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Factors influencing small-scale distribution of 10 macrolichens in King George Island, West Antarctica

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Abstract Lichens are among the main primary colonists in most terrestrial ecosystems of Antarctica, where the effects of environmental factors on spatial distribution of lichens are essential to understanding the functioning of Antarctic terrestrial ecosystems. We measured abundance of 10 frequently observed macrolichens and 15 environmental factors at a small scale (20 cm× 20 cm), in the ice-free areas of Fildes Peninsula and Ardley Island, King George Island, West Antarctica, and assessed the effects of environmental factors on the local distribution of these lichens. Canonical correspondence analyses (CCA) show that 8 out of 15 environmental factors, belonging to 4 sets of variables, are important in spatial distribution of the 10 lichens. Variation partitioning analyses show that most of the variation in distribution of the 10 lichens is described by the spatial heterogeneity of substrate, bird influence and microclimate and topography, whereas human impact has no significant effects.

Keywords **bird disturbance, canonical correspondence analysis, lichen ecology, maritime Antarctica, soil accumulation**

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0 Introduction

Lichens are widespread in diverse environments all over the world, due to their high ability to survive environmental extremes. They are among the primary colonists of Antarctic terrestrial ecosystems[1-2], and make up significant components of Antarctic vegetation[3]. They play important roles in biotic weathering of rocks and soil formation[4-8] and nutrient cycling processes[2], and provide suitable habitats for other organisms, such as mite and tardigrade species[3,9]. They also serve as reliable bio-monitors for evaluating global atmospheric transport and deposition of atmospheric contaminants[10-15].

In King George Island, 62 species were reported near the Korean Antarctic Scientific Station[16], and 104 taxa near the Polish Arctowski Station[17]. They occupy a wide range of diverse habitats due to their different responses to environmental factors[18]. Although the general ecology and distribution of these lichens have been described[3,16,19], factors influencing the distribution of these species need further study to better understand the mechanisms that govern the structure, function and dynamics of Antarctic terrestrial ecosystems. This is especially important under increasing human activity, which has been reported in King George Island to potentially impact diversity of local species, such as penguins[20].

The aims of this study are to quantify and test the relative effects of environmental factors and human impact on the cover of the 10 macrolichens in Fildes Peninsula and Ardley Island. These lichens were chosen because they are common in the investigated microhabitats, are easily identified in the field, and thus can be useful in elucidating the major factors influencing spatial distribution of lichens. The 10 macrolichens are *Caloplaca regalis*, *Cladonia borealis*,

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Himantormia lugubris, *Placopsis contortuplicata*, *Ramalina terebrata*, *Sphaerophorus globosus*, *Stereocaulon alpinum*, *Umbilicaria antarctica*, *Usnea antarctica* and *Us. aurantiacoatra*.

1 Materials and methods

1.1 Study area

The investigation was carried out in two localities of Antarctic Specially Protected Areas (ASPA): Fildes Peninsula (ASPA no. 125) and Ardley Island (ASPA no. 150). Both localities are situated in the southwestern part of King George Island (63°23′S, 57°00′W), South Shetland Islands, West Antarctica. Fildes Peninsula (62°12′S, 58°58′W) is 10 km long and 5 km wide. Ardley Island (62°13′S, 58°56′W), 2.0 km long and 1.5 km wide, is situated about 500 m east of the coast of Fildes Peninsula. They are in the maritime Antarctic region and are characterized by an oceanic climate with an average annual temperature of −2.5°C and the annual precipitation of 500 mm rainfall equivalent, falling as both rain and snow. High air humidity is maintained throughout the year, amounting on average to about 80%[17]. The topography is hilly with the highest peak no more than 200 m above sea level. The hills are largely free of snow and ice during the austral summer, and the vegetation is mainly dominated by lichens, mosses, algae, and cyanobacteria. Two species of phanerogams, *Colobanthus quitensis* (Caryophyllaceae) and *Deschampsia antarctica* (Poaceae), are sporadic in distribution and confined to patches with soil.

1.2 Field investigation

Field work was conducted in the 2009/2010 austral summer. A total of 360 plots each measuring 20 cm×20 cm, over an altitude gradient varying from sea level up to 200 m, were selected in various habitats to include as many of the potential microhabitats as possible. All plots contained at least one of the selected target species. These lichens were not found in the rivulets and marshy areas dominated by mosses[21], and so these habitats were not included in the investigation.

Percentage of lichen cover was estimated in each plot using the Braun-Blanquet method[22], adapted to Antarctic conditions[23-24]. Fifteen variables in 4 sets were recorded simultaneously in each plot (Table 1).

Table 1 Measured variables and the results of Monte Carlo permutation tests

Sets		Variables				Monte Carlo permutation results	
Name	Abbr.	Name	Abbr.	Units	Data type	*F*	*p*!
Microclimate and topography	{C}	Distance from ground	DG	cm	Continuous	10.56	0.000 5*
		Distance from coast	DC		Factor (1–3)	8.53	0.000 5*
		Water availability	WA		Factor (1–3)	2.53	0.017 0
		Light availability	LA		Factor (1–3)	1.79	0.080 5
		Altitude	Alt	m	Continuous	1.13	0.325 3
		Slope	Slo		Continuous	0.79	0.979 0
Substrate	{S}	Soil cover	SC	%	Continuous	41.22	0.000 5*
		Moss cover	MC	%	Continuous	8.52	0.000 5*
		Soil depth	SD	cm	Continuous	3.23	0.004 5*
		Rock size	RS	cm	Continuous	2.12	0.038 0
		Substrate roughness	SR		Factor (1–2)	1.35	0.200 4
Bird influence	{B}	Distance from bird excrement	DBE		Factor (1–3)	36.10	0.000 5*
		Distance from bird nest	DBN		Factor (1–3)	4.47	0.000 5*
Human impact	{H}	Distance from the closest road	DCR	m	Continuous	3.05	0.006 0*
		Distance from the nearest station	DNS	m	Continuous	0.99	0.423 3

Notes: "!" denotes the significant levels are Bonferroni-corrected (0.05/number of variables) and therefore different between sets of variables. "*" denotes that a specific variable is statistically significant at a Bonferroni-corrected significance level. The Monte Carlo permutation test was separately applied to each set of variables.

The microclimate and topography set {C} included 6 variables: (1) distance from ground (DG) representing the height of the substrate surface occupied by lichens; (2) distance from the coast (DC: 1=0–30 m (mostly dominated by rocks, with highest bird influence and high coverage of ornithocoprophilous lichens), 2=31–100 m (dominated by rocks with soil among rocks, and high bird influence but relatively lower coverage of ornithocoprophilous lichens), 3⩾100 m (environmentally diverse, with lowest bird influence and lowest coverage of ornithocoprophilous lichens)); (3) water availability (WA: 1=exposed with little capability to sustain water, 2=high capability to remain moist, 3=keeps moist over days); (4) light availability (LA: 1=exposed, 2=in cleft with most of the day in shadow, 3=completely sheltered); (5) altitude (Alt) measured using an altimeter; and (6) slope (Slo) angle.

The substrate set {S} had 5 variables: (1) soil cover (SC); (2) moss cover (MC); (3) soil depth (SD); (4) rock size (RS); (5) substrate roughness (SR) on an ordinal scale from 1 to 2 (1=smooth, 2=rough).

The bird influence set {B} consisted of distance from bird excrement (DBE: 1=0–2.0 m, 2=2.1– 5.0 m, 3⩾5.0 m; the thresholds were determined according to the distribution of lichens) and distance from bird nest (DBN: 1=0–5 m, 2=5.1–20 m, 3⩾ 20 m; the thresholds were determined according to the degree of bird trampling and distribution of lichens). The human impact set {H} consisted of distance to the closest road (DCR) and distance to the nearest station (DNS).

1.3 Statistic analyses

The computer program CANOCO 4.5 was used for all ordinations[25]. Detrended correspondence analysis (DCA) was used to estimate the amount of compositional turnover in standard deviations. Because the gradient length of the first DCA axis was 4.667 SD, canonical correspondence analysis (CCA) is therefore the appropriate method for these data[25-26].

Ten species, 360 plots and 4 variable sets consisting of 15 variables were subjected to a CCA analysis. The abundance data for each species, and continuous data were log-transformed, and rare species were downweighted. Diagrams were drawn in CanoDraw[25]. Biplot scaling with a focus on inter-species distance was used, and default settings were accepted in the rest of the analysis.

A set of sequential Monte Carlo permutation tests were separately applied to each variable set, under full model with the number of permutation=2 000, to test the significance of variables to be included in the model. The significance levels were corrected by a Bonferroni correction, which is a quotient of the desired overall significance level (α=0.05) divided by the number of variables. The significant explanatory variables were first subjected to a CCA analysis, then a Partial CCA with variation partitioning was conducted to estimate the proportions of variation in the species data explained by single sets of variables, and shared variation between the variable sets.

The selected variables were further subjected to an unrestricted Monte Carlo permutation test to determine which variables could potentially explain a significant amount of species/plot distribution along each CCA axis. The impact size of variables was estimated by comparing their correlations with axes[26]. Those variables with larger correlation coefficient have greater impact on the CCA axis. The t-value is regarded as an approximate guide and the critical value of significance at p=0.05 was set to 2.0[27]. Those variables with larger t-values than the critical value were regarded as significant in explaining the species/plot dispersion along the CCA axis under discussion.

2 Results

The Monte Carlo permutation tests applied separately to each set of variables show that the following 8 variables in the 4 sets can be included in the CCA analyses: DG and DC in {C}; SC, MC and SD in {S}; DBE and DBN in {B}; and DCR in {H} (Table 1). The other 7 variables were excluded because they were not significant in explaining the dataset (Table 1). The first four CCA axes are statistically significant (p = 0.000 5) and reflect 20.4% of species variation (Table 2).

Table 2 Summary of CCA analysis

	CCA axes			
	1	2	3	4
Eigen values	0.321	0.101	0.027	0.014
Species-environment correlations	0.767	0.482	0.353	0.242
Cumulative percentage variance of species data	14.1	18.5	19.7	20.4
Cumulative percentage variance of species-environment relation	67.7	89.1	94.8	97.8
Sum of all eigen values	2.275			
Sum of all canonical eigen values	0.474 (F = 11.541, p = 0.000 5)			

Notes: Eight explanatory variables were included in the analysis (Table 1).

2.1 Variation explained by the sets of explanatory variables

2.1.1 Pure variation

Variation partitioning shows that the pure bird influence variation [B|(C∪S∪H)] (that is the amount of variation explained by the bird influence set {B} along, but not shared with any other variable sets) is statistically significant. This is also true for the pure microclimate and topography variation [C|(S ∪ B ∪ H)], and the pure substrate variation [S|(C∪B∪H)]. The pure human impact variation

[H|(C∪S∪B)] is not statistically significant (p = 0.222; Table 3).

The largest faction of total variation explained (FTVE) by a single variable set when effects of other variable sets are excluded, is the pure substrate variation (FTVE=38.0%, Table 3, Figure 1), followed by the pure bird influence variation (FTVE=23.2%, Table 3, Figure 1) and microclimate and topography variation (FTVE=7.2%, Table 3, Figure 1). Only 1.5% of total variation explained (TVE) is attributable to the human impact variable set (Table 3, Figure 1).

2.1.2 Shared variation

The 4 sets of explanatory variables share variation (Figure 1). The largest shared variation is pooled between {S} and {B} (FTVE=21.1%), followed by variations shared by {C} and {B} (FTVE=13.9%), and {C} and {S} (FTVE= 12.9%, Figure 1).

When considering pure variation plus shared variation (that is the amount of variation explained by a single set of explanatory variables, with effects of other variable sets being included) {S} explained 63.3% of TVE, followed by {B} (49.4%) and {C} (24.7%). {S} and {B} together explained 91.6% of TVE. However, {H} explained 4.0% of TVE, and the variation was not statistically significant (Table 3, Figure 2).

Table 3 Partitioning of variation in distribution of the 10 lichens on 4 sets of variables

	Variation explained				Remarks
	VE	*F*	*p*	FTVE /%	
C	0.117	9.654	0.000 5*	124.7	Variation explained by {C}, shared with other sets of variables
S	0.300	18.050	0.002 0*	63.3	Variation explained by {S}
B	0.234	20.456	0.002 0*	49.4	Variation explained by {B}
H	0.019	3.048	0.004 0	4.0	Variation explained by {H}
C|(S∪B∪H)	0.034	3.342	0.002 0*	7.2	Variation purely explained by {C}, not shared with other variable sets
S|(C∪B∪H)	0.180	11.660	0.002 0*	38.0	Purely by {S}
B|(C∪S∪H)	0.110	10.733	0.002 0*	23.2	Purely by {B}
H|(C∪S∪B)	0.007	1.379	0.222 0	1.5	Purely by {H}
C∪S	0.356	13.117	0.002 0*	75.1	Explained by {C} and {S}, shared with other sets of variables
C∪B	0.285	12.711	0.002 0*	60.1	Explained by {C} and {B}
C∪H	0.127	7.010	0.002 0*	26.8	Explained by {C} and {H}
S∪B	0.434	16.676	0.002 0*	91.6	Explained by {S} and {B}
S∪H	0.318	14.398	0.002 0*	67.1	Explained by {S} and {H}
B∪H	0.242	14.097	0.002 0*	51.1	Explained by {B} and {H}
(C∪S)|(B∪H)	0.232	9.052	0.002 0*	48.9	Purely by {C} and {S}, not shared with other sets of variables
(C∪B)|(S∪H)	0.156	7.612	0.002 0*	32.9	Purely by {C} and {B}
(C∪H)|(B∪S)	0.040	2.606	0.002 0*	8.4	Purely by {C} and {H}
(B∪S)|(C∪H)	0.347	13.521	0.002 0*	73.2	Purely by {B} and {S}
(H∪S)|(B∪C)	0.189	9.197	0.002 0*	39.9	Purely by {H} and {S}
(B∪H)|(C∪S)	0.118	7.678	0.002 0*	24.9	Purely by {B} and {H}
(C∪S∪B)|H	0.455	12.656	0.002 0*	96.0	Purely by {C}, {S} and {B}, not shared with {H}
(C∪S∪H)|B	0.240	7.792	0.002 0*	50.7	Purely by {C}, {S} and {H}
(C∪B∪H)|S	0.173	6.760	0.002 0*	36.5	Purely by {C}, {B} and {H}
(S∪B∪H)|C	0.357	11.597	0.002 0*	75.3	Purely by {S}, {B} and {H}

Notes: Abbreviations for the sets of variables are given in Table 1; VE, variation explained; FTVE, fraction of total variation explained. The symbol "∪" stands for unions, while "|" indicates "without". "*" denotes that a specific variation is significantly explained at a Bonferroni-corrected significance level p=0.002 1 (0.05/24). VE is given in inertia units (IU). The total inertia is 2.275 IU, and the total variation explained is 0.474 IU (Table 2).

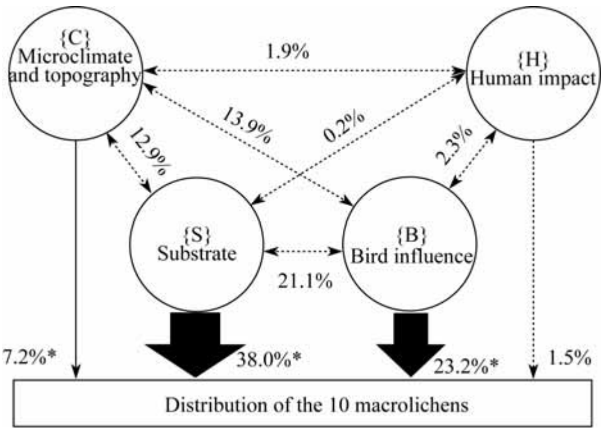

Figure 1 Path diagram of fractions of total variation explained purely by 4 variable sets, and shared variation between them. An arrow pointing from a variable set to distribution of the 10 macrolichens shows the fraction of total variation explained (FTVE) are purely attributable to this variable set, when effects of all other variable sets were removed. An arrow between variable sets indicates the FTVE shared by the two variable sets (effects of other variables were not removed). The solid lines and "*" indicate a specific FTVE is significant at p=0.002.

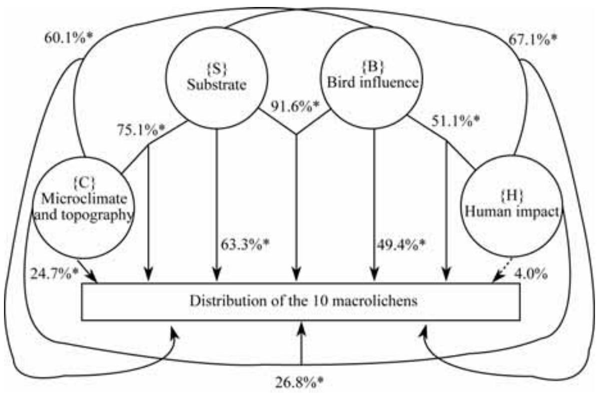

Figure 2 Path diagram of fractions of total variation explained by 4 variable sets and their combinations. An arrow pointing from one or two variable sets to distribution of the 10 macrolichens shows that the fraction of total variation explained (FTVE) are attributable to this variable set or the combination of the two variable sets (effects of other variable sets were not removed). The solid lines and values with "*" indicate a specific FTVE is significant at p=0.002.

2.2 CCA axes

2.2.1 CCA axis 1—Substrate and bird influence gradient

The first axis reflects 14.1% of species variation (Table 2). The most influential variables along axis 1 are SC and SD, as indicated by their highest correlation coefficients with axis 1 (r = −0.64 and −0.62, respectively, Table 4) and their long vectors (Figure 3). Both variables can significantly explain the potential spread of species and plots along axis 1 (t > 3.0, Table 4). The next most influential variable is DBE (r = −0.56), followed by MC (r = −0.49, Table 4); their explanatory power of species distribution along axis 1 are also significant due to their high t-values (Table 4). DBN and DG are significant in explaining species dispersion along axis 1 (t = −3.46 and t = 2.21, respectively), but their impact size is smaller (r = −0.38 and r = 0.31, respectively, Table 4). The other variables have minimal explanatory power of dispersion of species and plots along axis 1 (all t < 1.10, Table 4).

CCA axis 1 mainly reflects a substrate and bird influence gradient, where the left end of the axis represents habitats with deep soil and mosses (such as fellfield or expanses of surface soil), and lower bird excrement and bird population, while the right end reflects boulder and scree with little soil cover and higher bird influence (Figure 3).

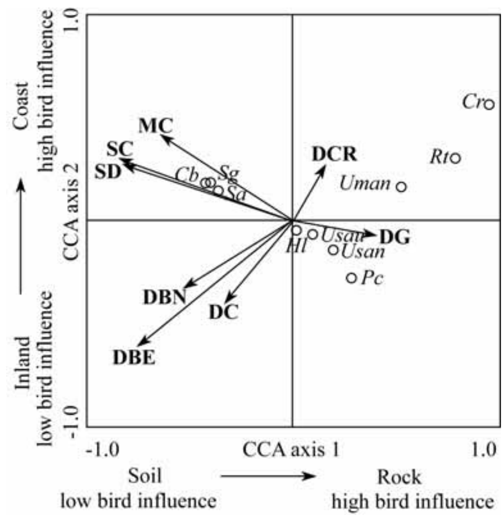

Figure 3 Lichen species and environmental variables on the biplot of canonical correspondence analysis (CCA) of the first and second axes. Abbreviations for species are: *Cr*, *Caloplaca regalis*; *Cb*, *Cladonia borealis*; *Hl*, *Himantormia lugubris*; *Pc*, *Placopsis contortuplicata*; *Rt*, *Ramalina terebrata*; *Sa*, *Stereocaulon alpinum*; *Sg*, *Sphaerophorus globosus*; *Uman*, *Umbilicaria antarctica*; *Usan*, *Usnea antarctica*; *Usau*, *Us. aurantiacoatra*. Abbreviations for variables are given in Table 1.

2.2.2 CCA axis 2—Bird influence gradient

The second axis reflects 4.4% of species variation (Table 2). The most influential environmental variable along axis 2 is DBE (r = −0.29), which has significant explanatory power of the species spread along axis 2 (t = −6.88, Table 4). The next most influential variables are MC (r = 0.20) and DC (r = −0.19), which can both explain dispersion of species and plots along axis 2 (all t > 2.1; Table 4).

Axis 2 mainly reflects the gradient of bird influence. The positive end of the axis represents the coast with bird colonies, penguin rookeries and an abundance of bird excrement, while the negative end represents the inland with little bird influence (Figure 3).

Table 4 Inter-set correlations and *t*-values (in parenthesis) of explanatory variables with CCA-axes

Variables	CCA axes			
	Axis 1	Axis 2	Axis 3	Axis 4
DG	0.31(2.21)*	-0.03(0.62)	0.21(5.03)*	0.08(1.43)
SC	-0.64(-3.96)*	0.14(3.01)*	0.06(-0.06)	-0.03(-0.58)
DC	-0.24(0.64)	-0.19(-2.51)*	0.01(1.82)	0.05(0.87)
SD	-0.62(-3.13)*	0.13(0.82)	0.12(3.01)*	-0.03(-0.87)
MC	-0.49(-5.09)*	0.20(3.71)*	-0.08(-2.45)*	0.11(3.06)*
DBN	-0.38(-3.46)*	-0.15(-1.34)	-0.02(-0.15)	-0.12(-2.94)*
DBE	-0.56(-6.64)*	-0.29(-6.88)*	0.03(-0.23)	0.04(1.87)
DCR	0.12(1.08)	0.12(-0.18)	0.13(2.94)*	-0.02(0.31)

Notes: Abbreviations for the variables are given in Table 1. "*" indicates that a specific variable has significant explanatory power of the species spread along the axis.

The third axis reflects only 1.2% of species variation (Table 2), its importance in interpreting the distribution of the 10 lichens is negligible.

3 Discussion

Substrate variation and bird influence are two major factors determining distribution of the 10 macrolichens, and jointly, they explain 91.6% of the TVE in the cover of the 10 lichens in King George Island (Figure 2). Variation in microclimate and topography is also an important factor, whereas human impact cannot be considered a key factor influencing the distribution of the 10 lichens.

3.1 Substrate variation

Substrate variation is the principle factor determining distribution of the 10 lichens. It explains 38.0% of the TVE (Table 3, Figure 1), and shares 21.1% of TVE with the set of bird influence variables (Figure 1). Environmental gradient reflected by CCA axis 1 also suggests that effects of substrate variation are often associated with bird influence (Figure 3).

In the set of substrate variables, three variables are significant in explaining the variation in species data: soil cover, soil depth and moss cover (Table 1). All three variables reflect soil accumulation in microhabitats.

Soils in the investigated area can be classified into non-ornithogenic and ornithogenic soil. The non-ornithogenic soils are generally poor in organic materials and available nutrients[8]. The ornithogenic soils are often dominant near bird colonies or penguin rookeries, where the bird droppings can significantly elevate the content of nutrients in both soil[8,28-31] and associated lichen thalli[32-34]. Accumulation of soil is necessary for the establishment of terricolous lichens, and the increased availability in ornithogenic soils can be beneficial for vegetation development, and the survival and growth of lichens that can tolerate or require these higher nutrient levels[32-35].

Usnea antarctica (*Usan*), *Us. aurantiacoatra* (*Usau*) and *Himantormia lugubris* (*Hl*) occur in diverse habitats, from bare rocks to fellfield with deep soil. *Caloplaca regalis* and *Ramalina terebrata* prefer coastal rocks with direct input of bird excrement, as indicated by their high species scores on both axis 1 and 2 (Figure 3). This demonstrates their ability to use soluble nutrients leached from excrement or ornithogenic soils and their tolerance of high levels of atmospheric ammonium derived from bird excrement[36]. The terricolous lichens, *Cladonia borealis* (*Cb*), *Sphaerophorus globosus* (*Sg*) and *Stereocaulon alpinum* (*Sa*) are often dominant lichens on soils and co-occur with mosses to form large stands of tundra vegetation[24], as indicated by the low species scores along axis 1 (Figure 3). They can be found on both mineral and ornithogenic soils, indicating that they can use the increased nutrients derived from birds.

3.2 Bird influence

The second major factor determining lichen distribution is variation in bird influence, which purely explains 23.2% of the TVE (Table 3, Figure 1). It shares 13.9% of the TVE with the set of microclimate and topography variables (Figure 1). In this variable set, distance from bird excrement and distance from nest are significant in explaining the species data (Table 1).

Although positive effects of bird excrement on soil nutrient availability and vegetation development have been demonstrated in many ecosystems in Antarctica[29,32-35], the negative influence of birds on lichen distribution can be readily seen from the dispersion of species (Figure 3) along CCA axis 2. Two ornithocoprophilous lichens, *C. regalis* and *R. terebrata*, are abundant in sites with high bird influence near the coast, while the other eight lichens are sparse in such microhabitats. Greater input of ornithogenically-derived nutrients does not necessarily support a greater species-rich lichen community[37], but favors a community dominated by ornithocoprophilous lichens[2].

Bird droppings can increase environmental salinity[1-2], which can greatly affect survival, growth and distribution of lichens[34]. *Caloplaca regalis*, *R. terebrata* and *Umbilicaria antarctica* can tolerate high levels of salinity[3], and they prefer coastal habitats with bird excrement (Figure 3). The other species, however, appear to be less salt tolerant. Although they can be found on ornithogenic soils, they prefer microhabitats far away from bird colonies and coast. Species such as *Us. antarctica*, *Us. aurantiacoatra* and *H. lugubris*, when growing near bird colonies, are sparse and restricted to cliffs or shelter microhabitats.

Animal trampling can also affect lichen distribution in maritime Antarctica by the effects of damage to the lichens thallus and disruption of soil stability[34,38-39]. On Ardley Island, a geological time scale study (about 2 400 years) showed that lichen abundance decreased whenever penguin populations increased, and vice versa[40]. A study conducted near the Polish Research Station on King George Island clearly showed a distinct zonation of vegetation related to penguin rookeries, where lichen richness decreased with decreasing distance from penguin rookeries[37].

The adaptation of lichens to bird trampling is related to growth form, thallus size and substrate preference. The reduced soil stability due to bird trampling makes the microhabitats unfavorable to terricolous lichens[3]. Crustose and dwarf lichens can survive greater penguin disturbance than the foliose, tall fruticose lichens[37]. The dwarf thallus of *C. regalis* (thallus commonly < 3 cm in height), and pendulous and soft thallus of *R. terebrata* on cliffs[3], may be helpful for both species in alleviating the damage of bird trampling[17]. The other lichens, either with a fruticose and stiff thallus up to 5 cm in height, or with a foliose thallus, are attached to the substrate by a single holdfast that can be easily damaged by birds[3]. Holdfast remnants or broken thalli of *Usnea* spp. were frequently observed on rocks near bird colonies.

3.3 Effects of microclimate and topography

The third most important factor is variation in microclimate and topography, which purely explains 7.2% of TVE (Table 3, Figure 1), and shares 13.9% of TVE with the set of bird influence variables and 12.9% with the set of substrate variables (Figure 1). Distance from coast and distance from ground are significant in explaining the distribution of the 10 lichens (Table 1).

Distance from coast is highly related to bird influence. In King George Island, bird colonies and penguin rookeries are often distributed along or near the coast, and bird concentrations generally declines with increasing distance from the coast[37]. Distance from ground is related to the degree of soil accumulation: Soil is commonly accumulated in flat and low-lying microhabitats, whereas soil cover and depth is low on the top of rocks.

Water availability is not statistically significant in explaining the distribution of the 10 lichens (Table 1). This is inconsistent with other studies documenting that water availability is one of the major factors influencing lichen distribution in Antarctica. For example, in the Soya and Prince Olav Coastal regions of East Antarctica with annual precipitation <150 mm, lichens are abundant in sites where an adequate summer seasonal moisture availability is maintained, but are generally absent or poorly developed in the dry or exposed sites[41]. A possible explanation is that water deficiency is not a limiting factor in King George Islands, due to the high precipitation (500 $mm \cdot a^{-1}$), high air humidity (about 80%)[17], and the capability of lichens to use water vapor from clouds[9,41].

3.4 Human impact

As noted by Øvstedal and Smith[3], human impact in Antarctica is on such a small and limited scale that no lichens are considered to be threatened by humans on the continent. This study also found that human impact cannot be considered as an important factor influencing distribution of the 10 macrolichens in King Gorge Island. Because the investigated sites were designated as ASPA, all activities that may be potentially harmful to native plants are strictly prohibited.

4 Conclusion

The CCA analyses show that the small-scale spatial distribution of the 10 macrolichen in King George Island, West Antarctica is mainly influenced by spatial heterogeneity of substrate, bird influence, and microclimate and topography, whereas humans have little impact.

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