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S. de La Peña-Lastra, C. Gómez-Rodríguez, A. Pérez-Alberti, Franck Torre, X.L. Otero. Effects of a yellow legged gull (Larus michahellis) colony on soils and cliff vegetation in the Atlantic Islands of Galicia National Park (NW Spain). CATENA, 2021, 199, pp.105115. 10.1016/j.catena.2020.105115 . hal-03392075

HAL Id: hal-03392075
https://amu.hal.science/hal-03392075

Submitted on 22 Mar 2022

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Effects of a yellow legged gull (*Larus michahellis*) colony on soils and cliff vegetation in the Atlantic Islands of Galicia National Park (NW Spain)

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Keywords:
Cliff vegetation
Nitrogen
Phosphorus bioavailability
Beta diversity
Principal component analysis

A B S T R A C T

Seabirds are powerful environmental modulators, generating major changes in soil properties and vegetation in areas where their breeding colonies are established. One of the largest yellow-legged gull colonies in the world is found in the Atlantic Islands of Galicia National Park. In this study, we performed seasonal monitoring, over a period of 5 years, of the flora and soil in eight subcolonies characterized by different densities of gulls. Soil nutrient concentrations differed significantly between the control site and the subcolonies, as well as between seasons; the concentrations of $N\text{-}NO_3^-$ and bioavailable P were highest in samples obtained at the end of the breeding season. Principal Component Analysis (PCA) transformed the environmental variables into three main components following varimax rotation. The PCA components were used as potential predictors in distance-based Redundancy Analyses (db- RDA) to explain turnover and also nestedness patterns in plant assemblages. Species turnover was explained by both natural (salinity) and nutrient gradients, while none of the relationships were significant in the nestedness analysis. Floristics inventories clearly revealed ruderalization of vegetation in the densest subcolonies, which led to total replacement of the most representative vascular plant species by eutrophic and ruderal species. PERMANOVA analysis showed that seagull density in 1991, when the seagull population was at its highest, could be used to group similar plant assemblages; however, this relationship was not observed for seagull density in 2011, which was 70–90% lower than in 1991. The study findings indicate that the environmental effects of seabird colonies are long lasting and that disappearance of the birds does not lead to restoration of the previous vegetation. The gull colony has irreversibly transformed the soil and vegetation of cliffs, generating a new environmental system.

1. Introduction

Seabirds are one of the most numerous bird groups in the world, including over 1100 million individuals and comprising around 3.5% of all birds (del Hoyo et al., 1996; Otero et al., 2018). During the breeding season, most species concentrate in large colonies in coastal areas, strongly impacting the vegetation and leading to the transformation of plant communities (Sobey and Kenworthy, 1979; Hahn et al., 2007; Hiradate et al., 2015, Zwolicki et al., 2016).

The effect that seabird colonies have on vegetation and flora is complex and multidirectional and as such is sometimes difficult to identify. Thus, low bird densities lead to increased biodiversity, plant biomass and plant height, as well as to enhanced seed dispersal, owing to "ornitheutrophication" of the soil (Anderson and Polis, 1999; Sanchez-Piñero and Polis, 2000; Otero et al., 2018). Nevertheless, seabird colonies often reach high densities, and the pressure they exert on the substrate and vegetation can dramatically transform characteristic plant formations in coastal environments. Uprooting of plants (for nest building), trampling, soil compaction and eutrophication greatly decrease the biodiversity of vegetation and lead to the introduction of allochthonous ruderal and nitrophilous species (Kamijo and Yoshinobu, 1995; Hiradate et al., 2015, Ishida 1996; Baumberger et al., 2012).

For the aforementioned reasons, newly established colonies can sometimes conflict with conservation programs that target certain

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species or communities. In the Atlantic Islands of Galicia National Park (AINP), a dramatic change in plant communities was observed in coastal cliffs where a yellow-legged gull colony was established, and a new plant community associated with the gull colony was described (e.g. *Calendulo algarbiensis-Parietarietum judaicae*; Guitián and Guitián, 1990). Nevertheless, most plant formations present in colonies within the AINP remain uncharacterized (Arcea, 1999). In addition to the formal description of plant communities (i.e. identification of the species in each plant assemblage), gradient analysis of vegetation can be used to investigate how plant assemblages respond to environmental factors, such as gull-driven eutrophication. This type of analysis should be based on appropriate metrics of biotic dissimilarity that enable discrimination of two opposed patterns: replacement of some species by others (i.e. turnover) and overall loss of species (Baselga, 2010).

The AINP includes one of the best representations of cliff vegetation in the NW Iberian Peninsula; in addition, some of the representative species are rare or endemic (Guitián and Guitián, 1990). The plant species are subjected to high levels of environmental stress (e.g. high salinity, strong winds, shallow soils), as well as to pressure from one of the world's largest yellow-legged gull colonies (*Larus michahellis*) (Barros 2015; Otero and Pérez-Alberti 2009). However, many of the factors influencing the distribution and dynamics of coastal plant communities are unknown. Long-term monitoring is used by different researchers and recommended for studies aiming to determine changes in habitats and species (Tilman, 1989; Stohlgren, 1995).

The "ornitheutrophication" (Otero et al., 2018) of marine ecosystems by seabirds is an environmentally important factor that substantially alters floristic diversity and plant community structure in colonies. The impact of faecal deposition by seabirds and other vertebrates (e.g. the Arctic fox) on the vegetation of subarctic ecosystems has been widely

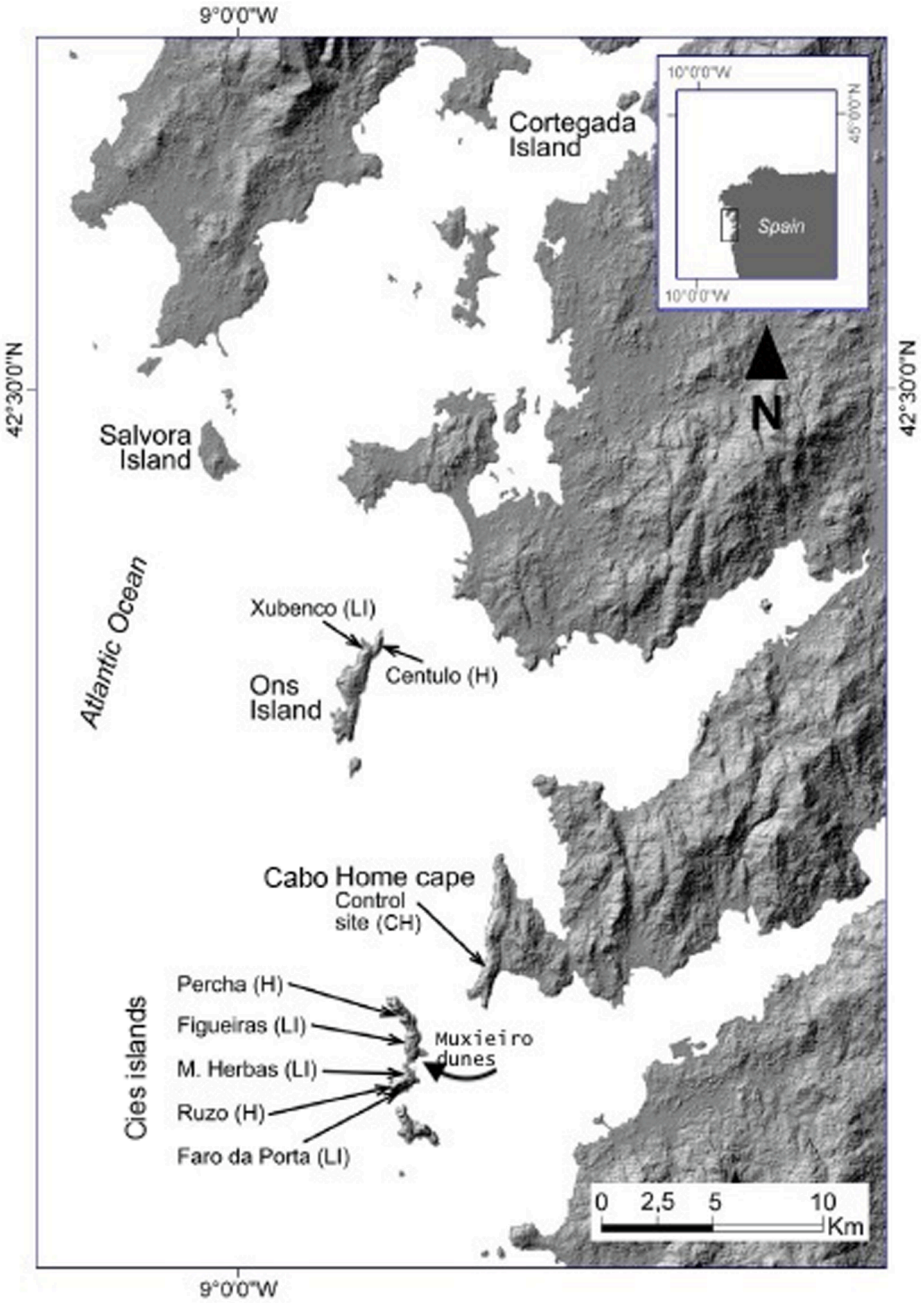


Fig. 1. Location of study plots within the Atlantic Islands of Galicia National Park (NW Spain). H: high seabird influence, LI: low-intermediate seabird influence, CS: no influence.

studied (Zhu et al., 2005; Croll 2005; Ellis et al., 2006; Zmudczyńska-Skarbek et al., 2015; Gharajehdaghipour et al., 2016; Fafard et al., 2019), while fewer studies have been conducted in temperate-humid areas (Sobey and Kenworthy, 1979; Breuning-Madsen et al., 2010; Baumberger et al., 2012; Vidal et al., 2000). In the present study, long-term monitoring of the effect of yellow-legged gull colonies on soils and cliff vegetation was conducted, and the relative importance of the following factors was analyzed by distance-based RDA analysis (dbRDA) of dissimilarity indices discriminating turnover and nestedness components of the variation in plant assemblage: (1) soil properties (pH, electrical conductivity), (2) macronutrient content ($N\text{-}NO_3^-$, $N\text{-}NH_4^+$, and bioavailable P), (3) gull influence (absent, low, intermediate and high density) in different subcolonies in the AINP and in a control site (without gulls)

2. Materials and methods

The Atlantic Islands Natural Park of Galicia (AINP) is located in the NW Iberian Peninsula (Fig. 1). Seven subcolonies of yellow-legged gull located on cliffs of the main archipelagos (Cíes and Ons) and also a control site with no gulls, located on a cliff in Cabo Home, were selected for study. The cliffs were selected on the basis of the distribution of the main plant communities described in previous studies (Arcea, 1999) and gull density (Fig. 2, Table 1, S1). Gull density in the AINP has undergone major variations in recent years: the population in the Cíes Islands decreased from 22,220 breeding pairs in 1991 to 3520 breeding pairs in 2015, while the population in the Ons Islands fell from 3747 breeding pairs in 1991 to 2242 in 2015 (Munilla 1997; Barros 2015; Supplementary Material Table S1).

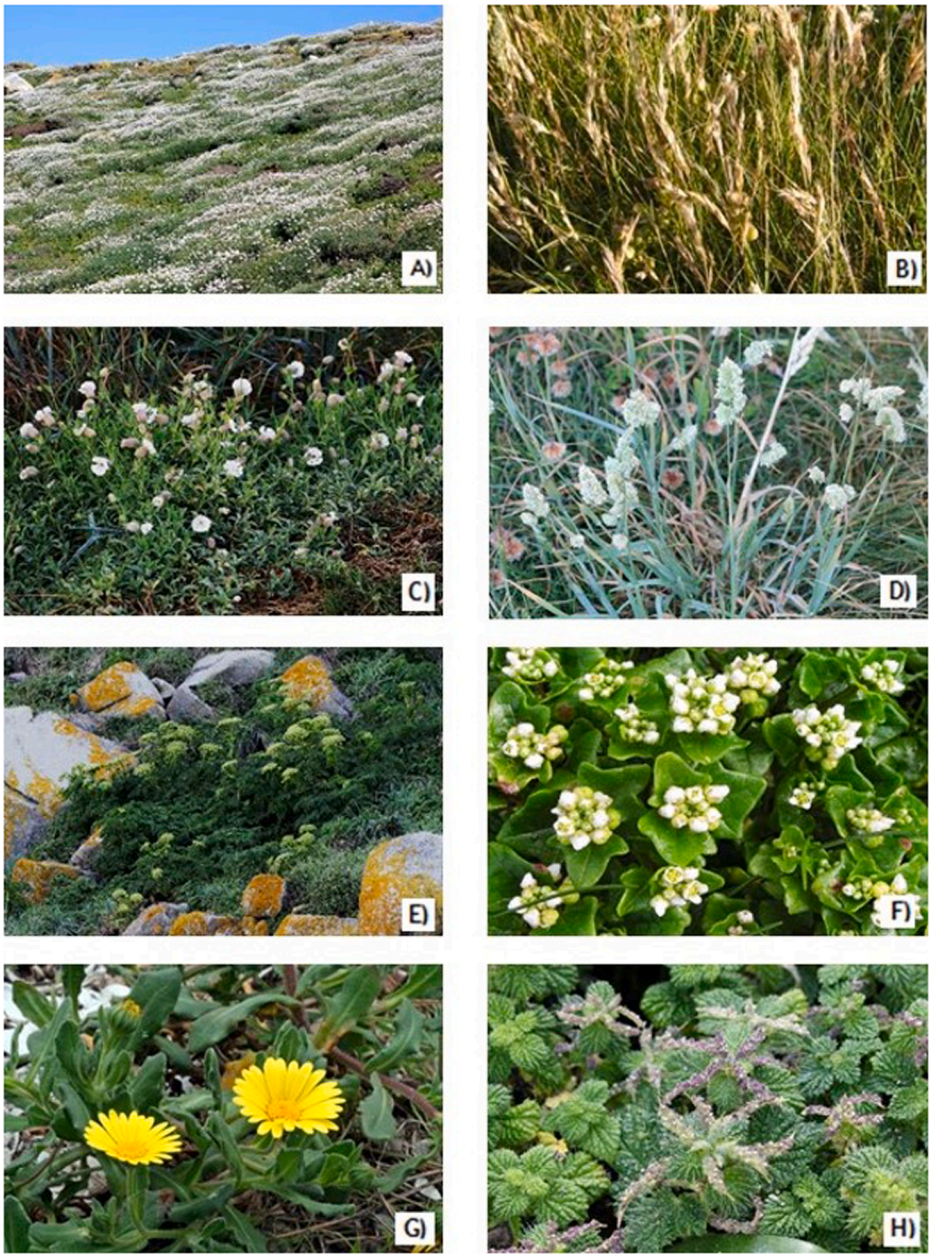


Fig. 2. Characteristic plant species of cliffs in the National Park. Receding species, presumably due to the action of seagulls: (A) *Armeria pubigera* meadow, (B) *Festuca rubra pruinosa*, (C) *Silene uniflora*. Ruderal eutrophic species that are dominant in cliffs with high seagull influence: (D) *Dactylis maritima,* (E) *Angelica pachycarpa*, (F) *Cochlearia danica*, (G) *Calendula suffruticosa algarbiensis*, (H) *Urtica membranacea*.

Table 1
Characteristics of plots in the AINP. The influence of seagulls was established on the basis of the census carried out in 1991 (see Table S2).

Atlantic island of Galicia Natural Park (Spain). Huso 29.					
Plot	Coordinates UTM (XY)	Orientation	Plant association	Representative species**	influence of gulls
Cabo Home (control zone)					
Cabo Home (plot CH)	511270.408 4680186.325	W	Grassland of *Armeria pubigera*	*A. pubigera*	Control plot, without seagulls
Cíes islands					
Monte Herbas (plot MH)	507595.772 4674540.514	N-NE	*Dauco gummnifer-Festucetum pruinosae*	*Festuca pruinosa; Koeleria glauca*	Low (<30 pairs ha^{-1})
Figueiras 1 (plot FIG1)	507,662,000 4675667.000	N-NO	*Cochleario-Matricarietum maritimae*	*Cochlearia danica; Matricaria maritima*	Intermediate (30–100 pairs ha^{-1})
Figueiras 2 (plots FIG2a,b)	507663.946 4675668.334	SW	Grassland of *Dactylis maritima y Silene uniflora*	*Silene uniflora; Dactylis glomerata*	
Faro Porta 1 (plots FP1a,b)	507173.000 4673353.600	S-SW	Grassland of *Armeria pubigera*	*A. pubigera*	High (>100 pairs ha^{-1})
Faro Porta 2 (plot FP2)	507120.000 4673364.000	S	*Calendulo algarbiensis- Parietarietum judaicae*	*Chrithmum maritimun; Calendula algarbiensis*	
Ruzo (plots RZ a,b)	507086.817 4673685.139	S-SW	Grassland of *Holcus lanatus*	*Holcus lanatus; A. pachycarpa*	
Percha Inf. (plot PERINF)	507452.250 4676835.310	N-NW	*Cochleario-Matricarietum maritimae*	*Cochlearia danica; Matricaria maritima*	
Percha Sup. (plot PERSUP)	507468.880 4676710.230	N-NW	Grassland of *Dactylis maritima y Silene uniflora*	*Silene uniflora; Dactylis glomerata*	
Ons Island					
Punta Centulo (plot CENA)	506376.120 4694105.095	N-NE	Community of *Angelica pachycarpa*	*A. pachycarpa*	*No data for 1991
Punta Xubenco (plots PXUB1 a,b)	505646.900 4693728.900	O-NO	Grassland of *Armeria pubigera*	*A. pubigera*	

* According to the guards of the National Park the density should have been Intermediate in Punta Centulo and Low-Intermediate in Punta Xubenco
** Representative species: plant species that give name to the plant association or are present with a high coverage, generally > 20%.

2.1. Sampling, floristic inventories and soil analysis

Soil sampling was performed at three different times a year in the periods 2011–2014 and 2016–2017: (1) February-March, before the gulls returned to the subcolonies; (2) August-September, at the end of the breeding season, i.e. when the impact of the gulls on the soil was maximal; and (3) December-January, after strong precipitation and in the absence of gulls.

One to three permanent sampling plots (7 × 5 m), depending on the environmental conditions of each cliff, were established in each subcolony (total, 14 plots). Targeted sampling was performed in each plot by randomly throwing a 50 × 50 cm metal square into the air 6 to 10 times and sampling within the area delimited by the square on the ground. The (0–15 cm) layer of soil was removed within three such squares and composite surface soil sample was obtained for each plot by mixing the three soil subsamples. The plant species present within each square were also inventoried. Cover of each was determined by the Braun-Blanquet method (1979): cover categories: 1: <10%, 2: 10–25%, 3:25–50%, 4: 50–75% and 5: >75%.

Soil analysis was performed on the fine soil fraction (<2 mm), after careful removal of the coarse plant debris (roots and stems): granulometry was determined by the Robinson pipette method; pH was determined in a soil: water ratio of 1:2.5 (Buurman et al., 1996); electrical conductivity (EC) was measured in a 1:5 soil/water suspension; and total organic carbon (TOC) was analyzed in a Leco CNS1000 autoanalyzer. Exchange cations (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, and Al^{3+}) were extracted using a 1 M NH_4Cl solution (Bertsch and Bloom, 1996), except for Al, which was extracted from 5 g of soil with a 1 M KCl solution. The concentrations of the exchange cations were determined by atomic absorption spectrophotometry (Perkin Elmer model 1100B). Exchangeable ammonium ($N\text{-}NH_4^+$) and nitrate ($N\text{-}NO_3^-$) were extracted from 5 g of fresh soil in 50 ml of a 2 M KCl solution (Mulvaney, 1996). Bioavailable phosphorus (P-ba) was extracted by the Mehlich 3 method (Mehlich, 1984). Briefly, the P-ba fraction was extracted from 2 g of air-dried soil in 20 ml of Mehlich-III solution (2 M CH_3COOH, 0.25 M NH_4NO_3, 0.015 M NH_4F, 0.013 M HNO_3 and 0.001 M EDTA), by first shaking the mixture for 5 min and then filtering it through a n° 42 Whatman filter. The extract was then stored at 3 ± 1 °C until analysis (Mehlich, 1984). The P-bio was determined colorimetrically by the molybdenum blue method, at a wavelength of 800-nm (Bowman, 1988).

2.2. Statistical analysis

In order to determine the impact of the gulls on cliff vegetation in the AINP, a group of 17 plant species were selected for analysis. The selected species had been identified in previous studies as typical of the plant communities on cliffs in the NW Iberian Peninsula or as ruderal (characteristic of disturbed environments) and nitrophilous species (Guitián and Guitián, 1989, 1990; Fernández et al., 2011, Veen et al., 2009). The characteristic and accompanying species in plant communities of cliffs in the NW Iberian Peninsula selected were *Angelica pachycarpa*, *Anthyllis vulneraria iberica*, *Armeria pubigera pubiger*a, *Crithmum maritimum*, *Festuca rubra pruinosa*, *Leucanthemum merinoi*, *Matricaria maritima*, *Plantago coronopus*, *Rumex acetosa biformis*, and *Silene uniflora*, while the ruderal (characteristic of disturbed environments) and nitrophilous species selected were *Calendula suffruticosa algarbiensis*, *Cochlearia danica*, *Dactylis maritima*, *Holcus lanatus*, *Leontodon autumnalis*, *Parietaria judaica*, and *Urtica membranacea*.

Two-way ANOVA was used to compare the influence of gulls (control, colonies) and season (spring, summer, winter) on soil nutrients, acidity and salinity (i.e. electrical conductivity) in the plots. All statistical tests were performed using SigmaStat software version 3.5.

Differences in plant community composition among plots were assessed following the beta diversity partitioning framework developed by Baselga (2010). Pairwise turnover and nestedness components of biotic dissimilarity were computed using the 'beta.pair' command in the R package "betapart" (Baselga and Orme, 2012). Community composition was based on presence/absence data of each plant species in each plot (species-by-site matrix) over the entire study period.

To assess the relationship between environmental variables and plant community composition, turnover and nestedness-resultant dissimilarity matrices were used as response variables in independent

distance-based Redundancy Analysis (db-RDA), which allows the use of non-Euclidean dissimilarity indices (Legendre and Anderson 1999). The mean and standard deviations of environmental variables related to natural gradients (i.e. pH and conductivity) and "ornitheutrophication" gradients (i.e. N-NH_4^+, N-NO_3^- and bioavailable P, P-ba) were first subjected to Principal Component Analysis (PCA) with varimax rotation. Three PCA components, accounting for 76% of the variance, were retained for downstream db-RDA analysis. A manual forward stepwise selection of predictors based on significant contribution to the model ($p < 0.05$) was applied using the 'dbrda' command in the R package "vegan" (Oksanen et al., 2018). Significance was assessed with a permutation test (n = 10,000) with sequential tests for each constraining variable conducted using the 'anova' command in the "vegan" package. When no significant predictors were selected, dissimilarities among plant assemblages were represented by Non-Metric Multidimensional Scaling (NMDS) implemented using the 'metaMDS' command in the "vegan" package.

In order to determine whether differences in plant community composition are related to current and/or historical gull densities, PERMANOVA (Anderson, 2001) was conducted using the turnover dissimilarity matrix, and the nestedness-resultant dissimilarity matrix was used independently as a response variable. The gull densities in 1991 and in 2011 were used as ordered grouping factors. Density levels represented by only one case were excluded from the analysis, resulting in two levels (high and intermediate) for 13 cases in 1991 and two levels (low and intermediate) for 14 cases in 2011. The analysis was conducted using the 'adonis' command in the "vegan" package.

3. Results

3.1. Soil properties and composition

3.1.1. General characterization of soils

Soils in the control site and in gull subcolonies showed limited development (15–25 cm depth). Texture was loamy sand to sandy loam, indicating a clear dominance of the sand fraction, with values over 78%, while silt (11.9 ± 2.8%) and clay (8.3 ± 2.6%) were much less abundant (Table 2, Fig. 3).

Mean organic C content was very high in most sites, exceeding 7% in all cases (Table 2). Regarding the cationic exchange complex, the dominant cation was Ca (mean values: 4.87–21.5 $cmol_{(+)}kg^{-1}$), followed by Mg (3.93–14.5 $cmol_{(+)}kg^{-1}$), Na (2.11–7.81 $cmol_{(+)}kg^{-1}$), and K (0.48–2.23 $cmol_{(+)}kg^{-1}$). Conversely, in almost all samples Al was either below detection limits (DL < 0.01 $cmol_{(+)}kg^{-1}$) or the values were very low (Table 2), which is consistent with pH in water values generally over 5.5 and with the presence of a quartz sand layer fossilizing the granitic substrate. Despite the higher concentrations of Na and Mg in seawater, the dominance of Ca in the soil cation exchangeable complex may be due to the greater affinity of colloids for this cation.

3.1.2. pH and electrical conductivity

The soil pH values were acidic in the control site and subcolonies, with mean values ranging between 5.0 and 7.0 (Table 3, Supplementary Material Table S2); no significant differences were observed between the control zone and the colonies, or between seasons (Table 3). Electrical conductivity ranged from environments with low ionic load to slightly saline environments. The lowest values corresponded to the Percha cliffs (PERSUP: 416 ± 227 μS cm^{-1}; PERINF: 574 ± 329 μS cm^{-1}, Table 3), while the highest mean values were observed in soils from the control site (CH: 1308 ± 1319 μS cm^{-1}, Table 2) and from the PXUB plot, in Ons Island (1060 ± 562 μS cm^{-1}, Table 3). EC differed significantly between the control site and colonies ($F_{1,679} = 54.739$, $p < 0.001$), as well as between seasons ($F_{1,679} = 86.223$, $p < 0.001$, Table 3, Supplementary Material S2), and the values were generally highest in winter.

3.1.3. Inorganic nitrogen in the soil

The concentrations of N-NO_3^- and N-NH_4^+ were significantly lower (N-NO_3^-: $F_{1,679} = 38.234$, $p < 0.001$; N-NH_4^+: $F_{1,679} = 12.555$, $p < 0.001$) in the control site soils (N-NO_3: 16.4 ± 13 and N-NH_4^+: 22.5 ± 18 mg kg^{-1}) than in gull subcolony soils (N-NO_3^-: 43.3 ± 37 and N-NH_4^+: 35.1 ± 33 mg kg^{-1}) (Tables 3, Supplementary Material Table S2). A gradient was identified in the subcolony soils, ranging from high values in sites with stronger gull influence (high density and long history of breeding), such as the Percha, Ruzo and Punta Centulo cliffs, to lower values in lower density and/or more recently established colonies (see also Otero et al., 2015, Table 3 and Supplementary Material Table S2). On the other hand, N-NO_3^- and N-NH_4^+ showed significant seasonal variations (N-NO_3^-: $F_{2,679} = 3.593$, $p = 0.028$; N-NH_4^+: $F_{2,679} = 4.283$, $p = 0.014$), with the lowest values occurring in winter, intermediate values in spring, and the highest values in summer (Table 3, Supplementary Material Table S2).

3.1.4. Bioavailable phosphorus (P-ba)

Mean P-ba concentration was significantly higher ($F_{1,679} = 42.072$, $p < 0.001$) in gull subcolony soils (162 ± 160 mg kg^{-1}) than in the control site (38.3 ± 22 mg kg^{-1}) (Table 3). However, no significant seasonal differences were observed ($F_{2,679} = 0.209$, $p = 0.811$, Table 2). Plot by plot analysis revealed a gradient from sites with the highest to the lowest gull influence, which was consistent with the results obtained for N: CH (control site) <Fig. 2 <MH <Fig. 1 <PERSUP <RZ <PXUB <FP1 <FP2 <PERINF <CENA (Supplementary Material Table S2).

3.2. Flora and vegetation

The total number of vascular plant species was similar across sites. A

Table 2
General characteristics of soils.

	pH	EC	TOC	Ca^{2+}	Mg^{2+}	Na^+	K^+	Al^{3+}
		μS cm^{-1}	%	Exchangeable Cations ($cmol_{(+)}$ kg^{-1})				
CH	5.80 ± 0.6	1308 ± 1319	13.2 ± 5.9	7.67 ± 2.7	11.2 ± 4.3	6.46 ± 2.6	1.62 ± 0.3	0.004 ± 0.007
Cíes islands								
MH	5.65 ± 0.4	726 ± 608	7.83 ± 3.7	4.87 ± 1.3	5.19 ± 1.6	2.82 ± 2.1	0.82 ± 0.6	<LD
FIG1	5.77 ± 0.3	729 ± 247	6.85 ± 1.9	12.8 ± 3.2	8.09 ± 3.5	2.89 ± 1.1	1.54 ± 0.3	0.01 ± 0.01
FIG2	5.98 ± 0.5	602 ± 383	7.27 ± 1.5	7.94 ± 1.9	10.2 ± 3.1	3.28 ± 1.9	1.46 ± 0.3	<LD
FP1	5.87 ± 0.6	1027 ± 572	17.9 ± 6.6	14.4 ± 3.8	14.0 ± 4.0	4.74 ± 2.1	1.43 ± 0.4	0.01 ± 0.02
FP2	6.87 ± 0.3	1051 ± 611	18.3 ± 4.6	17.5 ± 4.1	14.5 ± 4.1	5.81 ± 2.3	1.57 ± 0.8	<LD
PERSUP	5.29 ± 0.4	416 ± 227	15.1 ± 3.7	7.66 ± 3.2	3.93 ± 1.4	2.11 ± 0.9	0.58 ± 0.3	0.05 ± 0.07
PERINF	5.00 ± 0.3	574 ± 329	14.6 ± 3.0	11.0 ± 3.1	12.5 ± 3.4	4.13 ± 1.3	0.48 ± 0.3	0.35 ± 0.4
RZ	5.86 ± 0.5	548 ± 298	12.4 ± 3.2	18.5 ± 5.6	12.8 ± 5.1	4.25 ± 1.9	1.76 ± 0.7	<LD
Ons island								
CENA	5.44 ± 0.6	801 ± 520	17.5 ± 4.4	21.5 ± 7.9	11.7 ± 6.8	3.50±±±2.2	2.23 ± 1.4	<LD
PXUB	5.20 ± 0.5	1060 ± 562	16.0 ± 4.8	11.2 ± 4.8	12.3 ± 6.0	7.81 ± 4.2	2.01 ± 1.1	0.05 ± 0.05

LD: limit of detection. Al limit of detection = 0.01 cmol(+) kg^{-1}. Exchangeable cations (Ca, Mg, Na, K): n = 4; pH and CE (electrical conductivity): n = 60; TOC (Total organic carbon) n = 10. EC: electric conductivity

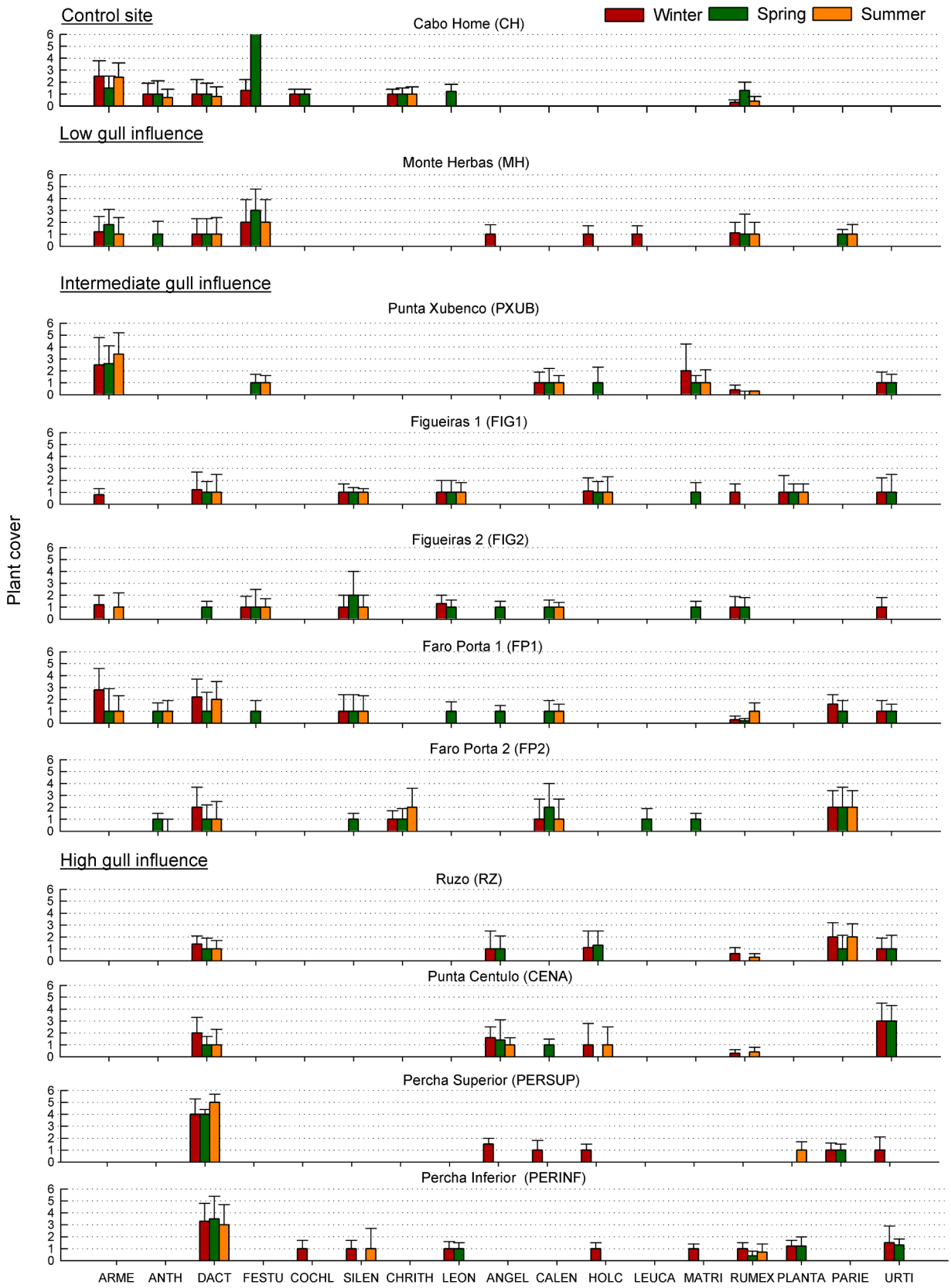


Fig. 3. Seasonal summary of inventories performed in study plots (mean ± SD). Values correspond to plant cover categories according to the phytosociological characterization scale by Braun-Blanquet (1979): 1= <10%; 2 = 10–25%; 3 = 25–50%; 4 = 50–75%; 5 = 75–100%. Characteristic species of plant communities in cliffs in the NW Iberian Peninsula were *Angelica pachycarpa* (Angel), *Anthyllis vulneraria iberica* (Anth), *Armeria pubigera pubigera* (Arme), *Crithmum maritimum* (Crith), *Festuca rubra pruinosa* (Festu), *Leucanthemum merinoi* (Leuca), *Matricaria maritima* (Matri), *Plantago coronopus* (Planta), *Rumex acetosa biformis* (Rumex), 2), and *Silene uniflora* (Silene). Characteristic ruderal (disturbed environments) and nitrophilic species were *Calendula suffruticosa algarbiensis* (Calend), *Cochlearia danica* (Cochl), *Dactylis glomerata maritima* (Dact), *Holcus lanatus* (Holcu), *Leontodon autumnalis* (Leon), *Parietaria judaica* (Parie), and *Urtica membranacea* (Urti).

Table 3
Seabird and seasonal influence on soil properties and nutrient concentrations (mean ± standard deviation, median in brackets) and ANOVA results. Two-way ANOVA results for seabird influence, season and site * season interaction. Statistically significant effects were found for seabird influence and season for each of the dependent variables. For electrical conductivity (EC), the interaction between seabird influence and season showed a statistically significant effect, which indicates that the effect of one factor depends on the status of the other. Significant values are shown in bold.

	seabirds influence		season			Influence	Season	interaction
	Without seabirds (n=72)	With seabirds (n=544)	Spring (n=174)	sum mer (n=185)	Winter (n=254)	*P*		
pH	5.78±0.5 (5.71)	5.69±0.7 (5.72)	5.71±0.7 (5.77)	5.64±0.8 (5.60)	5.74±0.6 (5.73)	0.193	0.675	0.271
EC (μS cm^{-1})	1412±1388 (1005)	730±19 (587)	647±407 (520)	624±557 (438)	1037±861 (752)	**<0.001**	**<0.001**	**<0.001**
N-NH_4^+(mg kg^{-1})	22.5±18 (16.9)	35.1±33 (27.4)	42.3±25 (35.9)	39.6±43 (30.6)	23.5±15 (21.8)	**<0.001**	**0.014**	0.103
N-NO_3^-(mg kg^{-1})	16.4±13 (13.4)	43.3±37 (31.1)	32.8±24 (28.4)	52.1±44 (42.9)	37.3±37 (24.0)	**<0.001**	**0.028**	0.410
P-ba (mg kg^{-1})	38.3±22 (33.0)	162±160 (122)	153±150 (109)	144±192 (88.4)	151±130 (110)	**<0.001**	0.811	0.896

total of 46 plant species were inventoried in the Cíes Islands subcolonies, while 49 species were inventoried in the control (Cabo Home) site and Ons Islands. However, analysis of the different subcolonies revealed substantial changes in floristic composition. Fig. 3 shows variations in plant cover for the 17 most frequent vascular plant species in cliffs within the AINP in relation to seagull influence (Table 1). Cover by the most representative taxa of plant communities in the NW Iberian Peninsula generally decreased as seagull influence increased. In the sites with the highest influence, species such as *Armeria pubigera, Chrithmum maritimum* and *Festuca rubra* are replaced by meadows dominated by the grass *Dactylis maritima* and with the presence of species characteristic of ruderal and eutrophic environments, such as *Urtica membranacea*, *Parietaria judaica, Chochlearia danica, Plantago coronopus* and *Matricaria maritima* (Gillham, 1960; Veen et al., 2009) or megaphorbic formations of *Angelica pachycarpa,* as on north-facing cliffs (e.g. Ruzo in the Cíes Islands, or Punta Centulo in Ons Island) (Otero et al., 2014).

The results obtained for each subcolony in relation to the degree of yellow-legged gull influence are detailed below (see also Supplementary Material Table S3). Note that a subcolony can include more than one plot, depending on the complexity of vegetation.

3.2.1. Site without gull presence

The total number of species in the control site was 29, and higher numbers were recorded in winter (15) than in summer (10). *Armeria pubigera* was the most abundant species (10–25% cover), followed by *Anthyllis vulneraria iberica, Dactylis maritima* and *Festuca rubra pruinosa,* with cover slightly below 10%. *Crithmum maritimum* was occasionally present. Moreover, *Daucus carota gummifer* was also present, while no ruderal or nitrophilous species, such as *Urtica membranacea, Holcus lanatus* or *Parietaria judaica*, were found (Fig. 3).

3.2.2. Sites with low and intermediate gull influence

The diversity and dominance of plant species were highest in plot Fig. 2 (30), followed by FP1 (27), MH (24), PXUB1 and Fig. 1 (22 each) and, finally, FP2 (13). In general, the numbers of different species were highest in spring and lowest in summer (Fig. 3, Supplementary Material Table S3).

Dactylis maritima, Armeria pubigera, Anthyllis vulneraria iberica and *Festuca rubra pruinosa* were the dominant species in plots MH, FP1, and PXUB1. However, the individual cover varied between plots. Thus, for example, in plot PXUB1, *Armeria pubigera* was the most abundant species on these cliffs (mean cover 25–50%), while *Festuca rubra pruinosa* was the most abundant species in plot MH, with cover varying seasonally between 10 and 25% and 25–50%. In plots Fig. 2, FP2 and Fig. 1, the dominant species were respectively *Dactylis maritima* and *Silene uniflora*, *Calendula algarbiensis* and *Parietaria judaica*, and *Cochlearia danica* and *Matricaria maritima* (Fig. 3, Supplementary Material Table S3).

The ruderal species *Urtica membranacea* was present in all the plots in some of the inventories (Supplementary Material Table S3). The invasive grass species *Panicum repens* (GEIB, 2007) also appeared in plot PXUB1.

3.2.3. Sites with high density of gulls

Ruzo (RZ) was the plot with the highest number of species (32), followed by PERINF (26), PERSUP (21) and CENA (15). Similarly to sites with low-intermediate influence, the number of species was highest in spring and lowest in summer (Fig. 3, Supplementary Material Table S3).

Dactylis maritima was present in all plots, with cover reaching 50–100% in PERSUP plot. However, *Parietaria judaica* was the species with the highest cover in plot RZ, and *Holcus lanatus* and *Angelica pachycarpa* were also abundant in RZ and CENA (Fig. 3, Supplementary Material Table S3).

In these plots, *Urtica membranacea* cover was much higher (i.e. it was one of the most abundant species in the plot, with cover generally > 20%) than in sites with low-intermediate influence, with cover even reaching up to 50% (Fig. 3, Supplementary Material Table S3).

3.3. Differences between plots

The environmental variability was summarized in three Principal Components, which accounted for 76% of the variance (Table 4, and Fig. 4). The first PCA component (RC1) was closely correlated with N-NO_3^- and P-ba (explained variance = 35%), while the second and third components were related to EC (i.e. salinity; RC2, explained variance = 22%) and N-NH_4^+ (RC3, explained variance = 19%), respectively.

RC1 and RC2 significantly explained the dissimilarity in plant communities derived from the replacement of some species by others (turnover: dbRDA $F_{2,12} = 4.4$, $p = 0.008$, explained variance = 42.4%), while no predictor was significant according to nestedness-resultant dissimilarity analysis (Fig. 4). In other words, N-NO_3^-, P-ba and electrical conductivity were related to changes in assemblage composition caused by the substitution of some species by others, but not to changes due to species loss. In the turnover analysis, both predictors explained a similar amount of variance, showing that their contribution to structuring plant assemblage composition was similar: RC1 (dbRDA $F_{1,12} = 4.8$, $p = 0.010$) explained 23.1% of the variance and RC2 (dbRDA $F_{1,12} = 4.0$, $p = 0.038$) explained 19.4% of the variance. Analysis of the turnover component of beta diversity revealed a historical signature, as

Table 4
Principal Component Analysis (PCA) loadings and explained variance. Varimax rotation was applied to PCA components. Loadings > 0.80 are shown in bold.

	RC1	RC2	RC3
pH	0.603	0.203	0.103
pH (SD)	0.257	0.523	−0.280
EC	0.076	**0.948**	0.200
EC (SD)	−0.130	**0.959**	0.011
NH_4^+	0.310	−0.051	**0.845**
NH_4^+ (SD)	0.286	0.113	**0.891**
NO_3^-	**0.867**	−0.136	0.298
NO_3^- (SD)	**0.804**	−0.145	0.402
P bioavailable	**0.826**	0.122	0.207
P bioavailable(SD)	**0.885**	0.077	0.068
Explained variance	35	22	19

EC: electrical conductivity; SD: standard deviation.

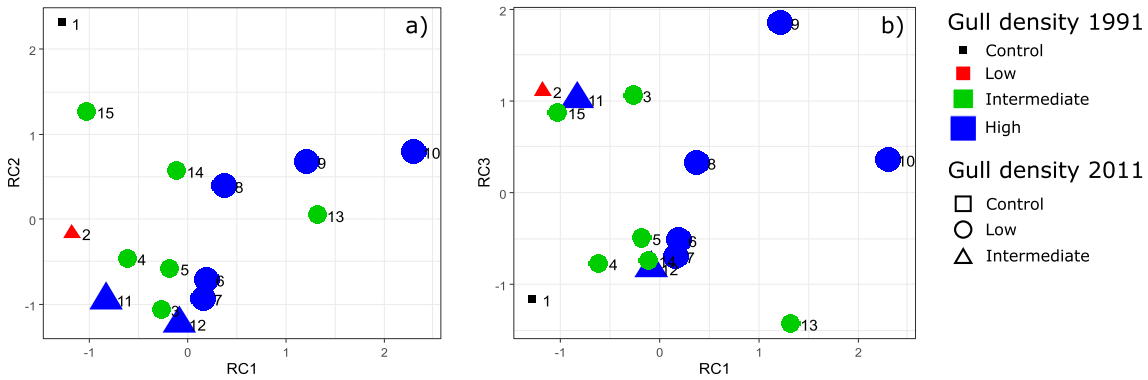


Fig. 4. Ordination (PCA) of sampling plots according to the environmental variables, as summarised by the Principal Component axes: RC1 and RC2 (a) and RC1 and RC3 (b). The first PCA component (RC1) was highly correlated with N-NO_3 and P-BIO, the second PCA component (RC2) with electric conductivity (i.e. salinity) and the third PCA component (RC3) with N-NH_4 (RC3). Size colour represent gull density levels in 1991: control (black), low (red), intermediate (green) and high (blue). Symbol shape represents gull density levels in 2011: control (square), low (circle), intermediate (triangle). An interactive 3D-scatterplot of PCA scores can be also found in Supplementary Material. Site numbers are: 1) Cabo_Home (CH; control plot), 2) Monte das Herbas (MH), 3) Figueiras-1 (Fig. 1), 4, 5) Figueiras 2 (Fig. 2) 6,7) Ruzo (RZ), 8,9) Faro da Porta 1 (FP1) 10) Faro da Porta 2(FP2), 11)Percha inferior (PERINF), 12)Percha Superior (PERSUP), 13) Punta Centulo (CENA), 14, 15) Punta Xubenco (PXUB). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

plant assemblages could be grouped according to gull density in 1991 (PERMANOVA $F_{1,11} = 4.82$, $p = 0.024$; $R2 = 0.30$, Fig. 5), although the results were not significant for gull density levels in 2011 (PERMANOVA $F_{1,12} = 2.41$, $p = 0.179$). No significant results were observed in the case of the nestedness-resultant component (density 1991: PERMANOVA $F_{1,11} = -0.86$, $p = 0.979$; density 2011: 371 PERMANOVA $F_{1,12} = 1.76$, $p = 0.22$).

4. Discussion

4.1. Soil ornitheutrophication

Seabirds establish breeding colonies in areas of land such as cliffs and other coastal formations, in some cases reaching high densities. The continued presence of large numbers of individuals in the same space strong alters the original characteristics of the habitat (Sobey and Kenworthy, 1979; Hahn et al., 2007; Zwolicki et al., 2016). The eutrophication gradient associated with bird colonies (ornitheutrophication) explains the observed variation in plant communities, with replacement of some species by others depending on the concentration of N-NO_3^- and bioavailable P in soil. Overall, the results showed that the presence of yellow-legged gull colonies in the AINP led to ornitheutrophication, with high concentrations of inorganic N and bioavailable P but not to salinization, which has been observed in Mediterranean colonies (García et al., 2002). The high levels of precipitation in the AINP (1419 mm; De La Peña-Lastra et al., 2019) favour leaching of salt from the soils (Otero et al., 2015).

Numerous studies have associated nitrogen enrichment with the loss of plant species diversity in temperate terrestrial ecosystems (e.g. Moore et al., 1989; Wheeler and Shaw, 1991; Stevens et al., 2004); for this reason, many authors refer to the species present in these environments as nitrophilous (Gillham, 1977; Hogg and Morton 1983). Our results also show a clear inorganic N enrichment. However, the effect of P on plant diversity has seldom been considered. In a study performed along a P gradient, Wassen et al. (2005) showed that many more endangered plant species persist under phosphorus-limitation than under nitrogen-limitation and concluded that phosphorus enrichment is more likely to be the cause of species loss than nitrogen enrichment. Our findings are

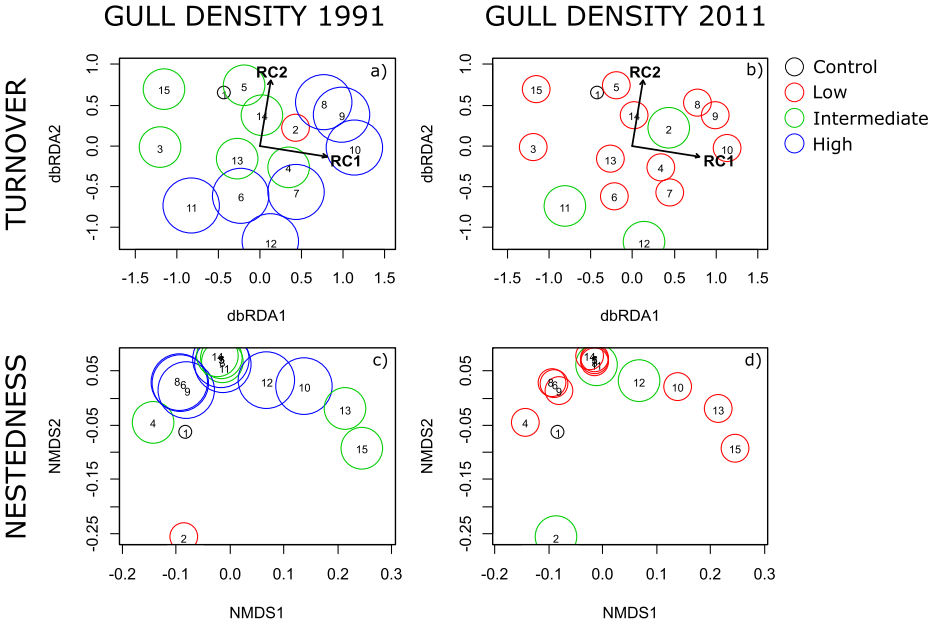


Fig. 5. Ordination (db-RDA) of sampling sites according to their plant species composition. Two separate ordinations were performed to describe the variation in plant communities due to the turnover (a, b) and nestedness-resultant (c, d) components of dissimilarity. Therefore, distances in the ordination space in (a, b) reflect the substitution of plant species between sites, while distances in the ordination space in (c, d) reflect richness differences in nested subsets between sites. Significant PCA correlates are shown for the turnover component (a, b) while for the nestedness component (c, d) no significant predictor was found in the distance-based RDA analysis, and hence a Non-Metric Multidimensional Scaling is used to represent the ordination of sampling sites. Size and colour represent gull density in 1991 (a, b) and 2011 (c, d). Site numbers are: 1) Cabo_Home (CH; control plot), 2) Monte das Herbas (MH), 3) Figueiras 1 (Fig. 1), 4, 5) Figueiras 2 (Fig. 2) 6,7) Ruzo (RZ), 8,9) Faro da Porta 1 (FP1) 10) Faro da Porta 2(FP2), 11)Percha inferior (PERINF), 12)Percha Superior (PERSUP), 13) Punta Centulo (CENA), 14, 15) Punta Xubenco (PXUB).

consistent with this idea. A major portion of N is leached from subcolony soils during the winter; therefore, in some subcolonies in the AINP, inorganic N content in early spring was observed to be similar to that in the control site (Otero and Fernández-Sanjurjo, 1999; Otero and Mouriño, 2002). However, the total P content (summer, 815 ± 189 mg kg^{-1} and winter, 1133 ± 194 mg kg^{-1}: Otero et al., 2015) and bioavailable P in soil remain high throughout the annual cycle as P is adsorbed to Fe and Al oxyhydroxides in acid soils (for further details, see Otero et al., 2015). In this respect, P enrichment in seabird colony soils is an irreversible process, with high concentrations of P persisting thousands of years after colony extinction (see Hawke et al., 1999; Sun et al., 2000; Otero et al., 2015). In addition, our results show that P bioavailability did not vary throughout the annual cycle (Tables 3 and S2), while inorganic N decreased significantly in winter (Table S2). Therefore, P should be considered a key geochemical factor in the mechanisms leading to changes in plant communities, and the species associated with colony soils should be termed "eutrophic vegetation" or "eutrophic plants" (Nagy and Proctor, 1997; Rotha et al., 2013) rather than nitrophilous plants, as they are usually referred to in the literature.

4.2. Effect of gull colonies on plant biodiversity and vegetation structure

Plant communities on cliffs in the NW Iberian Peninsula are arranged in strips that run approximately parallel to the coast according to their tolerance to salinity, wind-related effects and soil development (Guitián and Guitián, 1990; Fernández et al., 2011). However, this distribution is greatly altered in yellow-legged gull colonies within the AINP.

The control site corresponds to the *Crithmo maritimi-Armerietum pubigerae* association, a formation that typically occupies the lower section of cliffs in the NW Iberian Peninsula. This association is characterized by the presence of halochasmophytic herbaceous plants such as *Chrithmum maritimum*, *Armeria pubigera* and *Anthyllis vulneraria iberica*. This association persists on cliffs with a low influence of gulls, such as FP in the Cíes Islands and PXUB in the Ons Islands, although there are some changes in terms of the floristic composition and structure (Figs. 3 and 4). These differences manifest as lower levels of cover by species characteristic of this association and a higher variability in floristic inventories. The most relevant floristic aspects are the absence of *Daucus carota gummifer* and the presence of eutrophic and ruderal species (e.g. *Matricaria maritima, Parietaria judaica* or *Urtica membranacea;* Guitián and Guitián, 1990; Arcea, 1999). For these reasons, the assemblage could be considered a facies of the *Crithmo-Armerietum pubigerae* association, although more detailed studies are necessary to confirm this.

The *Dauco gummiferi-Festucetum pruinosae* association occupies the middle section of the slope, where some incipient soil formation is occurring. This herbaceous plant formation is mainly dominated by *Festuca rubra pruinosa,* with 75–100% cover, and *Daucus carota gummifer, Rumex acetosa biformis* and *Armeria pubigera,* with 10–25% cover (Rivas-Martínez, 1978; Fernández Prieto and Loidi, 1984). The most similar vegetation to this formation can be found in cliffs in the AINP such as Monte das Herbas (MH), a site with low to intermediate influence of gulls and corresponding to a recently established gull colony (≈30 years; Tables 1, S1) with low bird density (Munilla, 1997; Arcea, 1999). In this case, differences relative to the typical association manifest as lower cover by the species that define the association, the absence of *Daucus carota gummifer* and *Jasione gallaecica* and the presence of ruderal and eutrophic species (e.g. *Parietaria judaica*, *Urtica membranacea* and *Cochlearia danica*, Fig. 3).

The remaining cliff sites with intermediate to high gull influence showed a marked transformation in terms of floristic composition and structure of the vegetation relative to the typical associations on cliffs in the NW Iberian Peninsula. These differences were closely correlated with P-ba and $N\text{-}NO_3^-$ contents in soil and can therefore be attributed to the effect of subcolonies (Fig. 4). However, no pattern or gradient could be established for the effect of gulls on plants and vegetation in the AINP, possibly because the effect is due to the current and also the past presence of gulls on cliffs (see also Young et al., 2010; Baumberger et al., 2012; Magnússon et al., 2014), along with more local factors such as cliff slope and orientation (Guitián and Guitián, 1989). In this respect, Barcena et al. (1987) first referred to changes in plant communities in gull colonies within the AINP. This author observed that *Silene uniflora* meadows had been substituted by *Angelica pachycarpa* formations in northern cliffs of Monteagudo Island. Guitián and Guitián (1989) described new endemic haloornithocoprophilic communities (e.g. *Calendulo algarbiensis-Parietarietum judaicae, Cochleario danicae-Matricarietum maritimae* and *Angelica pachycarpa)* and assumed a nitrifying effect by gulls. More recently, Arcea (1999) tried to establish a pattern in the distribution of plant communities, taking into account the presence of seagulls as well as other environmental parameters, such as cliff orientation. However, the study findings did not enable a clear relationship among these factors to be established.

The distribution of plant species along this $N\text{-}NO_3^-$ and bioavailable P gradient in the soil reveals niche segregation (Fig. 5). Changes in nutrient availability affect interspecies competition, given that those species that can rapidly respond to increases in nutrients have a competitive advantage over species typical of oligotrophic environments (Hill et al., 2011; Tilman, 1986). Thus, in this case, species with a high resistance to environmental stressors (salinity, wind etc.) but a low tolerance to nutrient contributions, such as *Armeria pubigera, Festuca rubra pruinosa, Anthyllis vulneraria iberica* and *Crithmum maritimum* (Jefferies and Perkins, 1977; Kiehl et al., 1997; Otero et al., 2018), are replaced by species that are efficient users of $N\text{-}NO_3^-$ and bioavailable P (*Angelica pachycarpa, Holcus lanatus, Parietaria judaica,* and *Urtica membranacea*) (Zelenskaya and Khoreva, 2006; Critchley et al., 2002; Castroviejo, 1986–2012).

These findings are consistent with those of previous studies in which N, P, and K enrichment in soils of *Larus argentatus* colonies were found to lead to the replacement of native perennial meadows mainly composed of *Festuca rubra* by a pauci-specific plant community dominated by annual ruderal species such as *Atriplex hastata, Holcus lanatus, Poa annua, Rumex acetosa, R. crispus, Stellaria media* and *Tripleurospermum maritimum* (Sobey and Kenworthy, 1979). Likewise, Hogg and Morton (1983) observed the same phenomenon in ring-billed gulls (*Larus delawarensis*) in the Great Lakes (Canada). More recently, Baumberger et al. (2012) also observed ruderalization of vegetation in areas with high densities of yellow-legged gull (*Larus michahellis*) and found that lower densities of nests did not necessarily lead to the restoration of previous plant composition patterns. In the present study, the percentage of ruderal species ranged between 10% and 25% and was particularly high in those colonies with higher densities of yellow-legged gulls, as in Punta Centulo (CENA (in the Island of Ons), Percha (PERSUP, PERINF) and Ruzo (RZ) (in the Cíes Islands). Similar values have been observed in colonies in King George Island (Maritime Antarctic), where 25% of vascular plant species were found to be significantly associated with ornithogenic fertilization (Zwolicki et al. 2016). Moreover, these authors also observed that increases in nutrients led to a decrease in cover by some species, while eutrophic species such as *Prasiola crispa* became dominant.

4.3. Implications for management and research

Seabird colonies cause dramatic changes in plant communities, with native plants being replaced by new ruderal plant formations that are still poorly characterized. Soil ornitheutrophication is one of the factors explaining the observed changes in yellow-legged gull subcolonies. For approximately the last 15 years, yellow-legged gulls have been establishing new colonies within the AINP in areas considered of high environmental value due to the presence of rare or endemic species such as *Corema album*, *Iberis procumbens* and *Armeria pungens* (e.g. in the dunes of Punta Muxieiro and Rodas). For this reason, future efforts should be aimed at reducing the bioavailability of these two nutrients for a stronger focus on conservation management. In dune systems, the

combined addition of N and P has been observed to cause a decrease or even the disappearance of characteristic pioneer dune species and mosses (Lammerts and Grootjans, 1999).

For the above reasons, conservation of the aforementioned taxa and of priority habitats 2130 –Fixed coastal dunes with herbaceous vegetation ("grey dunes") and 2120 – Shifting dunes along the shoreline with *Ammophila arenaria* ("white dunes") within the AINP may be compromised if appropriate management measures are not implemented. The measures adopted should take into account the direct effect of gulls on plants (e.g. uprooting for building nests; trampling) as well as the bioavailability and mobility of N and P in dune system soils. In fact, the waters of the Nenos lagoon, in the Cíes Islands, currently show clear symptoms of eutrophication, which may have been one of the causes of the disappearance of the *Zostera marina* meadow approximately 15 years ago (for more details, see Otero et al., 2015).

5. Conclusions

Yellow-legged gull colonies are powerful environmental modulators that have greatly altered nutrient biogeochemical cycles in soils and floristic composition of plant communities on cliffs in the AINP.

Colony soils are significantly enriched in nutrients (inorganic N and bioavailable P), and therefore use of the term "eutrophic plant species" is probably more accurate than the commonly used "nitrophilous species".

Yellow-legged gull colonies have irreversibly transformed the cliff vegetation, generating a new environmental system that is exclusive to this National Park and which has not yet been well defined. Species whose presence seems to be favoured by the influence of seabirds include *Angelica pachycarpa, Holcus lanatus, Parietaria judaica* and *Urtica membranacea*, while *Armeria pubigera, Festuca rubra pruinosa, Anthyllis vulneraria iberica* and *Crithmum maritimum* seem to be receding in areas that are intensely impacted by gulls.

Finally, the colonization of new areas with a high environmental value, such as the Punta Muxieiro dunes, could substantially alter this habitat, classified as priority habitat due to its plant diversity, according to European Directive 92/43/CEE.

Authors' Contributions

SPL, XLO, and APA conceived and designed the study and performed the research; FT, CG-R, SPL and XLO carried out the statistical analysis; SPL, CG-R, AG and XLO wrote the paper with the collaboration of FT and APA.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors thank the authorities and guards at the Atlantic Islands National Maritime-Terrestrial Park for providing support during fieldwork. This work was financed by a 2016 Leonardo Grant for Researchers and Cultural Creators, the BBVA Foundation, the Autonomous National Parks Organization of the Spanish Ministry for the Environment, Rural and Marine Affairs (Ref. 041/2010) and the Consellería de Educación, Universidade e Formación Profesional-Xunta de Galicia (Axudas á consolidación e estruturación de unidades de investigación competitivas do SUG del Plan Galego IDT, Ambiosol Group, ref. 2018-PG036). Saúl de La Peña was in receipt of a predoctoral fellowship from the FPU Program of the Spanish Ministry of Education and Innovation. Thanks are also due to María José Santiso, for assistance with laboratory work, and to Esther Sierra Abraín, Pablo Montero and Adrián González, for help with sampling.

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