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Citation	Polar Biology, 2011, v. 34 n. 2, p. 307-311
Issued Date	2011
URL	http://hdl.handle.net/10722/145036
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Distribution and abiotic influences on hypolithic microbial communities in an Antarctic Dry Valley

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Received: 4 June 2010/Revised: 16 July 2010/Accepted: 20 July 2010/Published online: 7 August 2010
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Abstract The Miers Valley within the McMurdo Dry Valleys of Antarctica supports abundant quartz and marble substrates for hypolithons—microbial colonists on the underside of these translucent rocks. Three physically distinct hypolithic community types have been identified: cyanobacteria dominated (Type I), fungus dominated (Type II) or moss dominated (Type III). The distribution of the three types was mapped across much of the $\sim 75 \text{ km}^2$ area of the upper Miers Valley and correlated this with the measurements of selected micro-environmental variables. Type I hypolithons were most common and occurred at all altitudes up to 824 m, whilst Type II and Type III hypolithons were

less abundant and restricted to lower altitudes on the valley floor ($<415 \text{ m}$ and $<257 \text{ m}$, respectively). Whilst all colonized quartz effectively filtered incident UVB irradiance, transmittance levels for UVA and PAR varied markedly and were significant in determining hypolith type. Notably, the Type I hypolithons occurred under rocks with a significantly lower transmittance of photosynthetically active radiation than Type II and III hypolithons. Altitude and aspect were also significant factors determining hypolith type, and a role for altitude-related abiotic variables in determining the distribution of Type I, II and III hypolithons is proposed.

Keywords Miers valley · Antarctica · Cryptic microbial communities · Hypolithons · Microniches

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Introduction

The development of specialized cryptic microbial communities associated with and protected by lithic structures has emerged as a characteristic biotic feature of desert landscapes (Golubic et al. 1981; Friedmann 1982). These lithic communities are broadly divided into hypolithic (underneath rock), endolithic (inside rock) and chasmolithic (inside rock crack) communities (Cowan and Ah Tow 2004). Among these, the hypoliths have stimulated much recent interest due to their prevalence in hot and cold deserts (Warren-Rhodes et al. 2006, 2007; Pointing et al. 2007, 2009; Wood et al. 2008; Wong et al. 2010). The associated translucent rock, most commonly quartz or marble, allows transmission of sufficient light to support photosynthesis at a depth where other stressors such as moisture availability, UV irradiance and substrate stability are sufficiently minimized to allow the development of a microbial community (Cary et al. 2010).

Morphological studies have indicated that cyanobacteria are dominant in most hypoliths studied to date. In some hot arid deserts, hypoliths are colonized only by *Chroococcidiopsis* sp. (Warren-Rhodes et al. 2007), whilst in others, a more diverse range of taxa have been identified (Tracy et al. 2010). Polar hypoliths comprise a relatively diverse cyanobacterial assemblage comprising various Oscillatoriales, *Aphanocapsa*, *Aphanothece*, *Chroococcidiopsis* and *Gloeocapsa* morphotypes (Broady 1981, 2005; Cockell and Stokes 2004). Culture-independent molecular studies have revealed a greater cyanobacterial diversity (Wood et al. 2008) than identified by microscopy and have indicated the presence of diverse bacterial phylotypes (Pointing et al. 2009; Khan 2009). The hypolithic communities of the Dry Valleys region have been shown to be quite distinct from surrounding soil biota in the higher inland valleys (Pointing et al. 2009), whilst at lower altitudes, they share more commonality with surrounding edaphic microbial communities (Wood et al. 2008).

A fascinating recent discovery was the existence of distinct morphological classes of hypoliths from Miers Valley in the McMurdo Dry Valleys (Cowan et al. 2010). These were clearly delineated into Type I hypoliths dominated by cyanobacterial growth, Type II hypoliths dominated by fungal mycelia and Type III hypoliths dominated by mosses (see Fig. 1). The determinants of these different types of hypolithic communities are unknown although it has been proposed that they may represent successional stages (Cowan et al. 2010). In this study, we sought to identify the range of distribution for Type I, II and III hypoliths across the snow-free terrain of the Miers Valley, with particular reference to altitude (valley floor and valley slopes), aspect (north–south-facing slopes) and selected micro-environmental variables.

Methods and materials

Site and survey methods

The field location in the McMurdo Dry Valleys (Miers Valley) is a wide east–west-orientated valley (~11 km

in length and between 1.5 and 2.5 km wide) flanked by high northern and southern ranges (170–1,075 m altitude). The valley lies between the latitudes 78°06'S and 78°07'S and longitudes 163°44'E and 164°12'E (valley central coordinates: 78°05'S, 163°45'E). Hypolithic colonization was identified visually on white quartz and marble pebbles in the desert pavement. Sampling was undertaken at approximately 200-m intervals along a total traversed distance of approx. 36 km. At each site, sampling involved visual searching for 5 min/person to ensure equal search effort (and time). A series of transect lines were employed to provide regional and altitudinal coverage of the upper Miers Valley (see Fig. 2). These transects reflected terrain that could be safely traversed on foot and effort was made to include a variety of topographic features, including valley floor and slopes with a variety of aspects, and sites close to the potential sources of liquid water. All data were collected during the austral summer from 21 November 2009 to 17 December 2009.

Physical monitoring

For each hypolithon, the following were recorded in the field: Type I, II or III according to Cowan et al. (2010); GPS location and altitude (Garmin 60C) that was later integrated with a Geographic Information System (ArcView GIS v 9.3.1; ESRI, USA) to produce a distribution map; Rock dimensions (L × W × D; using a Vernier calliper); Incident and transmitted photosynthetically active radiation (PAR, 400–700 nm) (Licor Li-189 PAR sensor, Licor Inc, Lincoln, NA); Incident and transmitted UV_A and UV_B irradiance (UVX radiometer, UVP Inc, Upland, CA). Transmitted PAR, UV_A and UV_B were measured by placing the rock on the sensor (a collar of plasticine was used to prevent light leakage) and averaging readings from four 90° orientations. In addition, soil samples (<10 g) were also recovered from directly below each hypolithon into air-tight vials for subsequent water content analysis. Gravimetric moisture content was determined in the laboratory after heating to 105°C and re-weighing to constant dry weight over 24 h.



Fig. 1 Representative examples of type I cyanobacterial (a), type II fungal (b) and type III moss (c) hypoliths

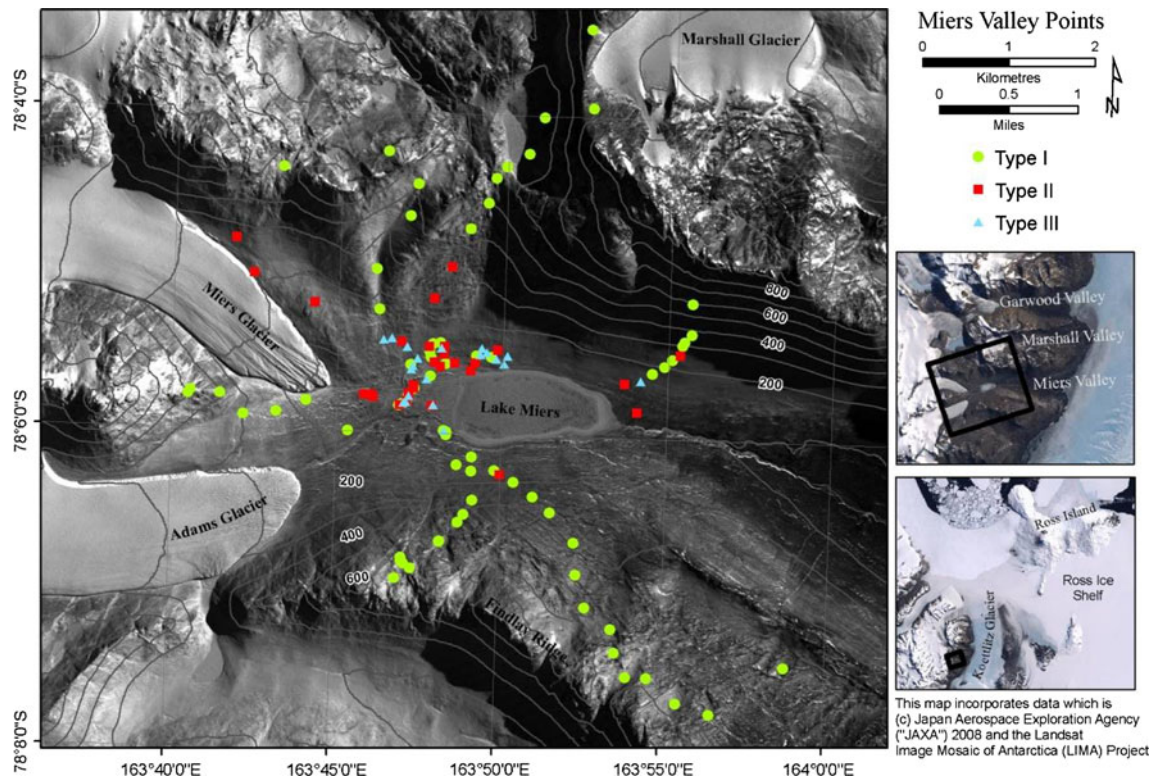


Fig. 2 GIS satellite map of the upper Miers Valley (in relation to the immediate coastal region and Ross Island (insets)) showing the distribution of different hypolithon types

Statistical analysis

All analyses were performed using PRIMER v6.1.6 (Clarke and Warwick 2001). ANOSIM (PRIMER v6.0) was used to determine whether each variable was significant in determining the distribution of Type I, II, III hypolithons. Significance was tested against 100 permutations. Multiple rank correlations (BEST, PRIMER v6.0) were used to determine the relative importance of variables alone and in combination.

Results and discussion

Quartz and marble substrates were ubiquitous throughout Miers Valley. These rocks form a niche for hypolithic refuge communities. An extensive survey of the valley floor, and north- and south-facing slopes revealed a wide distribution for colonized rocks (Fig. 2). However, the distribution of the three types was not homogeneous. The cyanobacterial Type I hypolithons represented the most frequently encountered colonization (74/126). These Type I hypolithons occurred throughout the valley floor and at all altitudes examined (171–824 m). The fungal Type II hypolithons colonized the substrates with markedly lower frequency (32/126). These Type II hypolithons were

restricted to the valley floor and lower slopes (170–415 m) with a south-facing aspect. Unlike Type I hypolithons, the fungal biomass of Type II hypolithons formed an extensive network in the soil surrounding the colonized rocks (Fig. 1). Field observations suggested that the Type II biomass stabilized the soil matrix surrounding colonized rocks. Type III moss-dominated hypolithons were least frequently encountered (20/126). These were restricted to a relatively narrow range at lower altitudes (171–257 m) on the valley floor and south-facing slopes. Unlike Type I and Type II hypolithons, which were attached to the rock substrate, Type III moss hypolithons were clearly integrated with the underlying soil substrate rather than the rock surface (Fig. 1). We acknowledge that in a heterogeneous terrain such as an Antarctic Dry Valley, various microclimates at different altitudes will inevitably exist. Such microclimates would create opportunities for colonization that may counter the patterns observed in this study. For example, we have observed that lake margins and areas of snowmelt at relatively high altitudes support extensive cyanobacterial surface crusts although these are absent elsewhere.

In order to begin to understand the environmental drivers of this interesting distribution pattern among Type I, II and III hypolithons, we measured substrate-related (PAR, UVA, UVB transmittance, rock dimensions) and environmental variables (location, altitude, aspect, soil

Table 1 Colonization frequency and abiotic factors for hypoliths throughout Miers Valley, Antarctica

Hypolith type	Number of colonized rocks	Aspect	Mean altitude (range) (m)	Mean transmittance (range) (%)			Soil moisture (range) (%)
				PAR	UV-A	UV-B	
I	74	VF, N, S, E, W	393 (168–824)	1.0 (0.1–12.5)	0.5 (0–2.5)	0.1 (0–6.4)	0.99 (0.14–7.32)
II	32	VF, N, S	220 (163–415)	1.9 (0.2–7.2)	0.7 (0–2.6)	0 (0–0.5)	0.24 (0.14–0.62)
III	20	VF, S	199 (170–257)	1.9 (0.5–5.2)	0.7 (0–2.0)	0.1 (0–0.1)	0.47 (0.16–3.23)

VF valley floor, N north-facing slope, S south-facing slope, E east-facing slope, W west-facing slope

moisture) (Table 1). Multivariate analyses of the possible influence of these variables on the type of colonization were conducted. A striking difference in the level of PAR transmitted by rocks supporting different hypolithon types was evident (ANOSIM, global $R = 0.17$, $P = 0.001$). Notably, the Type I cyanobacterial hypolithons colonized rocks with approximately 50% lower PAR transmittance than fungal or moss hypolithons. Similarly, UVA transmittance was significant in explaining whether a rock was colonized by Type I, II or III hypolithons (ANOSIM global $R = 0.111$, $P = 0.003$). All colonized rocks filtered near 100% of all UVB and so this variable could not explain differences in colonization, although it can be reasoned that effective UVB exclusion is a prerequisite for any colonization in view of its harmful effects on hypolithic microorganisms (Billi et al. 2000). The average dimensions of colonized rocks were not significantly different between hypolithon types.

The statistical analyses revealed a significant effect of altitude (ANOSIM global $R = 0.06$, $P = 0.034$) and aspect (ANOSIM global $R = 0.092$, $P = 0.001$) in determining hypolith type. Our data indicated a strong signal for declining complexity of hypolith communities with increasing altitude. The restricted distribution of eukaryotic hypolithons (Types II and III) to lower and south-facing slopes may reflect a requirement for relatively higher moisture availability and it has been postulated that this is partly derived from the melting of subsurface permafrost at lower altitudes (Cary et al. 2010). Soil moisture content of soils did not vary significantly with altitude or hypolith type. However, our soil moisture data reflect only a single point in time and so has limited ecological value (it was not significant in explaining hypolith types). Ongoing long-term environmental monitoring studies (<http://nztabs.ictar.aq/dv-geology.php>) will help to elucidate the abiotic drivers of diversity in the Dry Valleys. At altitudes above 415 m, only Type I cyanobacterial hypolithons were encountered, although inconclusive evidence for other types in sheltered niches at higher altitudes suggests more extensive landscape studies are necessary to validate this. We envisage that higher altitudes impose greater xeric stress to subsoil communities than lower altitudes, and extensive surveys of soil moisture in the McMurdo Dry

Valleys support this (Campbell et al. 1997). This is interesting since we observed an abundance of above-ground epilithic lichen (e.g. *Buellia* spp.) at higher altitudes, suggesting that above-ground niches experience greater moisture input at higher altitudes in this valley.

A combined statistical treatment (BEST analysis) including all variables from both substrate and environment revealed that the combination of variables that most satisfactorily explained the distribution of Type I, II and III hypolithons was PAR + UVA + altitude + aspect ($pw = 0.194$). This points to the interaction of a complex set of variables, both substrate and climate related, in determining hypolithon distribution.

A previous study suggested that Type I, II and III hypolithons constituted stages in a community succession (Cowan et al. 2010). Our data have identified potential environmental constraints upon such a succession. Substrate availability is not limiting since abundant colonizable but uncolonized rocks occur throughout the valley. We propose that the relatively severe micro-environmental conditions at high altitudes prevent the formation of the more sensitive Type II and III hypolithons. Conversely, under the more 'benevolent' conditions of the valley floor, these constraints are mitigated and all three hypolithic community types may develop.

This survey of hypolithon community distribution in Miers Valley provides a clear example of niche partitioning and altitudinal stratification, and mirrors pattern for higher plants in polar regions (Holtmeier and Broll 2005). However, whereas altitudinal stratification of higher plants is driven principally by temperature, our data suggest that the principal drivers for hypolithic community stratification in Miers Valley are complex. In hot deserts, both soil water content and temperature dictate the limits of diversity (Pointing et al. 2007) and metabolic activity (Tracy et al. 2010) and presumably community development processes, and these are likely also the principal drivers of biological processes in cold deserts such as Miers Valley.

Acknowledgments This research was undertaken under the auspices of the South African Antarctic Research Project, Australian Antarctic Division (ASAC 2355) and the Waikato University Antarctic Terrestrial Biology Research Program. We thank Irfan Jones and Brian Storey (Gateway Antarctica, Univ. of Canterbury, NZ) for

preparing Fig. 1. The authors gratefully acknowledge funding from the National Research Foundation (SA), the Hong Kong Research Grants Council (7733/08MM), Antarctica New Zealand and the NZ Foundation for Research Science & Technology (Terrestrial Antarctic Biocomplexity Survey, nzTABS).

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