

Niche breadth rather than reproductive traits explains the response of wetland monocotyledons to land-cover change

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Abstract

Question: We hypothesised that, even within the same plant functional group, there are specific distributions in land-cover classes and with land-cover change that are associated with niche breadth rather than reproductive strategy, and that the broader the niche of the species the better they cope with different land-cover classes and changes over time.

Location: The Llobregat Delta (Barcelona, Spain).

Methods: We analysed the distribution pattern of eight coexisting wetland perennial monocotyledons within human disturbance classes (obtained from the classification of land-cover categories in relation to their level of human disturbance) and changes in such classes from 1956 to 1999. We then compared species regional abundance and distribution patterns with seed dispersal type (wind dispersed versus non-wind dispersed species), vegetative spread (tussock versus caespitose-running species), and niche breadth (the number of phytosociological alliances in which each species is found).

Results: Regional abundance of the species was positively related to niche breadth, but was independent of reproductive traits. Similarly, distribution in human disturbance classes and their changes were associated with niche breadth rather than reproductive traits. In general, the more specialist the species, (i) the more they are concentrated in natural habitats, (ii) the less land-cover changes they are able to cope with, and (iii) the more they are restricted to stable change types, particularly to long-standing natural areas.

Conclusions: Ecological plasticity rather than dispersal capacity of dominant perennial monocotyledons determines their regional abundance and their ability to cope with recent and future land-cover changes in Mediterranean wetlands. As habitat specialists are less resistant to landscape change than generalists, floristic homogenisa-

tion may progress in these habitats with the likely scenario of increasing land-cover turnover.

Keywords: Catalonia; Habitat Conservation; Habitat Restoration; Human Disturbance Classes; Llobregat Delta; Species of Conservation Concern.

Nomenclature: Tutin et al. (1980).

Introduction

Any human-modified landscape has a mixture of different land-cover categories based on the degree of anthropogenic alteration to the natural ecosystems (Hobbs 2000). Changes in land cover can be defined as land transformations from one ecosystem state to another in terms of ecosystem structure, composition and function. Furthermore, any current land cover can be classified according to the identity and magnitude of the change it has experienced in the past.

At the regional scale, most emphasis has been placed on changes from natural to anthropogenically modified land cover (e.g., agriculture, pasture, rural and urban settlement) and their effects on ecosystem processes (Knops & Tilman 2000; Paruelo et al. 2001) and biodiversity conservation. However, changes in land cover can also be in the opposite direction: from intensively managed states back to semi-natural or natural states. These changes can be achieved after restoration or rehabilitation, especially in wetlands (Mitsch & Gosselink 1993; Comín et al. 2001; Edwards & Proffitt 2003). Spontaneous succession is also an important process in accomplishing some of the

restoration goals (Prach & Pyšek 2001), but alone it rarely yields restored sites that are ecologically equivalent to natural reference sites on timescales relevant to current conservation efforts. Indeed, restored wetlands commonly exhibit differences in their structure (e.g., organic matter, soil characteristics, vegetation) and species composition compared with longstanding natural sites (Klötzi & Grootjans 2001; Edwards & Proffitt 2003; van Duijn et al. 2003).

Changes in habitat affect plant species differently. Some species colonise, increase in abundance and expand their area of distribution, taking advantage of the disturbance associated with landscape change (Domènech et al. 2005; Pino et al. 2006). In contrast, other species might not colonise vacant sites, they might decline or even disappear locally during or after the land-cover change, especially if populations are small and the new habitat is not suitable for establishment and growth (Menges 1998; Maina & Howe 2000; Lindborg & Eriksson 2004; Lindborg et al. 2005).

A species' response to landscape change is primarily dependent on life-history strategies and trade-offs. Dispersal capacity in space and time directly determines a species' ability to colonise recently restored habitats (Maina & Howe 2000; Tikka et al. 2001) and is also inversely related to sensitivity to habitat loss and fragmentation, as reported for forests (Dupré & Ehrlén 2002; Jacquemyn et al. 2003; Vellend 2003; Kolb & Diekmann 2004; Verheyen et al. 2004), grasslands (Lindborg et al. 2005) and forest-crop mosaics (Geertsema et al. 2002). Clonal growth and poor dispersal capability allow species to persist in habitat fragments, leading to an 'extinction debt' (Vellend et al. 2006). Niche breadth (i.e., ecological amplitude) is also a key factor for explaining the current range of plant species (Kolb et al. 2006), but it also affects species' sensitivity to habitat loss and fragmentation (Dupré & Ehrlén 2002; Kolb & Diekmann 2004, 2005; Swihart et al. 2006) and even the potential response to global environmental change (Thuillier et al. 2005; Broennimann et al. 2006).

Understanding the biological and environmental determinants of a species' gain or loss in response to land-cover change and habitat fragmentation is of primary importance for conservation, as species change can have profound effects on ecosystem structure and function (Eviner & Chapin 2003). A number of recent studies have addressed this issue at multiple scales in a spatially explicit way. There are some examples of regional to continental approaches aimed at modelling future

distributions of plant species based on their life history, current niche and a set of global change scenarios (Thuillier et al. 2005; Broennimann et al. 2006).

Local approaches have commonly explored the role of species attributes in the colonisation of habitat fragments. There are a number of examples for forests (Jacquemyn et al. 2003; Vellend 2003; Kolb & Diekmann 2004, 2005; Verheyen et al. 2004) and semi-natural grasslands (Lindborg & Eriksson 2004; Lindborg et al. 2005) but, as far as we know, none for wetlands. The majority of these studies have compared current species' distributions to habitat extent and configuration. Only a few studies have linked species distributions to the historical legacy of changes in their present-day habitats (e.g., Jacquemyn et al. 2003; Domènech et al. 2005).

Our goal is to relate the distribution of eight wetland monocotyledon perennial herbs with similar life-histories but contrasting reproductive attributes and niche breadth to current land-cover classes and their recent (1956-1999) changes in the Llobregat Delta (Barcelona). We restricted the study to a closely related set of species to reduce the phylogenetic autocorrelation, which has affected several previous studies (Thompson et al. 1999; Kolb et al. 2006). All the selected species commonly occur in Mediterranean marshes and other wetlands, but show contrasting conservation concerns. Our hypotheses are that, (i) even for these closely related species with the same life forms and growing in similar habitats, species exhibit contrasting distribution patterns related to land-cover classes and changes according to species' biological and ecological attributes; and (ii) niche breadth rather than reproductive strategy is the primary correlate of a species response to changes in land cover: the more generalist the species are, the better able to cope with land-cover changes.

Methods

Study site

The study was conducted in the southern hemi-delta of the Llobregat River (Llobregat Delta hereafter), a 7000-ha area south of the city of Barcelona (Catalonia, NE Spain), which has undergone major land transformations in the last 50 years, including both ecosystem degradation and natural restoration. Despite the highly urbanised development of the area, it is still dominated by agricultural habitats. At present, marshlands and fixed dunes of

variable conservation status represent only 13% of the total land cover. The majority of the natural areas have been protected and included in the Spanish Natura 2000 network, but their conservation is threatened by intense land-cover change, water pollution and degradation. About 15% of areas occupying natural habitats exhibit moderate to intense degrees of degradation (more detail in Pino et al. 2006).

Study species

We selected eight perennial monocotyledons (Table 1) that are relatively similar in their biological traits. All colonise a range of coastal wetland communities having contrasting salinity and flooding regimes, including freshwater and brackish marshes. These species once dominated a set of plant communities previously widespread along wetland areas of the Mediterranean coast, including the majority of the study area, but have been severely reduced in extent by human disturbance. None of the study species is excessively restricted to a given area in the delta (patches of *Spartina versicolor*, the most restricted species, are scattered in an area of 8 km²). This selection criterion precluded the study of rare, highly threatened species included in red lists.

All the species selected have a perennial life form but differ in several attributes concerning their growth and reproductive strategy. *Phragmites aus-*

tralis has a running growth habit based on long, scarcely branched rhizomes. *Juncus acutus*, *Saccharum ravennae* and *Cortaderia selloana* have a tussock habit based on the production of a compact, highly branched rhizome that results in a clump-like form. *Juncus maritimus*, *Imperata cylindrica*, *Spartina versicolor*, and *Cladium mariscus* show an intermediate, caespitose growth habit, with relatively long and branched rhizomes that give rise to dense swards. Tussock species usually reproduce by seeds and show limited vegetative growth, whereas the remaining species mainly have high vegetative spread based on rhizome growth and division. No detailed information on seeds in soil is available for any of the species. *S. versicolor* seldom produces seeds in the study area (pers. obs.).

The study species also exhibit contrasting regional abundance and niche breadth. Regional abundance, inferred from distribution area in the delta, ranges from 6.2 ha for *S. versicolor* to > 560 ha for *P. australis* according to field mapping (see next section). The niche breadth of each study species has been estimated in terms of the number of phytosociological alliances in which each species is present in Catalonia, the administrative region (32 000 km²) to which the Llobregat Delta belongs and where there is highly variable topography, climate and land use (Pino et al. 2005). This number was recorded from the flora module of the Catalonian Database of Biodiversity (BDBC) project (Font & Ninot 1995), which is the product of the gathering, organisation and online exploitation of

Table 1. Main attributes of the study species in the Llobregat delta. ¹ = Tussock: perennial plants developing short, branched rhizomes giving compact tufts; Running: plants having a long, thin, less branched rhizome, extending indefinitely underground; Caespitose: intermediate between Tussock and Running types. ² = number of phytosociological alliances in which the species is present (based on BDBC relevés; <http://biodiver.bio.ub.es/biocat/homepage.html>). ³ = following the sigmatist phytosociological system of Braun-Blanquet (1932), developed in Bolòs et al. (2005).

Species	Area in the delta (ha)	Family	Life-form ¹	Reproductive mechanisms	Main seed dispersal mechanism	Niche breadth ²	Main community (phytosociological alliance) ³
<i>Cortaderia selloana</i>	28.5	Poaceae	Tussock	Seed	Wind	22	Diverse
<i>Phragmites australis</i>	563.2	Poaceae	Running	Vegetative/Seed	Wind	28	Reedbeds (<i>Phragmition australis</i>)
<i>Juncus acutus</i>	231.6	Juncaceae	Tussock	Seed	Not specific	17	Brackish rushbeds (<i>Juncion maritimi</i>)
<i>Juncus maritimus</i>	63.7	Juncaceae	Caespitose	Vegetative/Seed	Not specific	12	Brackish rushbeds (<i>Juncion maritimi</i>)
<i>Imperata cylindrica</i>	19.4	Poaceae	Caespitose	Vegetative/Seed	Wind	5	Dune rushbeds (<i>Imperato-Erianthion</i>)
<i>Saccharum ravennae</i>	28.7	Poaceae	Tussock	Seed	Wind	6	Dune rushbeds (<i>Imperato-Erianthion</i>)
<i>Spartina versicolor</i>	6.2	Poaceae	Caespitose	Vegetative/Seed	Not specific	5	Brackish rushbeds (<i>Juncion maritimi</i>)
<i>Cladium mariscus</i>	10.0	Cyperaceae	Caespitose	Vegetative/Seed	Not specific	4	Calcareous fens (<i>Magno-Caricion elatae</i>)

all floristic data in Catalonia (<http://biodiver.bio.ub.es/biocat/homepage.html>). This database presently accounts for >17 000 relevés, of which >15 600 (91%) have been classified into the classical phytosociological system (Bolòs et al. 2005). The number of alliances containing the study species ranges from four for *C. mariscus* to 28 for *P. australis*.

The study species also differ in their conservation concern. Stands of *C. mariscus* and *S. versicolor* have been prioritised in the Habitats Directive (Council of the European Communities 1992). *I. cylindrica* and *S. ravennae* have been included in local conservation lists. In contrast, *P. australis*, *J. acutus* and *J. maritimus* are common species in Mediterranean grasslands, with no special conservation concern, and *C. selloana* is an alien grass with recognised negative effects on Mediterranean marshlands (Domènech & Vilà 2006). No specific actions concerning either the introduction or control of this non-native grass have been taken in the study area.

Plant species mapping

In 2000, a detailed map of the study species locations in the Llobregat Delta was generated, mainly by field delineation of populations on 1:5000 orthophotomaps generated in 1999 by the Cartographic Institute of Catalonia (ICC). Field mapping was complemented by GPS tracking in order to include small populations, especially for the rarest species. Mapped locations were either monospecific stands or mixed stands in which the corresponding species was dominant. Minimum mapping area and minimum width of polygons were 100 m² and 10 m, respectively. A digital map containing the distribution areas of each species was generated by digitising the field cartography and adding GPS tracks using MiraMon, an in-house-developed GIS (<http://www.creaaf.uab.es/miramon>).

Land-cover/change mapping

Two land-cover maps of the Llobregat Delta for 1956 and 1999 were generated independently by on-screen photo-interpretation of orthophotomaps at a scale of 1:5000 using MiraMon. The map for 1956 was photo-interpreted on an orthophotomap generated *ad hoc* from black and white aerial photographs that were previously ortho-corrected, geo-referenced and assembled. The map for 1999 was directly photo-interpreted on colour orthophotomaps generated by the ICC. Both orthophotomaps were used

to generate land-cover maps of different levels of thematic resolution because of the contrasting colour and quality of images, and the availability of ancillary information on vegetation types in 1999 but not in 1956. In order to homogenise the results of photo-interpretation, to facilitate the comparison of maps and to reduce the number of categories to be analysed, the land-cover classes were reclassified into five human disturbance classes (hereafter, 'HD classes'; Fig. 1): (1) very low, corresponding to well-preserved marshlands and forests; (2) low, composed of marshlands and forests showing evident signs of disturbance (i.e., rubbish accumulation, high density of tracks, bare soil areas of human origin); (3) medium, corresponding to recently mowed agricultural fields still showing secondary grassland communities; (4) high, corresponding to croplands and bare soil areas; and (5) very high, including industrial areas, roads and railways. Grid versions (1 m pixel size) of the 1956 and 1999 HD class maps were generated and combined to produce an HD class change map with 25 (5×5) possible changes from 1956 to 1999. Changes were classified into three types: degradative, when the direction was to a more human disturbed class; restorative, when the direction was in the opposite direction; and stable, when the HD class did not change.

Species distribution according to HD classes/changes

The polygon coverages containing the current distribution of the study species were combined with (i) the grid version of the HD class map for 1999 and (ii) the grid with the HD class change map from 1956 to 1999. All combinations were performed using MiraMon. We used these maps to statistically test whether the observed distributions of the study species within HD classes and change types were significantly different among species. We also tested their departure from random, comparing them with the relative frequency of HD classes and change types in the whole study area (expected value). Comparisons were restricted to areas with very low, low and medium levels of disturbance in 1999, which were expected to concentrate the majority of the 1999 distribution area of the species. Since we limited the study to the deltaic plain, we can assume that all areas included in these HD classes are suitable for the wetland species (e.g., there are localities of freshwater and brackish marsh plants spread throughout the delta).

The distribution of HD classes, changes and change types (restorative, degradative and stable) were compared (i) among species (28 comparisons)

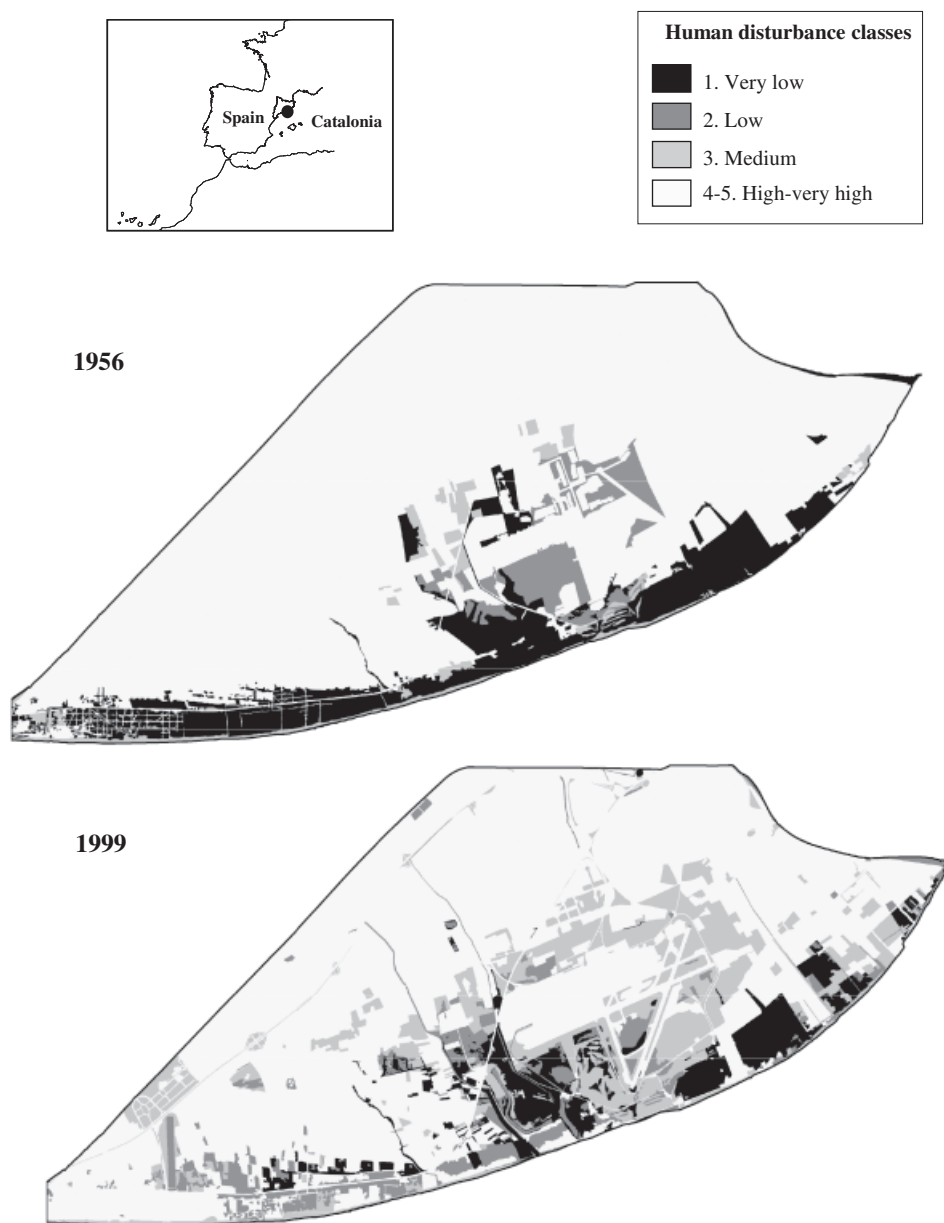


Fig. 1. Maps of human disturbance classes (obtained from the classification of land cover categories) for 1956 and 1999 in the Llobregat Delta (see text for more details).

and (ii) with those of the Llobregat Delta (eight comparisons) using the χ^2 test of goodness of fit. *P*-value was adjusted using the Bonferroni general method, considering the total number of comparisons ($n = 36$).

Species attributes according to regional abundance and HD classes/changes

Regional abundance and the percentage area of each HD class and change type in the Llobregat Delta were compared among species with contrast-

ing reproductive attributes using ANOVA. The species were previously scored as having wind-dispersed or non-wind-dispersed seeds, and tussock or caespitose-running vegetative spread (Table 1). The number of total, restorative, degradative and stable types was also compared between study species with contrasting reproductive traits using ANOVA. To avoid the number of change types being an artefact of the area occupied by a given species (as a smaller area provides less opportunity to sample the environment), we generated a coverage with points separated by 10 m from each other and covering all

the study area (650 000 points in total), and combined this layer with the HD class change map using MiraMon. We randomly selected 600 points falling within the distribution area of each species (covering 6 ha per species, the minimum distribution area, Table 1) and only tested the number of change types included in these points.

The association of ecological range with regional abundance, the number of change types, and the percentage area of each HD class and change type were explored using simple linear regressions. As in the case of reproductive traits, the number of change types was inferred from the 600-point subsample.

Results

Species distribution according to HD classes

In 1999, all study species were concentrated (> 99% of their distribution area) in the first three HD classes (very low, low and medium human disturbance), which together comprised 30.9% of the delta. The representation of species in very low and low HD classes together, from a low to high percentage, was as follows (Fig. 2): *C. selloana* < *P. australis* < *J. acutus* < *S. ravennae* < *I. cylindrica*, *S. versicolor*, *J. maritimus* and *C. mariscus*. Species followed different distributions within these two HD classes. Less than 10% of the total area of *C. selloana* was in the very low HD class; while values were 35-40% for *P. australis* and *J. acutus*, 55% for *S. ravennae*, 75% for *I. cylindrica*, and 95-100% for *S. versicolor*, *J. maritimus* and *C. mariscus*. In contrast, the medium HD class represented >70% of the total area for *C. selloana*,

45% for *P. australis*, 18% for *J. acutus* and 9% for *S. ravennae*; the rest of species were absent from this HD class.

Distribution in the first three HD classes was generally species-specific and significantly different from that of the whole delta, except for *P. australis* (Fig. 2). *S. versicolor*, *J. maritimus* and *C. mariscus* showed non-significant differences among their frequency distributions. Overall, species distribution was far from random in the three HD classes where they mostly occur: all species were over-represented in undisturbed classes, except for *C. selloana*, which was under-represented in this habitat.

Species distribution according to HD class changes

Frequency distribution across all HD class changes showed contrasting differences among species and between species in the study area. Only *P. australis* had no significant difference for the Llobregat Delta (Fig. 3). *J. acutus* showed a similar pattern to *P. australis*, mostly occurring in former high HD areas (agricultural) areas transformed to very low, low and medium HD areas (41.5%), but also in very low HD areas (preserved natural habitats) that have remained stable for this period of time (13.1%). *J. maritimus* was concentrated in very low HD areas, both stable (41.4%) and restored from high HD lands (30.7%). *C. selloana* had a distribution somewhat similar to that of *P. australis*. It was mainly distributed in medium HD areas formerly devoted to agriculture (62.2%) and low HD areas that had been restored to the very low HD class (17.2%); however, it was scarce in stable very low HD areas (6.6%).

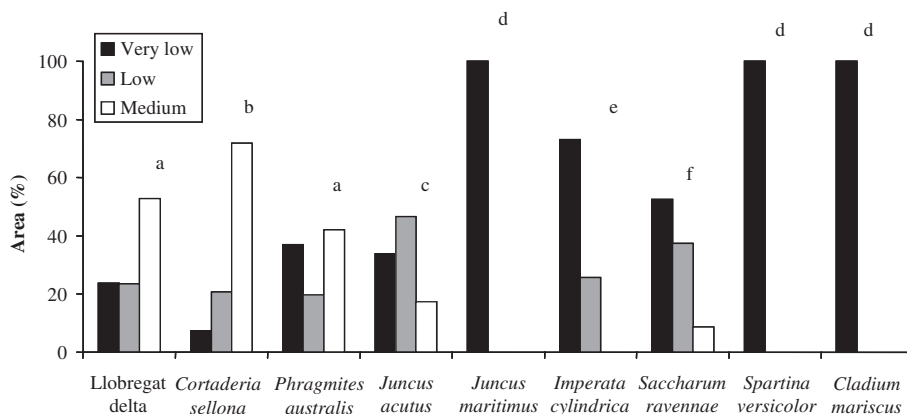


Fig. 2. Relative frequency distribution of human disturbance (HD) classes for each study species and for the whole Llobregat Delta in 1999. Different letters above columns indicate significant differences in HD class from distribution among species or with the Llobregat Delta according to a χ^2 goodness of fit test ($P < 0.05$; P -values were adjusted using the Bonferroni general method).

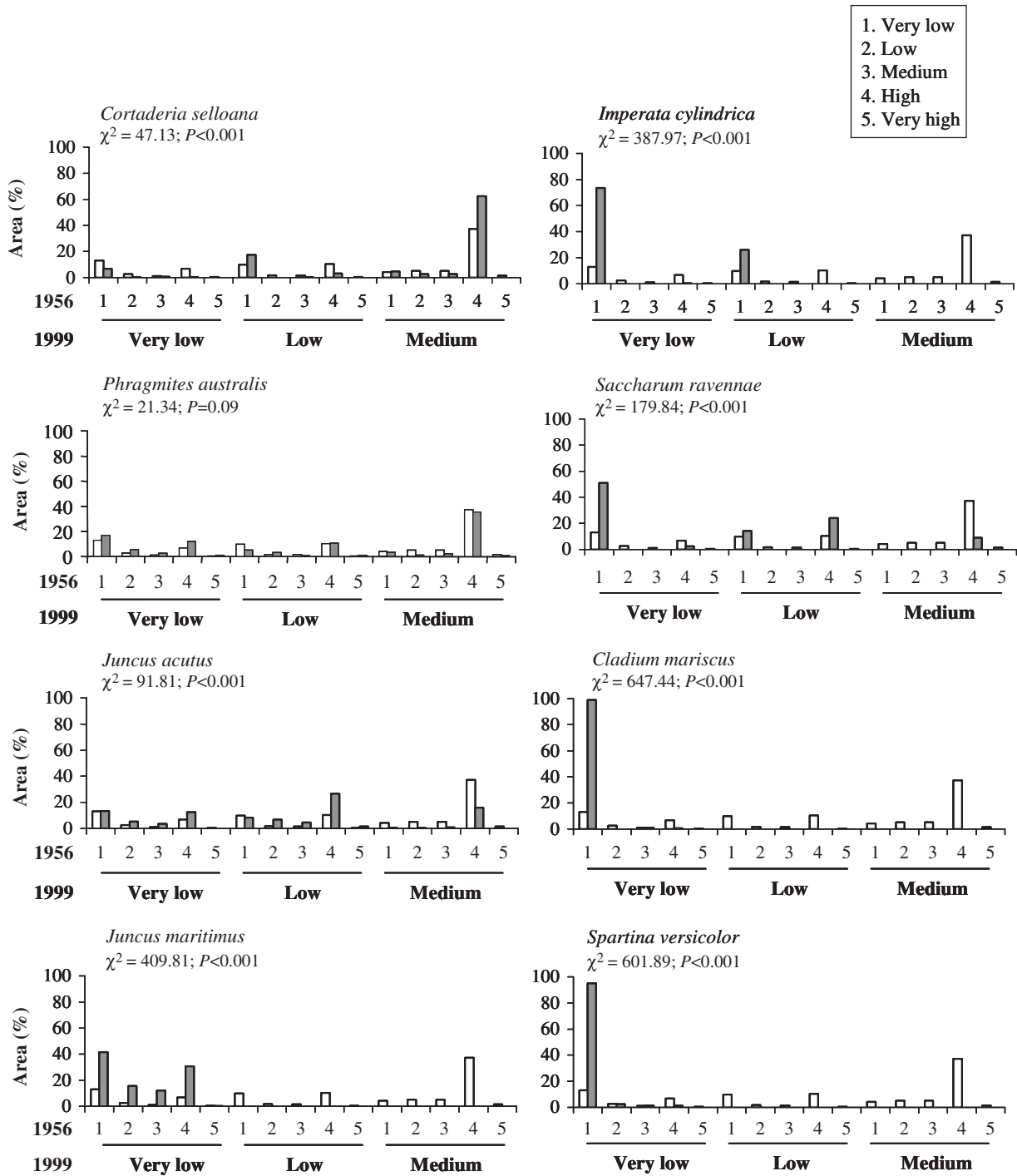


Fig. 3. Percentage of HD class changes from 1956 to 1999 in the distribution area of each study species (grey bars), compared with the percentages observed in the whole study area (white bars), and results of the corresponding χ^2 goodness of fit test comparing these distributions. Changes of 1999 agricultural and urban land cover were not considered because the distribution of the studied species is negligible in these land-cover classes. *P*-values were adjusted using the Bonferroni general method.

Of the 15 possible changes affecting the first three HD classes, *P. australis*, *J. acutus* and *C. selloana* were found in all, 13 and 11 respectively;

S. ravennae, *J. maritimus* and *I. cylindrica* were found in six, five and four respectively; and *S. versicolor* and *C. mariscus* were found in four and three,

respectively. Among the 15 class changes there are three possible degradation types, of which *P. australis*, *J. acutus* and *C. selloana* were found in all; *I. cylindrica* and *S. ravennae* in two, and *J. maritimus*, *S. versicolor* and *C. mariscus* in none. Of the nine possible restorative change types, *P. australis* was found in all, *J. acutus* in seven, *C. selloana* in five, *J. maritimus* in four, *S. ravennae* and *S. versicolor* in three, *C. mariscus* in two, and *I. cylindrica* in one. Finally, of three possible stable change types, *P. australis*, *J. acutus* and *C. selloana* were found in all, and the rest of the species in one (stable very low HD).

Stable, degradative and restorative change types corresponded, respectively, to 20, 19 and 61% of the area in the Llobregat Delta occupied by the first three HD classes in 1999 (Fig. 4). The frequency distribution of these change types was significantly different from those of each species, except for *P. australis*, *C. selloana* and *J. acutus*. Differences among species were significant ($P < 0.05$), except for *P. australis*-*J. acutus* and *S. versicolor*-*C. mariscus*. Stable change types were predominant for *S. ravennae*, *S. versicolor*, *C. mariscus* and *I. cylindrica*. In contrast, restorative change types, which are the most common in natural and seminatural habitats of the Llobregat Delta, were dominant in the other species.

Species attributes versus regional abundance and HD classes/changes

Regional abundance, the percentage area of HD classes, and number of change types showed no significant relationship to seed dispersal type, but species having wind-dispersed seeds had a greater

percentage area in degradative change types than did species with no specific dispersal mode. Vegetative spread had a stronger relationship to current distribution. Caespitose or running species had a significantly higher percentage area in the very low HD class than did tussock species, but the opposite was true in the low HD class. There were no significant relationships between vegetative spread and any variable concerning the number and percentage area of change types (Table 2).

Niche breadth (i.e., the number of phytosociological alliances) showed significant linear relationships with regional abundance and the percentage of very low and medium HD classes (Table 3). The broader the niche of a species, the higher was the regional abundance of that species and its percentage area in the medium HD class, and the lower the percentage area in the very low HD areas. Niche breadth was also linearly and significantly related to the number and percentage area of all change types, except for those involving degradation (the association was marginally significant for the number of degradative change types). Slopes of all regressions were positive, except for the percentage of stable change types.

Discussion

Our results indicate that, despite similarities in life-cycle strategy, the perennial monocotyledons studied in Mediterranean wetlands exhibit major differences in their (i) regional abundance, (ii) distribution in HD classes, and (iii) response to land-cover change in the Llobregat Delta. These differences are more strongly related to the niche breadth of the species than to the dispersal capacity, as

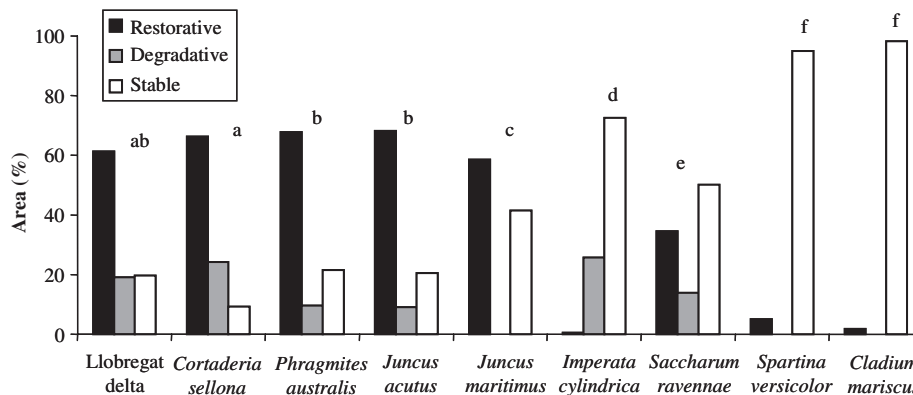


Fig. 4. Relative frequency distribution of HD class change types from 1956 to 1999 for each study species and for the whole Llobregat Delta. Different letters above columns indicate significant differences between species or within the Llobregat Delta according to a χ^2 goodness of fit test ($P < 0.05$; P -values were adjusted using the Bonferroni general method).

Table 2. Mean values (\pm SD) of HD classes and change types when comparing species with contrasting seed dispersal and vegetative spread attributes, and results of the corresponding ANOVA tests.

	Wind	Main seed dispersal mechanism				Vegetative spread		
		Non-specific	<i>F</i>	<i>P</i>	Tussock	Caespitose-Running	<i>F</i>	<i>P</i>
Regional abundance (ha)	77.87 \pm 105.79	159.95 \pm 268.87	0.323	0.591	96.27 \pm 117.20	132.50 \pm 241.86	0.056	0.820
Area (%) of HD classes								
Very low	42.5 \pm 27.6	83.5 \pm 33.0	3.621	0.106	31.3 \pm 22.6	82.0 \pm 27.8	7.029	0.038
Low	25.9 \pm 8.2	11.7 \pm 23.3	1.334	0.292	34.9 \pm 13.2	9.1 \pm 12.6	7.616	0.033
Medium	30.6 \pm 32.9	4.3 \pm 8.7	2.388	0.173	32.6 \pm 34.2	8.4 \pm 18.8	1.752	0.234
Number of change types								
Total	9.0 \pm 5.0	6.3 \pm 4.6	0.664	0.446	10.0 \pm 3.6	6.2 \pm 5.0	1.302	0.297
Restorative	4.5 \pm 3.4	4.0 \pm 2.2	0.061	0.813	5.0 \pm 2.0	3.8 \pm 3.1	0.346	0.578
Degradative	2.5 \pm 0.6	0.8 \pm 1.5	4.742	0.072	2.7 \pm 0.6	1.0 \pm 1.4	3.606	0.106
Stable	2.0 \pm 1.2	1.5 \pm 1.0	0.429	0.537	2.3 \pm 1.2	1.4 \pm 0.9	1.670	0.244
Area (%) of change types								
Restorative	42.3 \pm 31.8	33.4 \pm 34.9	0.141	0.720	56.4 \pm 18.9	26.7 \pm 33.5	1.908	0.216
Degradative	18.9 \pm 7.4	2.5 \pm 5.0	13.396	0.011	16.4 \pm 7.4	7.4 \pm 11.4	1.443	0.275
Stable	38.8 \pm 29.0	64.1 \pm 38.4	1.104	0.334	27.3 \pm 21.4	65.9 \pm 33.6	3.099	0.129

Table 3. Parameters of the linear regressions performed on niche breadth (number of alliances) versus HD classes and change types.

	<i>R</i> ²	df	<i>F</i>	<i>P</i>	y-intercept	slope
Regional abundance (ha)	0.613	6	9.490	0.022	- 88.03	16.73
Area (%) of HD classes						
Very low	0.548	6	7.260	0.036	98.96	- 2.91
Low	0.067	6	0.430	0.535	12.47	0.51
Medium	0.672	6	12.300	0.013	- 11.90	2.37
Number of change types						
Total	0.869	6	39.710	0.001	1.71	0.48
Restorative	0.832	6	29.670	0.002	0.95	0.27
Degradative	0.481	6	5.570	0.056	0.29	0.11
Stable	0.824	6	28.040	0.002	0.47	0.10
Area (%) of change types						
Restorative	0.744	6	17.400	0.006	1.09	2.97
Degradative	0.060	6	0.380	0.560	7.22	0.28
Stable	0.743	6	17.320	0.006	91.69	- 3.25

indicated by the low number of significant associations with seed dispersal type and vegetative spread.

The main seed dispersal mechanism of our study species was related only to the colonisation of degraded habitats (Table 2), and this probably reflects the widely known preference of wind-dispersed plants for vegetation gaps (Grime et al. 1989; Thompson 1992). On the other hand, vegetative spread was only related to HD class. The fact that running or caespitose species are more likely to concentrate in very low HD areas than are tussock plants reflects the tendency for undisturbed wetland communities to be dense, monospecific stands dominated by long-lived, large, rhizomatous, highly competitive perennials (Mc Naughton 1975; Eriksson 1992; Clevering 1995).

Generally, species abundance and persistence in changing landscapes is expected to be related to the ability of the species to colonise new sites, which, in turn, depends on the number of their individuals in surrounding areas, but also to their reproductive traits and dispersal capacity that determine their overall vagility. However, this is far from being universally proven. In forest landscapes, which are probably the best known case study, remnant habitat patches have been found to have a strong influence on the recovery of forest plant diversity (Jacquemyn et al. 2003; Vellend 2003), suggesting a significant effect of propagule pressure on the colonising capacity of species. The role of reproductive traits in species persistence and colonisation has also been highlighted. Verheyen et al. (2004) found that low seed production and the predominance of short-distance seed dispersal are primary negative correlates for the persistence of forest plant species in landscapes with high rates of habitat turnover. Jacquemyn et al. (2003) observed that patch occupancy was related to life-form, which, in turn, was correlated to seed mass and seed dispersal. Kolb & Diekmann (2005) also found that species having few and heavy diaspores without dispersal structures had low dispersability in space and time and therefore were more negatively affected by forest isolation. In contrast, other studies (Geertsema et al. 2002; Kolb et al. 2006) have found little association of life-history traits with forest species frequency at a variety of spatial scales, from local to national.

In the case of wetland monocotyledonous species of the Llobregat Delta, historical propagule pressure (i.e., abundance of target species in surrounding areas in 1956) and other non-studied dispersal mechanisms might have a significant

relationship with species regional abundance and persistence over time. There is no information on the pre-study distribution and abundance of the target species. However, this might not be relevant because many wetland species can be dispersed over large distances by birds (Santamaría & Klaassen 2002). This phenomenon would also obscure any association of the short-distance mechanisms studied in relation to species distribution in land-cover classes and changes. Nevertheless, we cannot expect a large effect of dispersal in time through persistent seed banks, since wetland perennial species commonly lack seeds with long-term dormancy mechanisms (Martínez-Sánchez et al. 2006). However, all these statements are quite speculative as no detailed information is available for the study species.

In contrast to reproductive attributes, regional abundance and responses to land-cover classes and changes were strongly related to niche breadth in our study species. Indeed, species found in more phytosociological alliances have higher regional abundance, and are able to cope with more land-cover changes. Nevertheless, these results can be affected by how we define niche breadth, because phytosociological alliances summarise a range of environmental factors (i.e., temperature, moisture, soil depth, bedrock), including human disturbance level. However, the risk of circularity in our analysis is reasonably limited by the fact that (i) species niche breadth has been determined independently of the Llobregat data, using the much larger geographical context – and environmental gradient – of the BDBC project, and that (ii) phytosociological relevés are traditionally focused on natural, quite well preserved habitats, and reflect the variation in environmental factors rather than in human disturbance levels. In fact, 90% of BDBC syntaxa with recorded presence of our study species can be classified as non-anthropogenic habitats (i.e., not belonging to the *Ruderali-Secalietea* phytosociological class). Therefore, the number of phytosociological alliances is, in our case, more an indicator of the range of environmental conditions than a measure of the variation in human disturbance level.

The role of niche breadth in determining species abundance and resistance to habitat degradation has been reported in a number of recent studies. In the herbaceous flora of Central England, species regional abundance was inversely related to a specialism index describing the niche breadth achieved (Thompson et al. 1999). Kolb et al. (2006) also found that forest plant specialists are generally less distributed than generalists in German decid-

uous forests. Jacquemyn et al. (2003) observed that species with more habitat requirements are, in turn, more sensitive to forest fragmentation, generally showing less capacity to colonise new habitat patches. Occupancy rates of forest fragments were also found to be positively related to niche breadth of vertebrates living in forest-crop mosaics (Swihart et al. 2006).

Bearing in mind that the low number of studied species limits the scope for conclusions, our study has identified several features relevant to conservation. First, as wetland monocotyledon specialists are less resistant to landscape change than generalists, our study highlights the difficulties of achieving the ecological integrity of natural sites when restoration relies solely on spontaneous succession. This supports the opinion, shared by most ecologists and conservationists, that the precautionary principle should play a pre-eminent role in any actions concerning these habitats, and that management efforts for the conservation of wetland habitats and species need to focus on the preservation and improvement of remnant natural sites, rather than on restoration of degraded areas.

The results also provide evidence of a possible mechanism for wetland plant homogenisation under the currently accepted scenario of increasing land-use/cover change. As McKinney & Lookwood (1999) stated, biotic homogenisation is the process whereby species with sensitive requirements ('the losers') will continue to have high extinction rates or will be reduced to surviving in small fragments of undisturbed habitats, while those widespread, broadly tolerant forms ('the winners') will spread and become increasingly dominant. We have found that wetland monocotyledon species of high conservation concern are more habitat-sensitive than the rest of the species, that they are more restricted to undisturbed areas, and that they are much less able to colonise change types than other relatively similar species. Consequently, an increase in land-cover turnover will penalise the former but benefit the latter, thus contributing to the homogenisation of the dominant flora in Mediterranean wetlands.

Acknowledgements. Funding was obtained from the Ministerio de Ciencia y Tecnología (REN 2000-0361/GLO and SEC2000-0836-C04-04 projects), and the European Commission Framework 6 Integrated Project ALARM (Assessing LArge scale environmental Risks for Biodiversity with tested Methods, GOCE-CT-2003-506675).

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Received 20 December 2007;

Accepted 21 July 2008.

Co-ordinating Editor: A. Symstad.