Interference competition in a threatened seabird community: A paradox for a successful conservation

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ABSTRACT

It is often assumed that conservation actions targeting a threatened community (e.g. habitat protection) will result in similar benefits for all species. However, complex interactions between species, such as interference competition, may result in displacement of subordinate, vulnerable species. We analysed here the spatio-temporal population dynamics of a threatened seabird community since the protection in the 1980s of several breeding sites at the Ebro Delta, western Mediterranean, Spain during 1980–2007. Competition for the most suitable patches was governed by body size, with smaller species avoiding associations with larger, dominant species. We tested whether the density increase of the larger species (yellow-legged gull *Larus michahellis* and Audouin's gull *Larus audouinii*) at La Banya (the highest quality patch within the Delta) affected species diversity at the local level. As expected, such diversity decreased, resulting also from the colonisation of other sites by smaller species, some abandoning the former area. The conservation paradox appeared because the interference competition was dominated not only by the largest species of the community, the yellow-legged gull, which is sometimes considered a pest species, but also by the vulnerable Audouin's gull, a flagship species which has ca. 65% of the total world population at La Banya. Nevertheless, the availability of alternative patches within the Ebro Delta ensured a high biodiversity at regional scale. Results highlight the role of turnover of competing species within a community in ecosystem function and stability, and the importance of alternative sites and dispersal abilities for the conservation of vulnerable communities.

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1. Introduction

Communities, together with simpler and more complex systems (i.e. species and ecosystems, respectively), have been recognised as one of the level of ecological structure on which conservation should devote most research efforts (Orians and Soulé, 2001). The structure of communities is partially governed by competition among species within a guild (Tilman, 1982; Schluter, 2000), with several consequences at ecological and evolutionary levels, such as competitive exclusion when resources are limited (e.g. Armstrong and McGehee, 1980). There is a large spatio-temporal heterogeneity in the patterns of community structure (e.g. Vitt and Pianka, 2005) and the recent effects of global change may have exacerbated such variability and altered the processes resulting from competition (Olden et al., 2004; Harley et al., 2006). Competition in conservation has been sometimes referred for introduced species and their effects on native biotas (e.g. Pimm, 1991; Sinclair et al., 2006; Rajbanshi and Pederson, 2007). Nevertheless, little is known about how interspecific competition in a community affects conservation in practice; in fact, many environmental policies, laws, and actions tend to ignore the effects of species interactions (Mills et al., 1993; Soulé et al., 2003). This is especially true for the effects of intra-guild competition, even though some communities (e.g. inhabiting relict habitats once very abundant) are formed by a high proportion of vulnerable species. For instance, it has been suggested that the removal of keystone-species may affect the whole community and even the whole ecosystem, although empirical evidences are few and the processes underlying such impacts (including competition) are poorly understood (Simberloff, 1988; Mills et al., 1993). In some cases, interspecific competition may affect the rarest species of the community,

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especially when they are also subordinates (e.g. by size) when exploiting the same resource (e.g. Abramsky et al., 2005; Carrete et al., 2006; van Veen et al., 2006). Such harmful consequences for some species of the community are typical of contest or interference competition (Krebs, 2001).

Here we analysed the conservation consequences of interference competition in a threatened seabird community in the Ebro Delta, a salt marsh of the western Mediterranean. This community is formed by a co-occurring assemblage of similar species in terms of trophic, and especially habitat overlaps (e.g. Fasola and Canova, 1992; Sadoul et al., 1996; Sadoul, 1997; Oro, 1999). From a conservation point of view, the community has a great value because is formed by twelve species, seven of which included in Annex I of the Birds Directive of the EU (http:// ec.europa.eu/environment/nature/legislation/birdsdirective/index_en.htm), and it holds 65% of the world population of Audouin's gull. It is well known the historical human occupation and alteration of ecosystems in the Mediterranean basin, resulting in extremely high rates of habitat loss, especially in coastal areas (Blondel and Aronson, 1999). During the 1980s, effective protection of many of the remaining wetlands has allowed most waterbird species to recover (Oro and Martínez-Abraín, 2007) but there are now evidences of increasing density-dependence processes resulting from a reduction in *per capita* resources, namely food and space (Oro, 1999; Oro et al., 2006; Tavecchia et al., 2007). Such density-dependence may in turn have increased interspecific interference competition for those resources. Asymmetric competition, which is common in ecological communities (e.g. Smith et al., 2004), also occurs in the present study and it is governed mainly by size: here, there is a hierarchy of dominance from the largest to the smallest species in the interactions, mainly predation, kleptoparasitism and interference competition for suitable space (Oro, 1996, 1998, 2002; Martínez-Abraín et al., 2003; Oro et al., 2004; Oro, 2008; see similar evidences from other Mediterranean regions in Sadoul et al., 1996; Valle and Scarton, 1999). Two species stand as dominant species not only by their size but also by their increasing population densities: the yellow-legged gull and the protected, flagship Audouin's gull. We tested here whether an increase of such dominant two species and the consequent increasing occupation of space have displaced smaller species out of the most suitable breeding area in the study site, as it has been suggested in other communities (e.g. Forero et al., 1996).

2. Materials and methods

2.1. Study area and model community

The study was conducted at the Ebro Delta (NE Spain: 40°37′N, 00°35′E). This wetland holds the largest breeding area of larids (gulls and terns) of the whole Mediterranean basin (ca. 32,000 pairs from 12 species). The most valuable areas of the Delta were protected in 1986, and particularly the Punta de La Banya, a 2500 ha peninsula connected to the rest of the Delta by a narrow 5 km long sand bar, which limits access of terrestrial predators and is easily preserved against human disturbances. After protection, La Banya can thus be considered a patch of high habitat quality for larids not only within the Ebro Delta but also in the whole western Mediterranean (e.g. Oro, 2002; Oro et al., 2004, 2006). The Ebro Delta is located in an area with one of the highest marine productivity of the whole Mediterranean (Coll et al., 2008) and the total protected surface in coastal habitats is large compared to most other similar Mediterranean marshes. As a result, some fitness indicators of habitat quality such as breeding success are very high (Oro and Ruxton, 2001; Oro et al., 2006). In addition, La Banya is the largest protected patch within the Ebro Delta and the most protected against perturbations (see above), which again results

in higher fitness indicators compared to other patches in the Delta (e.g. Oro, 2002). The total surface of the rest of the suitable breeding areas within the Ebro Delta was ca. 1100 ha. No important changes in vegetation and physical features have occurred during the study.

Seven species of larids listed in the Annex I of the Birds Directive of the EU breed in the marshes of the Ebro Delta (in taxonomic order, with species average body weight in parenthesis): Mediterranean gull *Larus melanocephalus* (300 g), slender-billed gull *Larus genei* (350 g), Audouin's gull *Larus audouinii* (620 g), gull-billed tern *Sterna nilotica* (235 g), Sandwich tern *Sterna sandvicensis* (220 g), common tern *Sterna hirundo* (175 g), and little tern *Sterna albifrons* (50 g); five species complete the community: yellow-legged gull *Larus michahellis* (1010 g), common black-headed gull *L. ridibundus* (290 g), lesser black-backed gull *Larus fuscus* (710 g), whiskered Tern *Chlidonias hybridus* (90 g) and lesser crested tern *Sterna bengalensis* (230 g); the last four species were not considered in our study because of the irregular counts available, of the different habitat occupied and of the low breeding numbers, respectively.

From 1980 to 2007, 13 complete counts of breeding pairs of the abovementioned eight species (1131 colonies; 202,158 nests) were performed both in the Punta de La Banya and in other areas of the Ebro Delta taking into account the differences in laying dates among species (Johnson and Krohn, 2001). Methods to census were standard for ground nesting species and thus similar for all species, with high detection rates (see also Barbraud and Gélinaud, 2005) and small (<4%) error counts (see Oro and Ruxton, 2001). Counts were performed by a team of 4–12 people (depending on the size and shape of both the whole colony and the sub-colonies) moving in a line back and forth throughout the dunes or the dikes where the nests were built. A strict time limit (varying with colony size) was always respected and no desertions were ever recorded. Counting efficiency was assessed by marking counted nests with a coloured small bead dropped into the nest in bands (see details in Oro and Ruxton, 2001). For very dense colonies (those of slender-billed gulls and Sandwich terns) it was not possible to perform census bands because the small surface occupied, but coloured small bead dropped in nests also ensured very low error counts (Oro, 2002).

2.2. Statistical analysis

Different quantitative approaches were used to test if the increase of large gulls at Punta de La Banya (including yellow-legged and Audouin's gulls) in the past 28 years has displaced the smaller species of the community to other sites at the Ebro Delta. The Shannon index of diversity (e.g. Gorelick, 2006) was calculated through time both for La Banya and for the rest of the Ebro Delta, and different functions (linear and non-linear) were fitted to assess the shape of variation with time in the two areas. Since all functions had the same number of parameters, we selected the best model relying only on the lowest value of deviance.

Furthermore, population growth rates were calculated for each species once again for La Banya and beyond for the study period (1980–2007); rates (noted by λ) were calculated using a regression model of $\log(N_{t+1}/N_t)$ with time (expressed as $\sqrt{t_{i+1} - t_i}$ to account for missing census as an offset of the model), forcing the intercept of the model to equal 0. The parameter of the slope of the model its 95% confidence intervals (CI) corresponded to the realized population growth rate and its CI, while its variance was estimated from the residual quadratic mean of the associated ANOVA.

Finally, we gathered the census data of the selected species (see above) to calculate the balance between population densities of each species inside and outside La Banya; this allowed us to standardize for the influence of environmental stochasticity in temporal dynamics of the study species. Thus, from now on we used B_{AI}

referring to such balance for species of Annex I, B_{Ag} referring to the balance in Audouin's gull numbers, and B_{Yg} to that of yellow-legged gulls. We applied a general linear model to analyse the relationship between B_{AI} and the explanatory variables B_{Ag} and B_{Yg}. We tested for normality and homoscedasticity and the goodness of fit of the model was also checked by R^2 values. A model including two factors and their interaction was described using an asterisk. Additive models were instead described using a "+" symbol. For instance, the model $(B_{Ag} * B_{Yg})$ designated a model where B_{AI} varied with B_{Ag} and B_{Yg}, with the effect of B_{Ag} potentially different at different values of B_{Yg}. Selection of the model was made based on Akaike's Information Criterion (QAICc, corrected for overdispersion and small sample sizes); the model with the smallest QAICc was selected as the most parsimonious, although models with close QAICc values (within 4–6 units) can also have meaningful support (Burnham et al., 1994, 1995; Anderson, 2008).

3. Results

The Shannon index of diversity decreased over time within La Banya, whereas increased during the same years in other areas of the Ebro Delta (Fig. 1). At the two areas (La Banya and outside), the regression quadratic models showed the lowest deviance, and their goodness of fit was reasonable (adjusted coefficient of determination, $R_a^2 = 0.471$ and $R_a^2 = 0.731$, respectively, Fig. 1). Even though the evolution of the Shannon index looked non-linear (e.g. rather sigmoid out of La Banya) and that there were few points at the beginning of the study (i.e. a low power to detect trends with reliability) some general pattern can be described. The two models showed a slight decrease of diversity in the two areas during the first years until the protection of the whole area; note that owing to a single count before protection, the shape of the curves in their beginning has to be considered with caution although a more robust data on the number of species did support such assertion (Fig. 1). Since protection, diversity was stable at La Banya until the mid 90s, and then decreased, whereas outside La Banya it increased steadily since the protection. The number of species breeding at each area showed the same pattern suggesting not only a
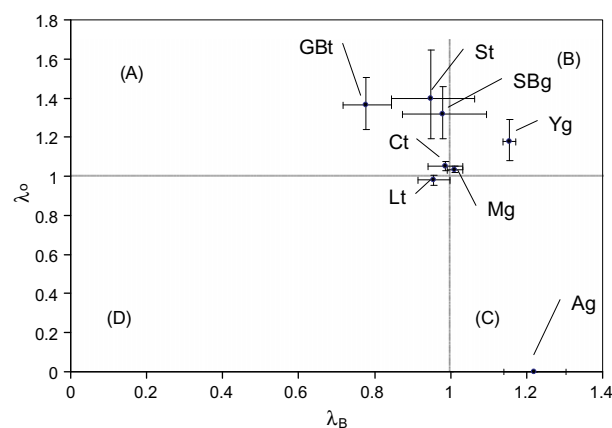
Fig. 2. State-space figure of population growth rate between 1980 and 2007 (with its 95% confidence intervals) of each study species at La Banya and out of La Banya (noted by λ_B and λ_o, respectively). Spaces A, B, and C showed the states of positive population growth rate of respectively: only out of La Banya, out and inside La Banya, only inside La Banya; space D showed the state of negative growth rate at the two areas. The lines of population stability ($\lambda = 1$) at each area are shown by dotted lines. Codes of species were Mg (Mediterranean gull), SBg (slender-billed gull), Ag (Audouin's gull), GBt (gull-billed tern), St (Sandwich tern), Ct (common tern), Lt (little tern) and Yg (yellow-legged gull).

Table 1

Model selection for the relationship between B_{AI} and the explanatory variables B_{Yg} and B_{Ag}, being B_{AI} the balance between inside and out of La Banya population densities of Annex I species (except Audouin's gull), Audouin's gull and yellow-legged gull, respectively. A model including two factors and their interaction was described using an asterisk. Additive models were described using a "+" symbol instead. N_p = number of parameters; QAICc = Akaike Information Criterion for small sample sizes; ΔQAICc = difference in QAICc values relative to the model with lowest QAIC; ω = weight of each model (Anderson, 2008). Selected model is in bold.

	Deviance	N_p	QAICc	ΔQAICc	ω
$B_{A1} \sim B_{Ag} * B_{Yg}$	**8,560,344**	**3**	**190.43**	**0.00**	**0.87**
$B_{A1} \sim B_{Yg}$	18,477,383	1	194.89	4.46	0.09
$B_{A1} \sim B_{Ag} + B_{Yg}$	18,464,244	2	196.88	6.46	0.03
$B_{A1} \sim B_{Ag}$	38,392,843	1	202.94	12.51	0.00
$B_{A1} \sim$ null model	62,590,050	0	206.31	15.88	0.00

decrease in population density within La Banya but also a shift of selected breeding area for small species. Such changes were thus attributable to different population dynamics of each species at the two areas; most small, vulnerable species of Annex I (except little terns) showed large population increases significantly higher than the value of stability ($\lambda = 1$) out of La Banya (Fig. 2).

The model that best fitted our data (i.e. with the lowest QAICc value and with most QAICc weight) on the balance between population densities of species of Annex I (except Audouin's gull) inside and outside La Banya, noted by B_{AI}, included the influence of yellow-legged and Audouin's gulls (B_{Yg} and B_{Ag}, respectively) and their interaction (Table 1 and Fig. 3A). Models suggested that the effect of the yellow-legged was stronger (Table 1), but that the addition of the effect of Audouin's gull explained more variance of the spatio-temporal dynamics of species of Annex I. Interestingly, a model with an interaction between the two largest species was much better than a model with an additive effect suggested a more complex effects on smaller species, probably resulting from the biological interaction between yellow-legged and Audouin's gulls (see Fig. 3B). This model had a much smaller deviance than the null model and explained 18% of the variance observed (see Fig. 3A).

4. Discussion

One of the main goals of conservation is to protect biodiversity, which is shaped by several levels of structures, including
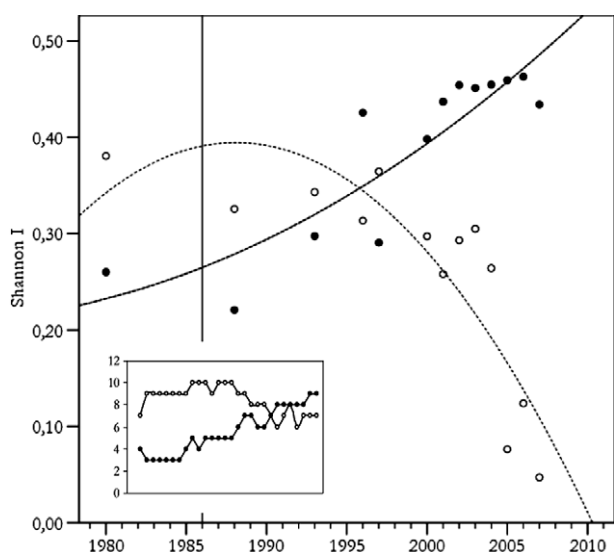
Fig. 1. Shannon index of diversity of the Annex I species (except Audouin's gull) during 1980–2007 at La Banya (open dots and dashed regression line) and out of La Banya (solid dots and regression line). Lines are quadratic regression models, which showed the best goodness of fit (see text). The vertical line shows the year of the legal protection of the whole Ebro Delta. The inner graph shows the dynamics of the number of species in the community at La Banya and out of La Banya for the same period; note that presence–absence of breeding species was available for all years.
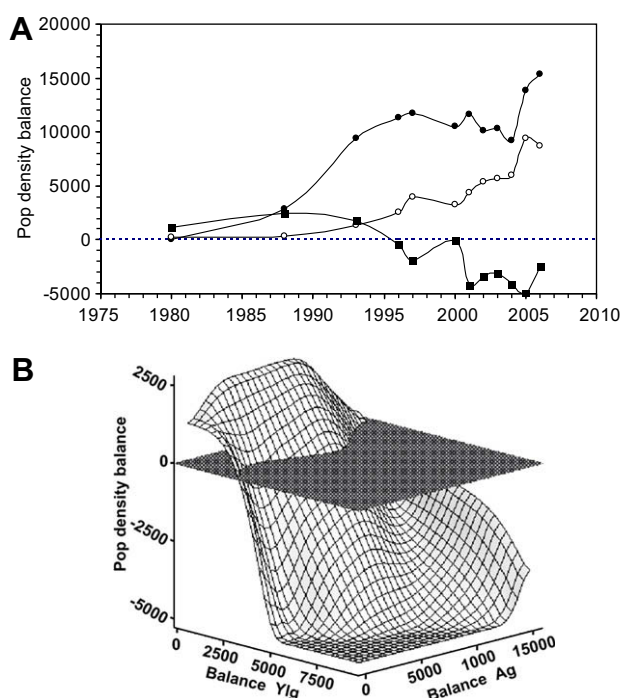
Fig. 3. (A) Balances in population density in and out of La Banya (as number of breeding pairs inside La Banya minus number of breeding pairs out of La Banya) in Audouin's gull (solid dots), yellow-legged gull (open dots) and the rest of Annex I species altogether (solid squares) during 1980–2006. (B) Smoothing regression surface using a lowess method by iteration of weighted least-squares on the same variables. The dashed line (A) and the horizontal surface (B) showed the balance of equal population density in the two areas.

communities. In fact, it has been argued (especially in marine eco-systems) that protection of sites should be based on communities rather than on single species (e.g. Angelstam, 1992; Boersma et al., 2001; Micheli et al., 2004). Nevertheless, communities have their temporal and spatial dynamics (the so-called metacommunities, see Holyoak et al., 2005), and the complexity inherent to such dynamics may pose a conservation challenge when we have to take into account the complex multispecies interactions (Frankel and Soulé, 1981). As such, competition between species is identified as one of the most important processes for community composition (Holyoak et al., 2005). At evolutionary scales, several hypotheses of community drift based on the rate of competitive displacement rely on at least three factors: the population densities of the species, the magnitude of their population fluctuations and finally the overall similarity of species in competitive abilities (Hubbell and Foster, 1986; Schluter, 2001). However, this last point has been disputed because there are evidences of asymmetries in competitive abilities, not only in evolutionary times, but also in short, ecological time periods. Some examples include invasive species displacing native communities (e.g. Schemel et al., 1990; Andersen, 1997; Rajbanshi and Pederson, 2007) but few cases deal with non-invaded communities, their dynamics and the consequences for conservation (e.g. Harmon et al., 2007).

Our results show how species densities in a community can change with time and space following unequal competitive skills driven by a hierarchy of body size. Brown (2007) also suggested that communities are not randomly organized in space and time, larger species being more abundant in small patches. Competition for suitable breeding habitat has been largely described in seabird communities (e.g. Burger and Shisler, 1978; Erwin et al., 1981; Fasola and Canova, 1996; Sadoul et al., 1996; Quintana and Yorio, 1998) as well as particular associations of species, which show that smaller species avoid breeding together with larger species of the community

(e.g. Oro, 2002; Oro et al., 2004). Our study had also the particularity that started before the protection of the Ebro Delta, so the spatio-temporal community dynamics departed at that time from a very poor community in population densities of all species and in their numbers (only three species bred in 1980 out of La Banya) to the largest and richest seabird community in the whole Mediterranean region. At spatio-temporal scale the displacement of smaller species increased as population densities of larger species (yellow-legged and Audouin's gull) increased within La Banya probably triggering in turn density-dependent mechanisms for suitable habitat (Oro, 2008). Interestingly, results showed that diversity decreased not as an additive effect of the density of the two largest species, but with a more complex pattern of interaction of such densities (see Fig. 3B). The influence of each of the largest species depended also on the density of the other, suggesting an interaction between the two dominant species, as already showed in previous behavioural studies of such competition (Arcos et al., 2001; Martínez-Abraín et al., 2003; Oro et al., 2006). For instance, results indicated that when low densities of the largest species the yellow-legged gull occurred, only highest densities of Audouin's gull would influence a dispersal of the smaller species out of La Banya (Fig. 3B).

Habitat scarcity may exacerbate the effects of interspecific competition because the dynamics of small, subordinate species can be limited by constrained dispersal to alternative sites (e.g. Abramsky et al., 2005; Brown and Sullivan, 2005). This adds a further concern about the importance of habitat loss as one of the major threats in the framework of global change (Millennium Ecosystem Assessment, 2005). Different species of a community can coexist even though the best competitors displace all other locally, because higher dispersal ability to sites not occupied by superior competitors can buffer the competitive subordination (Tilman, 1994; Schwartz et al., 2000). In our case, the rapid extinction–colonisation turnover of small species inside and outside La Banya has kept a rather constant increase of the biodiversity over the years following the protection of the whole Ebro Delta, even though the seabird community within La Banya has became poorer, governed by large, dominant species. The conservation paradox arose because such dominance was not only attributable to the largest species of the community, the yellow-legged gull, which is sometimes considered a pest species (Vidal et al., 1998; Oro and Martínez-Abraín, 2007), but also by the vulnerable Audouin's gull, a flagship species whose density has increased since its colonisation up to concentrate here ca. 65% of total world population. From this fact, protection of the site can be actually considered a conservation success, totally changing the conservation status of Audouin's gull (now considered as Near Threatened by the IUCN, see http://www.iucn-redlist.org/), at that time one of the most endangered seabird in the world, and allowing a rapid recuperation of population numbers and the progressive colonisation of new sites in the whole western Mediterranean. But at the same time, the consequences of such population increase (and a conservation success) are also an increase of interference competition within the community, a decrease of diversity and potentially a new conservation challenge. Importantly, this should not be perceived as a negative conservation state, but rather the natural spatio-temporal dynamics of the system. In a hypothetical scenario of no alternative breeding sites or at very low availability, the protection of a vulnerable species would paradoxically imply a lost in community diversity, including other threatened species (see Courchamp et al., 2003). The stability of the community is likely ensured by the environmental stochasticity affecting differently the breeding patches, i.e. switching the quality of a patch with time. In our case, La Banya has suffered in recent times from ecological stochastic perturbations (particularly predation and disturbances from terrestrial carnivores) affecting mainly the dominant species because their higher densities and the trend of predators to establish in their colonies (e.g. Ruiz-Olmo

et al., 2003; Tavecchia et al., 2007; Oro, 2008), which may allow the smaller species to recolonize the patch. This highlights the importance of considering large spatio-temporal scales in interpreting complex community dynamics and conservation in practice (Ricklefs, 1987). There are now evidences of unexpected effects other than competition (e.g. higher predation rates on target vulnerable species, sharp increase of common species, decrease of habitat availability) resulting from conservation actions widely accepted such as protection of habitat or eradication of alien species (Moyle and Light, 1996; Yanes and Suárez, 1996; Louda and O'Brien, 2002; Martínez-Abraín et al., 2004; Rayner et al., 2007; Tweedley et al., 2008). These studies confirm that ecosystems are complex systems and that conservation actions must incorporate as much of this complexity as possible to predict with more accuracy the resulting outputs (Green et al., 2005; Sergio et al., 2005).

5. Conclusions and conservation remarks

Looking at the conservation of the most vulnerable species of the community, the Audouin's gull, the protection measures set at the Ebro Delta and their most valuable areas can be considered a success, with an average annual population growth rate of 22% for that species. The species has been considered a paradigm for the conservation of Mediterranean islands and marshes always threatened by human factors such as habitat loss and fragmentation. However, conservation deals with complex systems and it requires of several quantitative challenges to respond to such complexity, including that of competition within communities (Green et al., 2005). A result from that competition was a decrease in diversity following an increase of the largest, dominant species, not only of the abundant and predatory yellow-legged gull, but also of the paradigmatic Audouin's gull. Natural systems are dynamic and governed by complex interactions, not only the most accepted of predator–prey but also other more subtle such as competition for suitable habitat among similar species of a community. This is why conservation measures and strategies may also be re-evaluated over the years to cope with the changes resulting from spatio-temporal population dynamics of vulnerable species.

Acknowledgements

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