Seabird colony effects on soil properties and vegetation zonation patterns on King George Island, Maritime Antarctic

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ABSTRACT

Seabirds are amongst the most important vectors transferring biogenic compounds from the sea onto land in the polar regions and, consequently, influencing the properties of soil and vegetation. We studied the influence of bird colonies (Adélie and gentoo penguins, giant petrels), on soil properties and plant communities on King George Island, Maritime Antarctic. We designated seven transects, each starting from the colony edge and running to a natural boundary feature, which were divided into contiguous sample plots where we identified specific plant taxa (*Prasiola crispa, Deschampsia antarctica, Colobanthus quitensis, Usnea* sp.), as well as hydrophilous and xerophilous ecological groups of mosses. Based on percentage contributions of each of these taxa, we distinguished six distinct vegetation zones along the transects, in which we measured physical (moisture, conductivity and pH) and chemical (NO_3^-, NO_2^-, NH_4^+, K^+ and PO_4^{3-} content) soil parameters. Our study confirmed that, with increasing distance from bird colonies, the concentration of nutrients and soil conductivity decreased, while pH increased. The vegetation zones were clearly related to this gradient of seabird colony influence, and occurred in the same sequence for all three bird species examined, although the largest colony of Adélie penguins had the strongest effect on vegetation. Similarly, the physical and chemical soil properties did not differ significantly between the colonies.

Keywords: vegetation zones, soil chemistry, environmental gradient, penguins, petrels

Introduction

Polar terrestrial ecosystems are defined as subsidiary because they depend largely on marine-derived nutrients (Odum 1989). Marine birds and mammals, which forage in the sea and reproduce on land, are amongst the most important vectors transferring biogenic compounds and organic material from the sea to land (Smith and Froneman 2008). Seabirds introduce these materials to the terrestrial food-web through their carcasses, dead chicks and eggshells, food scraps, feathers and guano, and they consequently influence the properties of soil and vegetation (Stempniewicz 1990, 2005; Sun et al. 2002, Bokhorst et al. 2007; Stempniewicz et al. 2007; Zhu et al. 2013, Zwolicki et al. 2013; Ziółek and Melke 2014).

In Antarctic terrestrial ecosystems nutrient availability and turnover are limited by low metabolic activity and low rates of primary production, which result from the short growing season and chronically low summer temperatures (Smith 1984). Vegetation develops on typically small ice-free areas, including those recently uncovered by glacier retreat (Cook et al. 2005; Convey and Smith 2006). The ‘Antarctic herb tundra formation’, one of the most widespread vegetation types in the maritime Antarctic, comprises mostly mosses and lichens and includes only two indigenous species of vascular plants, the grass *Deschampsia antarctica* Desv. (Poaceae) and the pearlwort *Colobanthus quitensis* (Knuth) Bartl. (Cariophyllaceae) (Greene and Holtom 1971; Smith 1972; Longton 1988; Alberdi et al. 2002).

Antarctic vegetation communities often develop in sites enriched by seabirds or marine mammals (Ryan and Watkins 1989; Smith and Froneman 2008), although this feature has perhaps been noted more widely and impressively in the High Arctic (Odasz 1994; Croll 2005; Zmudczyńska et al. 2009, 2013). Recently, changes have been recorded in the composition and abundance of avifaunal communities in the South Shetland Islands, especially decreases in penguin population numbers (Ciaputa and Sierakowski 1999;

Korczak-Abshire 2010). These changes may, therefore, significantly impact vegetation community structure and function. Areas that have been abandoned by penguins are rapidly colonized by complex plant formations, facilitated by both the considerable nutrient resources and the cessation of trampling by the birds (Tatur et al. 1997; Emslie et al. 1998; Juchnowicz-Bierbasz and Rakusa-Suszczewski 2002).

The significance of the large amounts of nutrients supplied by breeding birds has been recognized in many studies (eg. V. Smith 1978; R.I.L Smith 1984; Tatur and Myrcha 1984; Ryan et al. 1989; Myrcha and Tatur 1991; Hovenden and Seppelt 1995). Tatur (2002) calculated that the 30–50000 pairs of *Pygoscelis* genus penguins nesting on the west side of Admiralty Bay (King George Island) deposited about 6.35 tonnes of guano per day, equating to up to 10 kg of dry excreta per square meter of colony area during the breeding season. The impact of this fertilization is manifested particularly in the vegetation composition, diversity and abundance. Various studies have reported zonation of vegetation around nesting areas and colonies (Smith 1984; Zarzycki 1993; Olech 2002), in particular recognising the balance between increased plant diversity and growth rate associated with nutrient enrichment, and limitation of growth caused through both intense trampling and levels of fertilization exceeding those that can be tolerated by plants close to the colony (e.g. Smykla et al. 2007). However, as yet, no attempt has been made to quantify physical and chemical soil conditions underlying these vegetation patterns in the Antarctic.

Well-documented environmental changes, such as warming of the atmosphere and ocean around Antarctica resulting in melting of perennial snow, retreat of glaciers and reduced sea ice cover have taken place over recent decades and may change ecosystem structure and function in the maritime Antarctic (Convey et al. 2009; Chwedorzewska 2009; Turner et al. 2009, 2013, 2014; Convey 2011). Therefore, this study set out to describe the relationships between the physical and chemical properties of the soil and the development of specific vegetation zones. We tested hypotheses that the development of particular plant communities in the vicinity of seabird colonies is determined by: (1) nutrient composition, (2) nutrient concentration, and (3) colony type and species of seabird involved.

Materials and methods

Study Area

The study was conducted on King George Island (South Shetland Islands) during two expeditions from December 2005 to January 2006 and from December 2006 to January 2007 (Fig. 1). The study area was located in Antarctic Specially Protected Area 128 Ecology Glacier in the vicinity of the Polish Henryk Arctowski Antarctic Station. King George Island (61°50'–62°15'S, 57°30'–59°01'W), is the largest of South Shetland Islands archipelago, located 160 km from the Antarctic Peninsula, from which it is separated by the Bransfield Strait. The average annual temperature is 1.7°C. As is typical of the maritime Antarctic region, the island experiences a strong oceanic influence, with high humidity (84%) and considerable precipitation. It also exposed to strong winds that often reach hurricane force (Walton 1984; Convey 2013).

Notwithstanding the generally extreme environmental conditions, ice-free areas, constituting less than 10% of the island's area, host relatively well developed terrestrial ecosystems. King George Island, and in particular the western coast of Admiralty Bay, is one of the richest botanical areas both of the maritime Antarctic biogeographical region and of the entire Antarctic continent (Rakusa-Suszczewski 2003; Krzewicka and Smykla 2004). The island's vegetation is composed mainly of mosses, lichens, algae and cyanobacteria. Vascular plants are represented by two species, the Antarctic hair grass *D. antarctica* (Poaceae) and Antarctic pearlwort *C. quitensis* (Caryophyllaceae) (Smykla et al. 2007).

In general, vegetation development is concentrated in coastal areas, particularly close to those where marine birds and mammals breed and/or rest in high numbers. The most numerous vertebrate in the study area is the Adélie penguin (*Pygoscelis adeliae*, c. 15,000 breeding pairs), with other species represented by much smaller populations - gentoo penguin (*P. papua*, 30 pairs), kelp gull (*Larus dominicanus*, 40 pairs), southern giant petrel (*Macronectes giganteus*, 11 pairs), Brown skua (*Stercorarius antarcticus* ssp. *lonnbergi*, 225 pairs). Marine mammals, including the southern elephant seal (*Mirounga leonina*) and Antarctic fur seal (*Arctocephalus gazella*), also contribute to enrichment of the terrestrial ecosystem, while rapidly expanding regional populations of the latter have led to considerable damage and loss by trampling and over-fertilisation of large areas of maritime Antarctic terrestrial vegetation (Favero-Longo et al. 2012).

Collection of vegetation data

Data were collected in areas influenced by Adélie penguin, gentoo penguin and southern giant petrel colonies. Seven transects were designated on topographically similar profiles, each 1 m wide and ranging from 60 to 120 m in length, starting from the colony edge and running down the slope to a natural boundary feature, such as a stream, a small water body or the seashore. Three transects were defined close to an Adélie penguin colony, two from a southern giant petrel colony and two from a gentoo penguin colony (Fig. 1). Each transect was subdivided into contiguous sample plots (1×1 m), meaning that they included 60 to 120 sample plots depending on their length, and the study included a total of 568 plots.

Within all sampling plots along each transect we identified four specific taxa: *P. crispa, D. antarctica, C. quitensis* and *Usnea* sp., and additionally determined two ecological groups of mosses, hydrophilous (predominantly *Sanionia georgico-uncinata*) and xerophilous (including *Polytrichastrum alpinum, Syntrichia saxicola, S. princeps* and *Polytrichum piliferum*), and visually assessed their percentage contribution to total vegetation cover.

Physicochemical analysis of the soil

Sample plot selection for chemical analyses was determined on the basis of gradient analysis of vegetation (see below) using the first DCA axis for each transect separately. The plots with highest response of a given taxon/ecological group, as assessed by the highest percentage cover, were chosen for chemical sampling. The total number of soil samples collected for physical and chemical analyses was 72. Three samples of the surface layer of soil were collected from each of the plots (representing the five zones distinguished by the TWINSPAN classification on each of the six transects) from points lying on the same diagonal of each sampling plot (one from the centre and two from the corners of the plot). Samples were taken from the soil surface layer using a metal cylinder (diameter = 5 cm) to a depth of 10 cm. Each soil sample was separated into three subsamples of c. 80 cm^3, weighed to the nearest 0.1 g, and subjected to further analyses in order to assess:

1) Soil moisture [%] – by weighing a subsample before and after oven drying (120^{o}C) to constant mass.
2) Soil conductivity (µS cm^{-1}) and pH – samples of 80 cm^3 were mixed with 160 cm^3 of distilled water. The solution was shaken for ca. 20 min and then filtered through a sieve (0.5 mm diameter mesh). The conductivity and pH were quantified in the filtrate using a pH/conductivity/salinity meter CPC-401 (Elmetron).
3) Soil nitrogen (NO_3^-, NO_2^- and NH_4^+), potassium (K^+) and phosphate (PO_4^{3-}) content (mg 1000 g^{-1} soil dry mass) – samples of 80 cm^3 were mixed with 200 cm^3 0.03 N acetic acid. Closed vessels were left for ca. 60 min and shaken regularly. The solution was centrifuged for 15 min at 2500 rpm and filtered first through a sieve (0.5 cm

diameter mesh) and then through filter paper (MN 640 w, Macherey–Nagel diameter = 125 µm). Filtrates were analyzed using a photometer LF205 following standard procedures (Cygański 1994).

Data management and statistical procedures

Detrended Correspondence Analysis (DCA, unimodal gradient analysis) was performed to ordinate the vegetation plots and used to define plot selection for chemical and physical sampling (ter Braak and Smilauer 2012). Vegetation zone classification was performed using the TWINSPAN method under the following conditions: 6 cut levels: 0, 2, 5, 10, 20, 50 (%); minimum 5 samples by group size for a division, and maximum 7 indicators per division (TWINSPAN for Windows 2.3) (Hill and Šmilauer 2005). Differences between separate groups of vegetation and soil chemistry samples were examined using ANOSIM (analysis of similarities, with Monte Carlo permutation test) with one-way and two-way cross and nested comparisons design. Data standardization was performed only for physical and chemical variables. In order to illustrate the level of similarity between the identified vegetation zones and seabird colony types, a non-metric multidimensional scaling (MDS) was applied on the matrix of Euclidean distances between samples. These analyses were run on the log-transformed data [$x' = \log(x + 1)$]. Additionally, similarity percentages analysis (SIMPER) was used to define the contribution of each taxon/ecological group to dissimilarities between the distinguished groups. ANOSIM, MDS and SIMPER were run in Primer 6.1.5. (Plymouth Marine Laboratory, Plymouth, UK) (Clarke and Warwick 1994). For each of the physical and chemical soil parameters we conducted comparisons between the identified vegetation zones using non-parametric Kruskal-Wallis and *post hoc* Dunn tests using the STATISTICA 9.0 package (StatSoft, Inc. 2010).

Results

Vegetation analysis

On the basis of the TWINSPAN classification we separated six distinct vegetation zones along the transects. These were, starting from the colony edge:

1) *Prasiola crispa* zone (P) with *P. crispa* 100% relative ground cover, 2) *D. antarctica* and *P. crispa* zone (PD) – *P. crispa* 41% and *D. antarctica* 59% relative cover, 3) *D. antarctica* zone (D) – monospecific occurrence of Antarctic hair grass, with 64% relative cover, 4) mosses and *D. antarctica* (MD) –56% relative cover of hydrophilous mosses, with 25% cover of Antarctic hair grass, 5) mosses and lichens (ML) – mixed xerophilous moss community with relative cover of 31%, and the highest relative cover values recorded for macro lichens (*Usnea* sp. 7.5%) and *C. quitensis* (13%). Finally, we also defined a trampled (T) zone – including areas trampled by the birds and temporary ponds or puddles. Sampling plots included in this zone were present across the different zones in all transects, and are not included in the subsequent analyses. Percentage cover values and frequencies of occurrence of individual taxa are shown in Table 1.

Analysis of similarity between groups identified using TWINSPAN confirmed that they were distinct and that their membership was non-random (ANOSIM One-Way Analysis, Global Test; R = 0.79 p = 0.001). Pairwise comparisons confirmed that all the zones differed significantly (p = 0.001) (Fig. 3).

Soil physical and chemical characteristics in vegetation zones

Within the transects, the vegetation zones differed in terms of their overall physicochemical parameters (ANOSIM Two-Way Crossed Analysis, Global Test; R = 0.13

$p = 0.001$). Detailed comparisons for each of the physical and chemical soil properties revealed significant differences between the zones (all Kruskal-Wallis tests, $p < 0.001$, differences in *post hoc* tests $p < 0.01$).

Starting from the colony edge, clear gradients of measured ion concentrations and soil conductivity could be seen, with the highest values in the P zone and decreases through the successive zones (form P to ML; Fig. 4, Table 2). The P zone demonstrated the highest number of significant differences in terms of physical and chemical soil parameters in comparison with other zones. No significant differences were found between PD and D zones in any of the measured parameters. A distinct gradient was present in pH, which increased with progression from the colony edge and was significantly higher in the final ML zone than in other zones. The ML zone also had the lowest soil moisture values, differing significantly from all other groups except the P zone (Fig. 4g, Table 2).

Influence of seabird species on vegetation zonation

Similarity analysis revealed no significant differences between the three bird species in physical and chemical properties of soil measured within the identified vegetation zones (ANOSIM Two-Way Nested Analysis, Global Test $R = 0.22$ $p = 0.72$). Plant species composition within each of the five zones was also similar between the bird species (ANOSIM Two-Way Nested Analysis, Global Test $R = 0.13$, $p = 0.16$).

Two-Way Crossed Analysis, testing for differences between colony types regardless of any differences between the vegetation zones, revealed no significant differences in soil characteristics (ANOSIM Two-Way Crossed Analysis, Global Test; $R = 0.06$ $p = 0.11$). However, the transects near the Adélie penguin colony differed significantly from those associated with the other two bird species (ANOSIM, Two-Way Crossed Analysis Global Test; $R = 0.16$ $p = 0.001$, Pairwise Tests $p < 0.01$). MDS analysis (Fig. 3) confirmed that samples from the Adélie penguin transect did not share exactly the same similarity space as those from the other colonies. The main differences were among plots from the first three zones dominated by *P. crispa* and *D. antarctica* (P, PD, D). However, gentoo penguin and petrel colonies differed from Adélie mainly due to the samples from the final zone along the transect (ML) (Fig. 3). SIMPER analysis revealed average dissimilarities in vegetation composition between the Adélie and gentoo penguin transects of 53.9%, and between Adélie and giant petrel transects of 50.7% (Table 3). The Adélie penguin transect was characterized by substantially lower mean cover of hydrophilous mosses, contributing 47.1% of dissimilarity in comparison with the giant petrel transect and 19.1% with the gentoo penguin transect. The next largest contribution to differences between colony types was due to the presence of *D. antarctica,* whose average cover was greater on the giant petrel and gentoo penguin transects. Of the three bird species examined, the Adélie penguin transect was characterized by the largest cover of the alga *P. crispa*, which was the third most important contributor to dissimilarity between transects. Xerophilous mosses, *C. quitensis* and *Usnea* sp. were of minor importance in the differentiation between colony types (Table 3).

Discussion

In polar regions, vegetation patterns have been variously associated with proglacial chronosequences, topographical gradients (Frenot et al. 1998; Kojima 2002; Ohtsuka et al. 2006), and environmental gradients created by seabirds, with the latter having perhaps the most striking influence on vegetation development (Odasz 1994; Zmudczyńska et al. 2008, 2009; Zmudczyńska-Skarbek et al. 2013). On King George Island we found that, with increasing distance from bird colony edges through successive vegetation zones, the concentrations of nutrients and soil conductivity decreased, while pH increased. These results confirm in detail previous studies that have recognized that the presence of the seabird colonies leads to strong gradients in soil chemistry. Ryan and Watkins (1989) described a similar relationship near snow petrel nest concentrations in continental Antarctica and, in the High Arctic, tundra fertilization was much greater close to colonies, and gradually decreased along the colony-sea axis (Zwolicki et al. 2013; Ziółek and Melke 2014). High concentrations of mineral forms of phosphorus and nitrogen have been reported in surface waters draining from penguin breeding areas close to the location of the current study (Tatur and Myrcha 1983), consistent with the values measured here. We recorded the highest values of soil moisture in the central zones of the transects (PD and D zones). These data clearly imply that the differences in structure and composition of the distinct vegetation zones identified are likely to result from the interplay of multiple soil parameters (cf. Webb 1954).

Along the gradient in physical and chemical soil properties, we identified five distinct vegetation zones which were similar to those described by Smykla et al. (2007) in a study performed near a single gentoo penguin colony. With this characteristic zonation also being formed near Adélie penguin and giant petrel colonies, we consider that it may represent a general feature for different seabird species. The consistency of the vegetation pattern along the different transects may be in part a consequence of the small number of available plant taxa, giving a limited number of possible combinations, and also could reflect the reaction of the phytocoenosis reaction to direct disturbance caused by seabirds. Rapid nutrient inflow in the vicinity of bird colonies creates imbalanced communities, reflected in the simultaneous presence of pioneer (*P. crispa*) and climax species (*D. antarctica*) (compare with Smith 1972; Convey 1996). Phytocoenosis stabilization occurs with the separation from the strongest influence of a colony, and is evidenced by increasing number of species (MacArthur 1955, Smykla et al. 2007).

Adjacent to all three colonies, the closest community consisted only of mats of the nitrophilous foliose alga *P. crispa* overgrowing on over-fertilized habitat with low soil moisture level. This zone is also formed also under extremely variable pH conditions, which could be explained by microbially-mediated guano decomposition processes (Zdanowski et al. 2005). The second zone was rich in nutrients and characterized by the highest moisture content and lowest pH, as well as the presence of *P. crispa* and Antarctic hair grass *D. antarctica*. The third zone, with *D. antarctica* as a dominant species, is found on moist soil with moderate nutrient levels. The fourth zone was dominated by hydrophilous mosses growing on nutrient-poor habitats, with moderate soil moisture level. The fifth and final zone was covered by an open mixed mesic moss community that is typical of open fellfield habitats in this region (Ochyra 1998), representing the driest and most acidic soil environment. Smykla et al. (2007) noted that the general trend in the change of the vegetation structure between consecutive zones was marked by decreasing abundance of nitrophilous taxa such as *P. crispa*, with the simultaneous appearance and increasing abundance of nitrophobous species of mosses and lichens, therefore postulating that the penguin-derived fertility gradient was a major factor in determining the zonation pattern of vegetation.

Bird species differing in diet could potentially have a different impact on soil chemistry, as indicated by the differing effects of fish-eating and planktivorous bird colonies in the Arctic (Zwolicki et al. 2013). In the region of King George Island both penguin species feed primarily on krill (*Euphausia superba*), although gentoo penguins also consume a significant proportion of fish (Volkman et al. 1980). Giant petrels are the main scavenging seabirds in the Antarctic region, relying mainly on penguins, burrowing petrels and krill as reported on South Georgia (Hunter 1983). While such differences in diet could potentially influence soil physico-chemical properties and consequently the zonation in vegetation cover, there was no evidence for this occurring in our study Physical and chemical soil parameters did not differ significantly between the colonies, regardless of the clear gradients along the transects. This could be explained by the plasticity of giant petrel feeding strategies, where males and females can exploit different food resources during chick incubation: males scavenging on beaches and females foraging at sea mostly on krill, squid and fish (Hunter 1983). However, males also have the capacity to switch search modes and forage at sea (Gonzales et al. 2000; Forero et al. 2005). It is plausible that on King George Island the proportion of crustaceans, especially krill, in the giant petrel diet was larger than that reported in previous studies from South Georgia, and thus more similar to the two penguin species studied here. However, there were some more subtle differences in the mean cover values of specific plant taxa between the Adélie penguin colony and those of the other species, most apparent in the higher cover values of *P. crispa* and lower average cover of *D. anatarctica* and mosses. Thus, the largest colony (Adélie penguin) had the strongest effect on vegetation.

This study clearly demonstrates the significance of bird-derived nutrient enrichment to vegetation development. We found significant composition differences between successive vegetation zones, which were related to the clear differences in physical and chemical soil properties along gradients commencing at the colony edges. The pattern of vegetation zonation was independent of bird species and colony size.

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Table captions

Fig. 1. Location of transects in the study area. Tr-A1, A2, A3, - transects from Adélie penguin (*Pygoscelis adeliae*) colony; Tr-Pt1, Pt2 - transects from southern giant petrel (*Macronectes giganteus*) colony; Tr-G1, G2 – transects from gentoo penguin (*Pygoscelis papua*) colony (map by Pudełko 2002).

Fig. 2. Diagram of two way indicator species analyses (Twinspan) based on vegetation composition. P- *P. crispa* zone, T – trampling zone, PD - *D. antarctica* and *P. crispa* zone, D - *D. antartcica* zone, MD –hydrophilous moss and *D. antarctica* zone, ML - xerophilous moss and lichen zone. Numbers of plots presented for each group/division.

Fig 3. MDS plot showing ordination of samples based on the identified vegetation zones and colony types. P- *P. crispa* zone, PD - *D. antarctica* and *P. crispa* zone, D - *D. antartcica* zone, MD –hydrophilous moss and *D. antarctica* zone, ML - xerophilous moss and lichen zone.

Fig.4. Physical and chemical soil parameters in each vegetation zone. Significant differences ($p<0.01$) between zones are indicated by lines. Log_{10} transformation for NH_4^+, NO_3^-, NO_2^-, PO_4^{3-} and K^+ data performed for better data visualization. P - *P. crispa* zone, PD - *D. antarctica* and *P. crispa* zone, D - *D. antartcica* zone, MD –hydrophilous moss and *D. antarctica* zone, ML - xerophilous moss and lichen zone.

Table 1. Mean and relative ground cover (%) of taxa and ecological groups in the successive vegetation zones identified. P- *P. crispa* zone, T – trampling zone, PD - *D. antarctica* and *P. crispa* zone, D - *D. antartcica* zone, MD –hydrophilous moss and *D. antarctica* zone, ML - xerophilous moss and lichen zone.

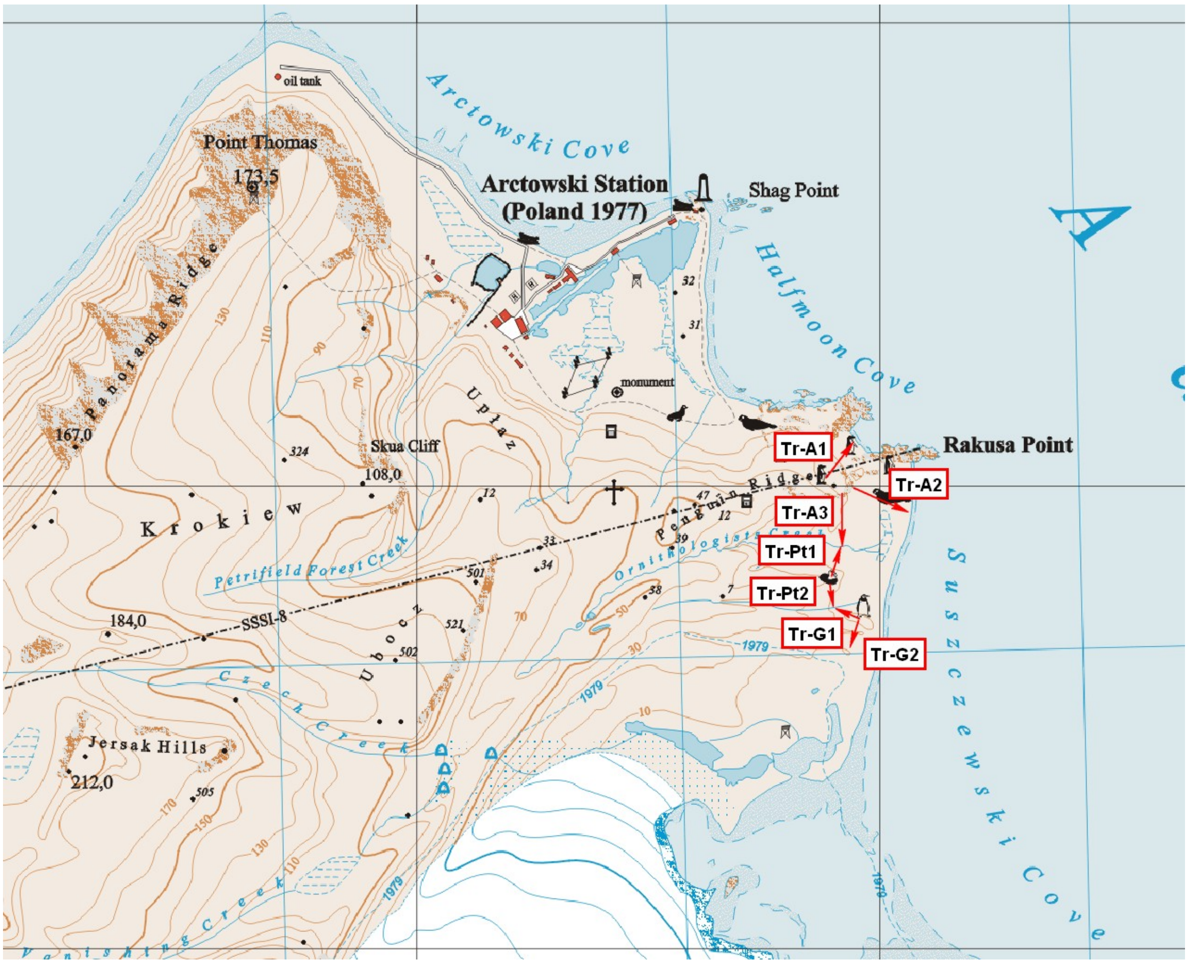
	Vegetation zones											
Taxon/ ecological group	P N = 163		PD N = 53		D N = 95		MD N = 144		ML N = 59		T N = 54	
	Mean	Relative	Mean	Relative	Mean	Relative	Mean	Relative	Mean	Relative	Mean	Relative
P. crispa	7.3	100	2.9	40.6	4.8	13.9	2.3	5.6	0.8	1.7	4.1	52.3
D. antarctica		0.0	4.2	59.4	22.1	63.6	10.5	25.3	9.9	21.5	1.7	21.3
C. quitensis		0.0		0.0	1.5	4.3	0.4	1.0	6.2	13.4		0
Hygrophilous mosses		0.0		0.0	3.8	11.0	23.4	56.2	11.5	24.9	2.1	26.4
Xerophilous mosses		0.0		0.0	1.8	5.2	4.1	9.7	14.3	31.0		0
Usnea sp.		0.0		0.0	0.7	2.0	0.9	2.1	3.4	7.5		0

Table 2. Median values and first and third quartiles (IQ - 25%, IIIQ - 75%) of measured physical and chemical parameters of soil in the identified vegetation zones. P- *P. crispa* zone, PD - *D. antarctica* and *P. crispa* zone, D - *D. antartcica* zone, MD –hydrophilous moss and *D. antarctica* zone, ML - xerophilous moss and lichen zone.

Soil parameters		Vegetation zones				
		P	PD	D	MD	ML
NH_4^+ (mg kg^{-1})	Median	58.0	10.4	7.9	1.5	1.2
	IQ	24.0	4.4	1.7	0.6	0.9
	IIIQ	582.3	17.3	27.3	12.0	1.8
NO_3^- (mg kg^{-1})	Median	192.3	80.4	51.9	12.3	2.7
	IQ	58.2	37.7	1.7	4.2	1.0
	IIIQ	393.1	202.8	123.5	23.2	5.5
NO_2^- (mg kg^{-1})	Median	4.6	0.8	1.2	0.3	0.1
	IQ	1.4	0.3	0.1	0.2	0.1
	IIIQ	12.7	6.7	2.8	0.7	0.2
PO_4^{3-} (mg kg^{-1})	Median	521.5	166.3	51.6	6.4	8.5
	IQ	119.2	144.8	12.0	3.9	1.5
	IIIQ	1605.4	294.1	280.7	72.0	14.3
K^+ (mg kg^{-1})	Median	309.5	60.8	40.6	24.6	19.4
	IQ	163.2	34.2	20.8	10.7	16.4
	IIIQ	1769.1	90.7	164.7	69.3	27.0
Soil moisture (%)	Median	22.7	33.2	32.3	21.4	15.5
	IQ	18.3	23.4	14.6	15.5	13.7
	IIIQ	31.1	55.9	51.9	57.1	19.2
pH	Median	4.2	4.1	4.4	4.8	5.4
	IQ	3.9	4.0	4.0	4.1	5.2
	IIIQ	6.8	4.2	4.7	5.1	5.6
Conductivity (µS cm^{-1})	Median	840.7	267.2	196.1	83.2	61.7
	IQ	334.2	182.4	115.0	60.1	55.0
	IIIQ	2438.0	341.4	291.1	98.4	104.0

Table 3. SIMPER analysis of vegetation composition between the studied bird colony types.

Taxon/ ecological group	Average cover %			Adélie vs Petrel		Adélie vs Gentoo	
	Adélie	Petrel	Gentoo	Average dissimilarity	Contribution %	Average dissimilarity	Contribution %
Hygrophilous mosses	7.7	51.6	31.72	23.85	47.08	19.08	35.38
D. antarctica	14.8	21.88	19.41	13.56	26.77	17.2	31.88
P. crispa	11.91	3.72	5.45	10.37	20.47	14.35	26.61
Xerophilous mosses	0.24	18.14	8.66	2.59	5.11	2.99	5.54
C. quitensis	0.01	3.27	1.36	0.14	0.29	0.18	0.34
Usnea sp.	0.08	1.23	0	0.14	0.28	0.14	0.25



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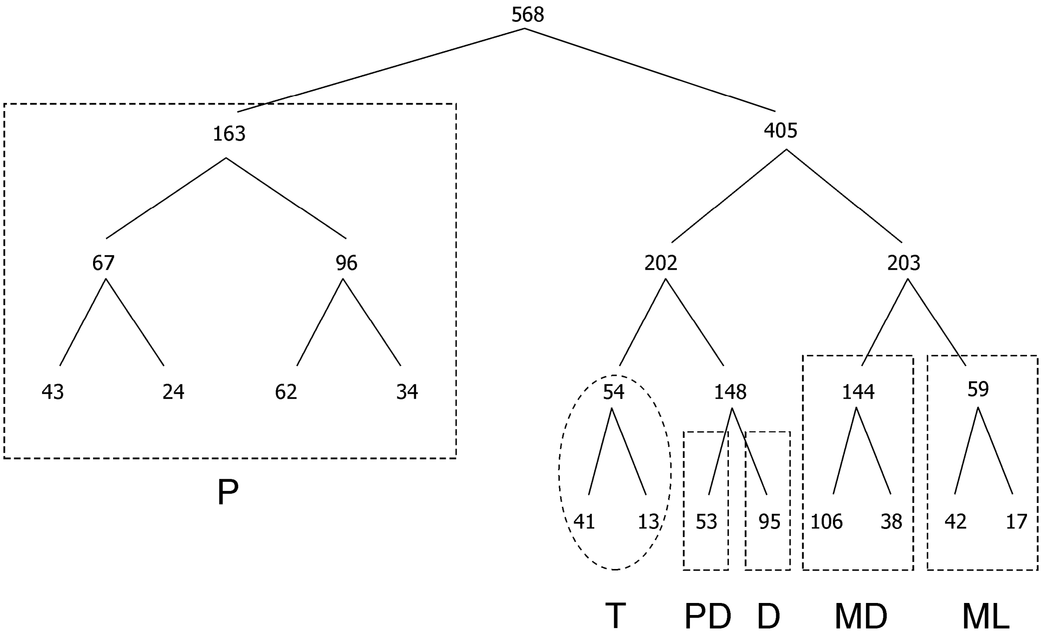

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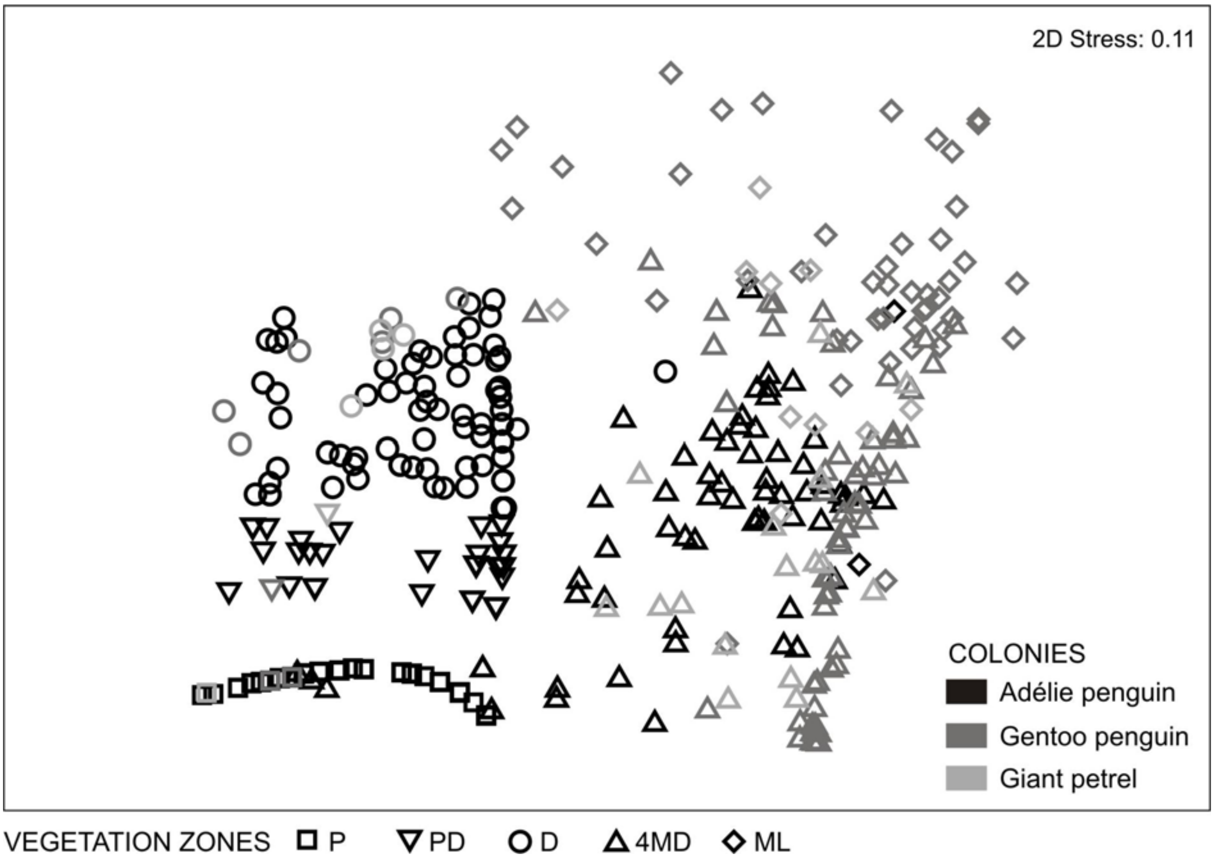

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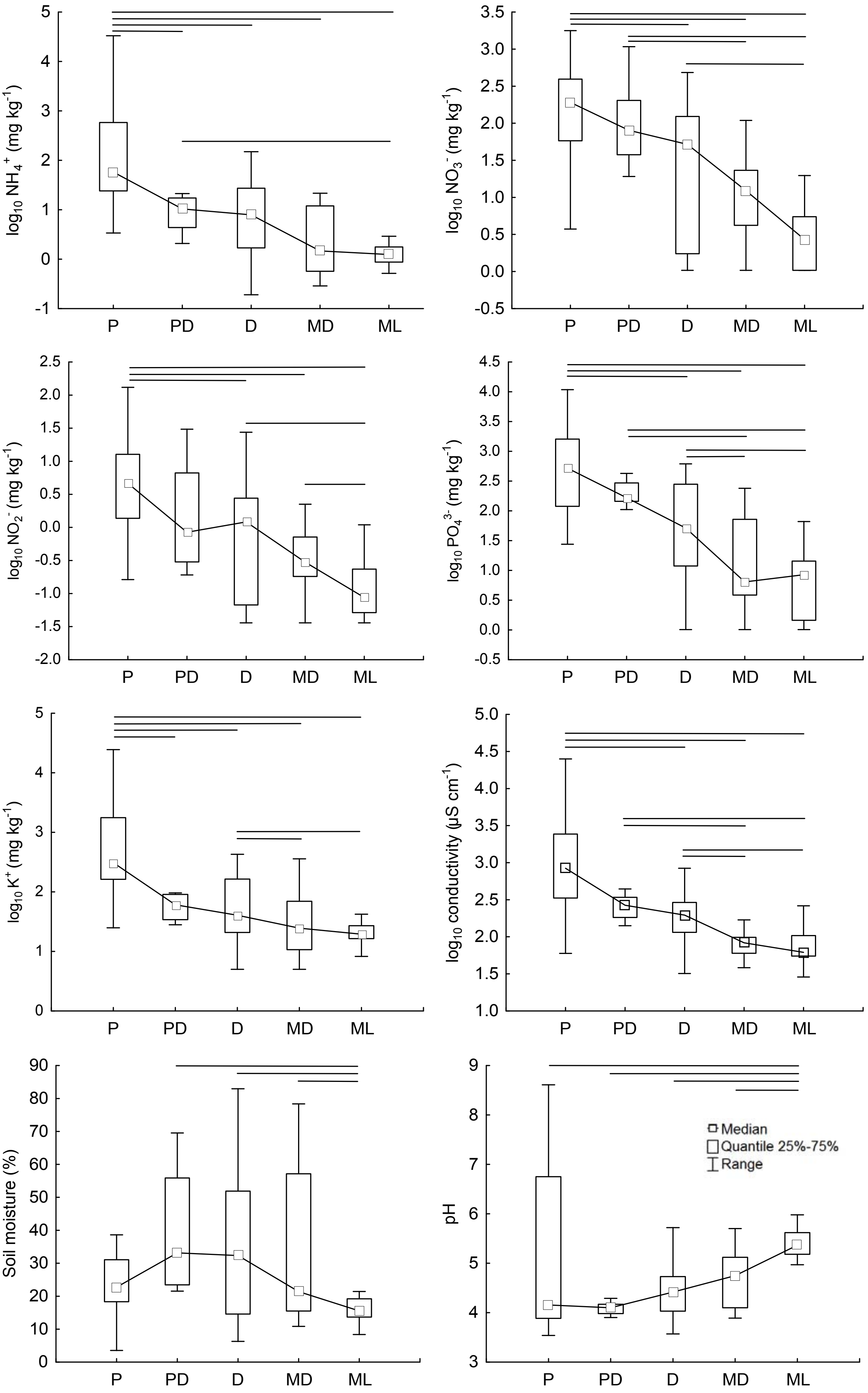

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