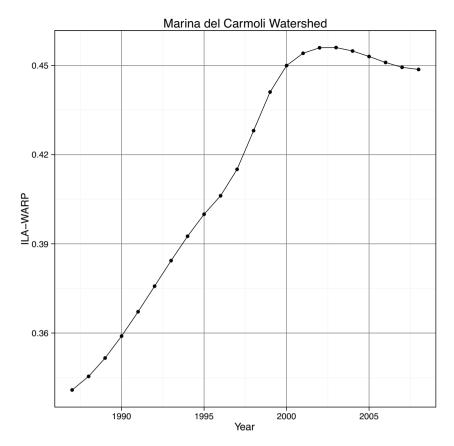
$$pwa_{sm} = fa\_ave\_ephs^4 (3)$$

An effective water availability parameter (ewa) for each plant community type was then computed depending on the drainage water input to the wetland ( $ILA_{WARP}$ ) as follows (Eq. (4)):

$$ewa = (1 + ILA_{WARP}) \times pw \tag{4}$$

#### 3.4. Conversion among plant community types

A conceptual diagram representing the conversion among plant communities types at each map cell is shown in Fig. 4. Water dependent conversion coefficients (*wdcc*) among different plant communities were included in the model as a way to represent the effect of increasing water inputs in the wetland on the relative ecological advantage of each specific plant community type over other. Eq. (5) shows this coefficient for the conversion from plant



**Fig. 3.** Wetland area relative percentage index of irrigated agriculture (*ILA*<sub>WARP</sub>) during the study period in the Marina del Carmolí wetland watershed according to remote sensing data.

community A to B. The lower the threshold value, the larger the conversion coefficient from one community type to another with the same water inputs. The threshold value for each conversion type ranged from 0.1 (from bare soil to reed beds) to 3 (from salt marsh to reed beds) and was estimated based on their known ecological tolerances (Álvarez Rogel et al., 2001, 2006, 2007).

$$wdcc_{AB} = \frac{ILA_{WARP}}{threshold_{AB}}$$
 (5)

The computed conversion rate ( $ccr_{AB}$ ) from plant community type A to B was therefore dependent on the effective water availability for B, the water dependent conversion coefficient from A to B and the potential growth of B (Eq. 6):

$$ccr_{AB} = ewa_B \times wdcc_{AB} \times pgr_B \tag{6}$$

Finally, the total conversion from plant community type A to B  $(tc_{AB})$  was dependent on the abundance of both plant community

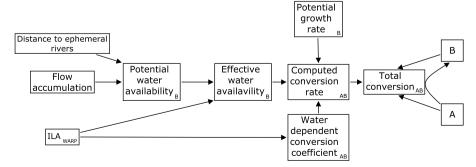
types, the computed conversion rate from plant community type A to B and a spatial limiting factor for plant community B related to the pixel size (Eq. (7)):

$$tc_{AB} = A \times B \times ccr_{AB} \times \left(1 - \frac{B}{25}\right) \tag{7}$$

For computing the change in abundance of each plant community type and bare soil, all total input and output flows were added up at each pixel and time step, together with potential salt marsh expansion from neighbouring cells.

#### 3.5. Model software

The model was developed starting from a basic dynamic model using Stella (ISEE Systems Inc., 2013) which was translated into R code using the StellaR software (Naimi and Voinov, 2012). Different available R libraries were used for model development, mainly



**Fig. 4.** Model diagram representing the conversion among plant communities. A and B subindices refer to the conversion from plant community type A to B. For more information see Sections 3.2–3.4.

**Table 1**Comparison of the area (ha) occupied by each plant community and bare soil after remote sensing (RS) and model results (MOD) for the years with initial and validation data.

	Salt steppe		Salt marsh		Reed beds		Bare soil	
	RS	MOD	RS	MOD	RS	MOD	RS	MOD
1984	179		2		0		134	
1992	149	155	72	54	0	15	93	80
1995	108	136	127	83	9	41	71	44
1997	104	124	99	96	32	53	79	30
2001	117	109	81	114	63	63	54	18
2008	90	90	121	137	74	65	29	12

the 'deSolve' package for solving differential equations (Soetaert et al., 2010) and the 'raster' package for the analysis of spatial data (Hijmans, 2013). The model code was finally wrapped as an R function that was then solved by numerical integration using the ode.2D function and the Euler integration method (Soetaert et al., 2010). State variables and spatial parameters were defined in the model as matrices in order to comply with the requirements of this function. The time step was set to 0.25 years and the 'Euler' method was selected as the integration algorithm. The model output is a matrix in which each row contains data from a specific time step and the columns correspond to all wetland pixels arranged by the different state variables. The total model execution took approximately one minute using one processor on a regular desktop computer with 4 GB of RAM. For validation purposes, the resulting wetland maps of abundances for each state variable were summarized into a categorical map in which each pixel was assigned the state variable with the highest abundance.

The model is freely available online as a standard R library, including all necessary input data sets and maps and documentation to run it (Martínez-López et al., 2014c). The development version of the model library is also available on an online collaborative environment (Martínez-López et al., 2013b) where advanced R users and modellers are able to run it and contribute to its development, as well as adapt it to their specific needs.

Several functions are included in the model library that allow a user to run the model, display and animate the simulation results, and change some optional parameters, such as the potential growth rate of the salt marsh and reed beds communities. Additionally, there is the possibility to establish random abundances and spatial configurations of the initial state variables, except for the reed bed community, in order to perform some model testing. Each function is documented according to the standard R documentation guidelines, which includes a description of the function, the input and output parameters, and some examples and optional explanatory notes, as recommended by Grimm et al. (2014).

#### 4. Model results and evaluation

Wetland plant community maps from years 1992, 1995, 1997, 2001 and 2008, obtained by means of remote sensing, with an overall accuracy ranging from 74% to 89%, were used as independent validation data for assessing the results of the model. Remote sensing maps were validated using field and aerial image data (Carreño et al., 2008; Esteve et al., 2008; Martínez-López et al., 2012).

The model was able to spatially simulate the abundance of the plant communities of interest in a timely manner during the study period, accounting for (1) the differential effects of the environmental parameters selected on each plant community; (2) the potential invasive effect of reed beds; and (3) the effect of dispersion of the salt marsh community. According to the values simulated by the model and those obtained by means of remote sensing (Table 1), between 1984 and 2008 the area of salt steppe was reduced by half,

**Table 2**Weighted average of fits (Ft) between wetland plant communities maps resulting from the model compared to the ones obtained by means of remote sensing, based on a mutiple-resolution-goodness-of-fit analysis. For more details see Section 4.

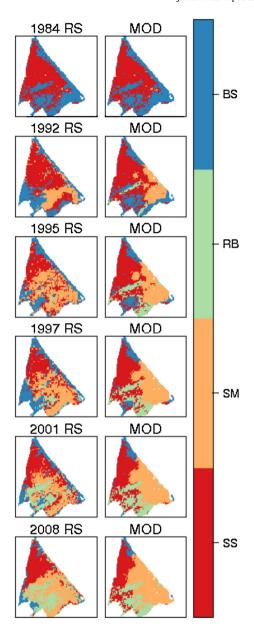
Year	Weighted average of fits (Ft)		
1992	0.77		
1995	0.75		
1997	0.70		
2001	0.66		
2008	0.74		

being mainly replaced by salt marsh, which became the dominant community. On the contrary, reed beds, practically absent in 1984, occupied 65 ha in 2008, after a significant expansion process which began in 1992. As a matter of fact, according to field data, reed bed patches were already present in the wetland in 1992. These were not mapped with the Landsat sensor due to their small size, but were clearly identified in the model results.

Results of the model showed high accuracy values in relation to the data obtained by means of remote sensing, which were used only for validation. Multiple-resolution-goodness-of-fit was performed for each validation year, comparing between the plant community maps resulting from the model and the ones obtained by means of remote sensing. Fits for moving windows of increasing cell sizes, a sequence of odd numbers from 1 to 113, were computed after an equation proposed by Kuhnert et al. (2005) and originally developed by Costanza (1989). The fits for each map were summarized into a weighted average with equal weights for all window sizes (Costanza, 1989). The comparison between the model-simulated wetland plant community maps and those obtained by means of remote sensing for each validation date showed accuracy values ranging from 0.66 to 0.77 (Table 2 and Fig. 5). Furthermore, the model showed almost no change in plant community abundance or dispersion during the study period when tested under a scenario of no drainage water inputs, in accordance with the model assumptions.

#### 5. Discussion and conclusions

Overall, this study demonstrates the suitability of open source software, such as R, for developing models that are open to the community and which are able to integrate complex historical environmental and biological variables over time and space. The model served as a research tool for testing plant community interactions and the relationships between plant communities and environmental variables in space and time. The model is easy to interpret, is mainly based on deterministic empirical data, and is openly accessible and easily reproducible. Furthermore, by means of the R library, the model could be extended by other researchers in order to include other conceptual wetland models of soil–plant relationships (González-Alcaraz et al., 2013), as well as addressing broader topics, such as the distribution, morphology and habitats of saline



**Fig. 5.** Wetland plant community maps over the study period after remote sensing (RS) and model simulated values (MOD). Legend: bare soil (BS), reed bed (RB), salt marsh (SM), salt steppe (SS).

wetlands (Castañeda et al., 2013). Additionally, the model could act as a scientific assessment tool to assist diverse environmental agencies in studying the responses of wetland plant communities to watershed agricultural pressures.

Wetlands are complex ecosystems exhibiting strong spatial heterogeneity, which makes them hard to study (Zhou et al., 2008; Fagherazzi et al., 2012). Therefore, including the spatial dimension of the main model parameters and state variables allowed us to better understand the distribution of each plant community type in response to the selected pressures. Results of the model clearly show the influence on this type of wetland of the expansion of irrigated agricultural areas in their watersheds. This explains the fact that conventional management strategies which ignore the hydrological processes occurring at watershed scale usually fail the protection and conservation goals of this type of ecosystem (Turner et al., 1995; Martínez-Fernández et al., 2014b). The relative changes between salt steppe, salt marsh and reed beds can be probably explained by the interaction between soil moisture and

conductivity gradients (González-Alcaraz et al., 2013). The initial increase of water inflows from the basin resulted in increased soil moisture and higher salinity, which favoured the expansion of salt marsh at the expense of salt steppe. At a later stage, around 1995, the increased water inputs reduced water salinity and allowed the expansion of reed beds. The net loss of salt steppe is very important since it is the habitat of Mar Menor wetlands with the highest interest from the point of view of the European Habitat Directive (Council of Europe, 1992).

The model library developed in this study can be easily linked with other modelling and GIS tools, such as Python, PCRaster and TGRASS, in order to expand its visualization capabilities or to build integrated models (Karssenberg et al., 2007; Schmitz et al., 2013; Gebbert and Pebesma, 2014). Besides, R gives access to classic and state-of-the-art statistical methods and it also possesses several libraries for obtaining directly biological and environmental data from the web, such as GBIF data (GBIF, 2013), which makes it suitable for web modelling approaches (Dubois et al., 2013). Although the model developed in this study is not computationally time consuming, R also offers several parallel computation libraries, allowing the implementation of large scale ecological models.

Between graphical interfaces and programming languages there are a wide variety of modelling tools available, that can help convert conceptual ideas into models (Costanza and Voinov, 2001). We agree that visual modelling environments that do not involve programming are easier to work with for high level users, especially for well developed models and non-advanced users. However, R also offers specific libraries, such as 'shiny' (RStudio Inc., 2013) and 'OpenCPU' (Ooms, 2014), that add graphical interface capabilities, which could be integrated in any existing model. Additionally, free and open source software offers a promising approach for developing standard modelling approaches, protocols and tools to collaborate in biodiversity research among researchers, students, decision makers and citizens in general (Jørgensen, 1995; Steiniger and Hay, 2009; Rocchini and Neteler, 2012). The adoption of an open source community approach is especially crucial to make progress on important conservation challenges, such as the implementation of large-scale ecological models to meet the Aichi Biodiversity Targets (COP 10 Decision X/2, 2010; Voinov et al., 2010).

Further development of this library by the authors is constantly ongoing. We aim to extend the library with other applications in a more generic context, such as model testing in similar wetlands, the inclusion of different and finer scale environmental variables and ecosystems, model sensitivity analyses, *etc.* Although the model library can be used independently from the original Stella model, the StellaR script (Naimi and Voinov, 2012) remains as a tool that allow modellers to connect both pieces of software for building and running new models in order to include a spatial dimension in their existing Stella models.

The use of online hosting repositories and platforms for collaborative model development, documentation and exchange should be encouraged, as seen in past initiatives, such as ECOBAS (Hoch et al., 1998; Benz et al., 2001). In this context, there are several free online repository hosting services, such as GitHub, BitBucket, SourceForge and R-Forge, that include additional functionalities to code sharing, such as version control, bug tracking, release maintenance, web and wiki services, which can be used as collaborative environments for model development (Wilson et al., 2013). Open scientific research is based on an open-source community through the use of such collaborative environments that facilitate model peer review, implementation verification (Augusiak et al., 2014), standarized model documentation (Grimm et al., 2014), replication of results and delivery of results to the public, especially for publicly funded science projects (Voinov et al., 2010; Poisot et al., 2013).

#### Acknowledgements

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#### Appendix A. Supplementary Data

Supplementary data associated with this article can be found, in the online version, at <a href="http://dx.doi.org/10.1016/j.ecolmodel.2014.11.024">http://dx.doi.org/10.1016/j.ecolmodel.2014.11.024</a>. These data include Google maps of the most important areas described in this article.

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