

# Catastrophic Bifurcation in the Dynamics of a Threatened Bird Community Triggered by a Planetary-Scale Environmental Perturbation

Pablo Almaraz<sup>ID\*</sup><sup>a,b</sup> and Andy J. Green<sup>c</sup>

<sup>a</sup>Departamento de Ecuaciones Diferenciales y Análisis Numérico, Facultad de Matemáticas,  
Universidad de Sevilla, Campus Reina Mercedes, 41012, Sevilla, Spain.

<sup>b</sup>Grupo de Oceanografía de Ecosistemas, Instituto de Ciencias Marinas de Andalucía, CSIC,  
Puerto Real, 11519, Spain.

<sup>c</sup>Departamento de Biología de la Conservación y Cambio Global, Estación Biológica de Doñana  
EBD-CSIC, Avda. Américo Vespucio 26, 41092, Sevilla, Spain.

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\*Corresponding Author: Pablo Almaraz. E-mail: pablo.almaraz@csic.es

**Abstract**

Ecological modeling has been traditionally dominated by a focus on the asymptotic behavior, but transient dynamics can have a profound effect on species and community persistence. We show a strong non-stationary coupling of ecological drivers in one of the world's major Mediterranean ecosystems, Doñana wetlands, which is currently threatened by many stressors. Recurrent changes in precipitation fluctuations triggered sudden reorganizations in community trends and population dynamics of a guild of ten wintering waterfowl species during a 36-year period. An anomalously dry and cold transient period in the Northern Hemisphere, induced by the volcanic eruption of Mt. Pinatubo in 1991, prompted an abrupt shift to an alternative regime of fluctuating species densities. Most species did not recover previous values even though local weather patterns and large-scale climatic conditions returned to normal values. Although the dynamical stability of the community is similar in both regimes, structural stability declined: the probability of feasibility dropped across time due to depressed population densities at equilibrium. A stochastic cusp catastrophe model fitted to the time series data suggests that the spatio-temporal persistence of cold and dry conditions in the wintering areas, coupled with warm and wet conditions in the breeding grounds, modulated local ecological conditions and induced hysteresis through behavioral shifts to alternative wintering sites. Our study provides empirical evidence for the existence of a catastrophic bifurcation triggered by a tipping point in the dynamics of an imperiled vertebrate community, highlighting the relevance of history and multi-stability in explaining current patterns in biological conservation.

**Keywords**

Alternative stable states; Doñana wetlands; Stochastic cusp catastrophe; Tipping point; Transient dynamics; Volcanism.

28

## Introduction

29 The stability of populations and communities in response to environmental perturba-  
30 tions is currently one of the most relevant research topics in the field of global change  
31 ecology (Bjornstad 2001; Post 2013; Vellend 2016; Yang et al. 2019). Despite the early  
32 appreciation that ecosystems might operate under more than one stable state (e.g.,  
33 Holling 1973; May 1977), the main focus of theoretical ecology is still dominated by the  
34 asymptotic stability of autonomous (time-independent) ecological models. However, a  
35 growing body of evidence suggests that many ecological systems might operate under  
36 nonlinear dynamics characterized by abrupt, transient shifts from one stable state to  
37 another, usually preceded by tipping points (Fukami and Nakajima 2011; Petraitis 2013;  
38 Yletyinen et al. 2016; Rocha et al. 2018; Clements and Ozgul 2018; Dakos et al. 2019;  
39 N. Chen et al. 2020). This behavior, commonly known as alternative stable states, is  
40 common in marine, freshwater, and terrestrial ecosystems (Steele 1996; Knowlton 2004;  
41 Capon et al. 2015; Gsell et al. 2016; review in Rocha, Peterson, and Biggs 2015).

42

43 In global change scenarios, understanding this non-linear behaviour is a major  
44 research goal (Rockström et al. 2009; Barnosky et al. 2012; Steffen et al. 2015; Nash  
45 et al. 2017). Progress in this field has been largely limited by semantic and statistical  
46 confusions on the specific mechanisms, processes and patterns involved in the char-  
47 acterization of alternative stable states (Suding, Gross, and Houseman 2004; Capon  
48 et al. 2015; Kuiper et al. 2015). A regime shift denotes a statistical change in the pa-  
49 rameters forcing a system, while a phase transition alludes to a change in the state of  
50 some attribute of the system (Scheffer 2009). From this it follows that regime shifts  
51 should usually translate to phase transitions, but the detection of the latter does not  
52 necessarily demonstrate the existence of the former (e.g., Rudnick and Davis 2003).  
53 Indeed, evaluating whether alternative states are stable is far from trivial (Scheffer  
54 2009; Stelzer et al. 2021). Alternative stable states give rise to hysteresis: under the  
55 same concurrent environmental conditions there may exist several stable states, and  
56 the location of the system in a particular state may be better explained by historical  
57 conditions than by present ones (Scheffer 2009; Clements and Ozgul 2018).

58

59 The overall consequence of this is that the abrupt phase transitions detected within  
60 ecological time-series are not always explicitly linked to the regime shifts potentially  
61 triggering them, thus yielding a rather phenomenological understanding of alternative  
62 stable states and regime shifts (Hastings 2004; Montoya, Donohue, and Pimm 2018;  
63 Hastings et al. 2018; Hillebrand et al. 2020). Thus, to date it is unclear how abrupt  
64 regime shifts at different levels of ecological organization are intertwined, and to what  
65 extent this non-linear behaviour stem from external disturbances or internal dynamics

(Scheffer 2009). For example, abrupt ecological disturbances have only recently been linked mechanistically to extreme climatic events, such as large volcanic eruptions and intense hurricanes (e.g., Kuhnt et al. 2005; Schoener and Spiller 2006; Vázquez-Loureiro et al. 2019; Osland et al. 2020). In particular, volcanism is regarded as one of the major perturbations not only to planetary climate (Osipov et al. 2021; Millán et al. 2022), but also to ecological systems at all organizational, temporal and spatial scales (Sadler and Grattan 1999; Oppenheimer 2003; Crisafulli et al. 2015; Jiang et al. 2022; Green, Renne, and Keller 2022; Z.-Q. Chen et al. 2022; Cabon and Anderegg 2022). One of the most recent major volcanic eruptions was that of the Mount Pinatubo on Luzon Island, Philippines, in 1991. This eruption is classified by geologist as a colossal event, with a return time between 50 and 100 years (e.g., Labitzke and McCormick 1992; Robock 2000). After producing the largest stratospheric volcanic aerosol cloud of the 20th century, the climatic impacts of Mt. Pinatubo eruption were of a planetary scale and lasted for several years (McCormick, Thomason, and Trepte 1995; Robock 2002; Douglass and Knox 2005). The Mt. Pinatubo eruption provided a natural experiment testing the response of the global atmosphere and biosphere to large geological phenomena (Soden et al. 2002; Church, White, and Arblaster 2005; Khodri et al. 2017; Booth et al. 2012). Consequently, a suite of ecological effects of this transient major perturbation were detected in several world ecosystems (Genin, Lazar, and Brenner 1995; Lucht et al. 2002; Gu et al. 2003; Kuhnt et al. 2005; Trenberth and Dai 2007). Nevertheless, by definition, the frequency of such events is rare, so there are few opportunities to study the effects of single major perturbations on ecological dynamics in the long-term, while accounting for system dynamics before and after the perturbation.

Using a 36-year (1978–2013) dataset of abundance fluctuations of a wintering waterfowl community, we provide evidence on the coupling of abrupt shifts in the environmental, anthropogenic and biological subcomponents in one of the largest and best preserved Mediterranean wetland ecosystems in the world (Doñana wetlands, SW Spain; Rendón et al. 2008; Almaraz et al. 2012; Green et al. 2018). This major ecosystem, historically supporting more than 1 million wintering birds from breeding grounds across the Palaearctic, is a Biosphere Reserve and includes a UNESCO World Heritage site. In spite of this, it is currently considered under severe threat due to several anthropogenic stressors, mainly groundwater abstractions and greenhouse-based agriculture (Scheffer et al. 2015; Green et al. 2017; Green et al. 2018; Camacho et al. 2022; Santamaría and Martín-Ortega 2023; Green et al. 2024). Waterbird communities are particularly useful for time-series analysis, because their populations are relatively easy to count, and can act as useful bioindicators of wetland biodiversity (Green and Elmberg 2014). Previous analyses (Almaraz et al. 2012) detected an abrupt shift in the wintering waterfowl community of Doñana wetlands synchronized with a climatically

105 harsh period lasting from 1992 to 1995. This low population density regime apparently  
106 became permanent even though local weather conditions returned to normal values.  
107 This transient period, characterized by anomalously dry and cold wintering seasons,  
108 is linked to the injection of massive amounts of sulfate aerosols by the eruption of  
109 Mt. Pinatubo (Robock 2002; Soden et al. 2002; Booth et al. 2012). These conditions  
110 persisted several years across the southern Palaearctic, with a reversed climatology  
111 in the northern Palaearctic characterized by warm and wet wintering seasons. Our  
112 main hypothesis is that the persistent anomalous conditions throughout the Palaearctic  
113 linked to Mt. Pinatubo eruption triggered a bifurcation between alternative stable states  
114 in the dynamics of the migratory wintering waterfowl of Doñana wetlands. Some  
115 evidence indicates that the drop in wintering waterfowl numbers in Doñana wetlands  
116 was synchronized with abrupt changes in the breeding and wintering populations of  
117 waterbirds communities across the Western Palaearctic (Ganter and Boyd 2000; Mitchell  
118 et al. 2008; Christensen and Fox 2014), and these changes were already hypothesized to  
119 be linked to the eruption of Mt. Pinatubo.

120

121 Here we suggest that the cold and dry wintering conditions in our study area during  
122 the transient anomalous period translated to persistent behavioral shifts in site selec-  
123 tion and migratory behaviour of waterfowl. Decision-making by individuals of social  
124 species can propagate to the population and community levels through well-known  
125 runaway mechanisms, such as social copying (Oro 2020; Oro et al. 2023). For example,  
126 environmental perturbations can induce highly complex ecological dynamics by linking  
127 individual decisions with permanent shifts in the fidelity to wintering or stopover sites  
128 and flyway routes of migratory animals (Almaraz and Oro 2011; Almaraz et al. 2012;  
129 Oro 2020; Oro et al. 2023; Piersma and Gils 2011). In waterfowl, winter philopatry is  
130 generally low due to highly plastic behaviour at the individual and population scales in  
131 response to weather fluctuations (Robertson and Cooke 1999; Adam et al. 2015; Clausen  
132 et al. 2018; Fox et al. 2023). Since there is a genetic, female-biased component to site  
133 fidelity, it can be hypothesized that long-lasting harsh conditions on the wintering  
134 grounds may prompt permanent shifts to alternative wintering sites and migration  
135 routes. We test this specific hypothesis using a suite of modeling approaches. First,  
136 we use Bayesian Dynamic Factor analysis and Hidden Markov Models (Almaraz and  
137 Oro 2011; Ward et al. 2022) to test for the existence of abrupt shifts and persistent  
138 alternative regimes in species- and community-level densities across time. Secondly,  
139 we fit a regime-dependent extension of a multivariate state-space model (Almaraz  
140 et al. 2012) to check for the existence of alternative stable states and shifting feasibility  
141 properties of the wintering community across different density regimes. Finally, we  
142 apply a stochastic cusp catastrophe model (Cobb and Zacks 1985) to test for the specific  
143 hypothesis that the existence of regime shifts and alternative stable states is linked to

144 the press-type perturbation of the Mt. Pinatubo eruption of planetary climate. From a  
145 conservation standpoint, the major implication would be that characterizing the history  
146 of an ecosystem is of paramount importance when management actions are directed at  
147 specific stressors that may not be currently operating (Scheffer 2009; Scheffer et al. 2015).

148

## 149 Material and Methods

### 150 Study area, environmental data and bird community time series

151 The Doñana wetlands are located in South-western Spain, and are composed of a com-  
152 plex mosaic of natural wetland ecosystems and artificial salt pans, ricefields, and fish  
153 farms within the large (>150.000 Ha) inner delta of the Guadalquivir river (Rendón  
154 et al. 2008; Almaraz et al. 2012; Green et al. 2018). This area is one of the best preserved  
155 Mediterranean wetland ecosystems in the world, and is one of the major wintering and  
156 stopover sites for waterbirds breeding throughout the Western Palaearctic. However, it  
157 is currently under threat from increases in water extraction and eutrophication from  
158 agricultural intensification, as well as from climate change (Marín and García 2006;  
159 Scheffer et al. 2015; Green et al. 2017; Camacho et al. 2022). A total of circa. 100 000 ha  
160 have been surveyed from the air on a monthly basis by the same three expert observers  
161 since 1973, providing total counts of the 10 most abundant wintering waterfowl (Anati-  
162 dae) species: the Pintail (*Anas acuta*), Shoveler (*Spatula clypeata*), Common Teal (*Anas*  
163 *crecca*), Eurasian Wigeon (*Mareca penelope*), Mallard (*Anas platyrhynchos*), Gadwall (*Mareca*  
164 *strepera*), graylag goose (*Anser anser*), Common Pochard (*Aythya ferina*), Red-crested  
165 pochard (*Netta rufina*), and Shelduck (*Tadorna tadorna*) (see Rendón et al. 2008 for count-  
166 ing methods). Complete data exist for every species from 1978 until nowadays. We used  
167 two estimated population sizes for each waterfowl species every year (December and  
168 January), and control for observation error through a state-space approach (Almaraz  
169 et al. 2012; see **Estimating community stability and feasibility** section below). The win-  
170 tering population size ranged from a minimum of 61.282 birds to a maximum of 534.460.

171

172 The size of the waterfowl population depends strongly on the amount of flooded  
173 surface in the natural marsh and in artificial habitats. The extension of ricefields depend  
174 on rainfall during previous winters, and not on the flooded area of the marsh, since  
175 their hydrology is different (Green et al. 2018). Therefore, in a given year of low rainfall,  
176 the natural marsh can be dry but the rice cover can still be high (Ramo et al. 2013; Rees  
177 et al. 2021). The fish ponds and salt pans are permanently flooded, and their surface  
178 area was expanded during the study period (Rendón et al. 2008; Walton et al. 2015.  
179 Different wetland types support different communities, and the natural marshes are

especially important for ducks and geese (Rendón et al. 2008; Sebastián-González and Green 2016). To assess the potential coupling between phase transitions in waterfowl populations and environmental dynamics, we used annual figures for the extension of winter flooding in the surveyed area, obtained from satellite imagery and averaged from November to February, for the surface covered with cultivated ricefields each year (see Almaraz et al. 2012 for details). Finally, we used monthly precipitation and temperature time-series gathered within Doñana National Park from 1978 onwards. We explored the structure of fluctuations in the precipitation time-series by extending the temporal analysis to the frequency domain through wavelet analysis (Torrence and Compo 1998; Cazelles et al. 2008).

190

## 191 Climatic and volcanic database

192 We constructed a synoptic climatology of the western Palaearctic, including both  
193 the breeding and wintering grounds of the ten waterfowl species considered, for  
194 the studied time period and during all seasons except summer. This included the  
195 region from 30N to 80N, and from 20W to 45E (Fig. 2). We extracted time-series  
196 data from the Version 3 (V3) of The Twentieth Century Reanalysis Project ([https://psl.noaa.gov/data/20thC\\_Rean/](https://psl.noaa.gov/data/20thC_Rean/)), developed by the Physical Sciences Laboratory  
197 of the National Oceanographic and Atmospheric Administration. We reconstructed  
198 the fields for air temperature and precipitation rate, and produced plots of composite  
199 anomalies for both variables: as suggested by the SDC and wavelet analyses, a transient  
200 dry and cold period was detected from 1992 to 1995. We thus compared the composite  
201 anomalies for air temperature and precipitation rate from 1978 to 2013 (excluding the  
202 transient period 1992-1995), with the composite anomalies of the transient period (1992-  
203 1995).

204

205 Several indices are available for characterizing the magnitude of volcanic eruptions  
206 (e.g., Crosweller et al. 2012; Constantinescu et al. 2021). The multi-decadal variability  
207 in the North Atlantic climate is under strong forcing by stratospheric aerosols (Otterå  
208 et al. 2010; Booth et al. 2012; Knudsen et al. 2014). Volcanic activity is one of the main  
209 natural sources of aerosols to the stratosphere (Otterå et al. 2010; Constantinescu et  
210 al. 2021), so an index of Volcanic aerosol optical depth of the stratosphere (SAOD, Booth  
211 et al. 2012) has been suggested as a surrogate for evaluating the impacts of Volcanic  
212 activity on global climate through the forcing of the upper atmosphere. We used the  
213 monthly AOD index for the Northern Hemisphere (35.2 °N and 58.7 °N) from Booth  
214 et al. 2012 as a surrogate for climatic forcing of volcanic activity in the breeding and  
215 wintering areas of Palaearctic waterfowl (See Fig. 1).

217

218

## Detecting community trends and regime shifts

219 We used Bayesian state-space Dynamic Factor Analysis (DFA; Almaraz and Oro 2011;  
 220 Ward et al. 2022) to detect and characterize major trends, and potentially regime shifts,  
 221 in the long-term wintering time-series of the waterfowl community. A DFA is a mul-  
 222 tivariate dimension-reduction technique analogous to Factor Analysis, and its main  
 223 goal is to extract the major temporal trends in abundance of the community emerging  
 224 from the simultaneous trend of each species, while accounting for observation error  
 225 (see Ward et al. 2022 for an introduction). It is thus a sort of joint species model where  
 226 the output is a suite of modeled community trends (factors) and a collection of factor  
 227 loadings representing the regression of each single-species temporal trend on every  
 228 common trend. A state-space DFA model has two equations: a (latent) process, or state  
 229 equation; and an observation or measurement model linking the state process to the  
 230 observations. The DFA can be written as:

$$\begin{aligned} \mathbf{x}_{t+1} &= \mathbf{S}(\mathbf{x}_t) + \mathbf{w}_t \\ \mathbf{y}_t &= \mathbf{Z}\mathbf{x}_t + \mathbf{e}_t \end{aligned} \tag{1}$$

231 were  $\mathbf{x}$  is an  $T \times K$  matrix of  $K$  latent trends (dynamic factors) and  $T$  years. The term  
 232  $\mathbf{S}(\mathbf{x}_t)$  represents smoothed functions capturing the autoregressive evolution of the  
 233 latent trends. These functions are constructed using P- or B-splines, Gaussian Predictive  
 234 Processes, or random walks (Ward et al. 2022). The process error of the latent trends  
 235 equation,  $\mathbf{w}_t$ , follows a multivariate normal distribution,  $\mathbf{w}_t \sim \mathcal{MVN}(0, \mathbf{Q})$  where  $\mathbf{Q}$   
 236 is generally assumed to be a  $T \times K$  positive semi-definite matrix. The trends  $\mathbf{x}_t$  are  
 237 linked to the observations  $\mathbf{y}_t$ , the wintering waterfowl counts of each species through  
 238 the observation or measurement model. We stress that we are using two counts each  
 239 winter, replicated in December and January each year, for each species, so that the DFA  
 240 is fully identified (see Almaraz and Oro 2011; Almaraz et al. 2012; Ward et al. 2022). In  
 241 this case,  $\mathbf{Z}$  is a matrix of estimated factor loadings, dimensioned as  $P \times K$ , were  $P$  is  
 242 the number of time series. Again, the residual observation errors are assumed to be  
 243 multivariate normally distributed,  $\mathbf{e}_t \sim \mathcal{MVN}(0, \mathbf{R})$ , where  $R$  is generally assumed to  
 244 be a  $T \times K$  positive semi-definite matrix.

245 We used flexible P-Spline functions for constructing the terms  $\mathbf{S}$  (Eilers and Marx  
 246 1996; Ward et al. 2022). We fitted a DFA with two common trends ( $K = 2$ ), and each  
 247 P-Spline was fitted with 16 knots; this is the value that minimizes the score from leave-  
 248 on-out cross-validation (see Ward et al. 2022). Since we implemented the DFA with  
 249 two replicated wintering counts each year, the model explicitly accounted for variable

observation errors among years (see Ward et al. 2022). After estimating the common trends, we used a Hidden Markov Model (HMM, Fraser 2008) with two regimes to detect and localize potential regime shifts in the common trends. HMMs were fitted to the two major trends. We fit the DFA in Eqn. 1 with the R package bayesdfa (Ward et al. 2022), which implements the Hamiltonian Monte Carlo NUTS algorithm of the Stan probabilistic programming language (Carpenter et al. 2017).

256

## 257 Modeling community dynamics

After characterizing the existence and location of the regime shift, we fitted a state-space Lotka-Volterra-Ricker (LVR) model to each of the regimes to evaluate their relative stability and feasibility properties (Almaraz and Oro 2011; Almaraz et al. 2012; Mutshinda, O'Hara, and Woiwod 2011). We denote the first regime identified by the DFA in the dominant common trend, or dynamic factor (Fig. 3) with the subscript 1 for each of the parameters, and the second regime with the subscript 2. The LVR regime-dependent state-space model can be written as:

$$n_{i,t+1} = \begin{cases} n_{i,t} + r_{1,i} \left( 1 - \frac{\sum_{j=1}^s \alpha_{1,ij} N_{j,t}}{K_{1,i}} \right) + \gamma_{1,i} F_t + \epsilon_{1,i,t} & \text{for } 1978 < t < 1992 \\ n_{i,t} + r_{2,i} \left( 1 - \frac{\sum_{j=1}^s \alpha_{2,ij} N_{j,t}}{K_{2,i}} \right) + \gamma_{2,i} F_t + \epsilon_{2,i,t} & \text{for } 1995 < t < 2013 \end{cases} \quad (2)$$

$$n_{i,0} = \begin{cases} \mu_{1,i,0} + \epsilon_{1,i,0} & \text{for } 1978 < t < 1992 \\ \mu_{2,i,0} + \epsilon_{2,i,0} & \text{for } 1995 < t < 2013 \end{cases} \quad (3)$$

$$y_{i,k,t} = \begin{cases} n_{i,t} + b_{1,i,k} + \tau_{1,t,i} & \text{for } 1978 < t < 1992 \\ n_{i,t} + b_{2,i,k} + \tau_{2,t,i} & \text{for } 1995 < t < 2013 \end{cases} \quad (4)$$

where  $n_{i,t}$  is the  $\log_e$  population abundance of each waterfowl species  $i$  during each winter, and  $N_{i,t}$  is the raw population abundance. Omitting the subscripts for each regime for the sake of clarity, the per-capita (intrinsic) growth rates of each waterfowl species is denoted by  $r_i$ . The interaction matrix  $\mathbf{A}$  is formed by the coefficients of inter-specific interactions scaled by the carrying capacities of each waterfowl species in the off-diagonal,  $\alpha_{ij}/k_i$ . The intra-specific coefficients in the diagonal,  $\alpha_{ii}$ , are  $k_i^{-1}$  (see Ranta, Lundberg, and Kaitala 2006; Mutshinda, O'Hara, and Woiwod 2009; Almaraz and Oro 2011). We regularized the interaction matrix through spike-and-slab priors on the coefficients of inter-specific interactions (see Almaraz et al. 2012 and the Supplementary Material). The parameters  $\gamma_i$  measure the impact of flooding extension,  $F_t$  on species-level population growth-rate during each regime.

276

277 The terms  $\epsilon_{i,t}$  represent the impact of process stochasticity on the abundance of  
 278 each species, with variance  $\sigma_i^2$ . These terms fill the diagonal of the matrix  $\Sigma$  in the  
 279 state equation: the diagonal of this matrix thus includes the variance of the unmod-  
 280 elled (stochastic) environmental factors impacting on single-species dynamics, while  
 281 the off-diagonal contains the (potentially) co-varying joint responses to the common  
 282 environment among all species,  $cov(\sigma_i, \sigma_j)$ . This matrix is, thus, positive semi-definite  
 283 and symmetric (Almaraz and Oro 2011; Almaraz et al. 2012). The initial state,  $n_{i,0}$  for  
 284 each waterfowl species in the vector of latent states is specified as a normal distribution  
 285 with mean  $\mu_{i,n_0}$  and variance  $\sigma_{n_0}^2$ ,  $n_{i,0} \sim \mathcal{N}(\mu_{i,0}, \sigma_{n_0}^2)$ .

286

287 Finally, the latent population abundances in Eqn. 2 are linked through the obser-  
 288 vation equations, eqn. 4, to the observed abundances in the aerial censuses,  $\mathbf{y}_{i,t}$ . The  
 289 observations contains two  $k$  values for each species  $i$  and winter  $t$ : one for December  
 290 and the other for January ( $y_{i,k,t}$  were  $k$  is the month). The column vectors  $\mathbf{b}_k$  include  
 291 the correction factors for the average fluctuation level of each wintering census (i.e. the  
 292 difference between December and January counts) and for each waterfowl species. The  
 293 correction factors for the December replicate were set to 0, while the other parameters  
 294 were estimated freely. This allowed for identifiability (Mutshinda, O'Hara, and Woiwod  
 295 2011; Almaraz et al. 2012). The terms  $\tau_{t,i}$  stand for the impact of measurement error  
 296 on latent state estimation for each species, with observation variance  $\rho_i^2$ . Again, these  
 297 measurement variances fill the diagonal of the matrix  $\Omega$ , and we also modeled the  
 298 potentially co-varying observation error between species in the off-diagonal terms:  
 299  $cov(\rho_i, \rho_j)$ .

300

301 We used Bayesian Markov Chain Monte Carlo (MCMC) through Gibbs sampling  
 302 to fit the regime-dependent state-space LVR model (Eqns. 2-4) to the waterfowl com-  
 303 munity time series (see Almaraz et al. 2012; Mutshinda, O'Hara, and Woiwod 2011).  
 304 The models were written in the JAGS probabilistic programming language (Plummer  
 305 2003), interfaced with the runjags package in R (Denwood 2016). We ran three parallel  
 306 chains for 130.000 iterations, discarding the first 100.000 as burn-in. We used the pack-  
 307 age ggmc (Fernández-Marín 2016) for diagnosing the convergence on the posterior  
 308 distribution.

309

### 310 Estimating community stability and feasibility

311 To evaluate the stability of the equilibrium for each community abundance regime  
 312 detected by the DFA, we constructed the Jacobian matrix of the LVR model (e.g., Ranta,

<sup>313</sup> Lundberg, and Kaitala 2006); for simplicity, we omit the subscript for each regime, but  
<sup>314</sup> we recall that there are two Jacobians. In the LVR discrete-time model the equilibrium  
<sup>315</sup> abundance vector,  $\mathbf{N}^*$ , is given by  $\mathbf{N}^* = \mathbf{A}^{-1}\mathbf{K}$ . The Jacobian matrix is then written as:

$$\mathbf{J} = \begin{pmatrix} 1 - \frac{r_1}{k_1} N_1^* & \cdots & -\frac{\alpha_{1s} r_1}{k_1} N_1^* \\ \vdots & \ddots & \vdots \\ -\frac{\alpha_{s1} r_s}{k_s} N_s^* & \cdots & 1 - \frac{r_s}{k_s} N_s^* \end{pmatrix} \quad (5)$$

<sup>316</sup> The criteria for the dynamical stability of a discrete-time system is that the spectral  
<sup>317</sup> radius of the Jacobian should be strictly less than 1 (Elaydi 2005), so we tested if the  
<sup>318</sup> modulus of the dominant eigenvalue of matrix  $\mathbf{J}$  (5) is contained within the unit circle in  
<sup>319</sup> the complex plane during the different regime shifts detected (see Results). We thus de-  
<sup>320</sup> fine the probability of dynamical stability as the frequency of spectral radii of the matrix  
<sup>321</sup>  $\mathbf{J}$  (5) that were  $< 1$  in the posterior distribution. If this condition is fulfilled during the  
<sup>322</sup> distinct regimes detected, this provides evidence of the existence of alternative stable  
<sup>323</sup> states. Further, we estimated the posterior asymptotic resilience of each distinct regime  
<sup>324</sup> as the inverse of the maximum absolute real part of the eigenvalue spectra (Arnoldi,  
<sup>325</sup> Loreau, and Haegeman 2016).

<sup>326</sup>

<sup>327</sup> Dynamical stability measures the asymptotic behavior of small perturbations of  
<sup>328</sup> the state variables of a linearized system in the vicinity of an equilibria. In contrast,  
<sup>329</sup> structural stability quantifies whole-system responses: the range of perturbations of  
<sup>330</sup> parameters of a dynamical system that produce the same qualitative dynamics (Thom  
<sup>331</sup> 1977; Almaraz et al. 2023). In ecology, a useful criteria for assessing structural stability  
<sup>332</sup> is the characterization of the feasibility domain (Logofet 1993; Roberts 1974): the range  
<sup>333</sup> of the environmental conditions yielding an equilibrium where all species have positive  
<sup>334</sup> abundances (Song and Saavedra 2018). In our case, this would imply that the poste-  
<sup>335</sup> rior distribution of the equilibrium abundance vector  $\mathbf{N}^*$  should contain only positive  
<sup>336</sup> values. Therefore, taking advantage of the effective propagation of uncertainty of the  
<sup>337</sup> Bayesian state-space approach, we define here the empirical probability of feasibility  
<sup>338</sup> as the fraction of strictly positive posterior samples of  $\mathbf{N}^*$ . Changes in this probability  
<sup>339</sup> between alternative stable states would indicate shifts in the structural stability of the  
<sup>340</sup> modeled system. That is, even though dynamical stability is conserved, structural sta-  
<sup>341</sup> bility could change as a consequence of changing impacts of environmental conditions  
<sup>342</sup> on the size of parameter space compatible with a feasible community.

<sup>343</sup>

344

## Stochastic cusp catastrophe modeling

345 Finally, we applied stochastic catastrophe theory (Cobb and Zacks 1985; Grasman, Maas,  
 346 and Wagenmakers 2009) to model the links between the global climatic transient forcing  
 347 induced by the Mt. Pinatubo eruption on the regime shifts in the wintering waterfowl  
 348 community. We hypothesize that this link operates through the press perturbation of  
 349 the large-scale weather conditions in the full distribution area of the studied water-  
 350 fowl species, namely the Western Palaearctic. This press perturbation reorganized the  
 351 wintering populations at a continental scale, with potentially long-lasting shifts in the  
 352 migratory behavior.

353

354 As a branch of nonlinear dynamical systems and bifurcation theory, catastrophe  
 355 theory, originally developed by René Thom (Thom 1975, 1977), has seen some appli-  
 356 cations in marine sciences over the last decades. For example, catastrophic dynamics  
 357 has been recently suggested as an explanation for the collapse of Atlantic Cod (*Gadus*  
 358 *morhua*) fisheries during the last decades (Sguotti et al. 2019). The perspective provided  
 359 by catastrophe theory is particularly relevant for systems characterized by sudden shifts  
 360 between alternative stable states induced by smooth changes in control parameters  
 361 (Casti 1982; Loehle 1989). In the Supplementary Material we describe in detail the  
 362 rationale behind catastrophe theory. In brief, our phenomenological hypothesis (Eqn.  
 363 6) is that the smooth temporal changes in the impact of the spatial flooding extension  
 364 can become nonlinear and discontinuous, and trigger regime shifts to alternative stable  
 365 states in the major community trend of the DFA, under the forcing of Volcanic-induced  
 366 shifts in planetary climate fluctuations. Namely, volcanic forcing, as measured through  
 367 the stratospheric aerosol optical depth (Booth et al. 2012) operates as a bifurcation pa-  
 368 rameter ( $\beta$ -parameter, (Grasman, Maas, and Wagenmakers 2009)), forcing the system to  
 369 go through a catastrophic bifurcation between alternative stable states that share a range  
 370 of environmental conditions. In contrast, flooding extension is an asymmetry parameter  
 371 ( $\alpha$ -parameter), measuring the skew in the distribution of alternative states across this  
 372 range of environmental conditions. This is indeed the region of hysteresis, where history  
 373 is important: where the system comes from is crucial to evaluate why it is now in the  
 374 state it is, and how can it be pushed to a desired state through, e.g., management actions  
 375 (Petraitis 2013; Scheffer 2009; Scheffer et al. 2015). The cusp catastrophe model would  
 376 take the form:

377

$$\begin{aligned}\alpha &= \alpha_1 F \\ \beta &= \beta_0 + \beta_1 SAOD \\ y &= \omega_0 + \omega_1 x_1\end{aligned}\tag{6}$$

378 where, as noted,  $\alpha$  and  $\beta$  are the asymmetry and bifurcation parameters, respectively,  
379 that are modeled as canonical variables (Grasman, Maas, and Wagenmakers 2009).  
380 These variables are smooth transformations of the control variables  $F$  (flooding exten-  
381 sion) and  $SAOD$  (stratospheric aerosol optical depth). The canonical variable  $y$  is the  
382 state of the system, here represented by the major community trend detected by the  
383 DFA,  $x_1$ .

384 We used the R package `cusp` to fit the cusp catastrophe model (Grasman, Maas,  
385 and Wagenmakers 2009). The cusp equilibrium surface, and the coefficients of the  
386 smooth transformation in Eqn.s 6,  $\alpha_1, \beta_0, \beta_1, \omega_0, \omega_1$ , were obtained through maximum-  
387 likelihood methods. The fitting of a linear and a non-linear (logistic) model was com-  
388 pared with the cusp catastrophe using information criteria and  $pseudo - R^2$ . Further  
389 details are given in Supplementary Material.

390

## 391 Results

### 392 Weather and climate fluctuations

393 Figure 1 shows the fluctuations in the stratospheric optical depth in the northern  
394 hemisphere, temperature, precipitation and spatial flooding extension of the study  
395 area from 1978 to 2013. While seasonality in the signal for temperature is strong and  
396 was never lost, precipitation did exhibit a more irregular pattern. The wavelet power  
397 spectrum is shown for precipitation (1E): the 1991-1995 period stands out as particularly  
398 irregular . Finally, the volcanic aerosol optical depth shows two salient peaks coinciding  
399 with the two largest volcanic eruptions of the study period (1A). The inset figure shows  
400 the standardized values for precipitation, temperature and flooding for volcanic vs.  
401 non-volcanic years. During volcanic years, the local weather was significantly cooler  
402 and drier, and the extension of the flooded area was therefore smaller.

403 The synoptic fields of composite anomalies for 1978 to 2013 obtained from the Twen-  
404 tieth Century Reanalysis Project (Fig. 2) reveal a clearly temporal and spatial divergent  
405 pattern at a continental scale: the reconstructed anomalies for temperature and precipi-  
406 tation rate for the period of transient climatic perturbation of the Mt. Pinatubo eruption  
407 (1991-1995) shows a particularly dry and cold period for southern Europe and northern  
408 Africa and a relatively warm and wet period for the northern Palaearctic (Fig. 2B, D).  
409 When excluding these years, this pattern is reversed: a relatively warm and wet period  
410 characterized winters in the southern Palaearctic (Fig. 2A, C).

411

## 412 Major trends in the community

413 The major waterfowl community trends modeled by the state-space Dynamic Factor  
414 Analysis (DFA) are shown in Figure 3. A first trend displayed a clear abrupt shift in 1992  
415 towards significantly lower levels, a shift that was sustained through time. In contrast, a  
416 second trend displayed a downward peak around 1992, and a further increase through  
417 time. A DFA with only one trend is a worse model relative to a two-trend model  
418 according to the leave-one-out cross-validation information criterion ( $\Delta\text{LOOC}$ : 53.872).  
419 Indeed, the Hidden Markov Model (HMM) of regime shifts, when applied to the first  
420 trend (Trend 1 in Fig. 3), suggested a highly significant shift in 1992. A HMM with  
421 no regime shift is a much worst predictor than a HMM with at least one regime shift  
422 ( $\Delta\text{LOOC}$ : 114.126). The fitting of the species-specific dominant trends to each time  
423 series is shown in Figure 4, with associated loading factors in Figure 5. The magnitude  
424 of the abrupt shift in 1992 differed somewhat among species, and is particularly strong  
425 for some, such as the Common Teal, the Eurasian Wigeon, the Gadwall, the Shelduck  
426 and the Graylag Goose. Overall, the DFA analysis suggests that the abrupt shift in 1992  
427 is a generalized dynamic shift across the community, with weak, subsequent recoveries  
428 only for some species.

429

## 430 Characterizing alternative stable states

431 According to the community regime shift detected by the DFA in 1992, and the transient  
432 period towards the second fluctuation level that started in 1995 (Fig. 3, 4), the state-  
433 space LVR model was fitted to two separate periods: from 1978 to 1992; and from  
434 1995 to 2013 (see Eqns. 2-4). The posterior quality checking of model fitting suggests  
435 that MCMC chains mixed well and showed evidence of convergence in both periods.  
436 Additionally, posterior predictive checks suggest that the fitted Bayesian state-space  
437 LVR model is able to reproduce closely the original time series for both regimes (see  
438 Supplementary Material). The impact of flooding extension on the growth-rate of the  
439 waterfowl species is generally positive for all species in both dynamic regimes. The  
440 probability of inter-specific interaction, as selected by the regularization scheme (see  
441 Supplementary Material), was very low in both periods (less than 0.04). Interestingly,  
442 the posterior probability of dynamic stability and resilience are similar for both periods  
443 (Figure 6A, B). While the posterior distribution of the dominant eigenvalues of the  
444 Jacobian are close to 1 in both periods, the linearized dynamics around the equilibrium  
445 are stable with a very large probability. This is strong evidence of alternative stable  
446 states.

447 The probability of feasibility, measured as the fraction of posterior equilibrium abun-  
448 dance vectors with strictly positive values, dropped from 0.992 before the Mt. Pinatubo

eruption to 0.634 after the event (Figure 6C, D). Although the probability of extinction was low for all waterfowl species, in all cases this probability increased in the second alternative stable state after the Mt. Pinatubo eruption (Fig. 7), particularly for the Gadwall. Overall, while dynamical stability does not change among regimes, structural stability drops after the explosion of Mt. Pinatubo.

454

### 455 Cusp catastrophe modeling

456 The results of the fitting of the cusp catastrophe modeling to the major community trend  
457 are shown in Table 1. The cusp model (Eqn. 6) is clearly the best one for explaining  
458 the observed pattern of covariation of the major community trend, the volcanic aerosol  
459 stratospheric optical depth (SAOD) and spatial flooding extension. This model accounts  
460 for the 95.4% of variance of the major DFA trend displaying a regime shift (Trend 1 in  
461 Fig. 3). The maximum-likelihood estimates, and their associated uncertainty, of the  
462 parameter of the cusp catastrophe model (Eqn. 6) are shown in the Supplementary  
463 Material.

464 The diagnostic plot for the fitted cusp catastrophe model (see Supplementary Mate-  
465 rial) suggests that all values are located in the region of the bifurcation set, providing  
466 strong evidence for the presence of a catastrophic bifurcation between alternative stable  
467 states. A 3D plot of the cusp catastrophe model (Fig. 8B) verifies that the waterfowl  
468 community fluctuated during the full 36 year period in the region of multi-stability.  
469 This is more clearly assessed in the transition plot of the major community trend (Fig.  
470 8C): two fluctuating regimes, clearly separated by an abrupt transition in 1992 after Mt.  
471 Pinatubo eruption (Fig. 8A), indicate a fundamental regime shift between alternative  
472 stable states after a tipping point in 1992. The hysteresis region covers all the fluctuating  
473 range of flooding extension.

474

## 475 Discussion

476 Our results provide an empirical example of a catastrophic bifurcation after a tipping  
477 point in a major threatened biodiversity hotspot induced by an abrupt geological dis-  
478 disruption, with global impacts on the atmosphere, the biosphere and the ocean. We have  
479 found a persistent regime shift between two alternative stable states in the wintering  
480 dynamics of a vertebrate guild of one of the world's most iconic wetland ecosystems  
481 (Scheffer et al. 2015) over a 36 year study period. As examples of abrupt shifts in  
482 birds, Durant et al. 2004 showed the existence of regime shifts in breeding parameters  
483 of a seabird linked to oceanographic changes in the Norwegian Sea, and Jenouvrier

et al. 2005 found discrete shifts in the cycling dynamics of three seabirds breeding in the Antarctic, correlated with changes in the climatic conditions of the Southern Ocean. In the present paper, a detailed pattern of covariation between external forcing variables and the fluctuations of a wintering waterfowl community conform very well to a cusp catastrophe, where the ecological dynamics depend not only on the local environmental conditions, but also on the external, large-scale forcing climatic conditions modulating the transition from a smooth, linear system behaviour to a discontinuous, nonlinear dynamic. Indeed, the modeled shift has been statistically linked to an abrupt perturbation of planetary climate for which a detailed forcing mechanism has been identified, namely the eruption of Mt. Pinatubo, Philippines, in June 1991 (Hansen et al. 1992; Labitzke and McCormick 1992; Robock 2000, 2002; Douglass and Knox 2005). A general, transient (2-4 years) worldwide cooling of the troposphere, inducing cold summers and warm winters in the Northern Hemisphere and a transient reversal of the global warming trend (Robock 2000, 2002; Lucht et al. 2002; Church, White, and Arblaster 2005; Smith et al. 2016), points to the Mt. Pinatubo eruption, with more than 20 megatons of  $\text{SO}_2$  injected into the stratosphere (Hansen et al. 1992), as the single most important geological event of the 20th century. The transient pattern of cooling in southern Europe and warming of Northern Europe immediately after the eruption was reproduced in this study, with evidence that this led to long-lasting shifts in the behaviour of migratory birds. Several biological signals have already been linked to the Mt. Pinatubo eruption, such as the remote control of net primary production (Lucht et al. 2002; Krakauer and Randerson 2003), shifts in deep-sea communities and oceanographic conditions (Hess et al. 2001; Kuhnt et al. 2005; Yao and Hoteit 2018), fish biology (Gaston, Woo, and Hipfner 2003), changes in coral survival (Genin, Lazar, and Brenner 1995), global hydrological cycles (Trenberth and Dai 2007), etc. Interestingly, a major result of our study is the finding that, while the identified alternative states were equally stable dynamically, structural stability, as measured through the probability of feasibility, dropped across time. Therefore, different metrics of community structure and dynamics should be taken into account for characterizing the ecological state of threatened ecosystems.

513

With more than one million birds wintering in some years, the study area is one of the most important wintering and stopover sites for migratory waterbirds in the Western Palaearctic, supporting more wintering waterfowl than any other site (Marín and García 2006; Rendón et al. 2008; Green et al. 2017; Camacho et al. 2022). The wintering conditions in this region are linked to the survival and breeding output in the breeding headquarters of many waterfowl species in the Western Palaearctic (Rendón et al. 2008; Almaraz et al. 2012; Green et al. 2017; Fox et al. 2023). Interestingly, Ganter and Boyd 2000 presented qualitative evidence of an arctic-wide decline in breeding performance of waterbirds in the summer following the Mt. Pinatubo eruption, with

523 potentially negative effects on wintering waterfowl populations in Southern Europe.  
524 This large-scale breeding failure in 1992 was confirmed by local studies with Eurasian  
525 Wigeon in Denmark and the UK (Mitchell et al. 2008), and by a reduced hunting bag of  
526 several waterfowl species in Denmark from 1982 to 2010 (Christensen and Fox 2014).  
527 Given the global relevance of Doñana marshes, it is very likely that the abrupt regime  
528 shift detected in 1992 was due to a combination of two factors: 1) a generalized failure  
529 of breeding success in the breeding grounds (Ganter and Boyd 2000; Mitchell et al. 2008;  
530 Christensen and Fox 2014); and 2) particularly harsh (cold and dry) conditions in the  
531 study area during the 1992 winter, compared to other continental wintering grounds  
532 (Fig. 2). As shown by the wavelet analysis of precipitation in the study area (Fig. 1),  
533 these conditions persisted until 1995. While the evidence suggests that most European  
534 waterfowl populations recovered rapidly from the 1992 breeding failure (Ganter and  
535 Boyd 2000; Mitchell et al. 2008; Christensen and Fox 2014), it is intriguing that the  
536 wintering population in Doñana entered an alternative stable state of significantly lower  
537 community abundance, even though local conditions returned to their normal statistical  
538 behavior. Although the stochastic cusp catastrophe model we use is a phenomenological  
539 approach (Casti 1979; Poston and Stewart 1979), we suggest a biological mechanism ex-  
540 plaining the regime shift to an alternative stable state induced by behavioural plasticity.

541  
542 Studies on waterfowl migration point to stronger breeding philopatry compared  
543 to site fidelity to wintering grounds in these taxa (e.g., Guillemain, Sadoul, and Simon  
544 2005; Davis et al. 2014; Clausen and Madsen 2016; Clausen et al. 2018). While geese  
545 and swans have been traditionally regarded as bearing stronger fidelity to wintering  
546 grounds relative to dabbling ducks and pochards (Robertson and Cooke 1999; Coulson  
547 2016), recent data suggest that geese are indeed plastic and can shift flyways with a high  
548 probability, even at the individual level (Clausen and Madsen 2016; Clausen et al. 2018;  
549 Fox et al. 2023). Pink-footed geese wintering in Denmark, the Netherlands and Belgium,  
550 show an average 54% probability of changing migrating strategy during a 25 year  
551 period (Clausen et al. 2018). At a continental scale, changes in migration propensity  
552 and shifts in flyways and wintering sites are common responses of European ducks to  
553 cold or warm spells (Ridgill and Fox 1990; Adam et al. 2015). Abmigration, the ability to  
554 shift flyways depending on environmental conditions, is indeed a common strategy in  
555 waterfowl: ringing data support the hypothesis that breeding populations of Palaearctic  
556 Common Teal can readily shift between North-Western European and Mediterranean  
557 flyway routes (Guillemain, Sadoul, and Simon 2005; Parejo et al. 2015). Importantly, site  
558 fidelity is usually female-biased in waterfowl and, contrary to other taxa, pair formation  
559 may occur in wintering grounds (Robertson and Cooke 1999). As a behavioral strategy  
560 under such a strong selective pressure, plasticity in migratory behaviour and wintering  
561 grounds in response to rapidly changing environments is thus regarded as adaptive in

562 waterfowl (Clausen and Madsen 2016; Clausen et al. 2018). We suggest that the abrupt  
563 regime shift detected in Doñana marshes, followed by an alternative stable state, may  
564 be a consequence of a permanent shift to alternative wintering grounds prompted by  
565 a perturbation-induced behavioral shift in philopatry. The reversed synoptic climatic  
566 conditions uncovered here during the transient Mt. Pinatubo perturbation (Fig. 2)  
567 point to an increase in quality for wintering conditions of alternative wintering grounds.  
568 These alternative sites may include new reservoirs in Spain (Navedo et al. 2012), and  
569 sites in eastern Spain and North Africa where wintering numbers have increased (Kleijn  
570 et al. 2014; de Arruda Almeida et al. 2019). Once waterfowl populations undergo a shift  
571 in site use in response to local changes in environmental conditions, they may become  
572 faithful to these new sites, even after the conditions in the original site improve (Clausen  
573 and Madsen 2016; Clausen et al. 2018). This is the behavioural mechanism giving rise to  
574 hysteresis (see below). Indeed, even though Doñana Marshes are considered the main  
575 wintering site for graylag goose in the Western Palaearctic, the negative shift detected  
576 in 1995 has not been reversed, and strong population increases have been observed in  
577 northern Spain and several European wintering sites from the mid nineties onwards  
578 (Madsen, Cracknell, and Fox 1999; Ramo et al. 2015). In particular, the Danish breeding  
579 population of Greylag goose is known to have largely abandoned Doñana marshes as a  
580 main wintering sites during the last two decades (Clausen, Heldbjerg, and Fox 2023).  
581 Our study covers up to 2013, and future research should assess whether the state in the  
582 community adopted from 1996 has remained stable in recent years, especially given  
583 the ongoing escalation in global warming. Since 2020, extreme drought and lack of  
584 flooded area in the natural marshes has led to exceptionally low numbers of wintering  
585 waterfowl (Camacho et al. 2022; Fox et al. 2023). It remains to be seen whether this will  
586 lead to a change to a new stable state.

587

588 Recently, theoretical and empirical approaches are addressing the study of nonlinear  
589 population dynamics in social species driven by behavioral rapid shifts in response to  
590 perturbations, social feedbacks and tipping points (Oro 2020; Oro et al. 2023). According  
591 to this perspective, changes in social behaviour induced by disturbances in breeding or  
592 wintering grounds may feedback at the population level to induce a highly non-linear  
593 dynamics, i.e., a population crash triggered by breeding site abandonment in response  
594 to predation (Almaraz and Oro 2011; Oro et al. 2023). In the case of Doñana marshes, we  
595 hypothesize that the regime shift to an alternative stable state induced by the transient,  
596 large scale climatic perturbation of the Mt. Pinatubo eruption, might be a remarkable  
597 example of non-linear feedbacks between behaviour and population dynamics: under  
598 this scenario, a persistent reversal of the synoptic climatic fields, with cold and dry  
599 conditions in the wintering area, might trigger a trans-generational plastic behavioral  
600 shift in migrating birds that persists even under the reversal of the normal synoptic

601 conditions. In this conditions, wintering birds might remain in alternative wintering  
602 grounds even if the local conditions return to normal. This might be the mechanism  
603 giving rise to hysteresis, as evidenced here in the cusp catastrophe model (Fig. 8).

604

## 605 Management implications of transients and multi-stability

606 In a rapidly changing world ecological dynamics over short time-scales, at which  
607 transient (non-asymptotic) dynamics may govern persistence, arise as a research area  
608 of paramount importance from pure and applied standpoints (Hastings et al. 2018).  
609 Processes operating with diverging spatial and temporal rates of change may yield  
610 surprises if tipping points, bifurcations and alternative stable states are not correctly  
611 identified (Watts et al. 2020; Williams, Ordonez, and Svenning 2021; Scheffer 2009).  
612 These fundamental scales may have an overriding effect on ecosystem supplies and  
613 resilience (Folke et al. 2004; Scheffer 2009). Predicting the consequences of transient  
614 environmental dynamics on biological systems is thus essential in global change ecology,  
615 with benefits ranging from improved knowledge on ecosystem functioning to informed  
616 management of harvested populations (Suding, Gross, and Houseman 2004; Scheffer  
617 2009; Francis et al. 2021). A major finding of our study is the decoupling of dynam-  
618 ical stability and structural stability at decadal time scales. We show how feasibility  
619 emerges as a key metric to evaluate the extinction risk of threatened communities in  
620 biodiversity hotspots at risk: while traditional measures of dynamical stability focuses  
621 on the asymptotic behaviour of systems, characterizing the changing feasibility domain  
622 of threatened communities might inform about the shifts in the structural fragility of  
623 already impacted ecosystems. The finding of hysteresis in the wintering waterfowl  
624 community of Doñana wetlands and a general decrease of feasibility, brought about  
625 by an increase in the probability of species extinction across decades, provides a clear  
626 conservation message: when evaluating the current conservation status of threatened  
627 ecosystems it is of paramount importance to untangle the detailed history of impacts  
628 that drove the system to its current status. In the case of Doñana wetlands, the history  
629 uncovered by the present work places in a novel context the already serious threats to  
630 the study area (Scheffer et al. 2015; Camacho et al. 2022; Green et al. 2024; Santamaría  
631 and Martin-Ortega 2023).

632

## 633 Acknowledgements

634 The comments from two anonymous reviewers greatly improved a previous version of  
635 the manuscript. PA was supported by a pre-doctoral fellowship through the program

636 Formacion del Profesorado Universitario FPU of the Spanish Ministry of Education  
637 (FPU16/00626), and by Proyectos FEDER and Consejería de Economía, Conocimiento,  
638 Empresas y Universidad de la Junta de Andalucía, by Programa Operativo FEDER 2014-  
639 2020 reference P20-00592. AJG was supported by Ministerio de Ciencia e Innovación.  
640 Proyectos de I+D+i PID2020-112774GB-I00 / AEI / 10.13039/501100011033. Census  
641 data were collected by the Monitoring Team for Natural Resources and Processes of the  
642 EBD-CSIC, and support was provided by the ICTS-RBD.

643

## 644 Data and code availability

645 All data and reproducible code is available in GitHub <https://github.com/palmaraz/>  
646 GuadaluShiftR and Zenodo <https://zenodo.org/records>.

647

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**Tables and figures****List of Tables**

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Table 1: Comparison of model fits between a linear model, a logistic model and the cusp catastrophe model.  $n_p$  is the number of parameters; pseudo –  $R^2$  specifies the proportion of variance explained by each model; *logLik* is the minimized log-likelihood function; AIC is the small-sample corrected Akaike Information Criterion, and BIC the Bayesian Information Criterion.

<b>Model</b>	$n_p$	pseudo – $R^2$	<b>logLik</b>	<b>AICc</b>	<b>BIC</b>
Linear	4	0.129	-20.678	50.647	55.690
Logistic	4	0.185	-19.504	48.299	53.343
Cusp	6	0.954	-10.426	35.749	42.353

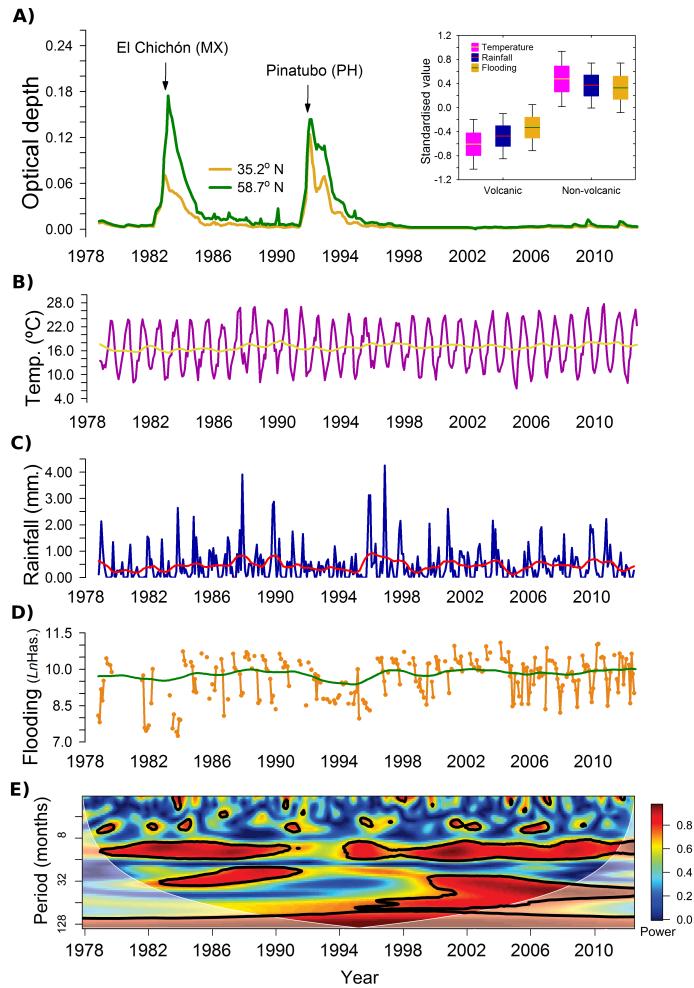


Figure 1: Temporal evolution at monthly steps of the environmental variables used in this study. **A)** Time series for the stratospheric aerosol optical depth (adim.) in the Northern hemisphere, in yellow and green at two different latitudes (Booth et al. 2012). The massive stratospheric aerosol injection events of the two largest volcanic eruptions of the study period, El Chichón (Mexico) and Mt. Pinatubo (Philippines), are located with arrows. The inset figure shows the box-plots for the average (horizontal line within each box), Standard Error (Box size) and Standard Deviation (whiskers) of the standardized variables of temperature, precipitation and spatial flooding extension, during volcanic years (1982-1983 and 1992-1995) and non-volcanic years. **B)** Monthly time series of temperature (°C) in the study area (Almaraz et al. 2012, in purple), with smoothed loess fitting in yellow. **C)** Rainfall (mm.) in the study area in blue, with smoothed loess fitting in red. **D)** Spatial flooding extension ( $\ln(\text{Has.})$ ) in the Doñana wetlands, including all types of flooded surfaces in orange, with smoothed loess fitting in green. **E)** Wavelet spectrum for the precipitation time series (Cazelles et al. 2008). Power values within black contours indicate statistically significant periodicity.

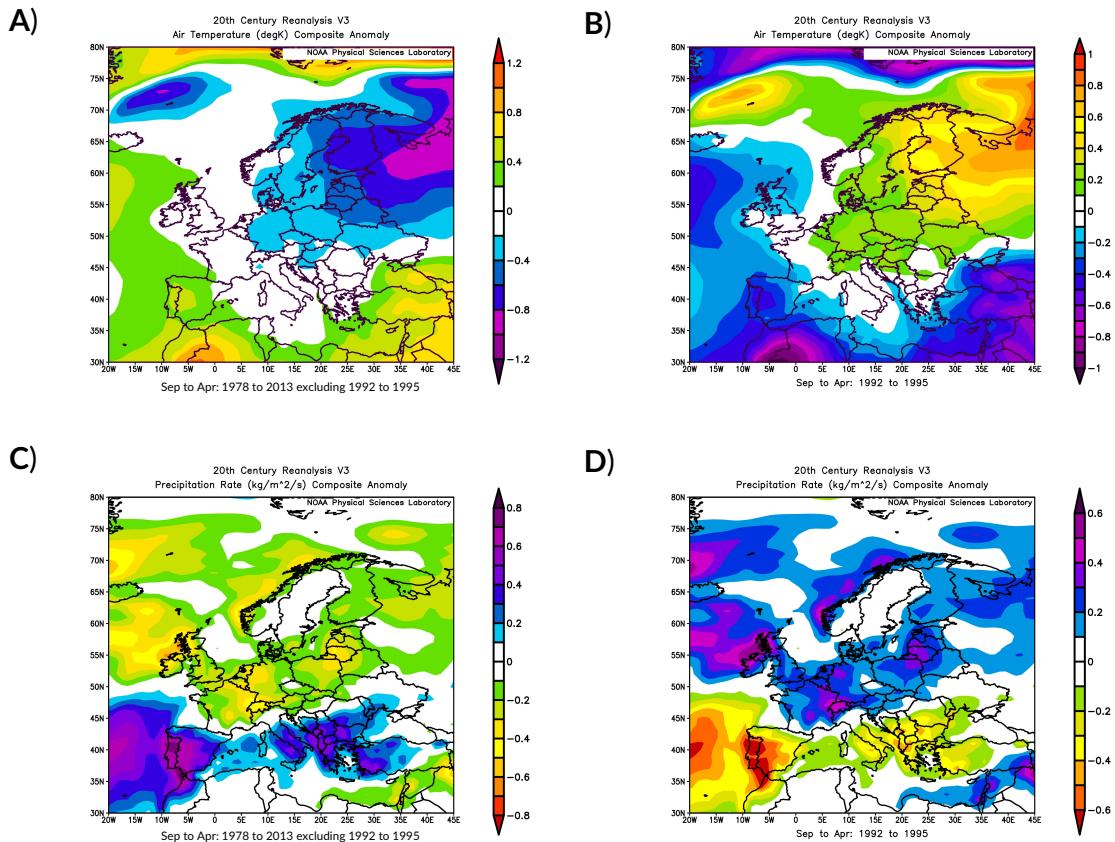


Figure 2: Synoptic fields of composite anomalies obtained from the V3 of the Twentieth Century Reanalysis Project ([https://psl.noaa.gov/data/20thC\\_Rean/](https://psl.noaa.gov/data/20thC_Rean/)). The composite anomaly from 1978 to 2013, excluding the transient period 1992-1995, is shown for air temperature (A) and precipitation rate (C). The composite anomaly for the transient period, 1992-1995, is shown for air temperature (B) and precipitation rate (D). The seasonal period considered excludes the summer months.

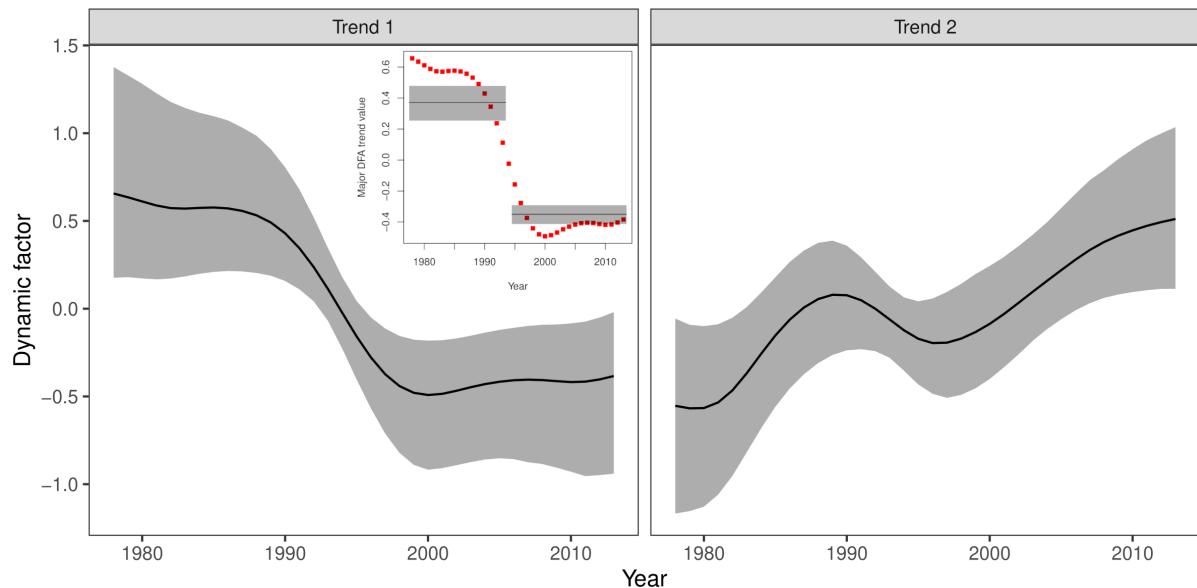


Figure 3: Posterior estimated community common trends in abundance of the state-space Dynamic Factor Analysis (Ward et al. 2022) applied to the wintering waterfowl community, and 95 % credible intervals. The inset figure in the common trend 1 shows the posterior regime shift identified by a Hidden Markov Model applied to the first common trend of the state-space DFA. The values of the common trend are depicted as red axes, and the average (and 95% Credible Intervals) of each regime is denoted in gray.

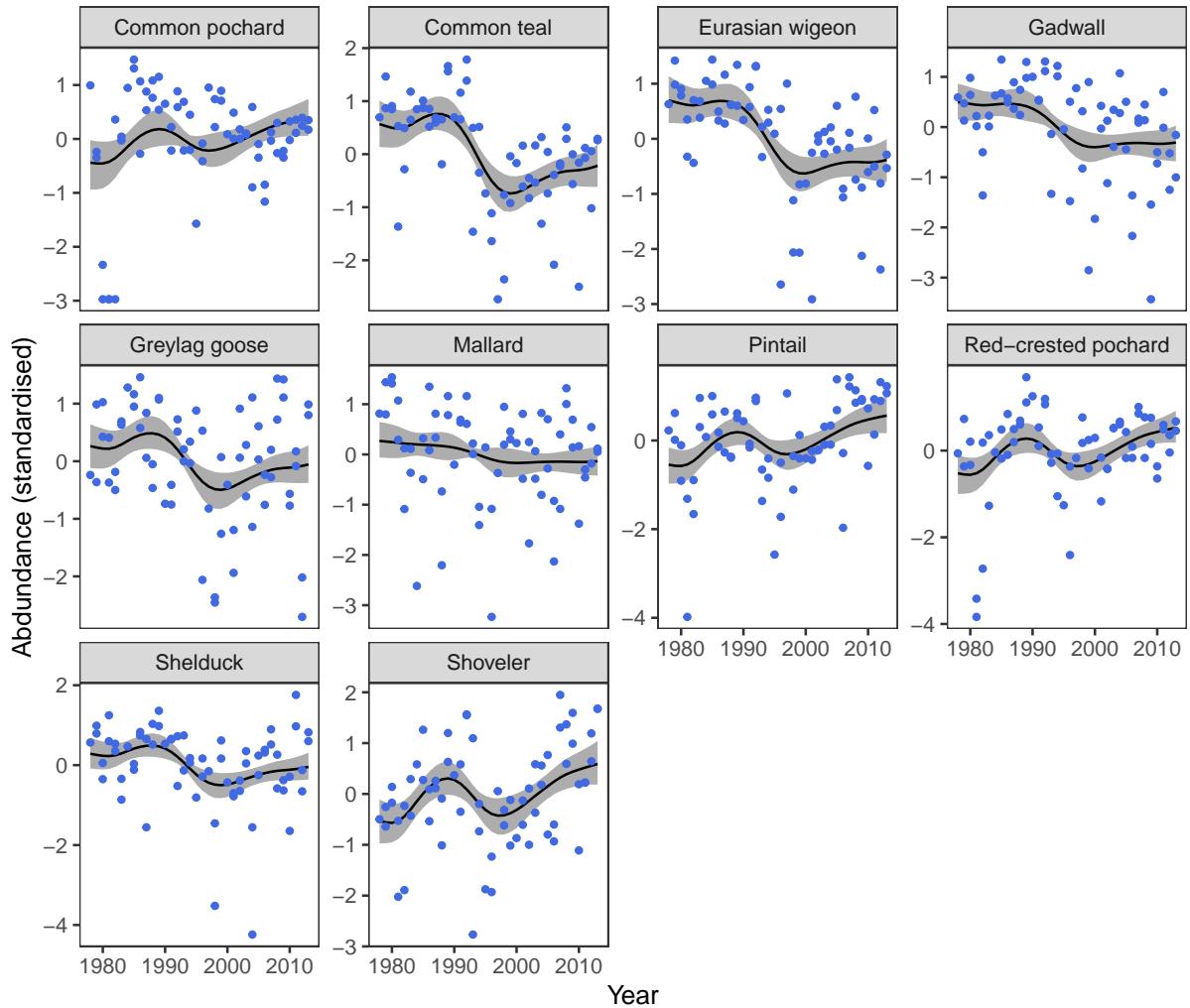


Figure 4: Posterior estimated common trends of the state-space Dynamic Factor Analysis for each wintering waterfowl species in Doñana wetlands, 1978-2021. The red dots denote the aerial count estimate for December and January of each wintering season. The solid line is the average posterior value of the common trend in Figure 3 yielding the largest factor loading for each species (Figure 5), and the shaded region is 95 % credible intervals.

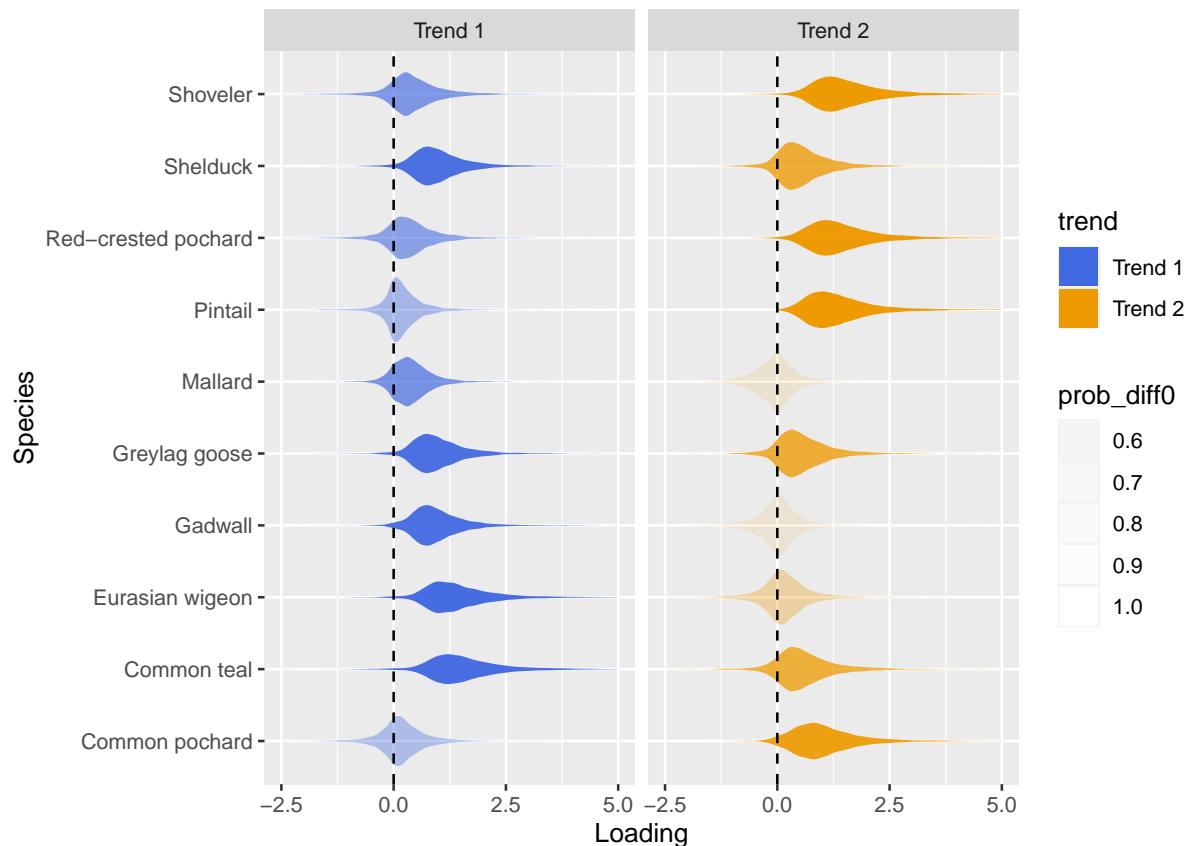


Figure 5: Factors loadings of the state-space Dynamic Factor Analysis for each wintering waterfowl species and each dynamic common trend (shown in Figs. 3 and 4). Violin plots include the posterior density for each loading and species, and the gray shading (prob\_diff0) is proportional to the probability that the loading is different from 0.

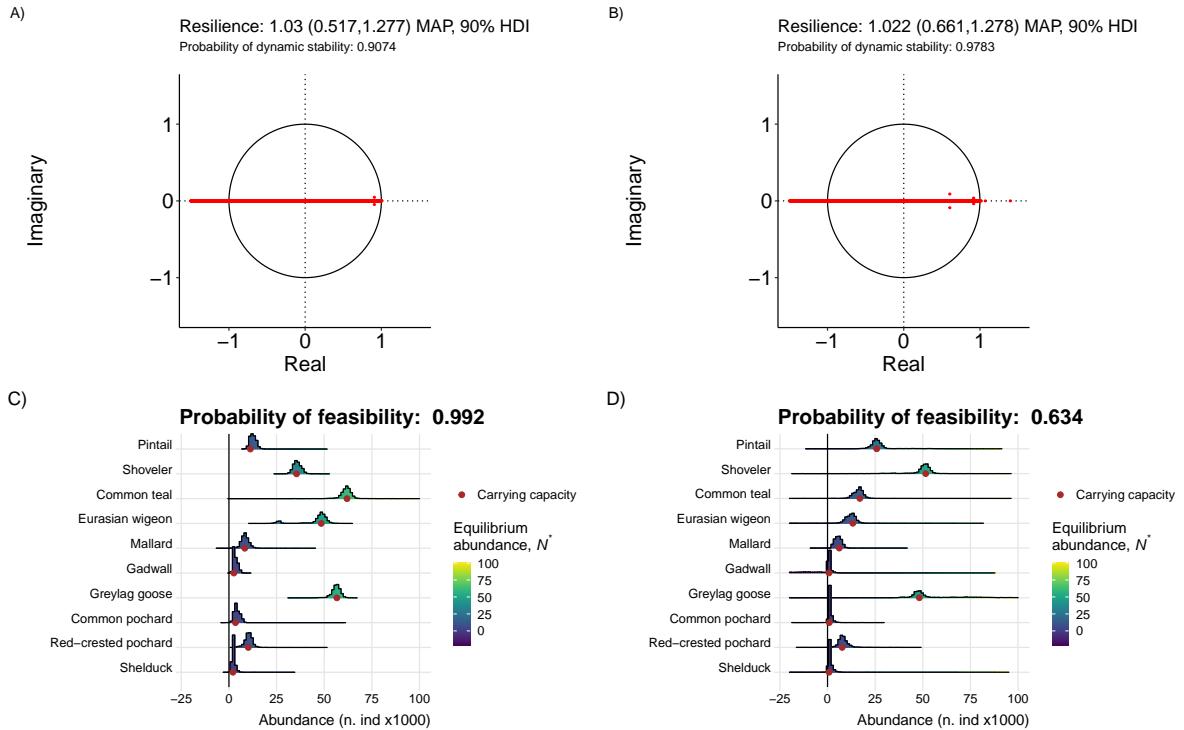


Figure 6: Probability of dynamical stability and feasibility of the wintering waterfowl community in Doñana marshes (1978-2013). Figures A) and B) show the distribution in the unit circle of the posterior eigenvalues of the Jacobian matrix 5 of the LVR state-space model (Eqns. 2-4) fitted to the pre-Pinatubo period (A, 1978-1992) and the post-Pinatubo period (B, 1995-2013). The probability of stability is the fraction of the eigenvalues (modulus) strictly smaller than 1 in the posterior distribution. MAP is the maximum a posteriori density, and 90% HDI the highest density interval (Makowski, Ben-Shachar, and Lüdecke 2019). Figures C) and D) show the posterior histograms of the equilibrium abundances ( $N^*$ ) and the posterior averages of the carrying capacities,  $k_i$  (Eqn. 2), for each waterfowl species (red dots) in the pre-Pinatubo period (C) and the post-Pinatubo period (D). The probability of feasibility for each period is the proportion of posterior estimated equilibrium abundance vectors in which the abundances are strictly positive for all species.

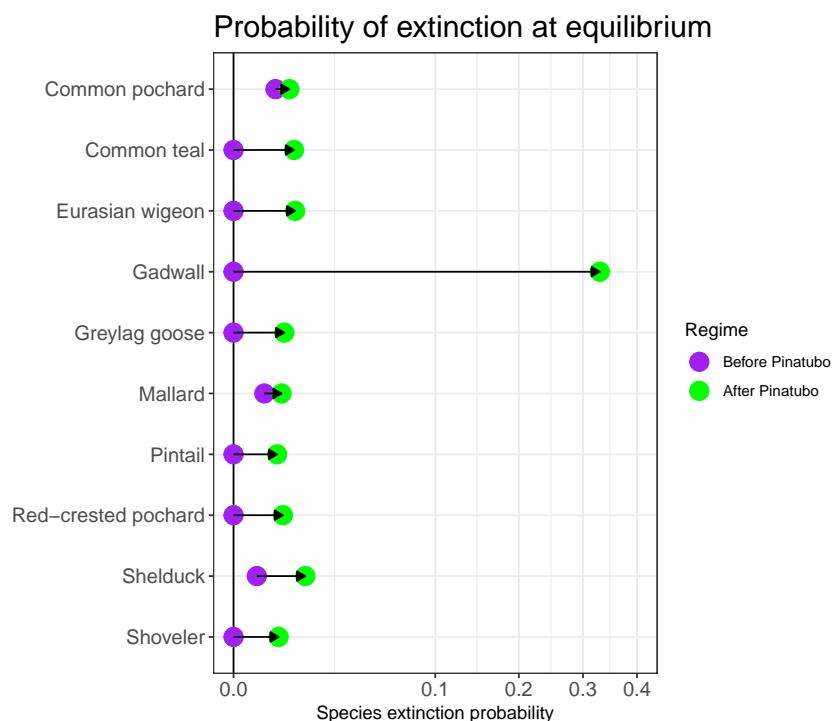
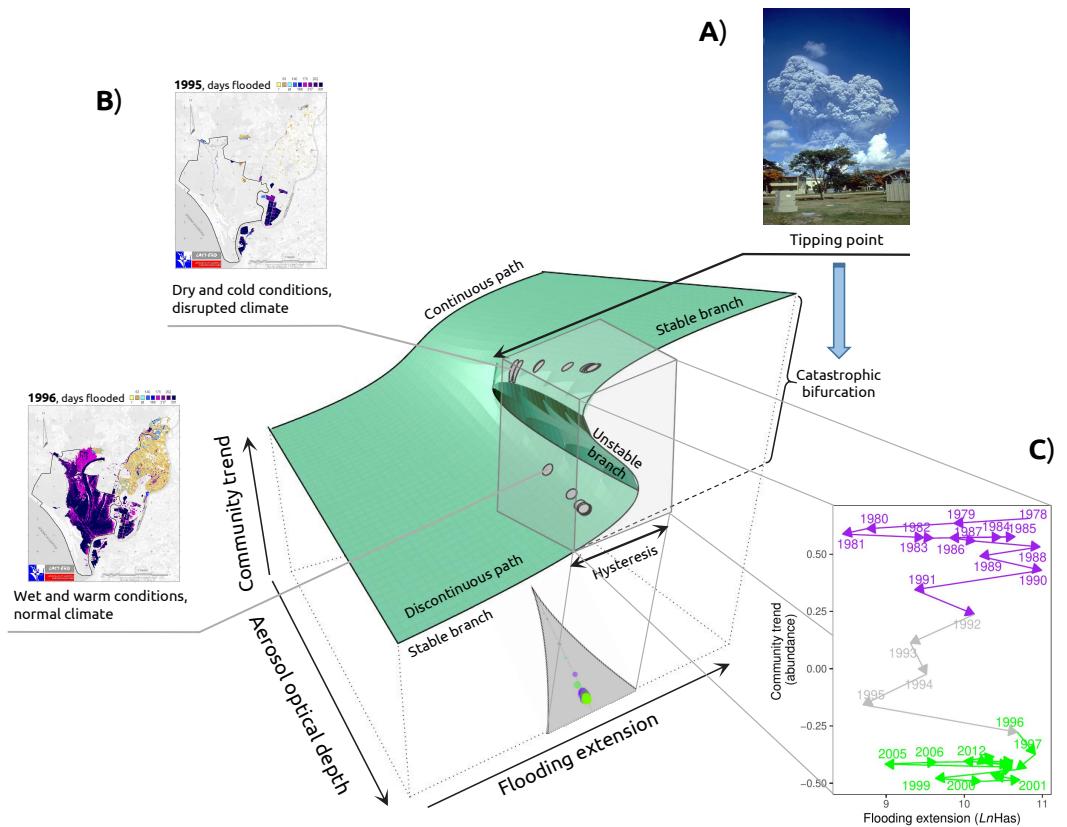


Figure 7: Change in the estimated probability of extinction at equilibrium for each waterfowl species in Doñana wetlands before (purple dots) and after the eruption of Mt. Pinatubo (green dots). From the posterior of the Bayesian regime-dependent state-space LVR model (Eqns. 2-4) fitted to the time-series of community abundance, this probability is calculated, for each species and alternative stable state, as the fraction of posterior estimated population abundances at equilibrium that are not strictly positive. Note the  $\sqrt{t}$ -transformation of the  $x$ -axis.



**Figure 8:** Diagram depicting the three-dimensional representation of the stochastic cusp catastrophe model (Eqn. 6) fitted to the major community trend (z-axis, Trend 1 in Fig. 3), as a function of the stratospheric aerosol optical depth (bifurcation parameter) and flooding extension (asymmetry parameter). The fitted values plotted in the maximum-likelihood cusp equilibrium surface (in green) are depicted as gray circles. In A), the tipping point (the cusp) of the model is represented by the eruption of Mt. Pinatubo of Philippines in April 2, 1991. As a press-type perturbation, it triggered a transient period of dry and cold wintering conditions in the Southern Palaearctic that lasted until 1995 (Robock 2002). Before the tipping point, fluctuations in waterfowl community abundance were located in the upper stable branch of the surface. In B), the small figures show maps of the numbers of days of flooded conditions in Doñana wetlands for two distinct years: 1995, at the end of transient period characterized by dry and cold wintering conditions; and 1996, a climatically normal year, with wet and warm conditions (see Fig. 2). The dynamic in year 1995 was evolving in the unstable (transient) branch of the surface. From 1996 onwards, the dynamics settled in the lower stable branch. The magnitude of the catastrophic bifurcation triggered by the tipping point is thus the difference in height between the two stable branches, while the size of the region of hysteresis is the amplitude of the stable states of waterfowl community abundance sharing the same environmental conditions. The gray cube in B), with height equal to the size of the catastrophic bifurcation, and width equal to the size of the hysteresis region, contains all the dynamics of the system, that takes place along the discontinuous paths. The bifurcation set is projected as a gray shadow in the floor of the cusp 3D surface, with the cusp as a critical point in the vertex. This set is represented in 2-dimensions in C), where the implicit temporal dynamics of the community abundance trend evolves with respect to the asymmetry parameter, namely flooding extension, from the first stable state (purple arrows) to the second stable state (green arrows) through the transient, unstable period (gray arrows). Flooding data provided by the LAST-EBD; Pinatubo public domain image from [Richard P. Hoblitt, USGS](#).