Living strategy of cold-adapted fungi with the reference to several representative species

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ABSTRACT
Our planet is dominant with cold environments that harbour enormously diverse cold-adapted fungi comprising representatives of all phyla. Investigation based on culture-dependent and independent methods has demonstrated that cold-adapted fungi are cosmopolitan and occur in diverse habitats and substrates. They live as saprobes, symbionts, plant and animal parasites and pathogens to perform crucial functions in different ecosystems. Pseudogymnoascus destructans caused bat white-nose syndrome and Ophiocordyceps sinensis as Chinese medicine are the representative species that have significantly ecological and economic significance. Adaptation to cold niches has made this group of fungi a fascinating resource for the discovery of novel enzymes and secondary metabolites for biotechnological and pharmaceutical uses. This review provides the current understanding of living strategy and ecological functions of cold-adapted fungi, with particular emphasis on how those fungi overcome the extreme low temperature and perform their ecological function.

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1. Introduction
Cold ecosystems are dominant in our planet and the temperatures of almost 85% of earth is permanently or seasonally below 5°C ranging from deep sea to alpine and from Antarctica to Arctic regions (Hassan et al. 2016). Cold conditions, together with other limiting factors (e.g. low water and nutrient availability, high hydrostatic pressure and oxidative stress, high solar irradiation), have a strong influence on whether a certain organism can survive or even successfully thrive in a given habitat (Margesin and Miteva 2011).

The classical definitions based on thermal dependence of growth kinetic parameters (Morita 1975) are used to classify cold-adapted organisms. Accordingly, psychrophiles have been defined as species that can grow at or below 0°C, with optimum growth temperatures (OGTs) of ≤15°C and maximum growth temperatures (MGT) of ≤20°C, while psychrotolerants can grow close to 0°C, with OGT >15°C and MGT >20°C. However, above definition is ambiguous and questionable to emphasise a MGT as an indicator of how well an organism is adapted to the cold habitat, because the temperature limits have been arbitrarily selected and do not correspond to clear separation of biological processes or environmental conditions. The terms stenothermal and eurythermal have also been proposed for organisms that grow over narrow and wide temperature ranges, respectively. "True" or "obligate" psychrophiles can be classified as stenothermal psychrophiles, whereas "facultative" psychrophiles or "psychrotrophs" can be classified as eurythermal psychrophiles (Russell 2006). Such a definition takes into account the fact that cold-adapted microorganisms with wide range of growth temperature are much more abundant in cold environments, probably because they can tolerate a broad range of temperature. Although concept of stenothermal and eurythermal psychrophiles seems more concise, classical concepts are still widely accepted. In this review, we will also use the general term psychrophiles with narrower range of growth temperature.

2. Cold-adapted fungi and their living strategies
Current knowledge about the cold-adapted fungi has shown that even the most extreme cold habitat harbours enormously diverse and metabolically
active fungal communities that constitute a large portion of low-temperature biodiversity. To survive in the harsh environments, fungal strains have developed series of living strategies and function as saprobes, symbionts, plant and animal parasites and pathogens to perform various ecological roles.

2.1. Fungal investigations in cold environments

Study on fungi in cold environments can be traced to the late nineteenth century (Bommer and Rousseau 1905; Brown 1906). Cold-adapted fungi belong to different phyla which have been reported from a wide variety of substrates from a broad geographical locations and diverse habitats.

The North and South Poles represent the coldest, driest and most inhospitable habitats in our planet. Paleomycological and paleoecological investigations have indicated that fungi have presented in Antarctica since at least the Permian period because diverse fossil fungi have been found from the Triassic and Jurassic Periods (Stubblefield and Taylor 1983; Taylor and Osborne 1996; Harper et al. 2012). In general, the fungal communities of Antarctic soils are dominated by filamentous ascomycetes and basidiomycete yeasts (Connell et al. 2008; Arenz and Blanchette 2011). Filamentous basidiomycetes that are typically known as wood-decay fungi in temperate ecosystems have been very rarely isolated in Antarctica (Blanchette et al. 2004; Ludley and Robinson 2008). Fungi in Zygomycetes are also isolated with some frequency in Antarctic (Lawley et al. 2004). Although the fungi in Chytridiomycota were considered to be not frequently encountered, they were isolated from Antarctic lakes and ponds with improved method (Paterson 1973). Bridge and Spooner (2012) listed over 400 fungal genera and more than 1000 species that had been reported from Antarctic regions and suggested that “fungi may be the most diverse biota in the Antarctica”.

The total number of known fungal species in the Arctic is more than 4350. Timling et al. (2014) sampled soils in paired plots along the North American Arctic Transect, which spans all five bioclimatic subzones of the Arctic. A total of 7834 fungal clones were grouped into 1834 operational taxonomic units (OTUs) which were assigned into 8 phyla, 24 classes, 75 orders, 120 families and 214 genera. Ascomycota dominated the communities, followed by Basidiomycota. Among 75 families of Ascomycota, members from Verrucariaceae were most abundant. Among 36 families of Basidiomycota, Inocybaceae was the most abundant. Five families in Chytridiomycota and one family in each of Zygomyctea, Glomeromycota, Blastocladiomycota and Neocallimastigomycota were detected, while Cryptomycota were only identified at the phylum level.

Fungi isolated from deep seas were first reported nearly 50 years ago (Roth et al. 1964), then a great number of fungi including some novel species have been published by both conventional culture-dependent (Raghu kumar et al. 2004; Gadanho and Sampaio 2005; Damare et al. 2006; Nagahama et al. 2006; Le Calvez et al. 2009; Singh et al. 2010) and culture-independent methods (Lai et al. 2007; Le Calvez et al. 2009; Nagano et al. 2010). Le Calvez et al. (2009) reported striking differences in their comparison of deep-sea fungal diversity assessed by culture-dependent and culture-independent methods. Generally, ascomycetes can be frequently and easily isolated in deep-sea environments, but chytrids and other basal fungi may be missed because many chytrids can not be isolated on solid growth media, especially those to which chloramphenicol has been added (Gleason and Marano 2011).

The Qinghai–Tibet Plateau, often called the “world’s roof” or “the third pole”, is the highest and largest low-latitude region with permafrost and glaciers in the world. The high elevation and low latitude make the Qinghai–Tibet Plateau a unique alpine ecosystem which possesses substantial new fungal species. Early mycology-based investigations mainly focused to macrofungi. Mao and Jiang (1993) investigated the macrofungi with commercial values in Tibet and described that 588 species belonged to 46 families, 173 genera. Compared with the polar regions, cold-adapted fungi in the Qinghai–Tibet Plateau were relatively poorly studied with the exception of the Chinese caterpillar fungus. A systematic survey on cold-adapted fungi had been conducted by Wang et al. (2015), with more than 1400 fungal strains isolated and 150 species including 6 new species identified and described from glaciers on the Qinghai–Tibet Plateau. Among those species, Phoma sclerotoides and Pseudogymnoascus pannorum were the most dominant species. Hassan (2015) isolated 77 fungal strains representing 24
fungal genera from Batura Passu and Siachen Glaciers in Hindu Kush and Karakoram mountains in Pakistan.

Except for being common in alpine, Arctic, Antarctic and deep-sea environments, cold-adapted fungi are also found in man-made habitats such as refrigerated environments where temperatures were often at or below 0°C. Many fungi isolated from the cold environments are cosmopolitan, i.e. Phoma herbarum is frequently isolated from the permafrost (Singh et al. 2006), as well as from soils of the temperate and subtropical zones (Domsch et al. 1980). Most of the cold-adapted fungi have wide growth temperature ranges. Epicoccum purpurascens is an example to have a minimum growth temperature at −3 to −4°C, an optimum at 23–28°C and a maximum temperature for growth at 45°C (Domsch et al. 1980). Only a few cold-adapted fungi with narrow growth temperature ranges were reported (Table 1).

2.2. Living strategies of cold-adapted fungi

2.2.1. Saprobides

Fungi are pivotal for the cycling of carbon and nutrients in cold ecosystems and the saprotrophic fungi actively decompose organic matters through excretion of a variety of hydrolases. A group of cold-adapted fungi decompose woody structures and artefacts left by the early polar explorers in Antarctic. Blanchette et al. (2004) first reported an unusual form of soft rot decay caused by Cadophora species which can cause degradation of the historic huts and artefacts. This type of decay has subsequently been found to be prevalent in historic woods and in soils from the immediate vicinity of the huts at many Antarctic locations and variety of filamentous fungi and yeasts such as Cadophora, Cladosporium, Cryptococcus and Geomyces species were discovered with a high frequency (Arenz et al. 2006; Arenz and Blanchette 2009; Blanchette et al. 2010). Although there are few woody plants on the Antarctic continent, researches provide strong evidence that Antarctic fungi are able to colonise and degrade-introduced wood and other organic materials (Blanchette et al. 2004, 2010). Held et al. (2005) found that Antarctic summer above 0°C and 75% relative humidity occurred for many weeks, which are conducive for fungal growing inside the historic huts on Ross Island. Air sampling of fungal spores in the interior and exterior areas of the historic huts demonstrated that Antarctomyces psychrotrophicus Cladosporium cladosporioides, Geomyces sp. and Pseudeurotium desertorum dominated the air environments within the huts and fungal spores are widespread particularly in the interiors of the huts (Duncan et al. 2010). Blanchette et al. (2010) reported that large numbers of degradative fungi colonised the exterior wood of Shackleton’s Cape Royds hut, presumably due to large carbon and nutrient input from the historic materials as well as introductions from the penguin colony nearby. Both culture-dependent and culture-independent methods demonstrated that low temperature may not adversely affect these fungal species unless they were out-competed by new arrivals or unfavourable changes in ecosystem domination occurred (Farrell et al. 2011).

A special group of fungi extensively studied in Antarctic is the rock-inhibiting fungi, which constitute an important part of epilithic and endolithic communities (Selbmann et al. 2014). To cope with the harsh conditions of the outside, these fungi adopt a particular lifestyle and live as so-called cryptendolithic and chasmoendolithic (Golubic et al. 1981) in microscopic niches inside the rocks (Nienow and Friedmann 1993; De Los Ríos et al. 2002). These fungi living on or within the rocks share similar morphological and physiological characteristics, such as slow expanding cauliform-like colony, barely differentiated structures and the presence of thick and heavily pigmented cell walls. Their morphological features are suitable to withstand harsh environmental conditions; for example, the meristematic growth allows them to keep optimal volume/surface ratio in order to minimise exchange with external stressors. Another remarkable character is the production of extracellular polymeric substances (EPS) which is involved in the protection against cycles of desiccation, freezing and thawing (Selbmann et al. 2002, 2005); EPS surround fungal structures (hyphae and conidia), as observed both in nature and in culture, create and maintain the proper micro-environmental conditions in the biofilms inside the rocks buffering pH and nutrient availability fluctuations (De Los Ríos et al. 2002). The Antarctic genus Cryomyces with highly pigmented structures showed a higher resistance to UV radiation compared with an Antarctic strain of
filamentous species *Arthrobotrys ferox*. However, a European strain of *Arthrobotrys oligospora* is more sensitive to UV than *A. ferox* (Zucconi et al. 2002; Onofri et al. Forthcoming). Most of the Cryptoendolithich black fungi show an extreme simplification of their structures and some are even unable to produce complex and well-differentiated reproductive structures, and propagules are produced directly from disarticulation of toruloid pre-existing hyphae. Some of them are mostly yeast-like organised and can formally conclude their life cycles with the production of a single cell being itself a resistant propagule. These high levels of simplification match very well with the prohibitive environment they colonised where the climatic conditions for active life happen just few days a year.

Nearly 90% of the volume of marine habitats is below 5°C and the deep seas which constitutes the largest unexplored habitat on our planet often have temperatures from −1 to −4°C (Frisvad 2008). Deep-sea sediments appear to be one of the potential niches for hidden fungal diversity and the fungal roles in the deep-sea sediments have remained neglected mainly due to the fact that they are not easily observed (Damare et al. 2008). Increased sighting of fungi after treating the deep-sea sediments with chelating agent suggested that fungi in deep-sea sediments may be involved in humic aggregate formation (Liu et al. 2002). Hyphal sheaths often have an adhesive role in the attachment of fungal mycelium to surface and particle entrapment (Hyde et al. 1986). Through concealing inside the microaggregates, which prevent the extracellular enzymes from diffusing away from the cells secreting it, these humic–enzyme complexes have an important role to play in overall nutrient dynamics of the sediments (Burns 1978). Protease is one of the several extracellular enzymes playing a major role in their nutritional requirements. Damare et al. (2006) demonstrated that 11% of the total fungi isolated from deep-sea sediments of Central Indian Basin showed low temperature-active protease production. The proteases from deep-sea fungi could be a potential source in the search for detergent enzymes (Raghukumar et al. 2009). Fungal polygalacturonases (PGases) are useful enzymes for clarification of fruit juices in the food industry. Two novel and active endopolygalacturonases at 0–10°C were purified from the culture supernatant of a deep-sea yeast *Cryptococcus* sp. which was isolated from the Japan Trench at a depth of 4500–6500 m (Miura et al. 2001; Abe et al. 2006). The hydrolytic activity of PGases remained almost unchanged up to a hydrostatic pressure of 100 MPa at 24°C. Interestingly, this strain was tolerant to CuSO₄ up to a concentration of 50 mM and showed high activity of superoxide dismutase, an enzyme

### Table 1. Cold-adapted fungi with narrow growth temperatures (psychrophilic fungi).

| Taxa                  | Growth temperature | Location/Substrate/Host                                                                 | Reference                  |
|-----------------------|--------------------|----------------------------------------------------------------------------------------|----------------------------|
| Mucor strictus        | OGT below 10°C     | Alpine soils                                                                            | Schipper (1967)            |
| Coprinus psychromorbidus | OGT between −8 and −3°C | Plant pathogen infecting cereals (winter wheat, oats), grass and conifers | Traquair and Smith (1982) |
| Typhula ishiokianesi  | OGT at 10°C        |                                                                                         | Hoshino et al. (1998)      |
| Typhula incarnata     | OGT between 5 and 10°C |                                                                                         | Nakajima and Abe (1994)    |
| Microdochium niveale  | OGT between 15 and 18°C |                                                                                         |                            |
| Sclerotinia borealis  | OGT between 4 and 10°C |                                                                                         |                            |
| Rhodotorula himalayensis | OGT at 4°C        | Soils of Himalayan mountain ranges                                                       |                            |
| Phoma herbarum        | OGT at 4°C         | Endophytic fungi of trees                                                                 | Moghaddam and Soltani (2014) |
| Humicola marvinii     | OGT below 15°C, MGT at 20°C | Soils in the Maritime Antarctic                                                        | Richard et al. (1997)      |
| Pseudogymnoascus destructans | OGT at 4°C | Hibernant bats                                                                          | Gargas et al. (2009)       |
| Pseudogymnoascus pannorum | OGT at 5°C | Soil and litter                                                                          | Flanagan and Scarborough (1974) |
| Thelebolus microsporus | –                  | Pangong Lake, Himalayan region                                                           | Anupama et al. (2011)      |
| Mrakia robertii       | MGT below 20°C     | Antarctic and alpine soils                                                                | Robin et al. (2010)        |
| Mrakia blolocation    | MGT below 20°C     | Northern Siberian glacier sediment                                                        | Margesin and Fell (2008)   |
| Mrakia cryononiti     | MGT below 20°C     |                                                                                         | Xin and Zhou (2007)        |
| Mrakia psychrophila   | OGT 10, MGT 18     | Antarctic soils                                                                          | Margesin et al. (2007)     |
| Rhodotorula psychrophila | OGT below 15°C | Alpine soils                                                                             | Wang et al. (2015)         |
| Tetrocladium ellipsoideum | OGT below 15°C | Glacier soils in Qinghai–Tibet Plateau                                                   |                            |
| Tetrocladium globosum | OGT below 15°C     |                                                                                         |                            |
| Tetrocladium psychrophilum | OGT below 15°C, MGT at 20°C |                                                                                         |                            |

OGT: Optimum growth temperature; MGT: maximum growth temperature.
responsible for scavenging superoxide radicals (Abe et al. 2001).

2.2.2. Plant mutualists

Lichen and mycorrhiza are ubiquitous fungal mutualism form and also dominant in the cold habitats. Mycorrhizal fungi play an important role in the functioning of cold ecosystems, where low water and nutrient availability restrict plant growth and productivity (Timling and Taylor 2012). The complex mycorrhizal structure, consisting of plant root and fungal hyphae, could enlarge the surface area for absorbing water and nutrients from soil, explore for nutrients more extensively than vascular-plant roots and mobilise organically bound nutrients. The fungal association provides the fungus direct access to the plant’s carbohydrates, while the plants gain benefits from improved mineral and water absorption through the fungal mycelia. It is estimated that 86% of the N obtained by Arctic plants is via mycorrhizal, notably ectomycorrhizal (ECM) fungi (Hobbie and Hobbie 2006). EMF genera were the most frequent and species-rich associated with plants in the Arctic (Bjorbaekmo et al. 2010; Deslippe et al. 2011; Geml et al. 2012). Coupled with previous sporocarp collections (Gardes and Dahlberg 1996), the frequently occurred fungal genera that either lack or produce sporocarps are Thelephora, Sebacina and Clavulina. EMF resulted from analysis of root tips and soil clones in Arctic revealed their extremely high richness (Bjorbaekmo et al. 2010; Geml et al. 2012), comparing with previous estimation based on surveys of above-ground ECM sporocarps. A large number of OTUs were detected in Arctic, with 137 OUTs on the roots of Dryas octopetala along a latitudinal gradient from Southern Norway to Svalbard (Bjorbaekmo et al. 2010), 73 ECM basidiomycete OTUs in soils on Svalbard (Geml et al. 2012) and 224 OTUs in the roots of three co-occurring species in the Low Arctic (Walker et al. 2011).

Lichens, the intimate and stable association between fungi and green algae/cyanobacteria, are the visually prominent life forms in most extreme ecosystems. In harsh environments, they have the general ability to photosynthesise at sub-zero temperatures, tolerance to low water potentials and high radiation levels, and the ability to utilise sublimed water from ice or air (Green et al. 1999). Lichens in the Antarctic ecosystems have been studied thoroughly. Some of the Antarctic species have a very wide geographic distribution and can be found in habitats of the extreme North or in high mountains (Sancho et al. 1999; Øvstedal and Lewis Smith 2001). Communities of chasmoendolithic lichens are common in granitic rocks. Cells of both algal and fungal symbionts occupy fissures and cracks of the lithic substrate with no clear heteromerous structure (De Los Ríos et al. 2005a). This kind of growth has been recognised and characterised for two species of Lecidea in Granite Harbour area (De Los Ríos et al. 2005b). The widespread distribution of this life-form in ice-free areas in Antarctica could be favoured by the high frequency of rock-freeze-fracturing phenomena (Cowan and Tow 2004). Remarkably, lichen associations are able to integrate photoprotective systems which provide higher resistance to oxidative damages than alga or fungus alone (Kranner et al. 2005). An increase of phenolic compounds content under UV exposition, which may prevent UV penetration into lichen thallus, as well as play a protective role as antioxidants, has also been observed (Buffoni Hall et al. 2002).

2.2.3. Endophytes

Endophytic fungi live inside healthy plants and synthesise an array of secondary metabolites that interact with and benefit their hosts. Studies dealt with fungal endophytes in cold ecosystems revealed high species diversity. Moghaddam and Soltani (2014) provided information on an endophytic association between bioactive cold-adapted fungi and trees in Cupressaceae living in temperate to cold habitats. The endophytic fungi from healthy foliar tissues of Cupressus arizonica, Cupressus sempervirens and Thuja orientalis (Cupressaceae, Coniferales) were identified, including 23 endophytic fungi in Doliomycetes. All of these fungi isolated at 4°C were able to synthesise secondary metabolites at this temperature. The evergreen Cupressaceae plants may benefit from their psychrophilic endophytic fungi during cold stress. Cold-adapted endophytic fungi associated with five dominant plant species were collected from the Baima Snow Mountain (altitude 4000–4300 m), Southwest China (Li et al. 2012). Forty-three taxa were identified based on the morphological characteristics and Internal transcribed spacer (ITS) sequences, of which Cephalosporium, Sirococcus, Penicillium and Aspergillus were the
dominant genera. Growth temperature tests indicated that 75% of the isolates from the Baima Snow Mountain were psychrotrophs and 14% were the transitional type between psychrotrophs and mesophiles, suggested that the endophytes from the Baima Snow Mountain possess a remarkable ability to adapt to cold environments.

2.2.4. Parasites

Fungal parasites are normally specialised microfungi attacking plants, other fungi and animals including human. Fungal diseases on plants are common in cold environments, such as rust fungi *Melampsora* that commonly cause mortality of willows (Parmelee 1989; Smith et al. 2004) and smuts (Ustilaginales) that parasitise plants of Cyperaceae (Scholler et al. 2003) in Arctic.

In higher latitude and high altitude regions, where winter is longer and harsh, a deep, persistent layer of snow insulates the roots and crowns of winter cereals, grasses, forages, ornamentals and shrubs, protecting them from winter injuries. However, the dark, humid environmental conditions are of favourite for the development of cold-adapted microorganisms. Snow moulds cause serious diseases of snow-covered plants when the temperature at the snow-plant interface remains around 0°C. Snow mould are taxonomically diverse and can attack not only perennial grasses and winter cereals, turf grasses and flowers, but also woody plants, such as first-year pine seedlings or the lower parts of tree branches under snow and occur commonly in high latitude regions. Generally, phytopathogenic fungi can survive in the form of spores and sclerotia, to concur the winter harsh condition, and develop mycelia under the snow cover and resume infection the following season (Smith 1993). Four different snow mould diseases caused by soil-borne fungi are pink snow mould (*Microdochium [Fusarium] nivale*), speckled snow mould (*Typhula idahoensis*, *Typhula ishikariensis* and *Typhula incarnata*), snow scald (*Myriosclerotinia borealis*) and snow rot (*Pythium iwayami* and *Pythium okanoganense*). Pink snow mould is the most widespread, occurring on wild grasses, lawns and winter wheat, but less destructive than speckled snow mould. In addition to speckled snow mould, *T. incarnata* is often found causing a root and crown rot of wheat and barley in the absence of snow cover (Matsumoto 2009).

3. Representative cold-adapted fungal species

3.1. *Pseudogymnoascus destructans*, a fatal pathogen causes bat white-nose syndrome

*P. destructans* (formerly known as *Geomycetes destructans*) is a psychrophilic fungus that causes white-nose syndrome (WNS) of hibernating and cave-roosting bats, a fatal disease that has devastated bat populations in parts of the United States and Canada. A visually conspicuous white fungus grows on the face, ears or wings of stricken bats; infiltration of the hyphae into membranes and tissues leads to severe damage (Meteyer et al. 2009). Bats that exhibit WNS have little or no fat reserves, which are essential for their survival throughout and after hibernation (Blehert et al. 2009). Although recent work on fungi associated with bat hibernacula uncovered many species of *Geomycetes* and allies, including *Geomycetes*, *Gymnostellatospora* and *Pseudogymnoascus* in the family *Pseudeurotiaceae*, *P. destructans* was demonstrated as unique pathogen of bats. The closest relatives of *P destructans* are members of the *Pseudogymnoascus roseus* species complex. There are no species phylogenetically close related to *P. destructans* providing evidence to support the hypothesis that this pathogen is non-native and invasive in eastern North America. Additional sampling from other regions of the world is necessary to better understand the evolution and biogeography of this important and diverse group of fungi (Minnis and Lindner 2013).

3.2. *Ophiocordyceps sinensis*, a valued fungus as the traditional Chinese medicine

The Chinese caterpillar fungus, *O. sinensis*, the so-called winter worm, summer grass in Chinese literature, is one of the most valued Chinese traditional medicinal fungi (Zhang et al. 2012). This fungus exhibits extremely high host specificity and colonises ghost moth caterpillars (*Thitarodes* spp.), making a parasitic complex that comprises the remains of the caterpillar and fungal sexual stroma. They are distributed in alpine regions of the Tibetan Plateau between 3000 and 5000 m as around the snow line and *O. sinensis* has an OGT at 15–18°C, but it can also survive at the temperature lower than −40°C in winter. Diverse bioactive ingredients and extensive medicinal effects (Chen et al. 2010; Lo et al. 2013) of
Chinese cordyceps have been found and they have been applied to treat a variety of ailments including cancer, impotence and fatigue (Stone 2008). Owing to the medicinal, economic, social and ecological importance, and the limited distribution mainly in China, O. sinensis had been nominated as the national fungus of China (Zhang et al. 2012).

The spatial patterns of genetic variation of Chinese cordyceps including both the parasitoidal fungus O. sinensis and its host insects indicated that O. sinensis and its host insects originated at similar divergence time and geographic regions in southern Tibet/Yunnan, followed by range expansion to their current distributions. Cophylogenetic analyses revealed a complex evolutionary relationship between O. sinensis and its host insects and both historical and contemporary events have played important roles in the phylogeography and evolution of the O. sinensis-ghost moth parasitoidism on the Tibetan Plateau (Zhang et al. 2014). O. sinensis is adapted to cold temperature with putative antifreeze proteins and mechanisms for increasing lipid accumulation and fatty acid unsaturation (Xiao et al. 2013). Recently, 31 strains of O. sinensis representing nearly all of its geographic range were analysed, and the results exhibited latitude-based population divergence and nature selection for population inhabitation towards higher altitudes on the Qinghai–Tibetan Plateau (Xia et al. 2017).

### 3.3. Mrakia psychrophila, a fungus revealing cold adaptation mechanism

*Mrakia psychrophila* was first described by Xin and Zhou (2007) from soil samples collected from Fildes Peninsula, Antarctica and its optimum and MGTs are at 10 and 18°C, respectively. The first integrated study on the genomic, transcriptomic and proteomic perspectives of *M. psychrophila* provided insights into the cold adaptation mechanism of psychrophilic fungi (Su et al. 2016). The comparative genomic analysis with that of other psychrophilic, thermophilic and mesophilic fungi indicated that *M. psychrophila* had a specific codon usage preference, especially for codons of Gly and Arg and its major facilitator superfamily transporter gene family was expanded. Transcriptomic analysis revealed that genes involved in ribosome, biosynthesis of unsaturated fatty acid and glycerol and energy metabolism were upregulated at 4°C, indicated that cold adaptation of *M. psychrophila* was mediated by synthesising unsaturated fatty acids to maintain membrane fluidity and accumulating glycerol as a cryoprotectant. In the meanwhile, genes involved in unfolded protein binding, protein processing in the endoplasmic reticulum, proteasome, spliceosome and mRNA surveillance were upregulated at 20°C, indicated that the death of *M. psychrophila* above 20°C might be caused by an unfolded protein response.

### 3.4. *P. pannorum*, a source for novel metabolites

*P. pannorum* is a soil-inhibiting fungus often associated with cold temperatures. It has been isolated from Arctic permafrost as well as the soils of Antarctica, glacier bank soils in some Asian countries (Deshmukh 2002; Arenz et al. 2006; Ozerkaya et al. 2008). This fungus maintains cell and membrane function at low temperatures by elevating levels of unsaturated fats and compounds with cryoprotectant properties such as trehalose and various polyols at low temperature (Finotti et al. 1996; Hayes and Mark 2012). *P. pannorum* is a slow-growing cold-adapted fungus, exhibiting growth below 0°C to as low as −20°C. Strains recovered from Antarctic cryopegs germinate at −2°C 2–3 weeks after inoculation. The fatty acid composition and metabolism of this species changed in response to environmental temperatures. Cultures isolated from different places exhibited morphological variations and different rates of glucose and lipid utilisation (Finotti et al. 1993, 1996).

*P. pannorum* produces a range of extracellular hydrolases including lipase, chitinase, urease and amylase (Hayes and Mark 2012). Some strains of *P. pannorum* isolated from cold habitats produce abundant cold-adapted α-amylases, which indicates its significant role as a desirable candidate in food processing. He et al. (2017) cloned the correlated gene AmyA1, and heterologously expressed it in *Aspergillus oryzae*. AmyA1 was also immobilised on magnetic nanoparticles and characterised. The detailed report of the enzymatic properties of AmyA1 gave new insights into fungal cold-adapted amylase and application study showed potential value of AmyA1 in the food and starch industries. Some bioactive metabolites also have pharmaceutical potentials, such as pannomycin, structurally similar
to a compound known to inhibit the ATPase, SecA, in the bacterial translocase pathway (Parish et al. 2009). Additional metabolites have been isolated from \textit{P. pannorum} including antimicrobial asteric acid derivatives called “geomycins”, which is active against \textit{Aspergillus fumigatus}, as well as Gram-positive and Gram-negative bacteria (Li et al. 2008).

4. Conclusions

Low temperature environments harbour large numbers of fungal species which have great ecological and physiological significance. Cold-adapted fungi are important resources for discovery of novel secondary metabolites and enzymes. There are limited fungi that have been successfully cultured from cold environments. Improved culturing methods and growth media are needed in order to isolate and culture diverse fungi from these environments, including those with unique physiologies to adapt to extreme habitats. Similarly, it is necessary to improve culture-independent methods for the enhanced detection of cold-adapted fungi, especially the development of better molecular markers for investigating true fungal diversity. The origination and evolution of some representative species that cause ecological crisis or have economic importance should be investigated in depth. Ecological function and adaptation mechanism of certain species will provide comprehensive understanding of cold-adapted fungi.

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