

Distribution patterns of a marsh vegetation metacommunity in relation to habitat configuration

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ABSTRACT: The identification of the factors behind the distribution of plant communities in patched habitats may prove useful towards better understanding how ecosystems function. Plant assemblages are especially important for wetland productivity and provide food and habitat to animals. The present study analyses the distribution of a metacommunity of helophytes and phreatophytes in a wetland complex in order to identify the effects of habitat configuration on the colonisation process. Ponds with wide vegetated shores and a short distance to a big (>10 ha) wetland, had higher species richness. The average percentage of surface covered by each species in all the wetlands correlated positively with the number of patches occupied by that species. Moreover, the community presented a nested pattern (species-poor patches were subsets of species-rich patches), and this pattern came about by selective extinction and colonisation processes. We also detected the presence of some idiosyncratic species that did not follow nestedness. Conservation managers should attempt to maximise the vegetated shore width and to reduce the degree of isolation to enhance species richness. Furthermore, a single large and poorly isolated reserve may have the highest level of biodiversity in emergent vegetation species in this wetland complex, however, the particular ecological requirements of idiosyncratic species should also be taken into account when managing this type of community.

KEY WORDS: Colonization · Extinction · Nestedness · Wetland · Phreatophytes · Helophytes

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INTRODUCTION

Disentangling the factors behind the distribution of animal and plant communities can prove useful to better understand how ecosystems function (Litchman & Klausmeier 2008). Many of these communities are distributed in patches, where suitable habitat areas for a set of species are surrounded by a matrix of non-available habitat. Metacommunities are species assemblages in patches that are linked by dispersed multiple potentially interacting species (Leibold et al. 2004). Several variables may affect distribution patterns in metacommunities, but the spatial configuration of patches and their habitat characteristics are

among the most important ones (Morin 1999). Therefore, studies on the distribution of metacommunities that account for these factors can provide relevant information for species management (see Parris 2006).

Wetlands are a clear example of patched habitats, especially in semi-arid regions. They support wet habitats in dry surroundings. Due to human activities, they are one of the most seriously threatened ecosystems in the world. One example can be found in the Mediterranean area, where natural wetlands have been reduced by 80 to 90% (Finlayson et al. 1992). Habitat loss and fragmentation have become one of the most important causes of species decline and loss, and have led to drastic changes in the struc-

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ture of plant and animal communities (Fahrig 2003, Cagnolo et al. 2006). Therefore, the landscape configuration of the resulting patchy habitats plays an important role in the distribution and abundance of species (Hernández-Stefanoni 2006). In this sense, it is important to acquire more knowledge about species distribution patterns to develop management measures for their conservation.

A common approach to studying the organisation of communities is to search for the distribution patterns and the processes causing these patterns (i.e. Barrett et al. 2010), such as the nested pattern in patchy habitats. When a community is 'nested', the species present in the poor patches are sub-samples of those present in the rich ones, and the same species tend to disappear from each patch in approximately the same order (Atmar & Patterson 1993, Patterson & Atmar 2000). Nestedness can be the outcome of different processes, the commonest being selective extinction, selective colonisation, presence of a nested habitat and passive sampling (Lomolino 1996, Wethered & Lawes 2005). Moreover, the nestedness theory has also been applied in conservation policies as it can be used in reserve design and to identify species of special interest (Fleishman et al. 2007).

When considering the usual patchy configuration of wetlands, not only because of their natural origin but also as a result of habitat fragmentation, the application of insularity models for marsh vegetation metacommunities might prove suitable (Pennings & Silliman 2005, Kunza & Pennings 2008). Understanding the repercussions of habitat patchiness on the distribution of these assemblages gains importance because they play multiple roles in the functioning of wetlands. Plant communities play a crucial role in fixing energy, supplying oxygen, and contribute to habitat structure (Cronk & Fennessy 2001). Furthermore, many animal species, some of which are globally threatened, depend on wetland emergent vegetation for their habitat (Mitsch & Gosselink 1993, Hawke & José 1996).

The present study analyses the distribution of vegetation in a wetland complex in order to identify how habitat configuration determines the distribution of plant species. For this purpose, 2 processes were studied:

(1) The importance of different environmental variables as predictors of species richness and community composition in relation to habitat configuration. We predicted that small, isolated patches would have a smaller number of species than large, clumped patches. We also expected some environmental vari-

ables to be important for the presence of marsh vegetation species.

(2) The effect of plant species coverage on species' ability to colonise patches. We predicted that the number of patches occupied by each species would correlate positively with the plant coverage of the community. We expected those plants with low-demand ecological requirements and high dispersal abilities to be more widespread. For instance, the species loss pattern would be ordered depending on the occurrence of each species (the 'nested' pattern). Moreover, we also studied the possible causes behind the nested pattern, and the implications for those species that do not follow that pattern (known as idiosyncratic species).

The results obtained in this study can be used in making decisions about how to maintain or maximise the species diversity of helophytes and phreatophytes in patched habitats, which can also be applied to their conservation and management.

MATERIALS AND METHODS

Study area

The study was carried out in a wetland complex of 22 marshes no further apart from each other than 30 km in the Baja Alpujarra (Southeast Iberian littoral, Almería, Spain; 36° 48' N, 2° 42' W), where there are no similar wetlands for at least a distance of 50 km. Each marsh consisted of a unique patch. The marshes were situated in a flat area (0 to 50 m a.s.l.) covered mainly by a matrix of greenhouses (Fig. 1) used to grow produce for human consumption (i.e. tomatoes, watermelons, paprika, cucumbers). The greenhouses are in general completely closed and the plants grown inside never appeared in the surveyed wetlands, and all the surveys were performed outside these greenhouses. Human action has an effect on the wetlands, but previous studies in the area have to date suggested that variables other than human influence are affecting the structure of the animal communities the most (Paracuellos & Telleria 2004, Paracuellos 2006a,b,c, 2008). Therefore, we believe our results are also applicable to other similar areas with or without the surrounding greenhouses. Rainfall in the area is scarce (annual range: 200 to 350 mm) and temperatures are mild (mean annual temperature range: 17 to 19°C, minimum average temperature: >6°C, annual fluctuation in temperature: ~13°C), these being typical of the Mediterranean environment (Capel 1990). The few unculti-

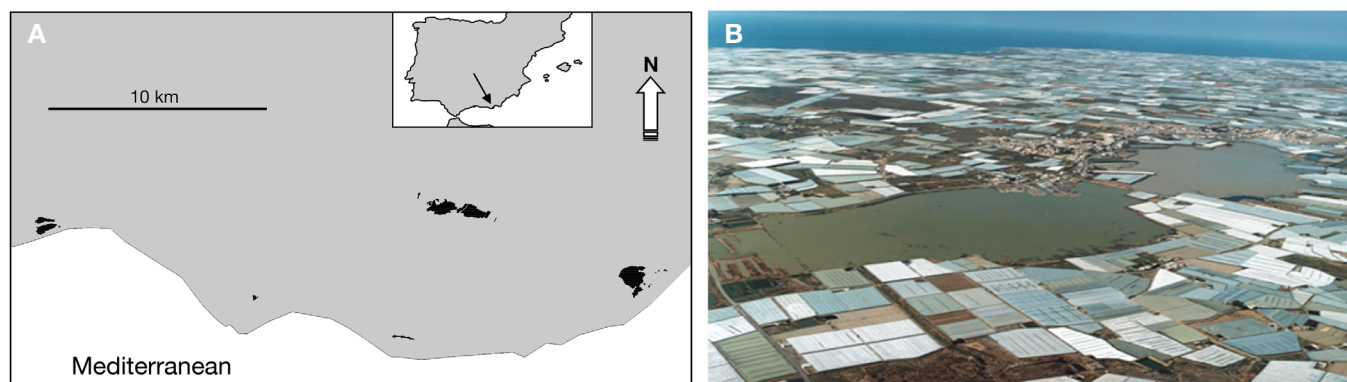


Fig. 1. (A) Geographical distribution of the study marshes (black areas). (B) Aerial photograph of a study wetland complex as islands of water in a sea of plastic (photo: Técnicas Fotográficas)

vated spaces available are usually colonised by natural Mediterranean shrubs (*Pistacia lentiscus*, *Rosmarinus officinalis*, *Thymus* spp.) (Mota et al. 1996). These wetlands are of a diverse origin since some are related to river deltas ($N = 4$), while others are abandoned salt pans ($N = 16$) or coastal salt marshes of an endorheic origin ($N = 2$). Several of these wetlands are legally protected and only management practices relating to conservation purposes are allowed. We included all the existing wetlands in the study area.

These wetlands are true islands for marsh-dependent species. They have open, permanent and deep, slightly salty water, which is often surrounded by a ring of emergent vegetation, composed mainly of helophytes and phreatophytes, which are dispersed mainly by wind and water. Helophytes occupy the lower marsh, while phreatophytes grow in the higher marsh (Casas et al. 2003, Giménez et al. 2003). The dominant species are *Phragmites australis* and *Tamarix canariensis* with 69 and 25% of coverage, respectively.

Field data

In each independent marsh, 14 variables were sampled (Table 1). As the marsh limits were well delimited, we considered that their separation (a distance of at least 20 m from the nearest marsh) was enough to consider them independent communities within the metacommunity. The studied variables are normally used in studies that assess relationships between marsh plants and environmental and spatial variables. The spatial variables (variables 1 to 8 in Table 1) were calculated using the ArcView GIS 3.1 software (Environmental Systems Research Institute 1992–1998) based on 1:2000 aerial photographs taken in 1998. The age of the wetlands in their pre-

sent ecological state and their origin were estimated using bibliography, historical documentation, authors' own data, personal communications and aerial photographs. In the spring of 1997–1998 (April to May), the identity and abundance of emergent vegetation species were sampled in each vegetation patch. The presence and coverage occupied by each species (9 in total: *Tamarix canariensis*, *Phragmites australis*, *Typha domingensis*, *T. latifolia*, *Juncus acutus*, *J. maritimus*, *Cladium mariscus*, *Bolboschoenus maritimus* and *Schoenoplectus litoralis*) were visually estimated within randomly chosen circles with a 25 m radius (1 to 20 circles per patch, depending on patch size). Low plant coverage facilitated visual estimations. Observations were made from one point. When the identity of a species was not clear, we subsequently verified the genus and species by getting closer to the individual plant. With this information, the following plant and patch characteristics were taken into account: (1) the number of species in each patch (sum of all the species found in the samples taken in each patch), (2) species abundance (the average value of the plant species coverage in marsh patches >10 ha, where insularity had to have a lower effect), and (3) the occupation frequency of marsh patches at species level.

Statistical analyses

To study the relationships among species and the spatial and environmental variables, ordination analyses were performed using CANOCO for Windows 4.1. This program enables partial analyses in which the influence of particular variables (termed 'covariables') is eliminated before the influence of the variables of interest (termed 'environmental variables')

Table 1. Environmental variables measured in the different marshes and sampling method used. *Variables logarithmically modified for the analyses

Variable	Method of sampling
1. Total surface	Open water surface + emergent vegetation surface delimited by means of digital planimetry
2. Surface covered by emergent vegetation	Digital planimetry
3. Percentage of shore occupied by emergent vegetation	Digital planimetry
4. Width of shore occupied by emergent vegetation	Digital planimetry
5. Distance to the nearest wetland*	Digital planimetry
6. Distance to the nearest wetland >1 ha*	Digital planimetry
7. Distance to the nearest wetland >10 ha*	Digital planimetry
8. Surface covered by wetlands in a 5 km radius	Digital planimetry
9. Maximum water depth	Mean values of various depth records measured about the center of the marsh at the moments of maximum flood during February 1998
10. Minimum annual salinity	Digital multiparametric probe at the moments of maximum flood during February 1998
11. Minimum concentration of total phosphorus in water	Colorimetry at the moments of maximum flood during February 1998
12. Average height of the emergent vegetation	Values visually estimated within circles of 25 m radius randomly chosen (1 to 20 per patch), during the 1997–1998 spring (Apr–May)
13. Age in its present ecological state	Bibliography, historical documentation, own data, pers. comm. and aerial photographs taken successively throughout the time. It refers to the state in the moment of the surveys
14. Pond origin	Bibliography, historical documentation, own data and pers. comm.

is tested. Ordination analyses are a descriptive/exploratory technique designed to analyse multiway tables containing some measure of correspondence between rows and columns (Legendre & Legendre 1998). Ordination analyses attribute scores to both species and the environmental and spatial variables so that the correlation between their scores is maximal given the best 'correspondence' between species and variables (Prodon 1992). Redundancy analyses (RDA) were selected from the different ordination procedures. RDA order species using axes that are linear combinations of the external variables, in such a way that the relationship between the species and these variables can be clearly seen. We included the UTM coordinates of the patches as covariables to account for spatial correlation. Significance was tested by the distribution-free Monte Carlo test (1000 permutations), in which the distribution of the test statistics under the null hypothesis is generated by random permutations of cases in the environmental data (Ter Braak & Šmilauer 1998). Multicollinearity was assessed by inter-variables correlation. Only one variable (the average percentage of surface covered by a species in the wetlands >10) was not included in the analyses because of its high correlation with the other variables (see 'Results').

To assess the existence of a nested pattern in community distribution, we constructed a matrix where each row and each column corresponded to a species and to a wetland, respectively. The matrix was reorganised to maximise nestedness in such a way that presences were packed in the upper left triangle of the matrix. We used the ANINHADO software (Guimarães & Guimarães 2006). This program uses a metric called matrix temperature (T), which is a measure of the disorder ranging from 0 (perfectly nested) to 100° (random). Similar results were obtained using the NODF (acronym for nestedness metric based on overlap and decreasing fill) metric (Almeida-Neto et al. 2008). The NODF metric quantifies 2 major properties for nestedness: whether marginal totals differ among columns and/or among rows, and whether the presences in less filled columns and rows coincide with those found in the more-filled columns and rows respectively (Almeida-Neto et al. 2008). The T of the matrix was calculated and compared with the T s of 2 null models. ANINHADO first uses a null model based on a random distribution of the presences assigned to any cell within the matrix, and then a second null model that assumedly controls the effects of passive sampling (Jonsson 2001). In our case, the presence of species i in patch j in the second null

model was the arithmetic mean of the presence probability of patch j (the proportion of presences in row j) and species i (the proportion of presences in column i). We calculated T of 1000 matrices of all the null models using Monte Carlo simulations. We then compared T of our matrix with the distribution of the simulated T s to test the significance of nestedness. When T in the observed matrix fell within the range of variation of any of the null models, the pattern was not considered nested. Moreover, the species that deviated from perfect nestedness were identified by a peak T and were termed as idiosyncratic. Therefore, a species was considered idiosyncratic if its T was higher than the system's T (Atmar & Patterson 1993).

We correlated the rank order of the wetlands in the final nested matrix to all the studied environmental and spatial variables to identify the possible causes of the pattern (Mc Abendroth et al. 2005, Heino et al. 2009). Spearman's rank (r_s) and Pearson (r) tests were employed in the correlations between variables according to the nature of the data using the SPSS 20.0 software (SPSS 2011). A significant correlation suggests that a community is packed in a predictable order due to the influence of the given variable. Statistical significance was set at $\alpha = 0.05$ for all the analyses.

RESULTS

The Monte Carlo permutation test provided strong evidence of a correlation between presence of marsh species and 2 external variables: distance to the nearest wetland >10 ha in size ($F = 4.00$, $p = 0.006$) and width of the pond's vegetated shore ($F = 2.15$, $p = 0.05$). The ordination plot illustrated that most species benefited from an increased vegetated shore width and from a shorter distance to another big wetland (Fig. 2). The effect of both variables was especially important for *Typha domingensis* and *T. latifolia*, while the effect for *Phragmites australis* was particularly low. The total observed variance of the first canonical axis was 69.6%.

Moreover, the average percentage of surface covered by a species in the wetlands >10 ha was related to the number of patches occupied by that species in the wetland complex ($r = 0.77$, $p = 0.01$), and was excluded from the model.

The distribution of the species in the wetland complex presented a nested pattern and the order of species loss in the vegetation patches was not random (matrix fulfillment = 47.4%, observed matrix $T = 9.1^\circ$; the entire estimated matrix T s differed significantly

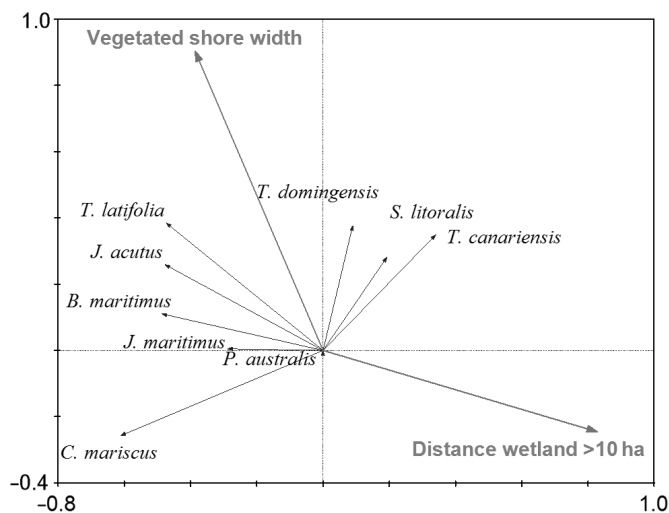


Fig. 2. *Tamarix canariensis*, *Phragmites australis*, *Typha domingensis*, *T. latifolia*, *Juncus acutus*, *J. maritimus*, *Cladium mariscus*, *Bolboschoenus maritimus* and *Schoenoplectus litoralis*. Redundancy analyses (RDA) ordination biplot of the marsh metacommunity. Species and environmental variables are represented by arrows that indicate the direction in which the variables are increasing. Longer arrows: stronger relationships between variables. Lines: plant species (black) and descriptive variables (grey)

from the observed matrix, $p < 0.001$ in null models I and II). The rank order of patches determined by the packed matrix correlated with the total surface ($r_s = -0.54$, $p = 0.01$), with the surface covered by emergent vegetation ($r_s = -0.66$, $p = 0.001$), and with the distance to the closest (>1 ha) patch ($r_s = 0.44$, $p = 0.04$). Moreover, 5 of the studied species were idiosyncratic (Table 2): *Tamarix canariensis*, *Schoenoplectus litoralis*, *Cladium mariscus*, *Juncus maritimus* and *Typha latifolia*. These species had higher T s than the T of the system and they did not follow a nested pattern. Besides, most species only presented mildly high T s compared with the system's T , and only 1 of them (*C. mariscus*) was much higher. On the other hand, both *J. acutus* and *Bolboschoenus maritimus* would be the first species to disappear through disturbance because they had low T and low coverage.

DISCUSSION

If we consider that the plant metacommunity in this study was mainly influenced by distance to the nearest wetland (>10 ha), our first prediction is partially supported by the field data. In general, we can state that the plant species composition in this wetland complex might be determined by a measure of the

Table 2. Presence (indicated by 'x') of the different emergent vegetation species in each marsh of the maximally packed matrix of distribution of helophytes and phreatophytes of the wetland complex. We indicate total surface, surface covered by emergent vegetation, and number of species for each wetland. We also indicate average coverage in patches >10 ha, number of occupied patches and Temperature (T) in the packed matrix for each species. *Idiosyncratic species with T higher than T of the system (9.1°)

Total surface (ha)	Veg. surface (ha)	No. of species	<i>Phragmites australis</i>	<i>Tamarix canariensis</i>	<i>Typha domingensis</i>	<i>Juncus acutus</i>	<i>Juncus maritimus</i>	<i>Bolboschoenus maritimus</i>	<i>Cladium mariscus</i>	<i>Schoenoplectus litoralis</i>	<i>Typha latifolia</i>
14.93	7.74	8	x	x	x	x	x	x	x		x
31.71	6.68	7	x	x	x	x	x	x	x		
1.05	0.43	6	x	x	x	x		x			x
49.73	27.77	6	x	x	x	x	x			x	
0.57	0.36	6	x	x	x	x			x	x	
0.47	0.25	6	x		x	x	x	x	x		
1.98	1	6	x	x	x	x	x	x			
7.75	7.74	5	x	x		x	x		x		
0.57	0.56	5	x	x	x		x	x			
88.57	16.45	5	x	x	x	x	x				
2.89	1.66	5	x	x	x	x	x				
59.52	6.43	4	x	x	x					x	
4.69	2.14	4	x	x	x					x	
1.59	1.24	4	x	x		x	x				
0.52	0.06	3	x	x	x						
9.12	1.35	3	x	x	x						
1.5	0.5	3	x	x	x						
0.83	0.3	2	x	x							
0.4	0.05	2	x	x							
0.1	0.05	2	x	x							
0.8	0.05	1	x								
0.2	0.05	1	x								
Helophyte			x		x			x	x	x	x
Average coverage >10 ha (%)			69.32	24.9	2.3	<1	<1	<1	1.67	<1	<1
No. occupied patches			22	19	15	11	10	6	5	4	2
Species T (°)			0.00	10.05*	4.64	0.60	11.10*	4.09	27.58*	12.57*	11.32*

degree of patch isolation. Several studies have confirmed the importance of patch area and degree of isolation to explain species abundance and richness in habitat patches (Petit et al. 2004, Sánchez-Zapata et al. 2005, Cagnolo et al. 2006, Sebastián-González et al. 2010). Indeed, area is also important because the distance to small patches was not selected as an explanatory variable. Patches >10 ha tend to have more surface covered by vegetation and higher species richness than smaller patches (Mann-Whitney U -test, both $p < 0.03$), and can function as a source of seeds in the metacommunity complex (Mouquet & Loreau 2003). Furthermore, none of the variables related to habitat quality (such as salinity or phosphorus concentration) influenced the metacommunity. This is probably because there were no marked variations between ponds in the values of these variables.

Plant coverage was an important predictor of a species' ability to occupy a patch (the interspecific occupancy–abundance relationship: reviewed by

Gaston et al. 1997, 2000). Therefore, the species covering higher percentages of wetland surface, such as *Phragmites australis*, *Tamarix canariensis* and *Typha domingensis*, also occupied a larger number of patches. On the other hand, the scarcer species occupied only a small part of the marshes, which was the case of *Bolboschoenus maritimus*, *Cladium mariscus*, *Schoenoplectus litoralis* and *Typha latifolia*.

We expected those plants with wider ecological amplitude and more diverse dispersal modes to be more geographically widespread. This evaluation was reinforced by the species' individual characteristics. *Phragmites australis* is the most widespread species in the area, and it is also distributed within a pond in many of the ecological zones created by the water level, although its optimum occupation is the intermediate zone (Coops & Van der Velde 1995). *P. australis* is dispersed by wind and water, thus implying short- and long-distance vegetative and seed propagules dispersal (Fér & Hroudová 2009). More-

over, *P. australis* presents high phenotypic and genotypic variations in relation to environmental factors such as climate, hydrology and salinity (Clevering & Lissner 1999). *Tamarix canariensis* can spread not only sexually by numerous tiny seeds that are dispersed by wind or water, but also vegetatively by adventitious roots or submerged stems (Merkel & Hopkins 1957, Brotherson & Field 1987). This species displays a pioneer strategy that benefits from dry seasons through its establishment on the margins of wetlands (Serrano et al. 2008). Helophytes are dominant in swamp vegetation and show marked local expansion due to rhizome spread and clonal growth, although hydrochory appears to be their main mode of dispersal (Grelsson & Nilsson 1991). Nevertheless, dispersal by air may be relevant for the plumed propagules in *Typha* spp., which confer them easy long-distance dispersal.

Conversely, *Bolboschoenus maritimus*, *Schoenoplectus litoralis* and *Cladium mariscus* produce fewer and larger fruits that are adapted to dispersal by water (Hroudová et al. 1997, Castroviejo 2008, Luceño & Jiménez Mejias 2008), and whose long-distance dispersal probably depends on transport by seed-consuming birds (De Vlaming & Proctor 1968). *Juncus maritimus* and *J. acutus* emerge respectively in the wetter and drier parts of high saltmarshes (Molina et al. 2003). These plants have reduced dispersal ability if compared to *Tamarix canariensis* because they produce small unplumed seeds that cannot be dispersed by wind. The wider ecological amplitude and dispersal modes of *Phragmites australis*, *T. canariensis* and *Typha domingensis* could, therefore explain their broad extension in our wetlands, in addition to their abundance.

The nested pattern found in the species' loss order in vegetation patches reveals that this order was, at least partially, predictable (Atmar & Patterson 1993). Assemblages of organisms with strong dispersal abilities, as in the studied species, may exhibit strong nested patterns of distribution (Cook & Quinn 1995). This pattern could have come about through selective colonisation and extinction because both area (both total surface and the surface covered by emergent vegetation) and isolation (distance to the closest patch >1 ha) correlated with the rank species order in the packed matrix. Therefore, we can state that large yet less isolated vegetation patches might hold all the species present in small, isolated patches (as in Lomolino 1996, Schouten et al. 2007). Of the other 2 more common causes of the pattern encountered, one was controlled by use of different null models (passive sampling; see Jonsson 2001), while the other

was the existence of a nested habitat (Wethered & Lawes 2005). The studied wetlands can be related to stratification in water depth and are structured as a central deep area surrounded by a gradient of concentric rings with progressively shallower water. This implies that when wetlands become smaller in size, there is generally a nested order in loss of habitat linked to zonation from deeper to shallower waters. Thus, deeper areas are lacking in small wetlands (see Paracuellos 2006a for a similar approach with waterbirds). Nevertheless, the present study refers only to emergent vegetation, usually located surrounding the open waters in this ecological zonation. The distribution of this vegetation can only be influenced by the existence of a nested habitat if total loss of the open water zone in any of the wetlands has previously taken place. As all the marshes retained some central open water, the nestedness found there does not seem to be caused by the existence of a nested habitat. It is important to note that nested habitats can also be generated by other abiotic habitat characteristics not included in this study, such as sediment oxygenation or maximum salinity, and further research is required to clarify this.

Idiosyncratic species are those species that do not follow the nested pattern (Patterson et al. 1996). When analysing nestedness in a metacommunity, idiosyncratic species are easily identified because their behaviour differs from that of the other species. They tend to be absent from species-rich sites and often appear in poor patches. Most of these species display this behaviour due to stringent ecological range requirements, which are only met in certain marshes independently of the other environmental variables of vegetation patches, such as surface or isolation. This may be certainly true for *Cladium mariscus*, *Schoenoplectus litoralis* and *Typha latifolia*, which are normally more affected by water eutrophication and soil salinisation than other helophytes with which they compete for resources (Duarte et al. 1990, Alvarez-Cobelas et al. 2001, Tanaka et al. 2004). Then, their presence in a patch may be restricted to those wetlands with low eutrophication levels and low salinity, even if these wetlands are not species-rich. Furthermore, the idiosyncratic behaviour of phreatophytes *Tamarix canariensis* and *Juncus maritimus* can be explained by the lack of their specific spatial niche in some small marshes or marshes with steep margins, and by the dynamics in vegetation succession, which occurs when grazing ceases, e.g. *J. maritimus*, thus provoking its disappearance (Bakker et al. 2009). Moreover, *T. canariensis*

sis woodlands are the late successional stage of semi-arid Mediterranean wetlands (Alcaraz et al. 1989).

The results of this study indicate that the degree of isolation and, indirectly, the size of wetlands, are important variables to describe the distribution of helophytes and phreophytes in the study system. From a general viewpoint, semi-arid wetlands with a low degree of isolation might normally contain the majority of emergent plant species' biodiversity. This is supported by the RDA and by the identification of the causes of the nested pattern. Therefore, it is necessary to pay special attention to more clumped, larger patches to guarantee the presence of a larger number of species. Moreover, the appearance of idiosyncratic species is principally related to their specific habitat needs rather than to increased patch surface. Consequently, in order to contribute to the global preservation of marsh-plant diversity, the conservation or restoration of a maximum number of wetlands should be a priority, as this favours habitat heterogeneity and the persistence of idiosyncratic species. However, small patches should not be forgotten as they may act as connectors or stepping-stones for many species.

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