

Studies on diversity of higher fungi in Yunnan, southwestern China: A review[☆]

Bang Feng, Zhuliang Yang*

Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, Yunnan, China

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ABSTRACT

Yunnan is exceedingly rich in higher fungi (Ascomycota and Basidiomycota). Given that the number of fungi (including lichens) occurring in a given area is, as Hawksworth suggested, roughly six times that of local vascular plants, a total of approximately 104,000 fungal species would be expected in Yunnan. However, to date only about 6000 fungal species, including roughly 3000 species of higher fungi, have been reported from the province. Although studies on Yunnan's fungi started in the late nineteenth century, significant progress has been made only in the last forty-five years. Over the first twenty-five years of this period, studies on fungal diversity in this area have largely been about taxonomy based on morphological characters and partially on geographical distribution. Over the past twenty years, the combination of both morphological and molecular phylogenetic approaches has become the preferred method to help understand the diversity and evolution of higher fungi. This review focuses on our current knowledge of how geological, geographical, and ecological factors may have contributed to the diversity patterns of higher fungi in Yunnan. Based on this knowledge, three aspects for future studies are suggested.

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1. Introduction

Yunnan Province, located in southwestern China, covers a total area of 394,000 square kilometers, about 84% of which is mountainous. The highest point is located in the north with an elevation of 6740 m, while the lowest point is in the south with an elevation of only 76.4 m above sea level. The average altitude of the province, similar to central Yunnan, is around 2000 m (<http://www.wcb.yn.gov.cn/arti?id=2>).

The complex topography and geography, highly variable climate, luxuriant vegetation, warm and wet currents from the Indian and Pacific Oceans in summer, and other abiotic and biotic factors, provided ample refuges during the Quaternary glaciations (Sun et al., 2017), and make Yunnan a favorable region for the

growth and reproduction of higher fungi. The extremely high fungal diversity in this area has attracted much attention from mycologists both at home and abroad.

Here we review studies of this area from the late 1880s to the present, based on which an up-to-date view is provided on the patterns of diversity of higher fungi in Yunnan and the mechanisms that drive that diversity, with a special emphasis on ecological, geographical and geological factors that may have influenced the diversity of local higher fungi.

2. Brief history of fungal diversity studies

As early as the Ming Dynasty, several ancient Chinese scholars, such as Lan Mao (1397–1476) and Li Shi-zhen (1518–1593), paid close attention to fungi for medical purposes. Records show that modern mycological research in China has a history of over 100 years (Zang and Li, 2008). Studies on higher fungi in Yunnan started at the end of the 19th century. Several western missionaries and explorers collected fungal specimens, together with plant and animal samples, from Yunnan for scientific studies. For example, J. M. Delavay made fungal collections from northwestern Yunnan in the

[☆] In memory of our inspiring mentor, Prof. Dr. Franz Oberwinkler (5. 1939–3. 2018), for his outstanding contributions to mycological studies and teaching.

* Corresponding author. Kunming Institute of Botany, Chinese Academy of Sciences, Lanhei Road #132, Kunming 650201, Yunnan, China.

E-mail address: fungi@mail.kib.ac.cn (Z. Yang).

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late 1880s, which were then studied by a French mycologist, N. Patouillard (1886, 1890). *Bovistella yunnanensis* Pat. (type, FH 1343) and *Hemiglossum yunnanense* Pat. (type, FH 4884) are probably the earliest novel species of higher fungi described from Yunnan (Patouillard, 1890). However, only a limited number of works were published thereafter. It was H. Handel-Mazzetti who collected a sizeable number of fungal specimens from Yunnan during the 1910s and deposited them at the Herbarium of the Institute of Botany, University of Vienna. His collections were examined by R. Singer (Singer, 1935) and by K. Keissler and H. Lohwag (Keissler and Lohwag, 1937).

In the 1940s, Prof. F. L. Tai from National Tsing Hua University, together with his colleagues and students, carried out important studies on fungi in Yunnan (Chiu, 1945, 1948a, b; Tai, 1944; Tai and Hung, 1948). Approximately 100 new species of Amanitaceae, Boletales, Geoglossaceae, Nidulariales and Russulaceae were discovered and described in Yunnan from 1944 to 1948. Reports by Teng (1963) and Tai (1979) published the most inclusive lists for higher fungi in China at the time and have been recognized as fundamental works for mycological research in China.

Over the past 45 years, significant progress, especially by field investigators, has been made on studies of the higher fungi of southwestern China. Supported by two projects, the Comprehensive Scientific Expeditions in the Qinghai-Tibet Plateau (including the Hengduan Mountains region, 1973–1983) and the Bioresources Survey and Evaluation (1988–1990), researchers at the Chinese Academy of Sciences surveyed higher fungi in the region. During this same period, more and more fungal species were reported from southwestern China (Ying et al., 1994; Zang et al., 1996), which significantly advanced our knowledge of higher fungi in the region.

From the 1880s to the beginning of the 21st century, species of higher fungi in China were recognized based mainly on morphological characters and partially on geographical distribution (Bandoni and Zang, 1990; Dai, 1999; Horak, 1987; Maekawa and Zang, 1995; Petersen and Zang, 1990; Yang, 1997; Ying et al., 1994; Zang, 2006, 2013; Zang et al., 1996; Zhuang et al., 2001). Over the past 20 or so years, molecular phylogenetic techniques have advanced rapidly and been used to study higher fungi in Yunnan. This has helped us better understand species diversity and systematics of several fungal groups, such as Agaricales, Boletales, Helotiales, Hymenochaetales, Pezizales, Polyporales, and Russulales (Chen et al., 2011; Chen et al., 2016; Cui et al., 2016; Dai, 2010; Ge and Yang, 2017; Ge et al., 2018; Gelardi et al., 2014; Han et al., 2016; Li et al., 2009, 2014a, 2014b; Popa et al., 2014; Song et al., 2014; Vincenot et al., 2017; Wang, 2017; Wang et al., 2009, 2015; Weiß et al., 1998; Wu et al., 2016a, 2016b; Zeng et al., 2013; Zhang and Dai, 2005; Zhang et al., 2004; Zhao et al., 2013a; Zhuang et al., 2016, 2017).

3. General features of higher fungi diversity in Yunnan

3.1. Two prominent regions of diversity in Yunnan

There are two regions rich in fungal diversity in Yunnan. One is the Eastern Himalayas and Hengduan Mountains located in northwestern Yunnan; the other is the tropical region of southern and southwestern Yunnan.

The Eastern Himalayas and Hengduan Mountains region is one of the world's 35 biodiversity hotspots (Mittermeier et al., 2000, 2005; Myers et al., 2000). The southern boundary of this region reaches down to Yunnan. Over 4000 fungal species, representing about 40% of known fungal taxa in China, have been reported in this area (Yang, 2005). About 500 type specimens of higher fungi were collected from this region and deposited in the Mycological Herbarium of the Institute of Microbiology (HMAS), the Cryptogamic

Herbarium of Kunming Institute of Botany of the Chinese Academy of Sciences (HKAS), and the herbarium of Beijing Forestry University (BJFC).

The Indo-Burma biodiversity hotspot partially overlaps the southern and southwestern parts of Yunnan, areas with typical tropical climate and vegetation (Myers et al., 2000; Yang, 2005). Over the last forty years, many studies on higher fungi in tropical Yunnan have been carried out (Yang and Zang, 2003; Zang, 1980, 1987; 2006, 2013; Zang et al., 1996; Zeng et al., 2013; Zhuang, 2001). In total, 5056 species of 1192 genera of higher fungi (including lichens) from the whole of tropical China were recorded in a monograph edited by Zhuang (2001). Some of these fungi are present only in tropical Yunnan (Li et al., 2015; Yang, 2000, 2015; Qin et al., 2014; Yang and Zang, 2003). Recently, new taxa of Agaricaceae and Cantharellaceae were described from tropical Yunnan (Ge and Yang, 2017; Shao et al., 2016).

3.2. Improved understanding of species diversity in higher fungi from Yunnan

To date, 17,427 species of vascular plants are known from Yunnan, including numerous endemic species (Zhang and Lu, 2017; Chen et al., 2017). Given that the numbers of fungi (including lichens) occurring in a given area are estimated to be about six times that of vascular plants (Hawksworth, 1991, 2001), about 104,000 fungal species may exist in Yunnan. Currently, about 6000 fungal species, including around 3000 species of higher fungi, have been reported from Yunnan (Yang, 2005; Yang et al., 2017b), suggesting that 95% of fungal species in Yunnan are likely undocumented.

Here we present studies on boletes (especially on the family Boletaceae) as an example to show that species diversity of higher fungi in Yunnan has been significantly underestimated. During the 1940s, Prof. W. F. Chiu carried out an excellent taxonomic study on Boletales in Yunnan and published one monograph on this order, recording over 54 species, including 46 species (and 18 novel species from Yunnan) of Boletaceae (Chiu, 1948a). From 1978 to 2006, Prof. M. Zang from the Kunming Institute of Botany, Chinese Academy of Sciences and Prof. J. Z. Ying from the Institute of Microbiology, Chinese Academy of Sciences, together with their colleagues, described at least 27 novel species of Boletaceae from Yunnan (for references, see Fig. 1). With advances in molecular

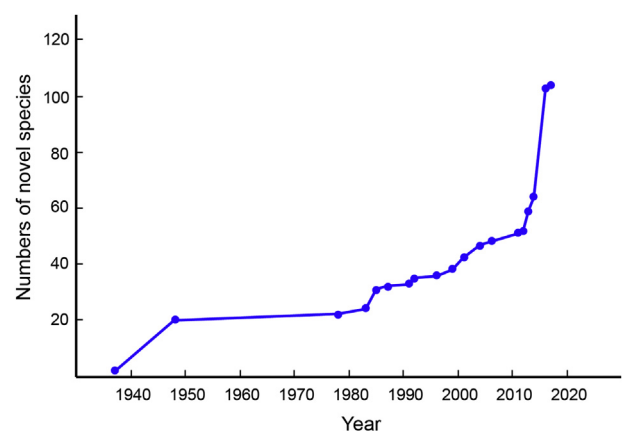


Fig. 1. Numbers of novel species within Boletaceae described from Yunnan since 1937. Data were retrieved from Chiu (1948), Keissler and Lohwag (1937), Li et al. (2011), Li et al. (2014b), Wen and Ying (2001), Wu et al. (2016a, 2016b), Ying (1987), Ying and Ma (1985), Zang (1983), Zang (1985), Zang (1991), Zang (1992), Zang (1996), Zang and Petersen (2004), Zang and Zeng (1978), Zang and Zhang (2004), Zang et al. (1999), Zang et al. (2001), Zang et al. (2006), Zeng et al. (2017), Zeng et al. (2013), Zhao et al. (2014) and Zhu et al. (2014).

phylogenetics over the last ten years, the number of new species within Boletaceae in Yunnan has exploded. Since 2011, 87 new species have been added to this family (Cui et al., 2016; Li et al., 2011; Wu et al., 2016a, 2016b; Zeng et al., 2017; Zhu et al., 2014), 56 of which were described based on type specimens collected from Yunnan (Fig. 1). At the same time, many species found in Yunnan, traditionally proposed to be conspecific with those reported from Europe and North America, were clarified as endemic to this area, China or East Asia (Cui et al., 2016; Feng et al., 2012). For example, a total of 24 porcini species were reported from China, most from Yunnan, based mainly on morphological features (Chiu, 1948a; Zang, 2006). However, most species reported in Chiu's and Zang's work were named according to descriptions of species found from Europe, North America or tropical Asia. Only two species, *Boletus violaceofuscus* W.F. Chiu and *B. reticuloceps* (M. Zang et al.) Q.B. Wang & Y.J. Yao, were originally described from Yunnan and Sichuan, respectively (Chiu, 1948a; Zang et al., 1993). Recent research (Cui et al., 2016; Feng et al., 2012; Zeng et al., 2014), which integrated molecular phylogenetic analyses and more detailed morphological observations that specifically emphasized the structure of pileipellis, revealed that the Chinese porcini have diverged greatly from their European and North American relatives. Fifteen species, 12 new to science, were subsequently documented (Cui et al., 2016; Dentinger, 2013; Feng et al., 2012; Zeng et al., 2014). Three of the 12 new species, namely *Boletus bainiugan* Dentinger, *B. shiyong* Dentinger and *B. sinoedulis* B. Feng et al., are traditionally collected and consumed by local people, widely traded in free markets, and exported to Europe. However, they were named as *B. edulis*, a species originally described from Europe, for a very long time (Chiu, 1948a; Zang, 2006). Similarly, one famous delicacy called Dahongjun, or "big red mushroom," which is consumed and traded in southern Yunnan and adjacent areas, was previously considered a European species, *Russula vinosa* Lindblad (Wang et al., 2009). However, it has been shown that this delicacy belongs to a species complex of at least three cryptic species (Li et al., 2010), and the species with a distribution in southern Yunnan was formally described as *R. griseocarnosa* X.H. Wang et al. (Wang et al., 2009). To correctly identify higher fungi in Yunnan remains a huge challenge, especially for species not commonly consumed by humans.

Changes were also made in the systematics of some groups of higher fungi. For example, Wu et al. (2014) constructed a comprehensive molecular phylogenetic framework of the family Boletaceae by using sequences of four gene fragments, along with which four new subfamilies were described. Close to the same time, over 15 new genera were proposed (Hosen et al., 2013; Li et al., 2011, 2014b; Wu et al., 2016a, 2016b), seven of which were with type locations in Yunnan. This research has largely improved our knowledge of the classification of Boletaceae. For instance, 18 species described by Prof. W. F. Chiu (Chiu, 1948a) have recently been transferred to ten genera, nine of which were proposed after 2011 (Li et al., 2011; Wu et al., 2016a; Zhang et al., 2017; Zhu et al., 2015).

4. Floristic relationships of higher fungi in Yunnan

The diversity of higher fungi in Yunnan may be the result of many factors, including but not limited to (1) geological events, (2) geographical factors, (3) diverse environments, and (4) co-evolution with host plants (Yang, 2005). The floristic relationships of higher fungi in Yunnan to other parts of the world were elucidated mainly based on morphological features in the past (Yang and Zang, 2003; Zang, 1980, 1987). However, with the inclusion of more and more molecular data in phylogenetic analyses since the late 1990s, our understanding of the evolution of higher fungi in

Yunnan, as well as those in China, East Asia and other continents of the world, has advanced significantly. Now, it is possible to construct more comprehensive molecular phylogenetic frameworks and illustrate geographical distribution patterns for certain fungal groups, which should help reveal evolutionary connections among fungal taxa from different continents, and address how such connections might have been formed (Cai et al., 2014; Du et al., 2012; Feng et al., 2012; Han et al., 2018).

4.1. Impacts of geological events

The mycobiota in China might have been influenced by orogeny, continental drifts, and climate changes in geological time. Since the collision of the Indian continent with Asia approximately 55 million years ago, tectonic activity in southwestern China has resulted in a series of dramatic landscape changes (Tapponnier et al., 2001) typified by the current topography of mountains and valleys nestled against the highest plateau on Earth. Due to the large-scale geological uplifts of the Qinghai-Tibet Plateau during the late Pliocene and Pleistocene, the arid areas in western and northwestern China spread further north and cover a much wider area (Zhang and Fang, 2012). Consequently, the fungal dispersals between East Asia and Europe virtually disappeared (Yang, 2005; Zhao et al., 2016a, b). Populations of the same species in East Asia and Europe, which were once continuously distributed across the Eurasian continent, may evolve independently and allopatric speciation may occur. This hypothesis has been supported by observations on the evolution of several fungal groups, such as *Morchella*, *Boletus*, *Amanita* sect. *Phalloideae*, and *Laccaria* (Du et al., 2012; Cai et al., 2014; Feng et al., 2012; Vincenot et al., 2017). Some closely related species, like *Boletus reticulatus* Schaeff. and *B. bainiugan*, can be found in Europe and southwestern China (Feng et al., 2012; Cui et al., 2016). In contrast, several species of *Hydnum* were shown to be shared by Europe and southwestern China, including Yunnan (Feng et al., 2016a). A possible explanation is that the Tethys region would have acted as a corridor for the dispersal of higher fungi between southwestern China and Europe. This hypothesis has been used to explain the discontinuous distribution of several plants in Europe and southwestern China (Sun, 2001).

Disjunctive distributions between East Asia and North America have been observed in several fungal groups, such as *Boletus*, *Morchella*, *Hydnum* and *Strobilomyces*, indicating possible historical mycobiota exchanges between these two regions (Du et al., 2012; Feng et al., 2012, 2016a; Han et al., 2018). Such historical exchanges would have been mediated by the Beringia route, which has repeatedly appeared and disappeared during different geological times, owing to historical climate fluctuations. Similarly, mainland East Asia was historically connected to Japan until the Last Glacial Maximum, which may have facilitated dispersals of fungal species between China and Japan. This has been supported by a recent study on *Strobilomyces*, in which 11 of 13 species were found to be shared by Japan and China (especially Yunnan) (Han et al., 2018). Other higher fungi shared by Japan and southwestern China include the species complex of *Tuber indicum* Cooke & Massee and *Singerocybe alboinfundibuliformis* (S.J. Seok et al.) Zhu L. Yang, J. Qin & Har. Takah (Kinoshita et al., 2011, 2018; Qin et al., 2014).

Historical fungal exchanges might have also happened between Southeast Asia and Yunnan. Han et al. (2018) indicated that after the African fungus *Strobilomyces* reached Southeast Asia through the boreotropics, it continued to migrate southward to Australia using continental fragments as "stepping-stones" between Australia and Asia, and then moved northward to East Asia via Yunnan. Thus, Southeast Asia might serve as a bridge for bidirectional migrations of fungi between Laurasia and Australia.

The sharing of fungal species between Yunnan and Southeast Asia has also been observed in *Hydnum* and *Cyptotrama* (Feng et al., 2016a; Qin and Yang, 2016).

Southwestern China is adjacent to South Asia. The Himalayas, formed by the uplifting of the Qinghai-Tibet Plateau, may act as a barrier for the biota exchanges between China and countries located to the west of the Himalayas. However, some fungal species in subalpine forests or alpine meadows, like *Boletus reticuloceps* and *Ophiocordyceps sinensis* (Berk.) G.H. Sung et al., co-occur both east and west of the Himalayas (Thapa et al., 2014; unpublished data). As taxonomic studies on higher fungi in the western Himalayas are quickly being accumulated, such distribution patterns are expected for more fungi in this region. Furthermore, evolutionary questions about how such distribution patterns have formed and the role the Himalayas plays in the microevolutionary processes of these fungi are worthy of further exploration.

4.2. Geographical factors

Geographical isolation, followed by allopatric speciation, would also have contributed to the endemic fungal diversity in southwestern China, as suggested by studies on several ectomycorrhizal and saprophytic fungal groups, such as *Chroogomphus*, *Phylloporus* and *Singerocybe* (Li et al., 2009; Qin et al., 2014; Zeng et al., 2013). For example, *C. tomentosus* (Murrill) O.K. Mill. was once assumed to be a putative disjunct species between western North America and East Asia (e.g., Imai, 1938; Redhead, 1989), but later studies revealed that the East Asian populations represent a distinct species related to *C. tomentosus* (Miller, 2003; Miller and Aime, 2001). Recently, geographical divergences of *Chroogomphus* in the Northern Hemisphere were further evidenced. Li et al. (2009) indicated that although several vicariously paired or closely related species of *Chroogomphus* were present in East Asia and North America, most species had relatively narrow distribution ranges in Far East Asia and central Europe.

4.3. Diverse environments

Climate, especially temperature and precipitation, affects the growth and distribution of fungi. The climate in Yunnan is significantly affected by monsoons. Monsoons bring abundant rainfall, and, as a result, humid tropical evergreen rainforests cover the southern part of the province. Central Yunnan generally has a subtropical climate, while the northern part shows a typical alpine climate. The diverse climate types and environments allow different fungi to specialize and thrive. For instance, *Imleria parva* Xue T. Zhu & Zhu L. Yang grows exclusively under subtropical mixed forests of *Pinus* and *Castanopsis* in southern Yunnan; *I. obscurebrunnea* (Hongo) Xue T. Zhu & Zhu L. Yang is distributed in forests dominated by Fagaceae in southern Yunnan; whereas *I. subalpina* Xue T. Zhu & Zhu L. Yang can only be found from subalpine forests with *Picea* and *Abies* as structural species (Zhu et al., 2014). Similarly, we observed that *Tricholoma highlandense* Zhu L. Yang et al. occurs on acid red soil in forests dominated by *Pinus yunnanensis* in the Yunnan Plateau between elevations of 2400 and 2800 m, while *T. sinopardinum* Zhu L. Yang et al. grows on calcareous soil in forests dominated by *Picea*, *Betula*, *Populus*, or *Quercus* in subalpine areas between elevations of 3300 and 4100 m (Yang et al., 2017a).

4.4. Co-evolution between fungi and host plants and fungal specificity to substrates

Plants of Pinaceae, Fagaceae, Betulaceae, Salicaceae, and Dipterocarpaceae are abundantly distributed in Yunnan, providing

ideal and diverse niches for various ectomycorrhizal higher fungi (Halling, 2001). Previous research has suggested that ecological speciation might have contributed to the high diversity of fungi (Li et al., 2009). For example, during the co-evolution of *Chroogomphus* and its hosts, host specificity generally increased, and host specificity would have driven some sympatric speciation events. For instance, *C. rutilus* (Schaeff.) O.K. Mill. had a sympatric distribution pattern with *C. purpurascens* (Lj.N. Vassiljeva) M.M. Nazarova, but with plant hosts in different subgenera of *Pinus* (Li et al., 2009).

Substrate specificity may drive speciation and evolution of saprotrophic fungi (Qin et al., 2018). For example, most species of the genus *Strobilurus* grow on decaying cones of various conifers. It was recently shown that some sympatric species of this genus are specific to certain substrates (Qin et al., 2018). For instance, *S. orientalis* Zhu L. Yang & J. Qin and *S. pachycystidiatus* Zhu L. Yang & J. Qin are restricted to dead cones of *Pinus armandii*, a five-needle pine, while *S. luchuensis* Har. Takah. & Taneyama only occurs on dead cones of three-needle pines, such as *P. yunnanensis*, and *P. luchuensis*. These findings suggest that substrate specificity might have contributed to the evolution of *Strobilurus*, in addition to geographical migration and vicariance events (Qin et al., 2018).

5. Microevolution of higher fungi in Yunnan and adjacent regions

Three of the world's 35 biodiversity hotspots, Mountains of Southwest China, Eastern Himalaya-Nepal-India and Indo-Burma-India-Myanmar, intersect in Yunnan (Mittermeier et al., 2005; Myers et al., 2000). This makes mountainous Yunnan and its adjacent regions ideal for studying the evolution of plants, animals, and higher fungi. Numerous phylogeographical studies have been carried out, mainly on plants and animals, to understand their evolutionary histories and the factors that drive their evolution. Two important hypotheses, "isolation of rivers" (Zhang et al., 2010, 2011) and "isolation of sky islands" (He and Jiang, 2014; Luo et al., 2015), have been proposed. These two hypotheses identify large rivers and high mountains as gene flow barriers for river-associated species and subalpine/alpine organisms respectively. Recent phylogeographic studies on the *Tuber indicum* species complex and the Alpine Porcini, *Boletus reticuloceps*, indicated that multiple factors, in addition to big rivers and high mountains, might have shaped the evolution of higher fungi in Yunnan and adjacent regions (Feng et al., 2016b, 2017; Fig. 2).

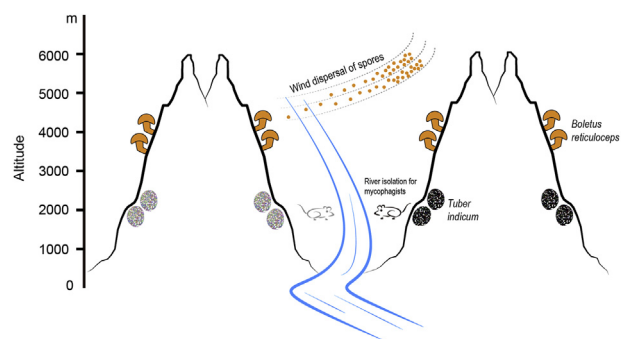


Fig. 2. A diagram showing how large rivers and high mountains may influence gene flow of hypogeous and above-ground mushrooms. Rivers may act as barriers to migration for mycophagists like mice and thus block gene flow of hypogeous mushrooms (like *Tuber indicum*). In contrast, above-ground mushrooms (like *Boletus reticuloceps*) can disperse their spores via winds and thus high mountains cannot block gene flow of such fungi. These conclusions are summarized from Feng et al. (2016b) and Feng et al. (2017).

The species complex of *Tuber indicum*, known as the Chinese black truffle, is distributed in southwestern China, Taiwan island of China, and Japan (Chen et al., 2011; Kinoshita et al., 2011, 2018; Qiao et al., 2018; Zhang et al., 2005). In southwestern China, its distribution is restricted to Yunnan and Sichuan, where three large rivers, Nujiang, Lancangjiang and Jinshajiang Rivers, run through. The species complex in this region contains two cryptic species, namely *T. indicum* Cooke & Massee and *T. himalayense* B.C. Zhang & Minter, although the nomenclature of these two species remains unresolved (Chen et al., 2011; Qiao et al., 2018; Zhang et al., 2005). By analyzing sequences from four gene fragments for over 300 individuals of *T. indicum* collected in its known distribution range, Feng et al. (2016b) revealed that large rivers in Yunnan and Sichuan could act as barriers to gene flow among different populations of *T. indicum*. Three major geographic groups, namely W, C and N, can be found in areas to the west of the paleo-Red River, between east of the paleo-Red River and south of the Jinshajiang River, and to the north of Jinshajiang River. As a hypogeous fungus that produces belowground ascocarps, the dispersal of spores of *T. indicum* is mainly dependent on the help of mycophagists, like mice and other small rodents (Maser et al., 2008). The existence of large rivers may form barriers to migration for such mycophagists, indirectly blocking gene flow of *T. indicum* (Feng et al., 2016b).

Boletus reticuloceps is an ectomycorrhizal fungus exclusively distributed under subalpine forests dominated by *Picea* and *Abies*. Its distribution pattern is similar to plants and animals that show an “isolated by sky islands” genetic structure. Surprisingly, Feng et al. (2017) suggested that gene flow of *B. reticuloceps* was not limited by high mountains in certain ranges, which means that “isolation of sky islands” may not efficiently influence the evolution of this fungus. One explanation may be that the on-ground fruiting bodies of *B. reticuloceps* bear spores that can be spread by wind over certain distances (less than 300 km, unpublished data). Despite this, three genetic groups, distributed in the East Himalayas (EH), northern Hengduan Mountains (NHM), and southern Hengduan Mountains (SHM), respectively, were identified in *B. reticuloceps*. Further analyses showed that ecological heterogeneity (especially precipitations and host plants) could have contributed to the divergence between the SHM and the NHM-EH groups, while physical barriers (the Mekong-Salween Divide) could have led to the divergence of the NHM and the EH groups (Feng et al., 2017).

6. Concluding remarks

This review and discussion has focused on studies using morphological characters, along with molecular evidence available since the beginning of the 21st century. As indicated by Wu et al. (2000), studies based on morphological characters alone can hardly provide a comprehensive understanding of fungal diversity and evolution. In order to further understand the diversity of higher fungi in Yunnan, special emphasis should be placed on (1) more international collaboration on fungal diversity, (2) reconstruction of molecular phylogenetic frameworks for fungal groups in higher ranks (such as order) and research on the evolution and ecological adaptations of higher fungi using genome-scale data, and (3) integration of multi-disciplinary approaches to investigate associations among higher fungi and other organisms, like host plants, and between fungi and environments.

6.1. Understanding fungal diversity and relationships from a global perspective

As summarized above, higher fungi in Yunnan show a great deal of endemism but also have evolutionary connections with species from other regions of the world. However, to date only limited

studies have considered fungal groups worldwide (Han et al., 2018; Hosaka et al., 2008; Matheny et al., 2009; Skrede et al., 2011). Thus, additional international collaborations are urgently needed to improve our understanding of fungal diversity and evolution from a global perspective.

6.2. Applying genome-wide analysis to study systematics, ecology and adaptations of higher fungi

From a single gene to multiple genes, the use of DNA sequences in phylogenetic analyses has revolutionized the study of fungal systematics, and this revolution is still being accelerated with the rapid development of sequencing techniques. Pioneering studies have exhibited the usefulness of genome-scale data and even genome sequences for the study of fungal systematics (Binder et al., 2013; Sato et al., 2017). A set of 80-gene data has helped better resolve relationships among different species of *Strobilomyces* (Sato et al., 2017). The small size of fungal genomes (about tens to hundreds Mb) makes genome sequencing for fungi much cheaper than that of most animals and plants. In addition, the costs for genome sequencing are gradually decreasing. Therefore, the application of genome sequences in the systematics of more and more fungal groups, especially at higher hierarchical ranks, like families and orders, is expected.

The use of genome sequences in studies of higher fungi is not restricted to systematics. There are many higher fungi that form ectomycorrhizal symbioses with several plant families, like Pinaceae, Fagaceae and Betulaceae. Several famous edible mushrooms in Yunnan, like boletes, truffles and *T. matsutake* (S. Ito & S. Imai) Singer, are ectomycorrhizal species. By using genome information, we can better understand how these commercial fungi interact with their host plants and subsequently provide guidelines for the artificial cultivation of these delicacies. Recently, the mystery of this mutualism has been partially uncovered by using genome and transcriptome information, involving a reduced complement of genes encoding plant cell wall-degrading enzymes (PCWDEs) and the addition of several mycorrhiza-induced small secreted proteins (MiSSPs) (Kohler et al., 2015; Martin et al., 2016). Interestingly, most of such MiSSPs are lineage-specific (Martin et al., 2016).

Ecological adaptation is a hot topic in evolutionary studies. In Yunnan and adjacent regions, several studies have been conducted to understand how organisms (especially animals) adapt to high elevations (Qiu et al., 2012; Yu et al., 2016; Zhao et al., 2013b; Zhou et al., 2014). There are numerous higher fungi distributed at high elevations, and how they adapt to such harsh environments remains unknown. Our current phylogeographic study on *Boletus reticuloceps* has suggested that ecological heterogeneity might have driven divergences between southern and northern populations in the Hengduan Mountains (Feng et al., 2017). Further study employing genome/transcriptome sequencing may help reveal the mechanism that drives the ecological adaptation of higher fungi like *B. reticuloceps*.

6.3. Interpreting interactions between higher fungi and environments

Higher fungi are important components of certain ecosystems, actively interacting with their living environments. The existence of certain ectomycorrhizal fungal group may influence the distribution of their host plants, and vice versa. Understanding such interactions between higher fungi and their living environments is a key goal in ecological studies and has attracted scientists' attention for a long time. Some attempts to elucidate these interactions in southern China have been made (Gao et al., 2013, 2015). Yunnan harbors a great deal of diverse vegetation. In certain places,

subtropical, temperate and subalpine forests are distributed vertically within distances as small as only tens of kilometers, making it ideal to address how higher fungi interact with different environments to form their current distributions. Such study urgently needs the integration of mycological and ecological approaches.

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