

Size-mediated non-trophic interactions and stochastic predation drive assembly and dynamics in a seabird community

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Abstract. Theoretical and empirical evidence suggests that body size is a major life-history trait impacting on the structure and functioning of complex food webs. However, long-term analyses of size-dependent interactions within simpler network modules, for instance, competitive guilds, are scant. Here, we model the assembly dynamics of the largest breeding seabird community in the Mediterranean basin during the last 30 years. This unique data set allowed us to test, through a “natural experiment,” whether body size drove the assembly and dynamics of an ecological guild growing from very low numbers after habitat protection. Although environmental stochasticity accounted for most of community variability, the population variance explained by interspecific interactions, albeit small, decreased sharply with increasing body size. Since we found a demographic gradient along a body size continuum, in which population density and stability increase with increasing body size, the numerical effects of interspecific interactions were proportionally higher on smaller species than on larger ones. Moreover, we found that the per capita interaction coefficients were larger the higher the size ratio among competing species, but only for the set of interactions in which the species exerting the effect was greater. This provides empirical evidence for long-term asymmetric interspecific competition, which ultimately prompted the local extinction of two small species during the study period. During the assembly process stochastic predation by generalist carnivores further triggered community reorganizations and global decays in population synchrony, which disrupted the pattern of interspecific interactions. These results suggest that the major patterns detected in complex food webs can hold as well for simpler sub-modules of these networks involving non-trophic interactions, and highlight the shifting ecological processes impacting on assembling vs. asymptotic communities.

Key words: allometric interactions; body size; community dynamics modeling; competition; ecological guild; hierarchical Bayes; Mediterranean Laridae; network; perturbations; population variability; predation.

INTRODUCTION

The way communities assemble and, eventually, disassemble through time and space remains an open question in ecology (Roughgarden 2009). Although classical models of community assembly regarded competition and predation as major forces driving multispecies dynamics (e.g., Orians and Willson 1964, Diamond 1975), their relevance as factors structuring natural communities has long been questioned (Connor and Simberloff 1979, Hubbell 2001). For example, some models emphasize the functional equivalence of different species within a given trophic level (Caswell 1976, Hubbell 2001), while others highlight the importance of stochasticity and phylogeny (Emersson and Gillespie 2008, Helmus et al. 2010) in the structuring and functioning of natural communities. The search for

patterns of interspecific interactions and stochastic forcing in natural communities is a central goal of current ecological and conservation research (Lande et al. 2003, Ranta et al. 2006). However, the statistical modeling of ecological interactions in natural multispecies communities was traditionally considered an elusive goal (Berlow et al. 2004, Emmerson et al. 2005, Wootton and Emmerson 2005), but the increasing availability of hierarchical modeling approaches have turned this into an area of active development (e.g., Ives et al. 2003, Mutshinda et al. 2009).

The evidence for the impact of competition and predation on community structure and dynamics is currently widespread (e.g., Chase et al. 2002). In particular, ecological relationships mediated by body size have been found common in food webs (e.g., Cohen et al. 2003, Emmerson et al. 2005, Wootton and Emmerson 2005, Berlow et al. 2009). Body size is a central trait in evolutionary ecology and is correlated with key parameters such as population density and several measures of community structure and dynamics

Manuscript received 2 February 2011; revised 17 May 2011; accepted 20 May 2011. Corresponding Editor: R. Greenberg.

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(Woodward et al. 2005, Wootton and Emmerson 2005, Berlow et al. 2009, Ritchie 2009). In recent years, the application of metabolic and allometric scaling rules (see Brown et al. 2004) to the assembly of theoretical food webs has shown that body size is a major life-history trait during this process at both evolutionary (Loeuille and Loreau 2005) and ecological scales (Berlow et al. 2009). Theoretical explorations show that allometric scaling rules have fundamental implications for the complexity and stability of model communities (Brose et al. 2006, Emmerson et al. 2005), and empirical evidence suggests that this is indeed the case for natural systems (e.g., Cohen et al. 2003, Emmerson and Raffaelli 2004, Brose et al. 2006). For example, the role of organism size on competitive interactions has received much attention over the years (e.g., Hutchinson 1959, Orians and Willson 1964, Wilson 1975, Persson 1985, Brown and Maurer 1986, Goldberg and Landa 1991, Leyequi n et al. 2007). Ecological theory states that species within guilds usually share a common evolutionary history, and thus, a similar size, and given that they compete for common resources the strength of interactions is expected to be greater within these ecological assemblages (Morse 1974, Wilson 1975, Connell 1980, Brown and Maurer 1986, Simberloff and Dayan 1991, Emerson and Gillespie 2008). Therefore, in stable communities (as opposed to assembling ones; Fargione et al. 2003), the per capita interaction coefficients among any pair of species are expected to be greater for similar-sized competitors (e.g., Brown and Maurer 1986, Leyequi n et al. 2007). In contrast, in assembling communities it can be expected that the variability in organism size during sequential community build up can yield divergent size-scaling rules of interaction strengths relative to stable communities (e.g., Buss and Jackson 1979, Goldberg and Landa 1991). This means that for a set of species engaged in resource competition large species are predicted to displace smaller ones during community invasion (Rummel and Roughgarden 1985), a process known as asymmetric competition (Morse 1974, Connell 1980, Schoener 1983, Persson 1985).

Although time series analyses of size-dependent interactions in natural communities are lacking, in particular for competitive interactions (Berlow et al. 2004, Wootton and Emmerson 2005, Emmerson et al. 2005), the evidence accumulated so far for the allometric scaling of trophic interactions suggest several predictions for the non-trophic dynamics of ecological guilds. First, a declining gradient in the magnitude of interspecific interactions across a body size continuum might be a signature of asymmetric competition (*sensu* Persson 1985). Second and more specifically, if size-mediated interactions impact upon long-term assembly dynamics; that is, if large species are able to numerically outcompete small ones during community invasion, the magnitude of the realized per capita interaction coefficients should scale positively with the body size ratio of competitors (see Goldberg and Landa 1991 for a

similar rationale). Unfortunately, the impact of size ratios of interacting species on long-term community and population dynamics is a largely unexplored issue for non-trophic interactions (e.g., Berlow et al. 2004, Wootton and Emmerson 2005).

Here, we tested the above predictions using nearly 30 years of multispecies monitoring of the largest breeding community of larids (gulls and terns) in the Mediterranean basin (Oro et al. 2009). This area hoards a guild of several seabird species with overlapping trophic and habitat requirements. Following site protection, the local populations of large gulls increased nearly exponentially (Oro and Mart nez-Abra n 2007). Some evidence for size-mediated asymmetric competition has already been found in single-species demography, feeding behavior, and spatial dynamics within the focal seabird community (e.g., Oro et al. 2006, 2009, and references therein, Tavecchia et al. 2007, Oro 2008). Therefore, this unique scenario constitutes a “natural experiment” testing whether body size is a major life-history trait driving the long-term assembly of a multispecies guild after a major ecological perturbation: the genuine invasion by ecologically dominant species (*sensu* Val ry et al. 2009) of a high-quality habitat ultimately driven by human intervention. Here our goal was twofold. First, we explored whether different temporal dynamic trends within the seabird community relate to an interspecific gradient in body size and to the onset of stochastic episodes of generalist predation from terrestrial carnivores. If body size drives long-term multispecies trends, we expected that population density should decrease and variability increase across time at a higher rate for smaller species (e.g., Pimm 1991). Besides, predation should induce shifts in community structure and interspecific synchrony (e.g., Lande et al. 2003, Ranta et al. 2006). Second, we fit a community dynamics model (Mutshinda et al. 2009) and tested whether a gradient in the relative contribution of the temporal variance components of each population, including ecological interactions, demographic stochasticity, and environmental noise, can be predicted from a body size gradient.

METHODS

Study area and seabird community

The study area is located at the Ebro Delta, northeast Spain (40°37' N, 00°35' E). This area holds annually ~32 000 breeding pairs from 12 seabird species (Oro et al. 2009), and is located in a marine shelf with one of the highest productivities of the whole Mediterranean Sea (Coll et al. 2008). The long-term monitoring was conducted at Punta de La Banya, a flat salt marsh, with spatially discrete dunes covered by halophilous vegetation. This area is a 2500-ha peninsula connected to the Ebro Delta by a narrow 5 km long sand bar (Oro et al. 2009). This spatial configuration, which remained virtually unchanged during the last 30 years, limited the access of terrestrial predators and the effect of human

disturbances, in particular, after 1986 when legal protection was implemented. Indeed, Punta de La Banya is a patch of high-quality habitat resulting in large breeding success among many seabird species relative to other Mediterranean habitats (e.g., Oro and Ruxton 2001, Oro et al. 2006, 2009, Tavecchia et al. 2007).

We focused in the analysis of time series for 10 species monitored from 1980 onward (see Appendix: Fig. A1 for supporting information): Yellow-legged Gull (*Larus michahellis*), Common Black-headed Gull (*L. ridibundus*), Lesser Black-backed Gull (*L. fuscus*), Audouin's Gull (*L. audouinii*), Mediterranean Gull (*L. melanocephalus*), Slender-billed Gull (*L. genei*), Gull-billed Tern (*Sterna nilotica*), Sandwich Tern (*S. sandvicensis*), Common Tern (*S. hirundo*), and Little Tern (*S. albigrons*). The last seven species are included in the Annex I of the Birds Directive 2009/147/EC of the EU (available online),⁶ and are thus under special protection. In particular, the Audouin's Gull is Globally Threatened, and the study area held 60% of its world population during the study period (see Oro et al. 2009). Selection of nesting microhabitat is similar among species. From 1980 to 2008, more than 1130 colonies and 200 000 nests were monitored at Punta de La Banya and in other areas of the Ebro Delta. Common methods for ground-nesting seabirds were employed for monitoring the number of active nests within the seabird community, while controlling for interspecific differences in laying dates. The survey yielded large detection rates and small (<4%) error counts (Oro and Ruxton 2001, see Oro et al. 2009 for further details). We measured body size as the mean mass of each species.

Several generalist predatory events by terrestrial carnivores have been recorded in the study area (Ruiz-Olmo et al. 2003, Tavecchia et al. 2007, Oro 2008, Oro et al. 2009). 1994 was the first year with a recorded predatory event by badgers (*Meles meles*), which preyed upon nests but not adults. From 1999 onwards, red foxes (*Vulpes vulpes*) regularly entered the study area preying upon nests, chicks, and adults. The disruption of predatory badgers significantly induced a 14% and 10% increase in the dispersal probability of young and experienced breeders, respectively, along with a significant reduction in fertility (Oro et al. 1999). Additionally, adult survival probability dropped by a 6% in the Audouin's Gull (Tavecchia et al. 2007) and 14% in the Yellow-legged Gull (Oro 2008) due to predation pressure by invading red foxes. Overall, from 1994 the presence of both species was regular, although unpredictable.

Common trends in multispecies dynamics

We used dynamic factor analysis (DFA; Zuur et al. 2003) to estimate common trends within our community time series. This method aims at extracting M indepen-

dent components (hereafter common trends) from a set of N population time series, and is particularly useful for short and nonstationary time series containing missing values (Zuur et al. 2003). The term \mathbf{y}_t is a vector of size N , containing the population densities of each species at time t . We considered the temporal values of the M common trends ($\boldsymbol{\beta}_t$) to evolve through time according to a first-order autoregressive process. Then, the standard DFA model can be written as

$$\begin{aligned}\mathbf{y}_t &= \mathbf{c} + \mathbf{Z}\boldsymbol{\beta}_t + \boldsymbol{\varepsilon}_t \\ \boldsymbol{\beta}_t &= \boldsymbol{\beta}_{t-1} + \boldsymbol{\tau}_t\end{aligned}\quad (1)$$

where \mathbf{c} is a constant vector of size N , and \mathbf{Z} is a M by N matrix containing the factor loadings of each species in the community, which represent the contribution of each population time series to every common trend; therefore, the examination of the values in matrix \mathbf{Z} allows the assessment of which group of species is related to the same common trends (Zuur et al. 2003). The term $\boldsymbol{\varepsilon}_t$ is a vector of size N representing the community process variance and having a multivariate normal distribution with 0 mean and covariance matrix \mathbf{R} , $\boldsymbol{\varepsilon}_t \sim \text{MVN}(0, \mathbf{R})$. This covariance matrix includes the terms for species-specific process error variances in the diagonal, and the terms for the process error covariances between every pair of species in the off-diagonal. The term $\boldsymbol{\tau}_t$ is a vector of size M representing the process variance of the common trends, having a normal distribution with 0 mean and diagonal matrix \mathbf{Q} , $\boldsymbol{\tau}_t \sim \mathcal{N}(0, \mathbf{Q})$. We fit the DFA to the community data set through Markov Chain Monte Carlo (MCMC) Bayesian integration (King et al. 2010). We constructed alternative DFA's with one, two, and three common trends (further trends made convergence unstable). We finally used DFA with two common trends because it reduced the deviance information criterion (DIC; see King et al. 2010). After estimating the canonical correlations between the time series of each species in the community and the fitted common trends (Zuur et al. 2007), an interspecific comparison of these correlation values in the bivariate plane allowed an easy estimation of a potential body size gradient.

To let the likelihood dominate the prior during the estimation of posterior distributions, we placed weakly informative priors on the parameters of the DFA (Gelman et al. 2004). The covariance matrix \mathbf{R} was modeled with an inverse Wishart prior, $\mathbf{R}^{-1} \sim \text{Wishart}(\boldsymbol{\Omega}, S)$, which is the conjugate prior for the covariance matrix of a multivariate normal distribution (Gelman et al. 2004). The number of degrees of freedom, denoted by q , was set to the rank of the scale matrix $\boldsymbol{\Omega}$, namely the number of species (S). This is the value expressing the weakest prior information. For the vector $\boldsymbol{\tau}_t$, we placed a uniform distribution on the standard deviation of the process error of each common trend i , $\tau_i \sim \text{Unif}(0, 10)$ (Gelman 2006). For location parameters, namely the constant levels in \mathbf{c} and the factor loadings in \mathbf{Z} , and initial values for the common trends ($\beta_{0,i}$), a flat

⁶ (http://ec.europa.eu/environment/nature/legislation/birdsdirective/index_en.htm)

normal distribution was used, $c_i, z_i, \beta_{0,i} \sim \mathcal{N}(0, 10^3)$. We constructed three independent Markov chains with dispersed initial values and ran them for 300 000 MC iterations. After discarding the first 200 000 as a burn-in period, the chains were thinned every 10 iterations to derive the posterior estimates of parameters in the DFA. Standard diagnostic tests were used to assess the convergence of the chains (Gelman et al. 2004). We used WinBUGS 1.4.1 to fit our model (Spiegelhalter et al. 2003), and a sample WinBUGS code for fitting the Bayesian DFA is given in the Supplement.

Structural shifts in community composition

We used chronological clustering (Zuur et al. 2007) to test for the presence of sudden temporal shifts in community structure and composition. With this method, a set of N sequential clusters differing in species composition can be identified within a multispecies database. Chronological clustering requires two parameters, namely the connectedness and the fusion level λ , which is a parameter quantifying clustering resolution. Given the pattern of missing data in our survey (see the Appendix), we used a small value for the fusion level ($\lambda = 0.05$), which is suitable for detecting the major shifts within a multivariate time series (Zuur et al. 2007). However, several larger values for parameter λ were considered to test for potentially more subtle shifts. In all cases, the connectedness parameter was kept low (0.2), although higher levels yielded similar results (not shown). The Euclidean distance matrix on the ln-transformed time series data was used as the dissimilarity measure in our setting. The groups obtained through chronological clustering can be used in a principal coordinate analysis (PCO; Zuur et al. 2007), and a posterior test can be applied to assess if the different groups detected by chronological clustering are similar among them or belong to essentially different community structures. Finally, to test for the potential effects of generalist carnivore predation on community dynamics, we calculated the pairwise interspecific correlations in population densities (Ranta et al. 2006) before and after the first predatory event in 1994, and tested whether these measures changed between both periods. Chronological clustering was performed with Brodgar 2.6.4 (Zuur et al. 2007), interfaced with R 2.11 (R Development Core Team 2010).

Time series modeling of community dynamics

We fitted a multivariate time series model to estimate the relative effects of both demographic and environmental stochasticity, as well as intra- and interspecific interactions, on population and community dynamics. From the following analyses, we excluded the time series for the Mediterranean Gull, which breeds only occasionally in low numbers, and the series for Common Black-headed Gull and Gull-billed Tern, given that both became extinct before 1999. The basic structure is a discrete-time stochastic Gompertz model including

interspecific interactions of the Lotka-Volterra type (Mutshinda et al. 2009). The term $n_{i,t}$ is the ln-transformed number of breeding pairs (hereafter density) of species i at time t . The model has the form

$$n_{i,t} = n_{i,t-1} + r_i \left[1 - \frac{\sum_{j=1}^S \alpha_{i,j} n_{j,t-1}}{k_i} \right] + \varepsilon_{i,t} \quad (2)$$

where r_i and k_i are the intrinsic growth rate and the ln-transformed carrying capacity of species i , respectively. The terms $\alpha_{i,j}$ represent the interspecific interaction coefficients, expressing the per capita effect of species j on i for all the species in the community (denoted by S ; Ranta et al. 2006). Finally, the term $\varepsilon_{i,t}$ represents the effects of unexplained (latent) environmental and demographic noise on the population dynamics of species i . Written in matrix form, Eq. 2 takes the compact form

$$\mathbf{n}_t = \mathbf{n}_{t-1} + \mathbf{R}(\mathbf{1}_S - \mathbf{A}\mathbf{n}_{t-1}) + \boldsymbol{\varepsilon}_t \quad (3)$$

where $\mathbf{n}_t = (n_{1,t}, n_{2,t}, \dots, n_{S,t})^\top$ is the vector of densities of the S species at time t ; \mathbf{R} is an $S \times S$ diagonal matrix with the intrinsic growth rates of the S species in the leading diagonal, $\mathbf{R}_{i,i} = r_{i,i}$, while $\mathbf{1}_S$ is an S -dimensional vector with all elements equal to 1. The vector $\boldsymbol{\varepsilon}_t = (\varepsilon_{1,t}, \dots, \varepsilon_{S,t})^\top$ is sequentially independent noise distributed according to a multivariate normal distribution, $\boldsymbol{\varepsilon}_t \sim \text{MVN}(\mathbf{0}, \boldsymbol{\Sigma}_t)$. The covariance matrix $\boldsymbol{\Sigma}_t$ can be decomposed into an environmental (C) and demographic component (\mathbf{D}_t), $\boldsymbol{\Sigma}_t = \mathbf{C} + \mathbf{D}_t$. The environmental matrix includes the variance of the latent environmental factors impacting on single-species dynamics in the main diagonal ($\sigma_{i,i}^2$), as well as the covariance terms for the pairwise joint responses to these factors, $c_{i,j}$ (for $i \neq j$), in the off-diagonal. The diagonal matrix $\mathbf{D}_t = [\delta_1^2/\exp(n_1), \dots, \delta_S^2/\exp(n_S)]^\top$ reflects the demographic variance affecting the dynamics of species S from time $t - 1$ to t , which scales inversely with population size (e.g., Lande et al. 2003). Finally, the matrix \mathbf{A} contains the coefficients for interspecific interactions scaled by the carrying capacities in the off-diagonal, $\alpha_{i,j}/k_i$. The coefficients $\alpha_{i,i}$ are normalized to 1 (Ranta et al. 2006, Mutshinda et al. 2009), so inverse carrying capacities ($1/k_i$) enter the main diagonal of matrix \mathbf{A} . Note that positive values for $\alpha_{i,j}$ denote that species j has a negative effect on the equilibrium population density of species i (e.g., Ranta et al. 2006). Given the size of our modeled community, 42 interspecific interaction coefficients need to be estimated. Since many of them will probably be around 0 due to the absence of a quantitative interspecific effect, we follow Mutshinda et al. (2009) and use stochastic search variable selection (SSVS) to automatically set these coefficients close to 0 during the MCMC simulation (see the Appendix). We used the Jacobian matrix of Eq. 3 fitted to the

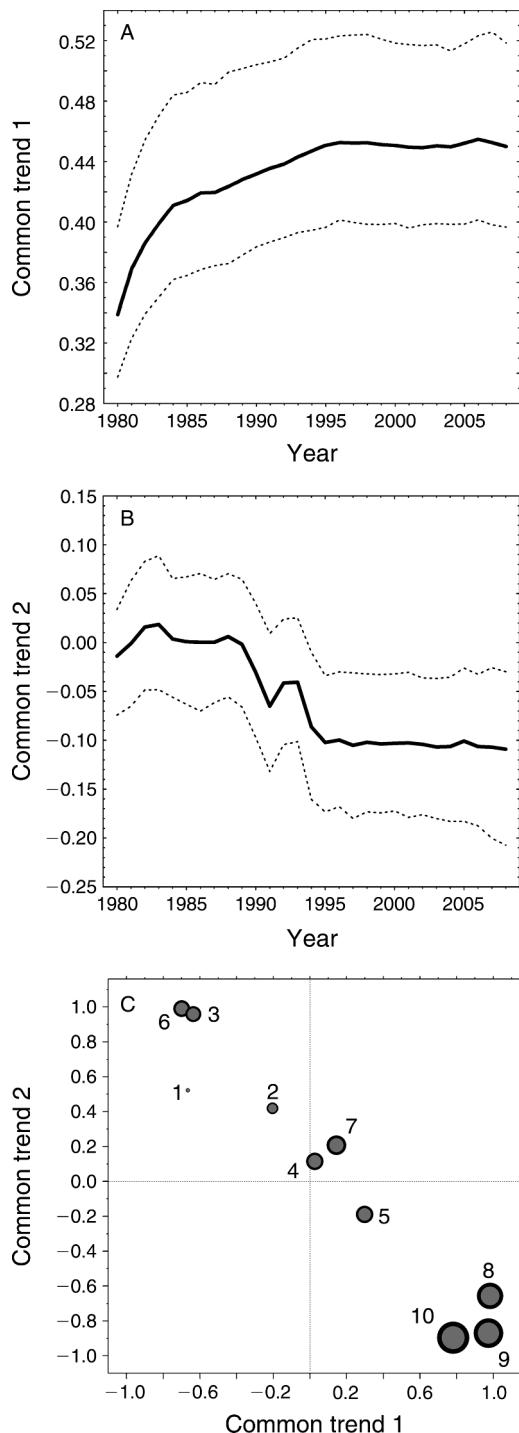


FIG. 1. Results of the Bayesian dynamic factor analysis (DFA) fitted to the multispecies seabird time series. (A, B) Time plots of the common trends modeled (solid line) and 95% credible intervals (dotted lines), and (C) ordination of the canonical correlations of each seabird time series. Circle size is proportional to the body mass of the corresponding species. Numbers are: 1, Little Tern; 2, Common Tern; 3, Gull-billed Tern; 4, Sandwich Tern; 5, Mediterranean Gull; 6, Common Black-headed Gull; 7, Slender-billed Gull; 8, Audouin's Gull; 9, Lesser Black-backed Gull; and 10, Yellow-legged Gull.

multispecies time series to estimate the local stability of the modeled community (see the Appendix).

The temporal variance of the specific population densities (Var_i) can be decomposed into the additive contributions from intra- and interspecific interactions, environmental forcing and demographic stochasticity, respectively:

$$\text{Var}_i = \left(\left(\frac{r_i}{k_i} \right)^2 \times \alpha_{i,i}^2 \times v_{i,i} \right) + \left(\left(\frac{r_i}{k_i} \right)^2 \times \sum_{j \neq i} \alpha_{i,j}^2 \times v_{j,j} \right) + \sigma_{i,i}^2 + \frac{\delta_i^2}{V_{i,i}} \tag{4}$$

where $v_{i,j}$ is the stationary variance for n_i , and $V_{i,j}$ is the stationary variance for $\exp(n_i)$. The matrix for environmental noise \mathbf{C} was modeled with an inverse Wishart distribution, $\mathbf{C}^{-1} \sim \text{Wishart}(\mathbf{\Omega}, S)$ (see the prior specification of the Bayesian DFA in *Methods: Common trends in multispecies dynamics*). The terms for intrinsic growth rates were given flat normal prior distributions $r_i \sim N(0, 10^3)$, while the carrying capacities were modeled through proper uniform distributions, $k_i \sim \text{Uniform}(l, m)$; hyperparameters l and m were selected to cover the range of biologically plausible values within our community. Finally, prior uniform distributions were placed on the standard deviation of demographic noise, $\delta_i \sim \text{Unif}(0,10)$. Three independent Markov chains with dispersed initial values were run for 300 000 iterations. The first 200 000 were discarded as a burn-in period, and the chains were thinned every 10 iterations to derive the posterior estimates of parameters. We tested whether the residual variance-covariance matrix of the fitted model conformed to the multivariate normality assumption using the Shapiro-Wilks test (Mutshinda et al. 2009), and checked the convergence of the chains using standard diagnostic tests (Gelman et al. 2004). We give a sample WinBUGS code for fitting the Gompertz stochastic community dynamics model in the Supplement.

RESULTS

Temporal dynamics of population and community trends

Across time, community size, measured as the total number of seabirds, showed a steady increase in the study area (Appendix: Fig. A1). In contrast, richness and diversity decreased accordingly, and this pattern is more evident from the mid-1990s onwards. Short-term population variability increased across time for small species, while remained stable or decreasing for large species (correlation between trend in short-term variability and body size, $r = -0.81$, $P < 0.01$; Appendix: Fig. A2). The DFA identified two opposite common trends within the seabird community (temporal cross-correlation, $r = -0.77$, $P < 0.001$; Fig. 1). The first one displays a decelerated increase across the study period: prior to 1995 the factor grows at a high rate, and then

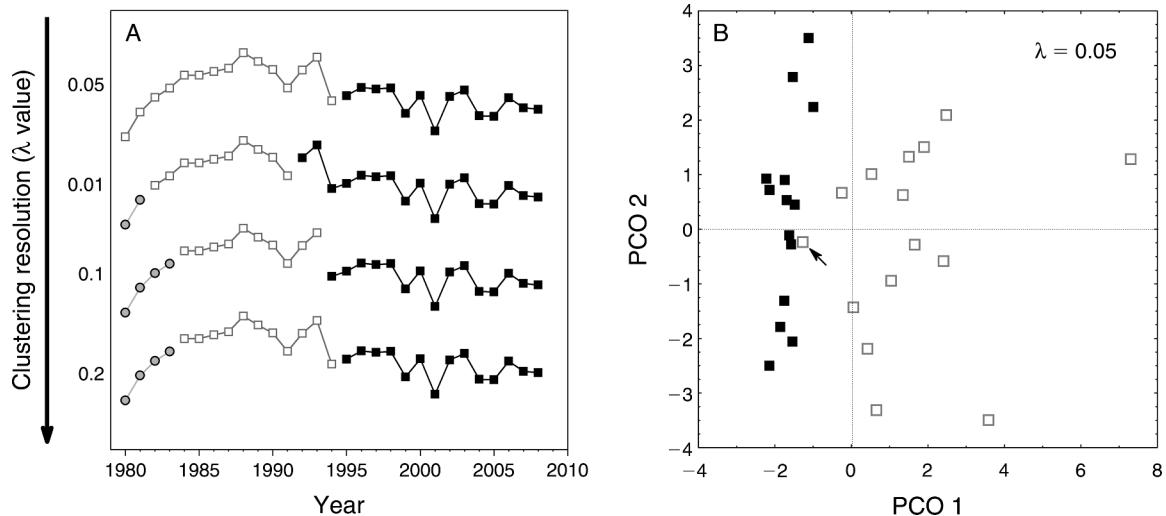


FIG. 2. Results of chronological clustering of the multispecies seabird time series. (A) Time plots of average community size with statistically significant clusters denoted by different symbols and fills. Clusters of increasing resolution are shown at growing levels of the fusion parameter λ . (B) The ordination of yearly cluster shown in the principal coordinate (PCO) plot at a small λ value. Open squares represent the years belonging to the first cluster, while solid squares are the years from the second cluster as depicted in panel (A). The arrow indicates the year (1994) of the onset of generalist predatory events.

levels off smoothly. The second dynamic factor shows the opposite trend, namely a drop until 1995 followed by stability. The canonical correlations of the population time series with these factors suggest an opposing pattern among different species, driven by body size. Large gulls with near-exponentially increasing trends (Yellow-legged, Lesser Black-backed, and Audouin's Gulls; Appendix: Fig. A1) correlate strongly and positively with the first factor ($r > 0.78$, $P < 0.01$), while negatively with the second ($r < -0.65$, $P < 0.01$). In contrast, smaller species fluctuating to extinction (Common Black-headed Gull and Gull-billed Tern) or to near extinction (Little Tern) correlate negatively with the first one ($r < -0.63$, $P < 0.03$) and positively with the second one ($r > 0.52$, $P < 0.01$) (see Fig. 1). This body size gradient is significant across the bivariate plane (multiple $R^2 = 0.62$, $P = 0.007$).

Temporal changes in community composition and effects of generalist predation

Results from the chronological clustering analysis are shown in Fig. 2. With small clustering resolution levels a major shift in community structure is detected in 1995 ($P < 0.001$), with no other significant shifts. At higher resolution levels (λ from 0.1 to 0.2), another significant shift ($P < 0.05$) is evident mostly in 1983. The ordination of the community structure for each year in the principal coordinate plane at a λ level of 0.05 suggests a clear structural shift after the onset of the second group in 1995. Fig. 3 shows the pairwise interspecific correlations in population density within the seabird community before and after the first recorded predatory event in the study area (year 1994). A nearly fourfold decrease in interspecific

synchrony (positive correlation) and anti-synchrony (negative correlation) was evident after this year.

Time series modeling of community dynamics

The dominant eigenvalue of the Jacobian matrix of the fitted community dynamics model is $|0.955|$, which suggest that the modeled community is locally stable. The relative impact of each modeled factor on the dynamics is variable among species (Fig. 4). At the community level, environmental stochastic factors explained the 63.7% of total variance. Demographic noise was negligible across species. Although the individual effects of per capita interaction coefficients are very small (see Appendix: Fig. A4) and the amount of variance explained by interspecific interactions is low across species (Fig. 4), body size is an excellent predictor of the amount of population variance explained by per capita interspecific interactions: The smaller the species, the more intense are the effects of interspecific interactions on its dynamics ($r = -0.96$, $P = 0.001$; Fig. 4B). Moreover, there is a positive correlation across species between the amount of variance explained by interspecific interactions and the trend in short-term population variability ($r = 0.77$, $P = 0.045$; see Appendix: Fig. A2); that is, species declining are under stronger per capita interspecific effects that species increasing. There is also a positive correlation between the magnitude of the interaction coefficients $\alpha_{i,j}$ and the body size ratio of the interacting species ($r = 0.57$, $P = 0.007$), but only for the set of interactions in which the species exerting the effect is larger than the species suffering it (Fig. 5). This means that the reduction in equilibrium population density of a given species caused by the interaction with other species in the community is higher the larger the external

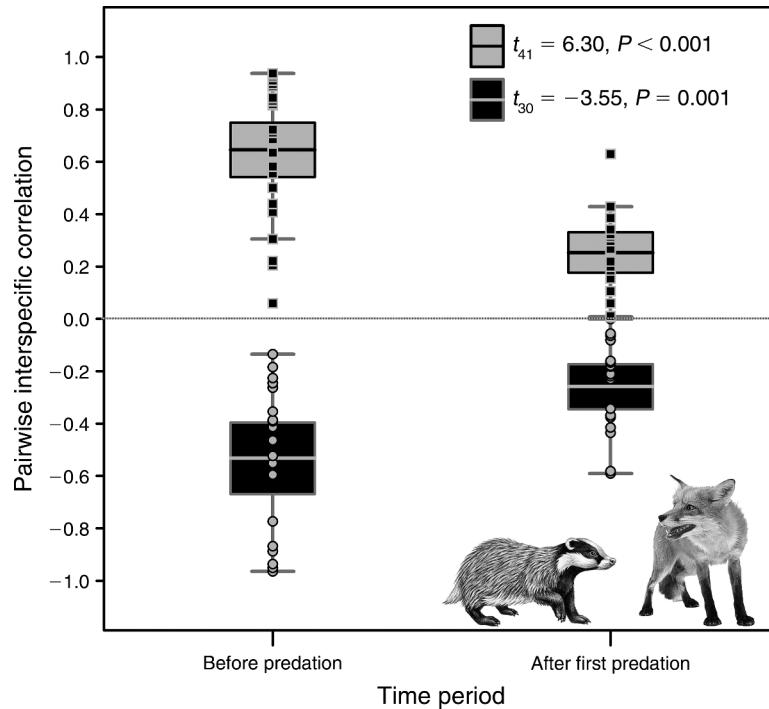


FIG. 3. Boxplots of the pairwise interspecific correlations between all the pairs of seabird time series before and after the first predatory event by terrestrial carnivores (badgers and red foxes). Boxes span the 95% confidence interval of positive (gray) and negative (black) cross-correlations, horizontal lines represent the mean, and whiskers cover the non-outlier range. Gray circles are the individual negative correlations, and black squares are the positive correlations. The average shift in correlation values were compared before and after 1994, with a *t* test for samples with unequal variances.

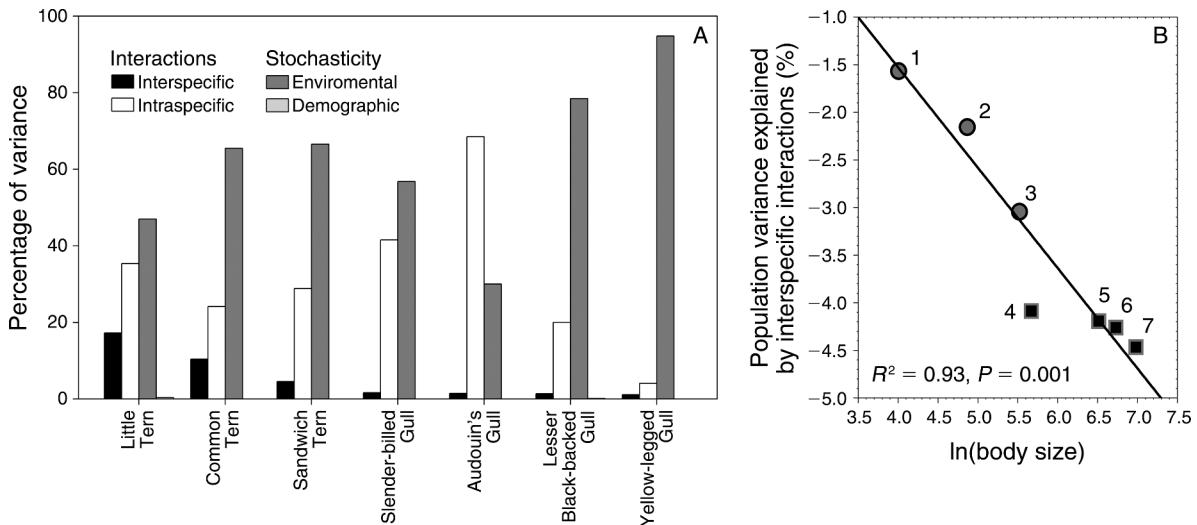


FIG. 4. Results of the fitting of the Gompertz stochastic community dynamics model to the seabird time series. (A) The percentage of temporal variance for the single-species dynamics attributable to interspecific interactions, intraspecific competition, environmental stochasticity, and demographic noise. (B) The reduced major axis (RMA) regression of the logit-transformed amount of population variance explained by interspecific interactions on the log_e-transformed body size of individual species. Results were obtained from 10 000 bootstrap-simulated data sets, and the jackknifed estimates are shown; the RMA equation is $y = 2.688 - 1.054x$; $R^2 = 0.93$, $P = 0.001$. Numbers are 1, Little Tern; 2, Common Tern; 3, Sandwich Tern; 4, Slender-billed Gull; 5, Audouin's Gull; 6, Lesser Black-backed Gull; and 7, Yellow-legged Gull. Gray circles represent *Sterna* species, while black squares denote species from the *Larus* genus.

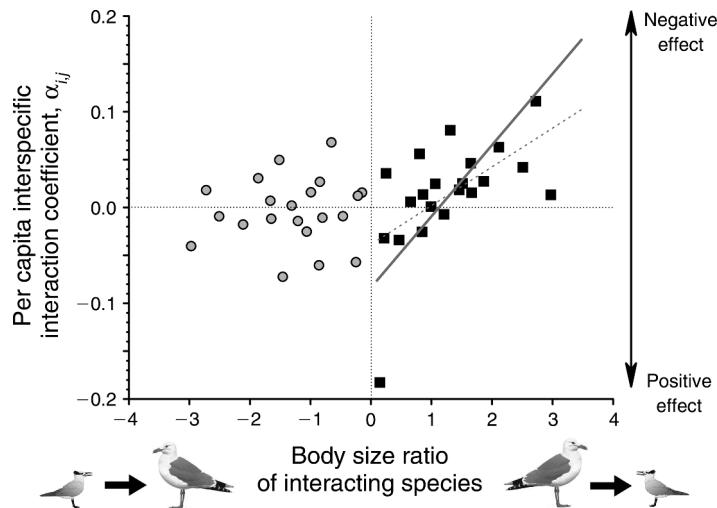


FIG. 5. Relationship between the magnitude of the per capita interspecific interaction coefficient ($\alpha_{i,j}$) and the body size ratio of every pair of interacting seabirds (w_j/w_i , where w is body mass). Positive values for the body size ratio indicate that the species exerting the effect is larger than the species suffering it (that is, $w_j > w_i$). Positive values for $\alpha_{i,j}$ denote that species j has a negative effect on the equilibrium population density of species i . A Bayesian cut-point analysis (Gelman et al. 2004) suggests that the correlation breaks down at a body size ratio of 0.0052 (posterior estimate for cut-point). For the set of positive body size ratios (solid squares), ordinary least squares (OLS) and reduced major axis (RMA) regressions are shown as a dotted and solid line, respectively. Results were obtained from 10 000 bootstrap-simulated data sets, and jackknifed estimates are shown; OLS equation, $\alpha_{i,j} = -0.039 + 0.041(w_j/w_i)$, $R^2 = 0.33$, $P < 0.01$; RMA equation, $\alpha_{i,j} = -0.085 + 0.075(w_j/w_i)$, $R^2 = 0.29$, $P < 0.01$.

species. In contrast, if the external species is smaller there is no clear effect on the focal population density.

Importantly, the results found here are robust to the pattern of missing data in our data set (see the Appendix).

DISCUSSION

Many world populations of large gulls increased at unprecedented rates in the last decades (Oro and Martínez-Abraín 2007), likely due to reduced human disturbance and increased food availability. In the study area, discards from commercial fisheries were the main driver of the population growth of all species, but particularly for large gulls, which dominate the interference competition for such resource (Arcos et al. 2001, Oro et al. 2009). In particular, food availability from discards strongly affects the breeding performance of most species in the study area (Oro et al. 2009 and references therein). Given that this resource is usually superabundant and largely predictable in space and time (e.g., Bartumeus et al. 2010), a relaxation of interspecific competition might be expected in this scenario. This is indeed the case for the breeding populations of Yellow-legged Gull, a generalist species, and the Audouin's Gull, a specialized nocturnal predator (Arcos et al. 2001). In general, there is a positive correlation between the size of predators and the size of their prey (Simberloff and Dayan 1991, Cohen et al. 2003), which might induce niche segregation in size-structured populations (e.g., Loeuille and Loreau 2005). Therefore, rather than the signature of competition for food (e.g., Ballance et al. 1997), the declining common trend

associated with small species in our study area likely reflects competition for breeding space, which triggered higher emigration from the study area (Tavecchia et al. 2007, Oro et al. 2009). Indeed, previous evidence revealed size-dependent microhabitat selection within the modeled community (see Oro et al. 2009), which point to interference competition for space (i.e., breeding habitat) as the process behind this pattern.

Demographic effects of stochastic predatory events by carnivores were strongly dependent on the differing efficiency among predatory individuals (Oro and Pradel 2000, Ruiz-Olmo et al. 2003, Cam et al. 2004, Oro 2008). The common trends driving multispecies dynamics have a nonlinear shape segregated according to a body size continuum, with drifting trajectories up to the mid-1990s and a subsequent stabilization. Indeed, an abrupt shift in community structure was detected a year after the first predatory episode, along with an abrupt decline in interspecific synchrony. These concurrent shifts in community structure and dynamics are the likely signature of generalist predation inducing a rapid reorganization of the seabird community. Interestingly, it is known that generalist predators are able to synchronize prey populations through shared predation pressure (e.g., Ranta et al. 2006), but we found the opposite effect. We think there are two non-mutually exclusive explanations for this. First, predators are only able to synchronize prey populations that display a similar density-dependent structure. We have shown that the modeled seabird time series display a range of population growth patterns. Indeed, for the Yellow-legged Gull, predation pressure was sometimes extreme-

ly high (Oro 2008), but in the long term, the dynamics of this species was clearly density independent. Besides, the failure of breeding output in the globally threatened Audouin's Gull induced by carnivore predators did not translate to changes in local recruitment, but to changes in emigration in spite of the clear density-dependent dynamics of this species (Oro and Pradel 2000, Tavecchia et al. 2007). Secondly, the recorded predatory events by carnivores in the Ebro Delta were characterized by a large temporal unpredictability, and the efficiency of predators was extremely variable among individual predators: While some of them were very efficient in killing hundreds of individuals in a single breeding season (Oro and Pradel 2000, Oro 2008), other caused virtually no damage (D. Oro, *personal observations*).

Ecological theory predicts that, for species to coexist, the strength of intraspecific competition must be larger than the magnitude of interspecific interactions within single trophic levels (e.g., Chesson 2000, Ranta et al. 2006). In our modeled community, the overall strength of intraspecific interactions was six times greater than the magnitude of interspecific interactions, a result in agreement with recent evidence across a range of natural communities (Houlahan et al. 2007, Mutshinda et al. 2009) and theoretical explorations (Kokkoris et al. 1999). Strikingly, however, body size alone is able to predict with a large accuracy the magnitude of interspecific effects across seabird species, and we found that the strength of per capita non-trophic interaction coefficients scales positively with the body size ratio of interacting species. Moreover, small species are simultaneously affected across time by stronger per capita interspecific effects, smaller population sizes and higher population fluctuations than larger species. This is a novel example of long-term asymmetric interspecific competition driven by body size on an assembling natural community. However, stochasticity still accounts for the largest portion of total community variance, and given that population fluctuations of small larids increased across time, driving two species to local extinction, we might expect to find strong per capita interspecific interactions destabilizing species dynamics (Pimm 1991, Chesson 2000, Ranta et al. 2006). We provide several nonexclusive explanations for this apparently counterintuitive finding. First, previous evidence has established that dispersal has been the main driver of the population dynamics of seabirds in our study area (Oro 2002, 2008, Oro and Pradel 2000, Oro and Ruxton 2001, Cam et al. 2004, Oro et al. 2009, Tavecchia et al. 2007). The high density of dominant species and/or conspecifics within a colony might simply trigger emigration of some individuals to adjacent colonies (Oro and Ruxton 2001), and in this case, the numerical signature of per capita interactions in time series of local population densities is diluted. Alternatively, although interspecific interactions are traditionally regarded as negative for at least one of the species

(but see Berlow et al. 2009), positive effects of the presence of conspecifics and/or heterospecifics on immigrants arriving to a colony may easily arise. Individuals may acquire information on the quality of a patch from the occurrence of species with similar habitat selection (e.g., Goodale et al. 2010). We have previously shown that conspecific attraction affected the settlement probability of Audouin's Gull in the study area and in other Mediterranean colonies (Oro and Pradel 2000, Oro and Ruxton 2001, Cam et al. 2004). Therefore, it is reasonable to assume that, during the initial colonization of the study area, large gull species benefited from breeders already there. From the mid-1990s, however, it is likely that the benefits obtained from conspecific and heterospecific attraction disappeared due to (1) the onset of density dependence, which operated through competition for space (Oro 2008, Oro et al. 2009) and emigration to adjacent colonies (Cam et al. 2004, Tavecchia et al. 2007); and (2) the onset of stochastic predation by generalist carnivores, which disrupted the pattern of interspecific correlations and community structure. In this scenario, the long-term strength of per capita interactions might thus be weakened. Finally, weak interspecific interactions can have strong community effects through cascading extinctions and the "noise-dampening" effect of rich communities (Berlow 1999). In our case, two species became locally extinct during the assembly process and the equilibrium density of others decreased accordingly, and it is possible that this shifting structure impacted upon lower trophic levels and regional dynamics (Oro et al. 2009). Moreover, the proportion of predictable variance in interspecific effects strongly increases with theoretical community richness (Berlow et al. 2009), and our sampled ecological guild, a sub-module of a larger interaction network, obviously misses other trophic levels with potentially large interspecific effects.

Overall, this study provides an empirical example suggesting that species within ecological guilds are able to coexist at the regional level through segregation in local population dynamical processes, even if the local communities decrease in diversity and richness. From a metacommunity perspective (Leibold et al. 2004) the implications are that size-dependent interactions at the local scale can be relaxed at the regional level through dynamic dispersal events induced by trophic (stochastic predation by carnivores) and non-trophic interactions (intra-guild competition for space; see Oro et al. 2009). Eventually, this can give rise to a heterogeneous spatiotemporal mosaic in the local demography and community dynamics ultimately driven by differences in body size (Ritchie 2009), and thus promote long-term species coexistence at the regional level.

ACKNOWLEDGMENTS

We are grateful to all the people participating in the seabird monitoring at the Ebro Delta over the years, particularly to Albert Martínez-Vilalta, Meritxell Genovart, Albert Bertolero, Julia Piccardo, José Manuel Igual, and Antoni Curcó, who

contributed to organizing and executing the censuses. Staff of the Delta de l'Ebre Natural Park also offered logistic support. P. Almaraz also is grateful to Antonio Delgado (EEZ-CSIC), Toni Sánchez-Zapata (UMH), and Paco Botella (UMH) for their support during the years 2009–2010. P. Almaraz also acknowledges the people at the IMEDEA for their insightful suggestions and fruitful discussions on several topics during his short visit there. Crispin Mutshinda provided valuable technical input. We are grateful to Jose M. Montoya and an anonymous referee for their constructive comments on a previous draft of the manuscript. Funds were provided by several agencies such as Generalitat de Catalunya, ICONA (Spanish Ministry of the Environment), and the Spanish Ministry of Science (grant ref. CGL2009-08298).

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APPENDIX

Further details on the estimation of the interspecific interaction coefficients, the local stability of the modeled community, and the effects of missing data on inference (*Ecological Archives* E092-166-A1).

SUPPLEMENT

The WinBUGS code used to fit the Bayesian dynamic factor analysis (DFA) and the Gompertz stochastic community dynamics model (*Ecological Archives* E092-166-S1).