

Estimating partial observability and nonlinear climate effects on stochastic community dynamics of migratory waterfowl

Pablo Almaraz^{1,2*}, Andy J. Green¹, Eduardo Aguilera³, Miguel A. Rendón¹ and Javier Bustamante^{1,4}

¹Department of Wetland Ecology, Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas (CSIC), Avda. Americo Vespucio S/N, E-41092 Sevilla, Spain; ²Laboratorio de Biogeoquímica de Isótopos Estables, Instituto Andaluz de Ciencias de la Tierra IACT (CSIC-UGR), Avda. de las Palmeras 4, 18100 Armilla, Granada, Spain; ³Ethology and Biodiversity Conservation, Estación Biológica de Doñana, CSIC, Avda. Americo Vespucio S/N, E-41092 Sevilla, Spain; and ⁴Remote Sensing and Geographic Information Systems Lab (LAST-EBD), Estación Biológica de Doñana, CSIC, Avda. Americo Vespucio S/N, E-41092 Sevilla, Spain

Summary

1. Understanding the impact of environmental variability on migrating species requires the estimation of sequential abiotic effects in different geographic areas across the life cycle. For instance, waterfowl (ducks, geese and swans) usually breed widely dispersed throughout their breeding range and gather in large numbers in their wintering headquarters, but there is a lack of knowledge on the effects of the sequential environmental conditions experienced by migrating birds on the long-term community dynamics at their wintering sites.

2. Here, we analyse multidecadal time-series data of 10 waterfowl species wintering in the Guadalquivir Marshes (SW Spain), the single most important wintering site for waterfowl breeding in Europe. We use a multivariate state-space approach to estimate the effects of biotic interactions, local environmental forcing during winter and large-scale climate during breeding and migration on wintering multispecies abundance fluctuations, while accounting for partial observability (observation error and missing data) in both population and environmental data.

3. The joint effect of local weather and large-scale climate explained 31.6% of variance at the community level, while the variability explained by interspecific interactions was negligible (< 5%). In general, abiotic conditions during winter prevailed over conditions experienced during breeding and migration. Across species, a pervasive and coherent nonlinear signal of environmental variability on population dynamics suggests weaker forcing at extreme values of abiotic variables.

4. Modelling missing observations through data augmentation increased the estimated magnitude of environmental forcing by an average 30.1% and reduced the impact of stochasticity by 39.3% when accounting for observation error. Interestingly however, the impact of environmental forcing on community dynamics was underestimated by an average 15.3% and environmental stochasticity overestimated by 14.1% when ignoring both observation error and data augmentation.

5. These results provide a salient example of sequential multiscale environmental forcing in a major migratory bird community, which suggests a demographic link between the breeding and wintering grounds operating through nonlinear environmental effects. Remarkably, this study highlights that modelling observation error in the environmental covariates of an ecological model can be proportionally more important than modelling this source of variance in the population data.

Key-words: climate fluctuations, community dynamics, data augmentation, Doñana, Hierarchical Bayes, measurement error, missing data, multivariate state-space model, North Atlantic Oscillation, population dynamics, waterfowl

*Correspondence author. E-mail: palmaraz@gmail.com

Introduction

Migratory species must cope with heterogeneous environmental conditions at large spatial scales throughout their annual cycles, and this can hamper the ability to predict their population sizes and regulating factors across time (Fretwell 1972; Webster *et al.* 2002; Newton 2004). The dynamic response of migrating populations to factors operating during the breeding, migration and wintering periods is translated among seasons through so-called carry-over effects (Webster *et al.* 2002; Norris & Taylor 2006). For example, there is empirical evidence from several bird species that local changes in habitat quality and environmental characteristics translate to changes in individual success between seasons and geographic locations (e.g. Sutherland 1998; Sillett, Homes & Sherry 2000; Gill *et al.* 2001). Among birds, waterfowl (ducks, geese and swans) provide particularly salient examples of extended migratory behaviour (Newton 1998, 2004; Kear 2005). Throughout the world, waterfowl populations usually breed widely dispersed over large geographic areas, but during winter large concentrations can occur in a few key areas (e.g. Weller 1988; Scott & Rose 1996). These local wintering gatherings can encompass a major fraction (Almaraz & Amat 2004a) or even the whole world population (Petersen, Larned & Douglas 1999) of single species.

In this scenario, factors operating at the wintering sites can be of critical importance for determining multi-annual population dynamics. For instance, many waterfowl species are the target of severe hunting pressure (Nichols, Johnson & Williams 1995; Newton 1998), particularly during the wintering season (Nilsson *et al.* 1999). Stochastic population dynamics analysis emerges as an instrumental approach for understanding the long-term dynamics of harvested waterfowl species, and the adaptive management of exploited waterfowl populations in North America has indeed pioneered the application of stochastic analysis to population ecology (e.g. Anderson 1975; see review in Nichols, Johnson & Williams 1995). Nichols, Johnson & Williams (1995) identified several major sources of stochasticity affecting ecological inference. First, *environmental variability* operating through habitat changes, local weather variation and large-scale climate fluctuations affects waterfowl populations world-wide (e.g. Almaraz & Amat 2004a,b; Ward *et al.* 2005; Kéry, Madsen & Lebreton 2006; Sedinger *et al.* 2006; Morrissette *et al.* 2010; reviews in Newton 1998; Sæther, Sutherland & Engen 2004). Secondly, *structural uncertainty* refers to the lack of knowledge on the precise mechanisms affecting population demography. For example, contradictory evidence has been presented in recent years on the prevalence of density dependence (Almaraz & Amat 2004a,b; Jamieson & Brooks 2004) and interspecific interactions (DuBowy 1988) in waterfowl populations. Thirdly, *partial observability* reflects the imprecision in the sampling of an ecological system. Processes are observed partially because they may yield data sets with unknown amounts of observation error and perhaps also missing data (Clark & Bjørnstad

2004; Freckleton *et al.* 2006). Assessing the relative impact of these sources of uncertainty should be the first step towards a sound ecological inference and adaptive management strategy for migratory waterfowl.

The possibility for strong carry-over effects linking environmental changes in wintering areas to breeding performance in waterfowl populations has been explored for single species (e.g. Morrissette *et al.* 2010), but the analysis of the long-term sequential environmental conditions experienced by migrating birds on major wintering areas is lacking. In the present paper, we analyse the long-term data (1978–2006) from 10 waterfowl species wintering in a major wetland of south-western Europe, the Guadalquivir Marshes (García-Novo & Marín 2006; Rendón *et al.* 2008; Kloskowski *et al.* 2009). This area is the single most important wintering site for waterfowl breeding in northern Europe (Scott & Rose 1996), with over a million birds recorded in some years (Nilsson *et al.* 1999; Rendón *et al.* 2008). Our main goal is to assess the relative impact of sequential large-scale climate variability across the life cycle, local environmental dynamics and biotic interactions on the long-term wintering multispecies dynamics. As is typical for long-term ecological projects (Clark & Bjørnstad 2004), the information arising from our monitoring programme contains missing data and observation error. To this end, here we develop a multivariate state-space model (MSSM) to assess the interaction between abiotic and biotic components in a hierarchical time-series model (e.g. Cressie *et al.* 2009; Knape *et al.* 2009). The novelty of our approach comes from the coupled modelling of two distinct hidden processes: one for the local environmental dynamics, represented by the stochastic fluctuations in the extent of spatial flooding dependent in a hierarchical manner on rainfall variability and large-scale climate fluctuations, and the other for the abundance of the waterfowl community, which evolves according to a stochastic dynamics model including biotic interactions together with large-scale climatic and local flooding effects. Thus, the structure of our model stems naturally from the ecological functioning of our study system (Jensen 2001; Almaraz & Amat 2004a), and partial observability is accounted for within both the environmental and biological process modelling. Given that observation error and missing data can both degrade the inference derived from population abundance models (e.g. Clark & Bjørnstad 2004; Dennis *et al.* 2006), a specific goal of our analysis was to test the impact of partial observability on the estimation of biological and environmental effects.

Materials and methods

STUDY AREA AND DATA BASE

The Guadalquivir Marshes, located in south-western Spain (Fig. S1 in Appendix S1, Supporting information), is one of the largest and best preserved Mediterranean wetland ecosystems in the world (García-Novo & Marín 2006). It contains a complex mosaic of

natural wetland and artificial salt pans, ricefields and fish farms within a huge (180 000 Ha) inner delta originated in the alluvial flood plain of the Guadalquivir river (see Fig. 1 and Fig. S1 in Appendix S1, Supporting information; García-Novo & Marín 2006; Rendón *et al.* 2008). The study area is largely protected as a Ramsar site (29 640 Ha), an EU Specially Protected Area (50 720 Ha), a Biosphere Reserve (77 267 Ha) and a UNESCO World Heritage site (29 640 Ha). In order to estimate the relative abundance of waterfowl, a total of 91 890 ha within the Guadalquivir Marshes have been surveyed from the air on a monthly basis since 1978 (see Rendón *et al.* 2008 for details). In this study, we analyse replicate censuses for December and January wintering counts up to 2006, most performed within 2 weeks; because the majority of migrating birds arrive in the study area by November (Rendón *et al.* 2008), these estimates yielded the largest repeatability, the smallest seasonal variance, and thus reflect the wintering population with a greatest accuracy. We focus on the 10 most abundant waterfowl species (Fig. 2): greylag goose (*Anser anser*), common shelduck (*Tadorna tadorna*), gadwall (*Anas strepera*), mallard (*Anas platyrhynchos*), northern pintail (*Anas acuta*), northern shoveler (*Anas clypeata*), common teal (*Anas crecca*), Eurasian wigeon (*Anas penelope*), common pochard (*Aythya ferina*) and red-crested pochard (*Netta rufina*). These species are easily detectable during the aerial surveys and cover a wide range of

population densities and life histories. In Table S1 of Appendix S1 (Supporting information), we summarize the population characteristics and the international importance of the study area for each species.

ENVIRONMENTAL AND CLIMATIC DATA

In wetlands, flooded surface area is a good surrogate for the amount of habitat and food resources available to birds (Newton 1998). Figure 1 shows the yearly variations in the spatial flooding extent during winter in the Guadalquivir Marshes. The spatial data for December and January replicates were estimated from satellite imagery. From 1978 to 1984, flooding data come from LandsatTM MSS imagery (<http://landsat.gsfc.nasa.gov/>) with a nominal 60 × 80 m pixel resolution; from 1985 to 2005, we used LandsatTM and ETM+ imagery with 30 × 30 m pixel resolution. The yearly amount of flooding within the study area depends almost exclusively on rainfall levels: the accumulated precipitation from September to January is a good predictor of the expected flooded area in January ($R^2 = 70\%$, $P < 0.001$). Owing to adverse environmental conditions (extreme cloudiness) and logistical problems (Landsat passage schedule), 11 years had to be treated as missing values using the cut() function in OpenBUGS (see below). Monthly rainfall data were obtained

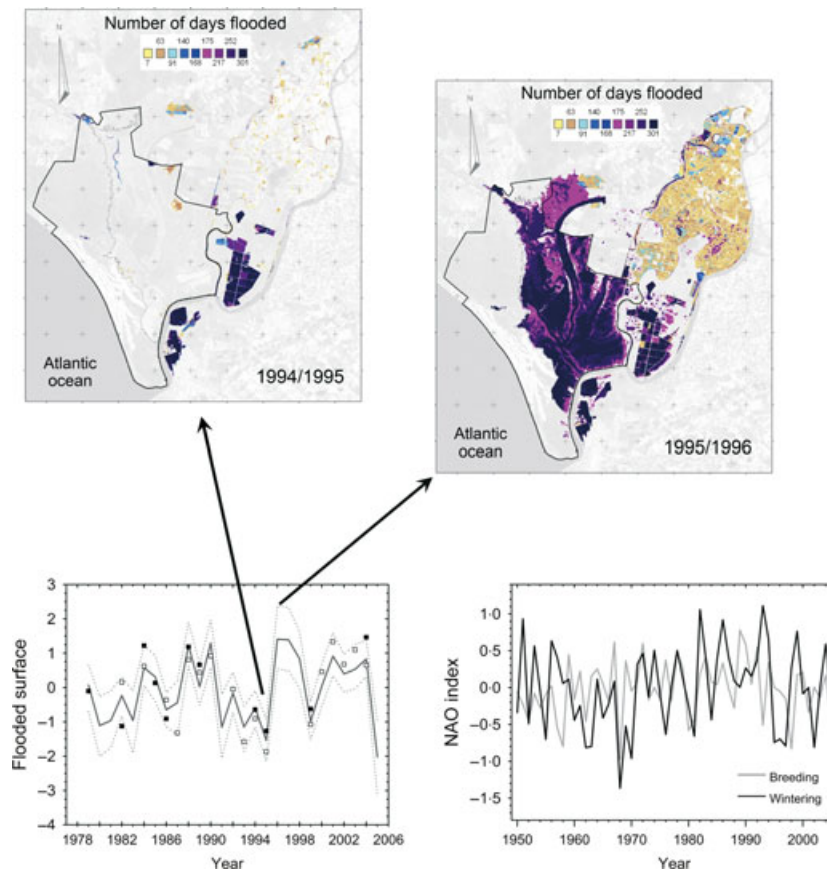


Fig. 1. Time series of spatial flooding extent during winter in Guadalquivir Marshes (lower left) and the North Atlantic Oscillation (NAO) index (lower right). The log-transformed satellite-derived estimates of flooding extent are shown for December (open squares) and January (black squares). Posterior predictions and 90% highest posterior density intervals for the hidden flooding states are shown with black and grey dotted lines, respectively. In the lower right, the NAO index during the last half century is shown for the breeding period (grey line), averaged from March to October, and the wintering season (black line, from October to January). In the upper level of the figure, the hydroperiod is shown for two consecutive years; this variable quantifies the number of days that each modelled pixel remained flooded in Guadalquivir Marshes, with 1 pixel = 900 m².

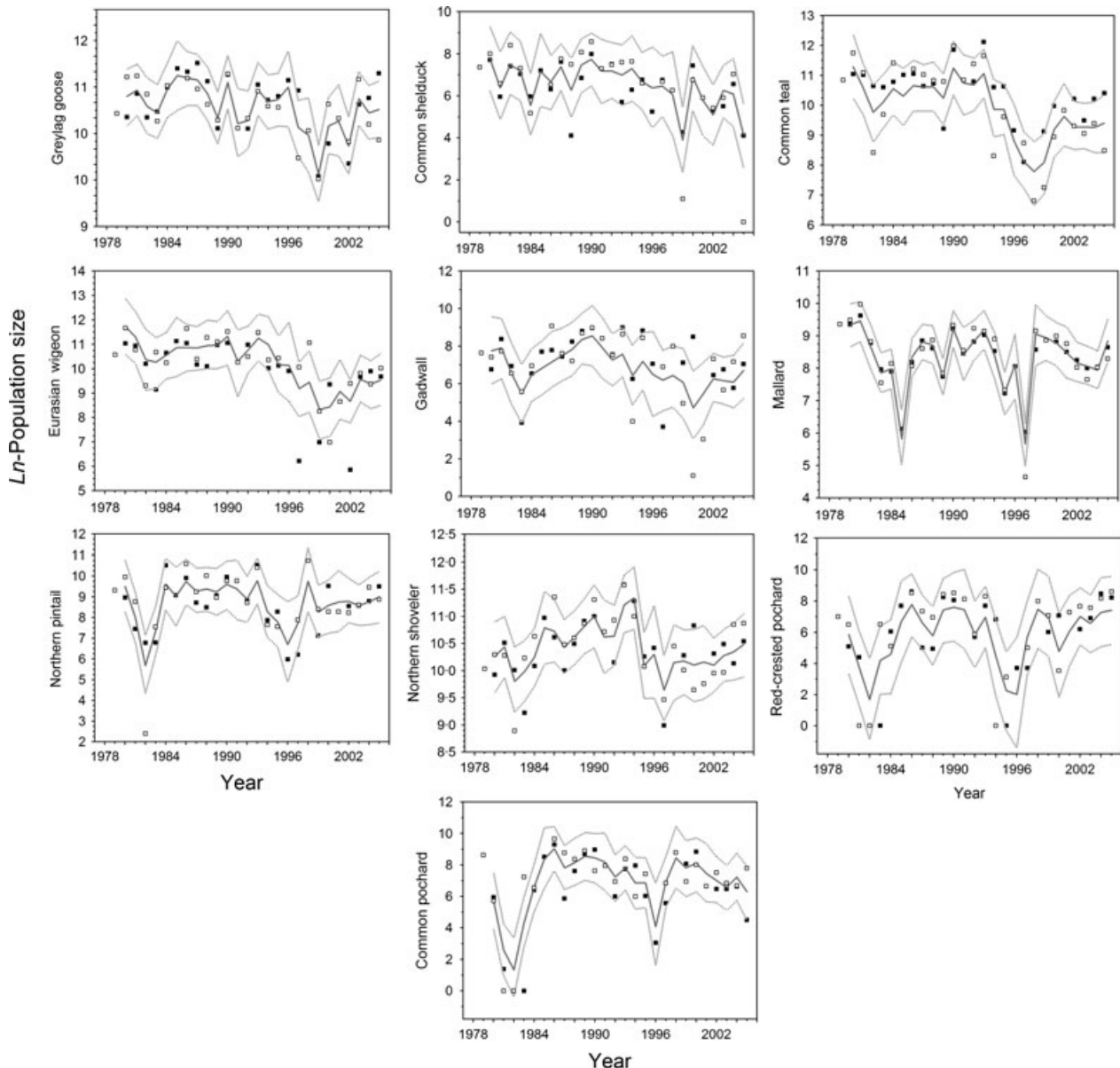


Fig. 2. Time series of winter aerial counts for ten waterfowl species in the Guadalquivir Marshes, and posterior states predicted by the stochastic Gompertz community dynamics model. The log-transformed population counts for December and January are shown as open and black squares, respectively. The grey line within each graph shows the posterior states estimated from the MSSM, while the grey dotted lines depict the 90% Bayesian highest posterior density interval of the estimates.

from the meteorological station within the Doñana National Park (Palacio de Doñana).

To assess the potential effects of climate on population abundance, we used the North Atlantic Oscillation (NAO) index as a large-scale climate proxy reflecting environmental conditions in the Northern Hemisphere (Hurrell *et al.* 2003). We obtained monthly NAO indices from the NOAA Climate Prediction Center (<http://www.cpc.noaa.gov/data/teledoc/nao.shtml>). The NAO is a north–south dipole of atmospheric anomalies, with one centre located over Greenland and the other spanning the central latitudes of the North Atlantic between 35°N and 40°N. Positive NAO phases are characterized by below-normal pressures over Greenland and tend to be associated with above-average temperatures and precipitations in northern Europe and the opposite in southern Europe. During prolonged periods dominated by a

particular phase of the NAO, the above patterns can be detected as far as central Russia and north-central Siberia (see Hurrell *et al.* 2003). These geographic patterns match quite well with the breeding range of the species studied (Table S1 in Appendix S1, Supporting information). We used a winter NAO index (see Fig. 1) to estimate the effect of climatic conditions on the abundance of waterfowl at a large spatial scale during wintering. Within our subset of species, the modal date of breeding onset is March. After the breeding period, all species moult during the boreal summer. In the Guadalquivir Marshes, the first migrants arrive in late October (Rendón *et al.* 2008). Therefore, we additionally used the NAO index averaged from March to October as a proxy for the lagged climatic conditions experienced by wintering waterfowl during their previous breeding and moulting period.

Modelling environmental forcing of stochastic community dynamics

PROCESS MODELS

Given that local weather is a function of large-scale climate (Almaraz & Amat 2004a), we assume rainfall variability during winter to depend on the wintertime NAO, and subsequently we specified flooding extent to depend on rainfall variability (see Fig. 3). Let r_t be the value of rainfall during winter at time t , w_t the wintertime NAO index at time t and F_t the hidden winter flooding extent at time t . Therefore, the environmental component of the study system, represented by the first two hierarchical levels in Fig. 3, takes the form

$$\begin{aligned} r_t &= \beta_0 + \beta_1 w_t + \eta_{r,t} \\ F_t &= \lambda_0 + \lambda_1 r_t + \eta_{F,t} \end{aligned} \quad \text{eqn 1}$$

where β_0 and λ_0 are constants and β_1 and λ_1 measure the impact of the NAO on winter rainfall variability and the subsequent effect of rainfall variability on spatial flooding, respectively; the terms $\eta_{r,t}$ and $\eta_{F,t}$ are the rainfall and flooding process noises, following normal distributions with mean 0 and constant variances σ_r^2 and σ_F^2 , $\eta_{r,t} \sim N(0, \sigma_r^2)$ and $\eta_{F,t} \sim N(0, \sigma_F^2)$. These variance terms are called the rainfall (σ_r^2) and flooding (σ_F^2) system errors.

For modelling the community dynamics process (the third hierarchical level depicted in Fig. 3), we used a stochastic Gompertz model including interspecific interactions of the Lotka–Volterra type and environmental effects (e.g. Muthinda, O’Hara & Woiwod 2011). We predict that environ-

mental fluctuations may have nonlinear effects on the fluctuations in the abundance of most species. For example, it is known that dabbling duck populations have an optimum habitat flooding extent, because depths too low or too high might prevent optimal foraging (e.g. DuBowy 1988; Kear 2005). Therefore, to test for potential nonlinearities in the functional effects of environmental variables, we included both linear and quadratic terms for the effects of flooding extent, NAO during breeding and NAO during winter. Let $n_{i,t}$ be the ln-transformed wintertime abundance of species i at time t and $z_{i,T}$ be the NAO index during the non-wintertime period at time $t-T$ where T is a variable time-lag accounting for variable age at first breeding attempt among species (see Discussion). The Gompertz community dynamics model with nonlinear environmental effects has the form

$$\begin{aligned} n_{i,t} &= n_{i,t-1} + r_i \left[1 - \frac{\sum_{j=1}^S \alpha_{i,j} n_{j,t-1}}{k_i} \right] + \gamma_{i,l} F_t + \gamma_{i,q} F_t^2 \\ &+ \varphi_{i,l} z_{i,t-T} + \varphi_{i,q} z_{i,t-T}^2 + \delta_{i,l} w_t + \delta_{i,q} w_t^2 + \varepsilon_{i,t} \end{aligned} \quad \text{eqn 2}$$

where r_i and k_i are the intrinsic growth rate and the ln-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). The parameters $\gamma_{i,l}$, $\varphi_{i,l}$ and $\delta_{i,l}$ denote the effects of flooding extent, NAO during breeding and NAO during winter, respectively, on the abundance of the i th species, for both linear (subscript l) and quadratic terms (q) of these variables. Given that the interpretation of quadratic

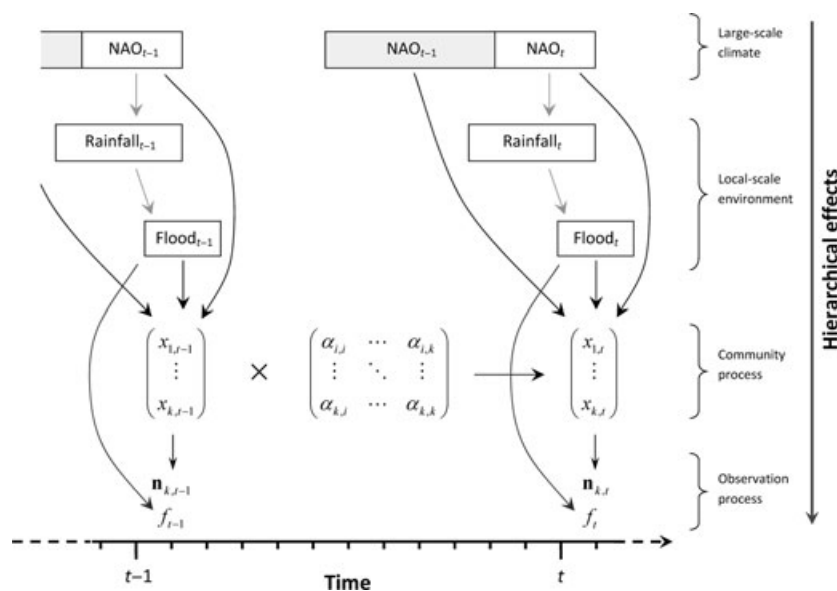


Fig. 3. Diagram depicting the structure of the MSSM fitted to the time series of the waterfowl community wintering in Guadalquivir Marshes. The graph depicts the flow of time, from left to right, and the flow of the hierarchy of effects, from the top to the bottom. In the upper part, the sequential effects of the North Atlantic Oscillation during breeding (grey box) and wintering (white box) are linked to the vector of population sizes both directly (black arrows) and indirectly through the local environmental effects (grey arrows). At the bottom, the vector for the observed abundances (denoted by n_k) and flooding values (f_t) are linked to the community and hidden flooding processes through observation models, respectively, while the population process vectors are linked across time through the community interaction matrix A (Levins 1968), containing the intra- and interspecific effects (the α 's). Shown are the effects for a single time slice (time t).

terms in a polynomial regression generally depends on the range of the covariates, we fitted semi-parametric Bayesian P-splines to the plots of waterfowl abundance vs. environmental variables to visually inspect that our parametric approach is correctly capturing the ‘nonlinearities’ of these effects (see Fig. S2 in Appendix S1, Supporting information). We did not fit P-splines in the MSSM because this made the convergence highly unstable.

A matrix \mathbf{A} can be derived from the above model containing the coefficients for interspecific interactions scaled by the carrying capacities in the off-diagonal, $\alpha_{i,j}/k_i$, and the coefficients for intraspecific interactions, $\alpha_{i,i}$, normalized to 1 ($1/k_i$) in the main diagonal; this is the so-called community matrix (Levins 1968). The vector $\boldsymbol{\varepsilon}_t = (\boldsymbol{\varepsilon}_{1,t}, \dots, \boldsymbol{\varepsilon}_{S,t})^T$ represents the effects of unexplained (latent) stochastic noise on the population dynamics of species i and is sequentially independent noise distributed according to a multivariate normal distribution, $\boldsymbol{\varepsilon}_t \sim MVN(\mathbf{0}, \boldsymbol{\Sigma}_t)$. The environmental matrix $\boldsymbol{\Sigma}_t$ includes the variance of the latent stochastic factors impacting on single-species dynamics in the main diagonal ($\sigma_{n,i,i}^2$), as well as the covariance terms for the pairwise joint responses to stochastic factors between all the pairs of species, $\sigma_{n,i,j}^2$ (for $i \neq j$), in the off-diagonal. The variance term $\sigma_{n,i,i}^2$ is thus the population system error for each species i . A graphical depiction of the MSSM is shown in Fig. 3.

The temporal variance displayed by the fluctuations in the abundance of every species can be decomposed into the joint contributions from biotic interactions and environmental forcing; the former factor refers to the role of intra- and interspecific interactions, while the later component refers to climatic and environmental variability, as well as other stochastic forces impacting on the temporal dynamics (e.g. Mutshinda, O’Hara & Woiwod 2011). It is straightforward to calculate the proportion of the single-species temporal variance in abundance attributable to every effect modelled through the MSSM, in the same way as the variance component estimation of a quantitative trait in genetics (Sorensen & Gianola 2002). To assess the overall effect of the modelled components at the community level, we estimate the total community variance as the sum of the single-species variance components. In Appendix S1, we derive the calculation of these variance components.

OBSERVATION MODELS

Because we have two replicated samples for both flooding extent and population abundance estimates, we can empirically estimate the observation error from the replicated nature of our survey in a fully identified model (see Dennis, Ponciano & Taper 2010; Knape, Jonzén & Sköld 2011; Mutshinda, O’Hara & Woiwod 2011). We denote $\mathbf{f}_k^T = [f_{k,1}, f_{k,2}, \dots, f_{k,T}]$ as the sequence of estimates for flooding extent derived from Landsat images for each k month and $\mathbf{y}_{i,k}^T = [y_{i,k,0}, y_{i,k,1}, \dots, y_{i,k,T}]$ as the log-transformed aerial estimates of population abundances for each species i during each replicated k census. We further considered the temporal distribution of the observation errors to be potentially corre-

lated across species (Knape *et al.* 2009), so a non-diagonal variance–covariance matrix $\boldsymbol{\Omega}_t$ was implemented in the sampling model for waterfowl counts; the measurement (observation) equations can thus be written as

$$\begin{aligned} f_{k,t}|F_t &\sim N(F_t + c_k, \tau_f^2) \\ \mathbf{y}_{k,t}|\mathbf{n}_t &\sim MVN(\mathbf{n}_t + \mathbf{b}_k, \boldsymbol{\Omega}_t) \end{aligned} \quad \text{eqn 3}$$

where c_k is the correction factor for the average fluctuation level of each flooding time series for each replicate sample k . The two $S \times T$ matrix $\mathbf{y}_{k,t}$ encompass the time series of waterfowl counts recorded during each replicate census as columns in two observation matrices, one for the December count ($\mathbf{y}_{1,t}$) and the other for the January census ($\mathbf{y}_{2,t}$); these matrices are jointly conditioned upon the $S \times T$ process state matrix \mathbf{n}_t including the time series of latent population sizes for each species as columns; $\mathbf{b}_k = (b_{1,k}, \dots, b_{S,k})^T$ are two column vectors encompassing the correction factors for the average fluctuation level of each replicate population abundance time series for each species and replicate census. To allow for identifiability, the correction factors for the December replicate (c_1 and $b_{1,1}$) were set to 0, while the other parameters were estimated freely. The term τ_f^2 is the observation error for flooding extent; the observation error matrix $\boldsymbol{\Omega}_t$ includes the error terms for the sampling variability of single-species surveys in the main diagonal ($\tau_{i,i}^2$), as well as the covariance terms for the temporally correlated observation errors between all the pairs of species, $\tau_{i,j}^2$ (for $i \neq j$), in the off-diagonal.

PRIOR SPECIFICATION AND PARAMETER ESTIMATION

We used Bayesian Markov chain Monte Carlo (MCMC) integration through Gibbs sampling (Gelman *et al.* 2004) to fit the MSSM. To finish model specification, we placed weakly informative priors on the unknown quantities in eqns 1–3. The location parameters were given flat normal distributions, that is, $\beta_0, \lambda_0, \beta_1, \lambda_1, \gamma_{i,\cdot}, \varphi_{i,\cdot}, \delta_{i,\cdot}, c_k, b_{i,k} \sim N(0, 10^3)$. The terms for intrinsic growth rates and carrying capacities were also given flat normal distributions $r_i, k_i \sim N(0, 10^3)$; these distributions were truncated at 0 to account for the biological fact that an intrinsic growth rate must always be positive; additionally, while k_i is supported in the entire real line, a negative value for the ln-carrying capacity would indicate a carrying capacity of < 1 individual, which does not make biological sense. For the scale parameters in eqns 1 (σ_r^2, σ_F^2) and 3 (τ_f^2), standing for the process and observation errors respectively, we placed uniform distributions on the standard deviations, $\sigma_r^2, \sigma_F^2, \tau_f^2 \sim \text{Unif}(0, 5)$ (see Gelman 2006). The covariance matrix for environmental noise ($\boldsymbol{\Sigma}_t$) and observation error ($\boldsymbol{\Omega}_t$) were modelled with inverse Wishart distributions, $\boldsymbol{\Sigma}_t^{-1}, \boldsymbol{\Omega}_t^{-1} \sim \text{Wishart}(\boldsymbol{\zeta}, S)$, which are the conjugate priors for the covariance matrix of multivariate normal distributions (Gelman *et al.* 2004). The number of degrees of freedom, denoted by q , was set to the rank of the scale matrix $\boldsymbol{\zeta}$, namely the number of species (S) which is the value expressing the weakest prior information. Given that we

monitored 10 species, 90 interspecific interaction coefficients need to be estimated. As many of them will probably be around 0 because of the absence of a quantitative interspecific effect, we use Stochastic Search Variable Selection (SSVS; George & McCulloch 1993) to automatically set these coefficients close to 0 during the MCMC simulation, so that model computation is not affected. We provide the rationale and working of SSVS within our setting in Appendix S1.

We initiated the MCMC simulation scheme with three chains with overdispersed initial values. Each chain was run for 110 000 iterations. The first 80 000 steps were discarded as a burn-in period. The following 30 000 iterations were used to construct the posterior distributions of the MSSM. The convergence of the MCMC simulation scheme was assessed by visually inspecting the posterior trace of the Markov chains and by estimating the cross-correlation among the parameters and hidden states in the model (Gelman *et al.* 2004). The goodness-of-fit of the MSSM was evaluated by plotting the realized residuals in the MSSM vs. the predicted hidden states and by constructing the quantile–quantile plots (e.g. Gelman *et al.* 2004; Knape *et al.* 2009). In Bayesian analysis, a realized residual is estimated from the expected value of the hidden states and observations given the data and the posterior parameter estimates. We used posterior predictive checking (Gelman *et al.* 2004) to assess whether the MSSM is capable of recovering the main processes underlying the temporal fluctuations in flooding extension and waterfowl abundance from synthetic data sets simulated from the fitted model (see Appendix S3 for further details). We wrote the MSSM in the BUGS language (Thomas *et al.* 2006), and the BRugs package (OpenBUGS version 3.0.3) running on R 2.13.0 (R Development Core Team 2011) was used to carry out the analyses. We give a sample BUGS code implementing the MSSM in Appendix S2.

ESTIMATING THE EFFECTS OF PARTIAL OBSERVABILITY ON INFERENCE

Although the impact on ecological models of observation error in population counts is well known (e.g. Dennis *et al.* 2006; Freckleton *et al.* 2006), the role of missing data on ecological inference has seldom been explored (Clark & Bjørnstad 2004). Recently, the availability of replicate counts and the precise specification of the observation error distribution have been shown to be critical for an unbiased estimation of ecological effects of biotic interactions (Dennis, Ponciano & Taper 2010; Knape, Jonzén & Sköld 2011), but little is known about the expected effects of missing data on ecological time-series models, even though their negative impacts on inference are known to be severe in some cases (Nakagawa & Freckleton 2008; Boone, Ye & Smith 2009).

To address the effect of partial observability on parameter estimation, we sequentially fitted alternative MSSMs to different sets of reconstructed data bases. First, we averaged the replicate observations (*sensu* Knape, Jonzén & Sköld 2011) for both waterfowl populations and flooding extent while

retaining the original pattern of missing data. Secondly, by taking advantage of the Gibbs sampler as a data augmentation technique (Gelman *et al.* 2004; Boone, Ye & Smith 2009), we used the time series of rainfall variability to predict the missing data in the replicate estimates of flooding extension through MCMC integration (see eqn 1). Through data augmentation, specific parameters associated with probability distributions (so-called augmented data) are added in the model as surrogates for the missing values, so that the variability in these distributions provides the uncertainty emerging from the missing values. Suitably, the Gibbs sampler can marginalize these distributions during posterior simulation (see, e.g., Boone, Ye & Smith 2009). The pattern of missing data in the replicated time series of waterfowl counts did not have an appreciable effect on inference owing to the small number of unavailable censuses, so we focus only on the flooding data where the amount of missing data is larger (see Fig. 1). This strategy resulted in six reconstructed data sets: (i) two sets where no observation error is considered in waterfowl counts, with and without missing data; (ii) two sets where no observation error is considered in the estimates of flooding extent, with and without missing data; and (iii) two final sets where both waterfowl counts and flooding extent were considered to be measured without error, with and without missing data. The MSSM was then fitted to this six reconstructed data sets, and the resulting posterior estimates for the variance components of biotic interactions and environmental forcing were compared to the results with the original data base where the patterns of both replicated observations and missing data were correctly specified.

Results

ASSESSING CONVERGENCE, GOODNESS-OF-FIT AND MODEL ADEQUACY

There was no evidence for the non-convergence of the three posterior Markov chains, which displayed a relatively good mixing during the MCMC simulation (Figs S1 and S2 in Appendix S3, Supporting information). The posterior correlations between the terms in the full parameter vector, including the hidden flooding states and latent population abundances, were virtually 0 or very small overall (Fig. S3 in Appendix S3, Supporting information). Interestingly, the posterior autocorrelations in the MCMC estimation of the dynamic states were nearly always close to 0 (see Fig. S3.1 in Appendix S3, Supporting information). Finally, the posterior cross-correlations between the linear and quadratic terms estimating the climatic and environmental effects on community abundance were virtually always close to 0, as were the cross-correlations between the biotic interaction coefficients and the system and observation error variances and covariances (see Fig. S3.2 in Appendix S3, Supporting information). The residuals of the MSSM were mostly uncorrelated ($r < 0.2$) and displayed no systematic pattern with respect to the predictions (Fig. S4 in Appendix S3, Supporting information). With only small deviations in a few data points, they

displayed a Gaussian shape across species and replicated observed time series (Fig. S5 in Appendix S3, Supporting information). Finally, both the process error matrix Σ_t and the observation error matrix Ω_t conformed to the multivariate normality assumption (Shapiro–Wilks test, $P > 0.05$).

In Appendix S3, we provide the results of the posterior predictive checking conducted with the MSSM. Even with as few as 10 simulated data sets, our model is capable of capturing the underlying ecological processes from the simulated data to a large degree (Fig. S6 in Appendix S3, Supporting information). In the majority of the cases, the average value of the distribution of posterior parameters estimated with the predicted data sets lies very close to the original sampling estimates.

ENVIRONMENTAL AND STOCHASTIC COMMUNITY DYNAMICS

Parameter estimates for the environmental component of the MSSM are shown in Table S2.1 of Appendix S1 (Supporting information). According to the correction factor for the average fluctuation in observed flooding level (c_k), no systematic sampling bias was detected in the observation model, but the term for observation error (τ_j^2) was 2.37 times larger than the

term for process error (σ_j^2). A moderate signal of the NAO is evident on winter rainfall variability (21.8% of explained variance), as well as a large impact of rainfall variability on flooding extent (87.3% of explained variance; see Fig. 1). Therefore, the downscaled effect of the NAO on hidden flooding extent accounted for 19% of interannual variability in local environmental conditions.

For eight of 10 species, the correction factor for the average fluctuation in observed abundance suggested no systematic sampling bias in the observation model (b_i ; Table S2.2 in Appendix S1, Supporting information). Posterior estimates for observation error variance were generally large, with observation error being on average 1.26 times larger than process error across species (Table S2.2 in Appendix S1, Supporting information). Some 72.6% of the community variance could be explained by environmental stochasticity (41%) and large-scale climate plus local environmental effects (31.6%; see Fig. 4a). Only 4.6% of this variance is accounted for by interspecific interactions: the Bayes Factors averaged 0.488 across the 90 modelled potential interactions, which provide evidence against the inclusion of any interspecific effect in the stochastic community dynamics model. The remaining community variability (22.8%) could be ascribed to intraspecific interactions; however, given the large

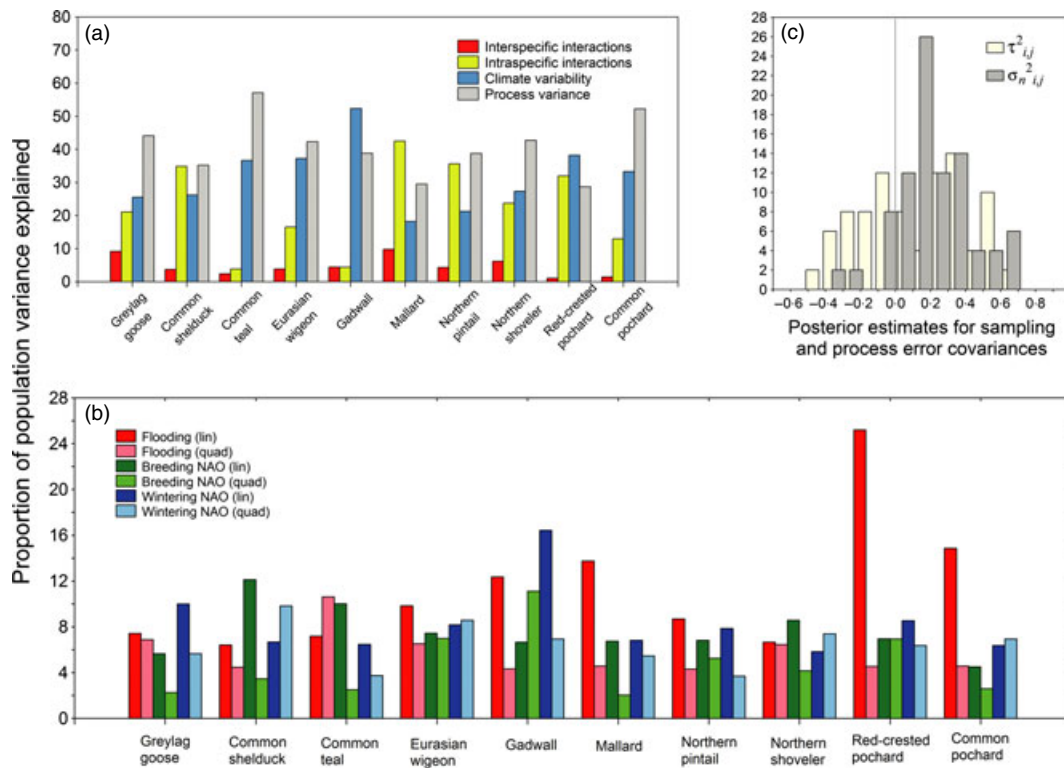


Fig. 4. Results of the fitting of the MSSM to the abundance time series of ten waterfowl species wintering in Guadalquivir Marshes. The bar plot in (a) shows the amount of population variance in the time series for each species (in %) that is explained by the four major sources of variability considered in the community model: interspecific interactions, intraspecific interactions, climate variability and process variance. The bar plot in (b) shows the amount of environmental variance in the dynamics of each species that is explained by linear (lin) and quadratic (quad) terms for the flooding extent, the North Atlantic Oscillation (NAO) during breeding and the NAO during wintering. The figure in (c) shows the frequency distribution of the posterior estimates for the temporal correlation in observation error ($\tau_{i,j}^2$, in white) and residual process error ($\sigma_{n,i,j}^2$, in grey) for each pair of species.

mobility of waterfowl within the wintering period (see Discussion), this figure is likely an overestimate for some species. The distribution of the correlation coefficients measuring the residual interspecific synchrony in process error ($\sigma_{n_{i,j}}^2$) and the covariation in observation error ($\tau_{i,j}^2$) yielded average posterior estimates of 0.20 and 0.12, respectively (Fig. 4c). A model with uncorrelated observation errors yielded a worse fit than the MSSM with correlated errors (DIC: 1591.7 vs. 1491.3, respectively).

Flooding extent of the study area during winter accounted for 38.6% of the community variance, while the wintering and breeding NAO index explained 33.6% and 27.9% of this variability, respectively (Fig. 4b). The impact of flooding extension was particularly important for diving ducks (common and red-headed pochards; Fig. 4b, Table S2.3 in Appendix S1, Supporting information); in contrast, the NAO conditions during breeding and winter prevailed for dabblers and particularly for the shelduck. The largest effect size for the breeding NAO forcing of wintering abundance of greylag goose and common shelduck was found at a 3-year lag. Overall, 63% of the posterior estimates for linear terms and 60% of the quadratic terms in the MSSM did not overlap with 0 (Table S2.3, Supporting information). Segregated according to linear vs. nonlinear effects, 61.6% of the community variance was accounted for by the linear environmental terms in eqn 2, while 38.4% was ascribed to quadratic terms. According to the sign of these environmental effects, 6 of 19 linear terms and 17 of 18 quadratic coefficients were negative. This suggests essentially concave relationships between environmental variables and wintering population size, where the largest wintering population sizes are located at approximately intermediate values of the environmental drivers (see Fig. S2 in Appendix S1, Supporting information).

IMPACT OF PARTIAL OBSERVABILITY ON MODEL ESTIMATION

Accounting for missing information through data augmentation yielded a 50.9% increase in the estimated variance component for climatic and environmental variability at the community level (see Fig. S3a in Appendix S1, Supporting information). These increases were most evident for the diving ducks and the common teal. Accordingly, a sharp decrease was observed in the estimated impact of environmental stochasticity (42.9%) and interspecific interactions (28.1%). These figures averaged 30.1%, 39.3% and 23.5% across species, respectively (Fig. S4 in Appendix S1, Supporting information). This increase in the community variance explained by environmental and climatic variability was mainly attributable to a rise in the estimated effect of hidden flooding extension (136.1%), which averaged 50.1% across species; in particular, the magnitude of the quadratic terms rose dramatically for nearly all species (Fig. S3b in Appendix S1, Supporting information).

The effect of ignoring observation error and missing data on estimates of biotic interactions was variable across

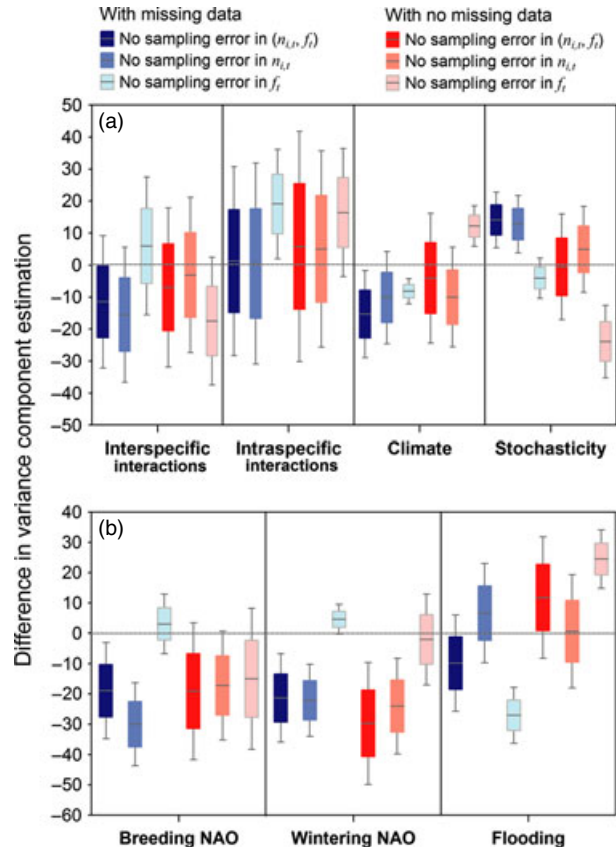


Fig. 5. Effects of observation error and missing data on the estimation of the variance components in the MSSM. The figure in (a) shows the proportional difference (%), averaged across species) in the estimation of the variance attributable to biotic interactions and environmental variability between models ignoring observation error in population abundance ($n_{i,t}$), flooding time series (f_t) and both ($n_{i,t}, f_t$), and a model fully accounting for partial observability; the results are shown for the original pattern of missing data (shades of blue) and for a model accounting for missing information through data augmentation (shades of red). On (b), these differences are shown segregated for the three environmental variables modelled (North Atlantic Oscillation (NAO) during breeding, NAO during winter and flooding extent). A negative (positive) value in the difference for a given setting and variance component suggests that the misspecification of the structure of partial observability causes a decrease (increase) in the estimated component for that setting. In the box-plot, the mean is shown as a horizontal line, while the boxes span one standard error and the whisker denotes the 90% confidence interval. The raw data are the values of each variance component for every species modelled.

species, and no consistent pattern is found at the community level (Fig. 5a). However, neglecting observation error had a dramatic effect on variance component estimation for environmental forcing and stochastic effects: on average, environmental forcing is underestimated by 15.3% (maximum specific underestimation of 38.8%) and environmental stochasticity overestimated by 14.1% (maximum overestimation of 32%). Interestingly, the magnitude of intraspecific interactions (density dependence) was overestimated by an average 19.1% when observation error was neglected in the time series of flooding extension, but not in the time series of population abundance; in this latter case, observation error

had no clear effect on the estimates of density dependence. In general, the effects on variance component estimation of accounting for missing information through data augmentation were weakened when observation error was sequentially dropped from the analysis (Fig. 5a). Data augmentation did increase the estimated variance component of climatic effects and decreased the effect of environmental stochasticity even when observation error was neglected, but these shifts were of smaller magnitude relative to the case where observation error is correctly specified (compare Fig. S3 in Appendix S1, Supporting information with Fig. 5a).

When observation error is completely omitted from the MSSM, the variance components for the three environmental forcing variables are jointly underestimated (Fig. 5b): an average 18.9% for the breeding NAO index (up to 58.9%); 21.4% for the wintering NAO index (up to 49.1%); and 9.9% for the flooding extent (up to 34.3%). Remarkably, when the observation error terms were alternatively dropped from the MSSM, an opposing pattern emerges: neglecting observation error in the waterfowl counts caused a large underestimation of the variance components for large-scale climate forcing (26.1% on average, up to 63.9%), but no effect is evident for the local flooding effect. In contrast, neglecting observation error in the estimation of flooding extent caused an underestimation of spatial flooding effect (27.4% on average, up to 43%), but no clear effect is evident on the estimation of large-scale climate forcing. Across species, the amount of bias in the estimation of environmental effects when observation error is neglected is greater the larger the estimated effect in the correct MSSM ($r = 0.64$, $P = 0.044$, $n = 10$). Again, the effect of data augmentation on variance component estimation is weakened when observation error is neglected (Fig. S3 in Appendix S1, Supporting information and Fig. 5b).

Discussion

The abundance of migratory species can be influenced by conditions in the breeding grounds, the stop-over areas and/or the wintering quarters (Newton 2004; Sæther, Sutherland & Engen 2004). Survival and fecundity are expected to be positively affected by warm and wet springs in waterfowl (Johnson, Nichols & Schwartz 1992), and supplies during winter and migration have been shown to affect the body condition and subsequent reproductive success on the breeding grounds in several species (e.g. Nilsson & Persson 1994; Bêty, Gauthier & Giroux 2003; Ward *et al.* 2005; Kéry, Madsen & Lebreton 2006; Morrissette *et al.* 2010). Warm and wet conditions are correlated with positive phases of the NAO in northern Europe (Hurrell *et al.* 2003). Interestingly, conditions during breeding, moulting and migration, as measured through the NAO index, impacted nonlinearly on the long-term dynamics of most species. We suggest that lagged climatic conditions might affect wintering waterfowl numbers through two mechanisms: (i) an increase in the proportion of pairs breeding and/or in the survival of young of the year until arrival on wintering grounds (Johnson, Nichols &

Schwartz 1992; Newton 1998), which gives rise to a direct numerical signal during winter. This mechanism seems to be operating in the dabbling duck populations and the red-crested pochard; and (ii) through a cohort effect, by which an increase in body condition of ducklings raised with good weather enhances subsequent productivity when recruited to the breeding population (Almaraz & Amat 2004b). This latter effect has been found in other waterfowl populations (Christensen 1999; Sedinger & Chelgren 2007) and usually operates at the population level with a time-lag similar to the age of first breeding (Almaraz & Amat 2004a). Nilsson, Persson & Voslamber (1997) showed that the survival rates up to fledging of young Scandinavian geese were larger for birds feeding on more productive grasslands, and the productivity of these ecosystems is known to be affected by the NAO (e.g. Kettlewell *et al.* 2006). This suggests that the finding of a 3-year lag in the impact of the NAO during breeding on the abundance of greylag goose and common shelduck, which usually start reproduction when 3 years old (Kampe-Persson 2002), might be the signature of a cohort effect operating in the breeding grounds: geese and shelducks born and raised in better climatic conditions (i.e. during positive NAO phases) might be expected to survive in better body condition until maturity (e.g. Bêty, Gauthier & Giroux 2003). Interestingly, the quadratic terms measuring the lagged impact of the NAO during breeding on wintering waterfowl abundance were mostly negative, which indicates that during periods of extremely favourable environmental conditions in the breeding grounds, the abundance of subsequent wintering populations declines. We suggest that during these warm and wet periods, a fraction of the reproductive population remains in the breeding grounds (see below), because these conditions in northern Europe (positive NAO phases) are negatively correlated with subsequent weather conditions in the Mediterranean basin (Hurrell *et al.* 2003).

The impact of spatial flooding extent was proportionally larger at the community level than the large-scale climate forcing. Because diving ducks are more strongly dependent on deep waters with open vegetation than dabbling ducks (Murkin, Mokin & Ball 1997), it is not surprising that the strongest effect of flooding on abundance was indeed found in the red-crested and common pochards. Interestingly enough, as with the large-scale climatic signals, a large portion of the quadratic coefficients for the spatial flooding effect were negative, which suggests that the magnitude of environmental forcing on waterfowl abundance is depressed when the conditions are either extremely wet or extremely dry. We suggest that the mechanisms behind this pattern differ among species and with the spatio-temporal scale of the effect. First, in the Guadalquivir Marshes, the greylag goose feeds mainly on tubers of *Scirpus* spp. (Amat 1995), and only secondarily on rice fields and grassland. However, when water levels are too high, the accessibility of *Scirpus* tubers drops, so the estimated negative effect of flooding extent on population abundance might reflect the negative impact of depressed *Scirpus* availability during extreme wet years. As shown here, lagged good conditions in the breeding grounds

produce an increase in the number of geese wintering in the study area. When flooding extent is too high or too low, geese are forced to abandon the National Park and winter in sub-optimal habitats where food availability is lower and hunting pressure is high (Calderón, Máñez & García 1991; Nilsson *et al.* 1999). During extreme climatic conditions, disturbance levels for greylag goose are thus expected to be higher and foraging conditions worse.

Secondly, positive phases of the NAO are correlated with cold and dry wintering conditions in the Mediterranean basin (Hurrell *et al.* 2003; Almaraz & Amat 2004a). In our case, this is reflected by the negative impact of the NAO index on rainfall variability. Most dabbling ducks in Europe display a large spatial mobility during winter in response to harsh (cold and dry) weather conditions (Ridgill & Fox 1990). Therefore, positive NAO phases most likely force migratory birds to shift their wintering headquarters, and even their flyway (Guillemain, Sadoul & Simon 2005) to areas with better conditions; during these periods, most birds might thus remain closer to their breeding grounds in Northern latitudes (Scott & Rose 1996) and consequently depress local wintering populations in the study area. In contrast, during extreme negative NAO phases, climatic conditions are optimal (warm and wet) throughout the Mediterranean basin and southern Europe, and then migratory birds distribute throughout a wider spatial area. Again, the net effect is a reduction in local wintering populations. Using neck-banded geese breeding in Sweden, Nilsson & Persson (1994) showed that those birds wintering in the Guadalquivir Marshes had a significantly lower productivity than those wintering in the Netherlands, and these differences have been attributed to migration costs induced by rainfall variability in the Guadalquivir Marshes (Nilsson *et al.* 1999). It is very likely that this mechanism operates in other species as well, and it provides a link between wintering conditions in the study area and subsequent breeding performance in northern Europe operating through weather variability. Overall, these mechanisms provide a plausible explanation for the nonlinear climatic forcing of waterfowl dynamics.

Accounting for partial observability is currently at the core of time-series modelling research in ecology (de Valpine & Hastings 2002; Clark & Bjørnstad 2004; Cressie *et al.* 2009). In regression modelling approaches, it is known that measurement error in the independent variable causes attenuation in the estimated coefficient (i.e. the regression parameter is biased towards 0; Carroll *et al.* 2006). The presence of observation error in population counts is thus known to introduce severe bias in the estimation of biotic interactions (e.g. Dennis *et al.* 2006; Freckleton *et al.* 2006); in contrast, the effects of measurement error in climatic covariates on the statistical estimation of biological dynamics remain largely unexplored. Remarkably, we have shown that a strategy ignoring observation error in both environmental and population survey data induces a coherent underestimation of local environmental and large-scale climate effects on community-wide waterfowl abundance, as well as an overestimation of environmental stochastic effects. The extent of

underestimation of environmental effects on population dynamics was higher the larger the estimated effects on the correct model. Lindén & Knape (2009) showed that the estimation of environmental effects in population dynamics can be biased in the presence of autocorrelation in the environmental driver. However, we found no evidence of autocorrelation in either the NAO index or the flooding time series. It is known that observation errors in the estimation of weather and climate variability can be large (Hegerl, Jones & Barnett 2001), but this source of variance is usually neglected in ecological time-series analyses. To our knowledge, our study provides the first empirical example showing that modelling observation error in the environmental component of an ecological model can be proportionally more important than modelling this source of variance in the biological component (e.g. population size), as it jointly underestimates the biological effects of environmental fluctuations and overestimates the effects of density dependence. If our results are common to other modelling approaches, this opens up the possibility for a previously unappreciated source of uncertainty in the estimation of ecological effects of climate change and variability.

In conclusion, we have found that local-scale environmental fluctuations, driven by weather variability, were the major factor impacting on the dynamics of a multispecies wintering community migrating at a continental scale. In contrast to previous suggestions (Stenseth *et al.* 2003; Hallett *et al.* 2004), these results show that large-scale climate indices might not always predict ecological processes better than local weather (see also Almaraz & Amat 2004a; Knape & de Valpine 2011). Additionally, few ecological examples of community-wide nonlinear climate forcing currently exist. Deciphering the functional form relating climate fluctuations to population dynamics is not a trivial task (Sæther, Sutherland & Engen 2004; van de Pol *et al.* 2010). Future climate changes, operating through shifts in both the mean and variance of climatic variables, can have unexpected effects on ecosystem behaviour if potential nonlinearities underlying the climate effects on demography are not correctly specified (e.g. Drake 2005).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Supplementary material and results.

Appendix S2. BUGS code for fitting the multivariate state-space model.

Appendix S3. MCMC convergence diagnostics, model goodness-of-fit and posterior predictive checking.

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