



Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Protected wading bird species threaten relict centenarian cork oaks in a Mediterranean Biosphere Reserve: A conservation management conflict

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ARTICLE INFO

Article history:

Received 26 January 2010

Received in revised form 30 October 2010

Accepted 6 November 2010

Available online xxxx

Keywords:

Quercus suber

Stable isotopes

$\delta^{15}\text{N}$

$\delta^{13}\text{C}$

Indirect effects

Colonial waterbirds

Heronry

Doñana

ABSTRACT

Conservation management conflicts frequently arise when an overpopulation of a protected organism has negative effects on other valuable elements in the same ecosystem. We studied the interactions between a colony of protected tree-nesting wading birds and a remnant population of centenarian cork oaks that was part of the formerly dominant forests in the Doñana Biological Reserve (SW Spain). A significant increase in the tree mortality rates has been recorded in areas that are yearly influenced by the bird colony.

We analysed a cohort of surviving trees using a gradient of nesting bird influence. Tree-nesting history, bird isotopic signature ($\delta^{15}\text{N}$), tree health-related parameters (defoliation, $\delta^{13}\text{C}$ and leaf surface coverage by faeces) and several soil variables were evaluated. Bird influence was related to increased soil salinity. This increase correlated to increased water-use efficiency for the leaves and to crown defoliation, suggesting that the heavily occupied trees are under higher stress and in poorer health condition than the unoccupied ones. We tested structural equations models (SEM) that were based on hypothesised bird effects on the health of the trees. Soil-mediated effects of the nesting birds best explained the symptoms of the declining health of the trees, whereas the percent of leaves' surface that was covered by faeces did not improve the fitted SEM model.

For the reserve's managers, a challenging trade-off exists between preserving the relict trees, which have a high genetic diversity and a key ecological role in these savannah-like ecosystems, and maintaining the current nesting area for these protected, but expanding, wading birds.

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1. Introduction

The establishment of natural reserves with a high protection status is a valuable tool to preserve endangered species and ecosystems (Arcese and Sinclair, 1997; Sinclair et al., 2002). However, in some cases, a high effective protection status is not enough to guarantee the conservation of a natural area. Unforeseen species–species or species–environment interactions may lead to undesirable results, including habitat degradation, a decline in the number of key species or losses in plant or animal diversity (Asner et al., 2009; Oro et al., 2009).

Under certain circumstances, plant–animal interactions may have detrimental effects on the plant communities in natural reserves. Overgrazing and overbrowsing by herbivores is frequently reported as an undesired result of the protection of some natural

areas (Herrera, 1995; Henríquez and Simonetti, 2001; Harrison et al., 2008; Asner et al., 2009). Other potentially harmful effects of animals (such as nesting, roosting, trampling and burrowing), allied to intensive plant occupation or soil alteration, have also been reported in protected areas (Sobey and Kenworthy, 1979; Mulder and Keall, 2001; García et al., 2002; Hebert et al., 2005).

One specific example of the effects of animals in natural reserves is the damage done to trees by tree-nesting/roosting waterbirds colonies. This type of damage has been reported in natural areas of America (Miller, 1982; Dusi and Dusi, 1987; Belzer and Lombardi, 1989; Hebert et al., 2005), Australia (Baxter, 1992; Baxter and Fairweather, 1994), Korea (Mun, 1997), the Russian Federation (Zelenskaya and Khoreva, 2006) and Japan (Ishida, 1996, 1997; Fujiwara and Takayanagi, 2001; Mizota, 2009). In Europe, Ligeza and Smal (2003) and Żółkoś and Markowski (2006) have reported the deleterious effects of cormorants and protected wading bird colonies on centenarian trees in Polish natural reserves. Alterations in the composition of the soil and/or direct mechanical/

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chemical effects were the most cited causes of damage to the trees by the nesting/roosting colonial waterbirds. As far as we know, no studies have been carried out on the detrimental effects of these tree-nesting colonial birds on Mediterranean oak forests.

In previous studies in protected Mediterranean islands (García, 2005; García et al., 2002), we found that colonial-nesting seabirds induced significant changes in soil salinity. These changes were paralleled by increased ^{15}N levels and by ^{13}C changes in the leaves of shrubs, suggesting that the soil alterations could affect the water-use efficiency (WUE) of leaves. Bird-induced soil changes significantly affected the distribution of the woody salt-tolerant plant species that inhabit these islands. Therefore, we concluded that changes of a similar nature may be much more damaging for long-lived, salt-sensitive species such as the cork oak, which thrives on the leached, acidic sands in the Doñana Biological Reserve (DBR) (Clemente et al., 1988; Siljeström et al., 1994).

In this paper, we studied the bird–soil–tree interactions in a cohort of centenarian cork trees that were distributed along a gradient of influence of colonial-nesting wading birds in the DBR (SW Spain). Along the last four decades, the cork oak tree mortality rate in the areas repeatedly occupied by wading birds during the nesting season has been significantly higher than the mortality rate recorded in the areas that have not been frequented by nesting birds (Ramo et al., 2009).

The aims of the study are the following: (1) to determine whether the cork oak decline detected in the Doñana Reserve is related to the present and past influence of nesting wading birds; (2) to investigate the mechanisms involved in the bird–soil–tree interactions by testing alternative structural equations models (SEM) on different direct and indirect (soil-mediated) bird effects on the health status of the trees; (3) to provide the Reserve managers with information to allow them to make evidence-based adaptive decisions and (4) ultimately, contribute to solve a potential conflict in this conservation management.

We hypothesise that the present health status of the trees may be explained, for the most part, by their history of wading bird occupation. We also hypothesise that changes in the soil composition that were caused by these birds, particularly those that increase solute concentrations in the soil as a result of the mineralisation of large amounts of bird debris, may play a central role in the observed centenarian tree decline.

2. Materials and methods

2.1. Study site and species

Doñana (SW Spain) is one of the main European protected areas for waterbirds (Rendón et al., 2008). In 1964, 6795 ha were protected under a Biological Reserve order; in 1969, it was extended to 54253 ha and declared a National Park (1969), Biosphere Reserve (1981) and World Heritage site (1994). The climate in this area is of Mediterranean-type, with an average annual rainfall of about 550 mm, which mainly occurs (>80%) between October and March and an average temperature of 16–17 °C. Some valuable aquatic and terrestrial Mediterranean ecosystems surround the Guadalquivir river estuary in this area, which were threatened by agricultural (the drainage and cultivation of marshlands, forest cutting and intensive farming of crops on the inland sands) and touristic development before being protected (Fernández-Delgado, 2006). The National Park comprises about 30,000 ha of clayey marshlands and about 25,000 ha of dunes, sparse forests and shrublands on sandy soils (Montes et al., 1998). The cork oak (*Quercus suber* L.) forests were devastated (>95%) by human exploitation (mainly for timber and charcoal) during the 17th to 20th centuries. The few thousand remaining trees formed a savannah-like scrubland (“dehesa”) that was historically managed for cork

and cattle production and for game hunting (Granados-Corona et al., 1988). Currently, these trees grow on acidic and nutrient-poor sandy soils that have a seasonally shallow water-table (1–3 m) (Clemente et al., 1988; Siljeström et al., 1994).

The present study was carried out in the Biological Reserve (6795 ha) at the core of the National Park. Following the Biological Reserve creation, all tree exploitation practices, such as cutting, pruning and cork extraction, ceased in order to preserve the remaining large centenarian trees. In addition, an important wading bird colony was naturally established in the reserve. Seven protected wading bird species nested on the centenarian cork oaks and in the nearby riparian vegetation: the white stork (*Ciconia ciconia*), the spoonbill (*Platalea leucorodia*), the grey heron (*Ardea cinerea*), the little egret (*Egretta garzetta*), the cattle egret (*Bubulcus ibis*), the squacco heron (*Ardeola ralloides*) and the black-crowned night-heron (*Nycticorax nycticorax*). Currently, these species usually occupy the trees in a broad ecotone between the scrublands and the marshlands known locally as “Vera”, during the nesting season (from February to July). The number of birds in the colony varies from year to year (from 150 to 13,000 pairs), depending on the marsh flood level (Ramo et al., 2009). We estimate that approximately 70% of the centenarian cork oaks of the “Vera” have been affected at some level by the colony. This percentage decreases to 30% if we consider the total number of centenarian cork oaks in the Biological Reserve. About 40% of the centenarian trees in the ecotone have died in the last four decades (Ramo et al., 2009).

2.2. Data gathering

We selected 60 centenarian cork oak trees that spanned the gradient of the wading bird occupation. This selection was based on the frequency of the occupation experienced by each tree over the precedent 24 nesting seasons (NestFreq, data gathered by the Doñana Monitoring Team). In the late dry season (August–September) of 2008, we collected information about the crown health for each tree and simultaneously sampled soil and leaves for analysis.

2.2.1. Crown health evaluation

Crown health status was evaluated by two methods: (1) by a visual estimation of the crown density on a standardised and fixed scale of six degrees (from 0, a dead tree, to 5, a healthy reference tree), which is locally used every year for monitoring purposes and is known as the Crown Density Index (CDI) and (2) by a quantitative estimation of the crown transparency (CT, the amount of skylight visible through the live portion of the crown) by digitally processing lateral digital photographs of the tree crowns using the program ENVI v4.0 (RSI, 2003).

2.2.2. Sampling of leaves and soil

In each tree, the leaves were sampled at about a 6 m height at the four cardinal orientations of the outer canopy and were mixed to form a single sample (per tree) for the analysis. Topsoil (0–10 cm depth) and subsurface soil (10–25 cm) samples were collected at the projection of the leaf sampling points and bulked to get a single sample per tree.

Leaf samples were washed for about 20 s with a solution of 0.1 g L⁻¹ phosphate-free detergent and rinsed twice with distilled water. They were oven-dried (70 °C) and finely ground. Soil samples were air-dried, crushed, sieved (<2 mm) and finely ground.

2.2.3. Percentage of the leaf surface covered by faeces

In each of the four cardinal leaf sampling points, five leaves were sampled at random at a middle height of the outer of the canopy. These 20 leaves were independently evaluated by two different observers for the percentage of their surface that was covered by bird faeces. For each tree, the average percentage of the leaf sur-

face covered by faeces (%LC) was approximated by averaging the estimates across all of the sampled leaves.

2.2.4. Soil chemical analyses

Total salinity (Electrical Conductivity, EC) and water-soluble nitrate (NO_3) and phosphate (PO_4) concentrations were determined in 1:5 (soil:water) extracts using a conductimeter and standard spectrometric methods (Sparks, 1996), respectively. To relate the measured salinity values with the published critical ranges (Richards, 1954; Shaw, 1999), we estimated the conductivity values for the soil saturation extracts (EC_{SE}) by making a calibration curve. Values in the soil saturation extracts took into account the effect of the variable soil water-holding capacity on the salt concentration in the soil solution, whereas the values in the 1:5 extracts took into account the total soil salt content on the basis of weight. Because bird debris is highly enriched in nitrogen and phosphorus, we estimated the percent of the dissolved nitrate plus phosphate ($\% \text{NO}_3 + \text{PO}_4$) with respect to the total amount of anions in the soil solution, and these values were used as an index of the ornithogenic anions along the gradient of bird influence. The total amount of anions in the solution (in $\text{mmol}_e \text{L}^{-1}$) was calculated as ten times the EC (in dS m^{-1}) (Shaw, 1999).

2.2.5. Isotopic analysis

Topsoil $\delta^{15}\text{N}$ and leaf $\delta^{13}\text{C}$ values were determined with a precision of about 0.2 per mil using an EA-IRMS (elemental analyser-isotopic ratio mass spectrometer) in continuous flow mode.

High $\delta^{15}\text{N}$ values were expected in soils that receive carnivorous bird debris because of the ^{15}N enrichment that occurs along the aquatic food chains and the isotopic fractionation that occurs during ammonia volatilisation from bird products (Mizutani et al., 1986; Mizutani and Wada, 1988).

Leaf $\delta^{13}\text{C}$ values are considered a time-integrated index of the intrinsic leaf water-use efficiency (WUE, i.e. the ratio of the carbon gain to transpired water). Both the WUE and the $\delta^{13}\text{C}$ values are usually higher for drought-tolerant species or populations. Within a given species and population, higher WUE and leaf $\delta^{13}\text{C}$ values are expected in water-stressed plants (Ehleringer and Cooper, 1988). Water stress induces closing of leaf stomata and fixing of most of the CO_2 that enters during the short stomata openings, reducing carbon isotope discrimination and increasing leaf $\delta^{13}\text{C}$ values (Fry, 2006). Ionic toxicity can also decrease photosynthesis by decreasing carboxylase activity. This decrease in activity frequently occurs in a later phase of salinity stress that follows an early phase dominated by osmotic stress (Munns et al., 1995).

2.3. Data analysis

The relationships between the wading bird occupation, soil and leaf alterations and tree health status were first explored using correlation analyses (Pearson or Spearman, depending on the nature and distribution of the correlating variables). To summarise and test the hypothesised multivariate relationships between bird, soil and tree variables, we performed a SEM analysis using the measured (manifest) variables as indicators of the hypothesised underlying (latent) factors causing the observed changes in the analysed system (see Iriondo et al., 2003).

SEM allows for the testing of causal relationships that link wading bird, tree and soil variables. A series of alternative causal models are derived from previous knowledge and the observed empirical patterns. Each alternative model entails a series of causal assumptions that condition the structure of the variances and covariances of the variables and that can be tested against the observed data. The parameters of a system of linear equations that relate latent factors and manifest variables are fitted in order to maximize the correspondence between the modelled covariance

matrix and the observed covariance matrix. A model is considered an adequate fit to the data when their assumptions cannot be falsified, that is when the null hypothesis is not rejected (i.e. p -values exceed the selected significance level, usually 0.05). Otherwise (usually $p < 0.05$) the tested model is rejected as a potentially worthwhile explanation of the overall observed relationships between the variables involved in the studied system. Therefore, unlike most statistical testing procedures, here we are interested in models matching the data i.e. in accepting instead of rejecting the null hypothesis.

In the present study, the main hypothesis underlying the tested models is that a higher frequency of bird occupation produces an accumulation of N- and P-enriched organic debris and that the mineralisation of this debris increases the concentration of the soluble salts (mainly nitrates and phosphates) in the soil. In addition, these augmented soil salinity levels increase the level of plant stress (and hence increased leaf WUE) and contribute to a decline in tree health. Direct chemical and physical damages may also occur because of the accumulation of faeces on leaves and because of the mechanical effects of birds on leaves and twigs. This damage could have a significant effect on tree health status, and therefore, they have been included in the model. Bird effects on tree health can be classified into two categories: “explicit direct” (i.e. including additional measured variables which are indicators of direct bird effects on tree crown) or “implicit direct” (based on the assumption that crown status significantly co-variates with direct bird pressure and establishes a specific direct path in the tested model).

To test these multivariate hypotheses, with consideration for all of the empirical evidence simultaneously, the SEM included five underlying latent factors: wading bird influence (BIRD), soil salinity (SALINITY), leaf water stress (STRESS), crown health status (HEALTH) and the average percentage of the leaves' surface covered by bird faeces (LCOVER). We used the following as indicators of these unmeasured latent factors: the nesting frequency (NestFreq) and the topsoil bird isotopic signature ($\delta^{15}\text{N}_s$) for BIRD; the surface (EC_{0-10}) and subsurface (EC_{10-25}) soil salinity values for SALINITY; the leaf $\delta^{13}\text{C}$ values for STRESS; the CDI and CT for HEALTH and %LC for LCOVER. All latent factors, except BIRD, were considered endogenous (i.e. influenced by another factors).

We tested three competing models: (1) in the first model (Model I), only the indirect effects of the birds on tree health were considered, (2) the second model (Model II) was based on both indirect and implicit (unmeasured) direct bird effects and (3) the third model (Model III) included a factor (LCOVER) that accounted for a measured explicit direct bird effect.

When necessary, the variables were transformed (log, arcsin) to minimise violations of the required assumptions (normality, homoscedasticity). Deviations from multivariate normality were tested by evaluating the Mardia coefficient. Model fitting was based on the covariance matrix between the indicator variables and the maximum likelihood function (ML). The goodness of fit was evaluated using the chi-squared test, the root mean square error of approximation (RMSEA), the standardised root mean-square residual (SMRR) values and the Joreskog–Sörbom's Goodness of Fit (GFI) index. For the RMSEA and SMRR, values close to 0 are desirable; those ≤ 0.05 are indicative of a very good fit of the model. For GFI, values close to 1 are desirable; those ≥ 0.95 are indicative of a very good fit of the model. To select among the competing models, we used the sample-size corrected version of the Akaike Information Criteria (AIC_c), which estimates the lost information by approximating the full reality with the fitted model. For each model, we calculated the Akaike weights (w_i), which are interpreted as the probability that the model i is the best model given the candidate set of models (Johnson and Omland, 2004). This procedure allows for a powerful information theory-based ranking of the competing models and for a selection of either the best model or

a weighted-average model when no single model is overwhelmingly supported by the data (i.e. $w_{ibest} > 0.9$). As an additional criterion to select among the nested competing models, we used the chi-squared difference test (Bentler, 2006).

All statistical analyses were performed using the EQS (Bentler and Wu, 2007) and the Statistica (Statsoft, 2004) packages. Type I error inflation resulting from repeated tests was controlled at the 5% level using the Benjamini & Hochberg's False Discovery Rate (FDR) approach, as recommended by García (2003).

3. Results

3.1. Environmental ranges

The frequency of the wading bird occupation of the studied trees (NestFreq) ranged from 0% to 92% of the nesting seasons since 1985. As expected for a steep gradient of colonial carnivorous bird effects, a wide range of soil $\delta^{15}\text{N}$ values ($\sim 13\delta$ units) was found in the soil under the studied trees (Table 1).

Leaf $\delta^{13}\text{C}$ values varied over a large range ($\sim 6\delta$ units) given that all the studied trees were conspecific and spread in a relatively uniform area, indicating a wide gradient of leaf WUE values. Crown transparency values fell within a 10-fold range, whereas the average percentage of the leaf surface covered by faeces at the end of the nesting season exceeded 75% in some trees.

Soil salinity levels varied up to 75-fold along the studied gradient and were considerably (2–3 times) higher in the topsoil than in the subsoil. The salinity values that were estimated for the saturation extracts reached levels that are considered potentially harmful for salt-sensitive species ($>2 \text{ dS m}^{-1}$, Shaw, 1999) in heavily occupied sites. Water-soluble nitrate and phosphate varied >2000 and >900 -fold, respectively, along the studied gradient of bird effects, ranging from a negligible fraction of the total dissolved anions up to $>85\%$ of the total in the salinised soils (Fig. 1).

3.2. Oak decline symptoms and bird influence

We found that both the long-term nesting frequency and the soil's bird isotopic signature were significantly and negatively related to the crown health status (i.e. positively related to CT and negatively related to CDI, Table 2) of the studied centenarian oaks. Both indicators of the cumulative bird influence were positively correlated with leaf ^{13}C enrichment, suggesting that leaf WUE and water-stress increased along the bird influence gradient. Furthermore, this increased water-stress-related leaf isotopic signature seems to be an attribute of unhealthy trees because it

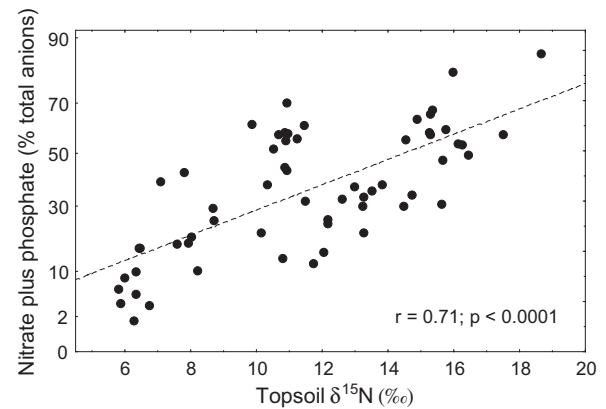


Fig. 1. Variation of water-soluble soil nitrate plus phosphate levels along the gradient of the bird inputs, indicated by the topsoil ^{15}N isotopic signature. Original Y-values (percentage data) were transformed using the arcsin-sqrt transformation.

showed a strong positive correlation with the crown transparency CT and a strong negative correlation with the CDI values (Table 2).

On the other hand, the percentage of the leaf surface that was covered by bird faeces was significantly correlated with the level of ornithogenic salts in the soil, but no significant correlations were found with the indicators of water-stressing conditions or of crown health status.

3.3. Soil-mediated effects on trees

We found a close relationship between the available indicators of bird activity (NestFreq, $\delta^{15}\text{N}_s$) and the overall soluble salt concentrations in the surface (EC_{0-10}) and the subsurface (EC_{10-25}) soil horizons (Table 2). Unexpectedly, both indicators of long-term cumulative bird influence were more closely related to subsurface than to surface soluble salt concentrations, probably related to the leaching/downward translocation of the bird derived products through the soil profile. Soil $\delta^{15}\text{N}$ values were a better quantitative predictor of the overall soil salinity levels than the corresponding long-term nesting frequency, suggesting that a direct quantitative relationship may exist between topsoil levels of ornithogenic N (and other elements associated to wading bird inputs) and soil salinity. This link was further reinforced in terms of the increased relative importance of the two main ornithogenic anions (nitrates and phosphates) along the wading bird influence gradient, as reflected in the soil $\delta^{15}\text{N}_s$ values (Fig. 1).

Table 1

Basic statistics (median, range and maximum/minimum) of the measured variables. The salinity values of the soil saturation extracts (SE) take into account the effect of soil water-holding capacity on the salt concentration in the soil solution, whereas those in the 1:5 extracts take into account the total soil salt content on a weight basis.

Variable	Abbrev.	Median	Minimum	Maximum	Max./min.
Nesting frequency (%yr, since 1985)	NestFreq	33	0	92	–
Leaf $\delta^{13}\text{C}$ (‰)	$\delta^{13}\text{C}_l$	–29.8	–31.9	–26.1	–
Soil $\delta^{15}\text{N}$ (‰)	$\delta^{15}\text{N}_s$	11.4	5.8	18.7	–
Crown Density Index (1–5)	CDI	3	1	5	–
Crown transparency (%)	CT	12.2	4.9	44.0	9
Leaf surface covered by faeces (%)	%LC	5.4	0.0	76.7	–
Topsoil salinity (1:5, dS m^{-1})	EC_{0-10}	0.17	0.03	2.20	73
Topsoil salinity (SE, dS m^{-1})	sEC_{0-10}	0.52	0.09	5.46	59
Subsurface salinity (1:5, dS m^{-1})	EC_{10-25}	0.05	0.02	0.59	37
Subsurface salinity (SE, dS m^{-1})	sEC_{10-25}	0.31	0.07	5.21	75
Nitrate (mg kg^{-1})	NO_3	62.3	2.2	4650	>2000
Phosphate (mg kg^{-1})	PO_4	122	2.0	1849	>900
$\text{NO}_3 + \text{PO}_4$ (% total dissolved anions)	$\text{NO}_3 + \text{PO}_4$	36.4	1.5	85.9	59

Table 2

Matrix of correlations between the measured variables. All values, except those labelled as ns, were declared significant after controlling for the False Discovery Rate at the 5% level. All correlation values corresponded to Pearson correlation coefficient, except those with Crown Density Index (CDI) that corresponded to Spearman correlation coefficient. See Table 1 for variable abbreviations.

	%LC	CDI	CT	NestFreq	$\delta^{13}\text{C}_L$	$\delta^{15}\text{N}_S$	EC _{0–10}	EC _{10–25}	NO ₃
CDI	–0.26 ^{ns}								
CT	0.06 ^{ns}	–0.66							
NestFreq	0.20 ^{ns}	–0.37	0.48						
$\delta^{13}\text{C}_L$	0.19 ^{ns}	–0.65	0.58	0.29					
$\delta^{15}\text{N}_S$	0.23 ^{ns}	–0.44	0.47	0.81	0.38				
EC _{0–10}	0.25 ^{ns}	–0.37	0.35	0.54	0.49	0.54			
EC _{10–25}	0.32	–0.45	0.42	0.66	0.46	0.61	0.86		
NO ₃	0.42	–0.43	0.30	0.51	0.42	0.61	0.80	0.73	
PO ₄	0.35	–0.41	0.36	0.72	0.38	0.84	0.72	0.76	0.77

3.4. A Structural equation modelling analysis of the bird–soil–tree interaction

The results of the SEM analysis for the three hypothesised models are summarised in Table 3 and Fig. 2. Model II had the best values of significance (highest *p*-value), of overall fit indexes (GFI > 0.95, SRMR and RMSEA < 0.05) and of AIC (lowest value). According to the Akaike weights (w_i) criterium, the probability that model II is the best approximating model is 0.78, compared to 0.20 for model I and to 0.02 for model III. In contrast, the chi-squared difference test concluded that the direct effect introduced in Model II did not represent a significant overall improvement over Model I ($p = 0.99$), whereas the fraction of the explained variance of the overall tree health condition was higher in the model that was based solely on the bird indirect effects (Model I).

Model III, which assumed that direct faecal deposition on tree leaves significantly contributed to tree decline, was clearly outperformed by the first two models (Fig. 2, Table 3).

In summary, we found strong empirical support for that hypothesis advocating a prominent role for the indirect (soil-mediated) effects of colonial wading birds on the health status of the trees, although some unmeasured significant direct bird effects seemed to exist.

According to the model based on the measured significant effects (Model I), the intensity of the bird influence, evaluated both by the nesting frequency and by the isotopic signature, may directly explain over 50% of the overall (i.e. both in the surface and subsurface horizons) increase in soil salinity. This increase in salinity explained 35% of the observed water stress symptoms (increased ^{13}C). A close negative relationship between the STRESS factor and the HEALTH factor was found. About 88% of the crown health status was explained by the accepted hypothesised model.

Table 3

Model comparison. Different criteria for the goodness of fit and significance to evaluate the performance of the tested models are included. See text for further details.

Tested effects	Model I Indirect	Model II Indirect + direct path	Model III Indirect + measured direct
<i>Significance/goodness of fit</i>			
Chi-square	15.2	8.5	17.0
DF	11	10	15
<i>p</i>	0.17	0.58	0.32
AIC _c	7.81	5.14	12.80
w_i	0.20	0.78	0.02
SRMR	0.07	0.03	0.05
RMSEA	0.08	0.00	0.05
90% CI	(0.00, 0.17)	(0.00, 0.12)	(0.00, 0.14)
Joreskog–Sorbom's GFI	0.93	0.96	0.93

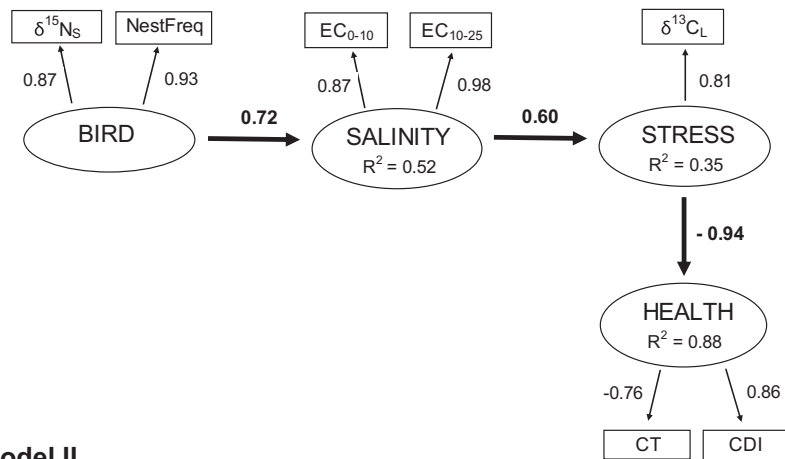
4. Discussion

The Doñana World Heritage site, comprising highly threatened aquatic and terrestrial Mediterranean ecosystems, has received the highest protection status (IUCN Category Ia, Strict Nature Reserves). However, the increase in herbivorous populations over the last four decades have impaired the regeneration of cork oak (Herrera, 1995) and could threaten the survival of the cork oak population.

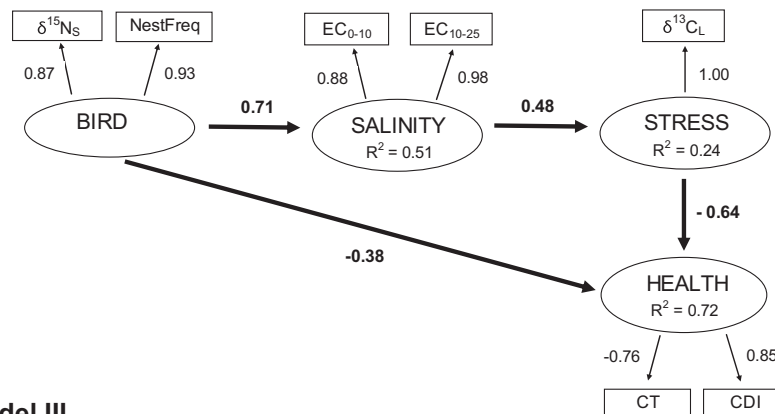
Management conflicts frequently arise when different endangered species (or groups of species) require contradictory conservation strategies. The larkspur (*Delphinium montanum*) versus the chamois (*Rupicapra rupicapra*) in the Pyrenees (Simon et al., 2001); three endangered endemic subspecies of scavenger birds, which feed on introduced goats and rabbits, versus highly endangered native plants, which are threatened by goat proliferation, in the Canary Islands (Gangoso et al., 2006); the elephant (*Loxodonta africana*) versus native endemic flora in South Africa (Lombard et al., 2001) and the green turtle versus seagrass meadows in the Lakshadweep Islands (Lal et al., 2010) are all examples of these conflicts. Ecosystem management and the identification of keystone species have been proposed to solve the conflicts associated with single-species management (Simberloff, 1998).

Large colonial tree-nesting waterbird populations have become a large problem for environmental managers (Telfair et al., 2000; Hebert et al., 2005). In some cases, valuable remnants of native forests have been threatened by colonial tree-nesting birds (Hebert et al., 2005). In natural areas of central Europe, recent reports have been published about the detrimental effects of colonial wading birds on tree species (Ligeza and Smal, 2003; Żółkoś and Markowski, 2006). Our results support such findings; in the warm and seasonally dry Mediterranean-type climate of southern Europe, an intense and persistent occupation of trees by colonial wading birds induces large changes in the soil composition and contributes to the decline observed in the studied population of the centenarian cork oaks. We found a close relationship between the overall soil salinity level and the concentration of ornithogenic soluble anions, which points to a wading bird-mediated soil salinisation process that has detrimental effects on tree health. Direct negative effects from nest building and faeces covering the surface of the leaves (inhibiting photosynthesis and/or respiration and producing chemical damages, Ishida, 1996) could also be important to explain tree decline; however, these effects seem to be less influential than the soil-mediated effects on the crown health status of the trees. In our case study, some unmeasured chemical or mechanical direct effects seemed to be significant for tree decline and warrant more research. For example, large nest accumulation occludes significant tree leaf areas and often causes broken branches; nest construction frequently involves twig collection and lose of leaves, bird drops tend to produce visible chemical injuries on leaves. These per-

Model I



Model II



Model III

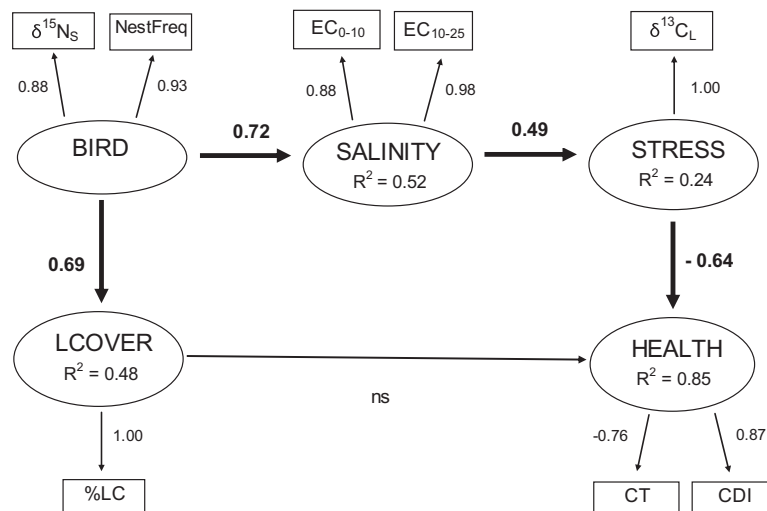


Fig. 2. Results of the SEM analyses for three hypothesised models of wading bird influence on tree health status. Model I considers only soil-mediated (indirect) effects on tree health, Model II assumes both direct and indirect bird effects on crown health status, and Model III includes a factor (LCOVER) accounting for an explicit measured direct bird effect. See Table 3 for significance and goodness of fit information. All path (regression) coefficients shown are standardised and were significant at the 5% level, whereas those labelled as ns were non-significant. R^2 values indicate the proportion of variance of the latent endogenous variables explained by the model. Arrows between measured (squares) and latent (ellipses) variables represent the correlations between these two kinds of variables. Abbreviations for latent variable names are: BIRD = wading bird influence; SALINITY = soil salinity; STRESS = leaf water stress and HEALTH = crown health status. See Table 1 for the abbreviations of the manifest variables' names.

ceived, but not measured, direct bird effects on trees could account for the observed results.

Special attention should be given to areas with semiarid climates where the indirect effects of birds may be enhanced by in-

creased water-stressing conditions, such as those predicted for the climate change in Mediterranean regions (Bates et al., 2008). The expected warmer and drier conditions would boost the evaporative demands, enhance the intensity and persistence of the

increased solute concentrations and therefore aggravate the negative bird–soil–tree interaction.

There are no in-depth studies about the ecological role played by these large cork oak trees that are scattered in the extensive herbivore-resistant scrublands which occupy most of the Doñana stabilised sand dunes. However, it is well known that they seasonally provide food for deer, wild boars, small mammals (Herrera, 1995) and birds, nesting structures for raptors (Calderón et al., 1987; Suárez et al., 2000; Sergio et al., 2005) and suitable breeding dens (old hollow oaks) to endangered Iberian lynx (*Lynx pardinus*, Fernández and Palomares, 2000). Additionally, as demonstrated by studies in other ecosystems, large, scattered trees may act as keystone structures that provide a disproportionately large contribution to the functioning of the ecosystem relative to their biomass, both on local and landscape scale (Belsky and Canham, 1994; Dean et al., 1999; Herrera and García, 2009; Manning et al., 2006; Marañón et al., 2009; DeMars et al., 2010; Fischer et al., 2010). Due to the impossibility of quickly replace these large centenarian trees, their accelerated elimination has unpredictable effects on the whole ecosystem that are difficult to reverse.

The high genetic diversity within these few hundred large trees is remarkable (de Heredia and Gil, 2006), and these locally adapted genotypes should be preserved despite the fact that belong to *Q. suber*, a widespread and abundant Mediterranean tree species (see also Lorenzo et al., 2009). The maintenance of the genetic connectivity among tree populations and the preservation of genetic material and focal points for future large-scale restorations (Manning et al., 2006) are additional reasons to protect this remnant oak population.

For the Doñana managers, a challenging trade-off exists between maintaining the nesting area for the protected, although expanding, wading birds (Rendón et al., 2008; Tablado et al., 2010) and preserving the relict, large, scattered trees, which have a great genetic diversity and play a key ecological role in these savanna-like ecosystems. What can managers do to solve this conflict? If no action is taken, new trees will be used by the colony as the occupied trees die, and the problem will increase. Is it possible to remediate the soil to minimise the adverse effects on the oaks while maintaining the bird colonies? No previous essays of successful soil remediation practices in natural reserves have been reported in the literature. The remediation measures currently available for highly eutrophicated soils (e.g. in poultry or pig farms) typically involve chemical treatments (e.g. Moore and Miller, 1994; Moore et al., 2000) or the introduction of accumulator plant species (Delorme et al., 2000; Sharma et al., 2007); in addition, they are usually applied after the source of pollution has been eliminated. Therefore, none of the known soil remediation treatments would be recommended for yearly application in a natural reserve while maintaining the source of pollution. Mechanical intercept of falling dung and removal of this material at the end of each nesting season seem to be unworkable in this Reserve and could cause other unexpected negative effects, as those related to rain interception and interaction with large herbivores.

One possible alternative would be to relocate the colony to another location where the vegetation has a lower conservation value and can be more easily replaced. There are some examples of successful relocation operations. In South Carolina, the construction of a new port terminal led to the relocation of a colony of about 500 pairs of black-crowned night herons to a mitigation site (Crouch et al., 2002). In the Camargue (France), a mixed colony of more than 300 pairs of little egrets, cattle egrets and black-crowned night herons, which were located in an unprotected area, were led to a new location inside a biological reserve (Hafner, 1982, 2000). In the case of Doñana, the large size of the colony would likely make relocation much more difficult.

5. Conclusions

In this study, we have found consistent evidence linking the wading bird occupation and the morphological and physiological signs associated with this occupation to the centenarian cork oak decline in the Doñana Biological Reserve (SW Spain).

The fitted structural equations models showed a significant indirect bird–soil–tree health path. No fit improvements were observed after including one measured direct bird effect (surface of leaves covered by faeces); however, several unmeasured and potentially relevant direct bird effects emerged from the analysed models.

Rising soil salinity levels, which were associated with increased concentrations of ornithogenic salts (nitrates and phosphates) that alter plant water-use efficiency by increasing water and/or photosynthetic stress, emerged as a potential main mechanism through which the colonial birds may be indirectly causing the decline of this salt-sensitive tree species.

Predicted warmer and drier scenarios by climate change for the Mediterranean region may increase the deleterious effects of the tree–nesting wading birds on the cork oak trees.

A complex trade-off exists for managers between preserving the relict centenarian large scattered trees, which represent a 'hot spot' of intraspecific diversity, have a key ecological role and have a very slow rate of recruitment and growth, and maintaining the current nesting area for several protected but expanding wading bird species.

Acknowledgements

We are grateful to the Consejería de Medio Ambiente (Andalusian Government) and to the Organismo Autónomo Parques Nacionales for financial support and to the Doñana National Park and Doñana Biological Reserve managers for the use of their facilities and the support to carry out the field work. Héctor Garrido, Eduardo Aguilera and Rubén Rodríguez provided us with valuable information about the wading bird colony. Doñana Monitoring Team members and Eduardo Gutiérrez, Juan S. Cara, Paula Madejón, Pilar Burgos and Vanessa Peiró helped us with the field and/or laboratory analyses. Three anonymous referees helped us to greatly improve the paper. LVG, CA, AM, MTD, LGA and TM were supported by the INTERBOS (CGL2008-4503-C03-01), the DECALDO (091/2009) and the BIOGEOBIRD (P09-RMN-4987) projects.

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