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OPINION

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Roof of the world: Home and border in the genomic era

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Himalaya and the Tibetan Plateau, known as the 'land of snow' and the 'roof of the world', is home to tens of millions of indigenous people who live with a staggering amount of biological diversity. In the past decade scientists have applied genomic tools and methods to substantially advance the understanding of phylogeography and genetic mechanisms behind high-elevation adaptation of local biota. However, contributions from indigenous researchers and native institutions are underrepresented in this scientific endeavour. We point to the higher degree of indigenous contribution within the discipline of conservation biology and how recognizing the prominence of traditional ecological knowledge (TEK) could deliver keen molecular ecological insights. Since the Himalaya-Tibet ecological interface spans five countries, comprehensive biogeographical and phylogeographical taxon sampling in the region requires multi-national collaborations across indigenous lands as well as indigenous community participation at both national and international levels. For the next generation of indigenous molecular ecologists, researching and cataloguing the evolutionary history and genetic information of the Tibetan and Himalayan landscape is a race against the melting glacier. At the roof of the world, their scientific judgement and stewardship will have environmental impacts that percolate far beyond indigenous lands.

KEYWORDS

Himalaya, indigenous land, Tibetan Plateau, traditional ecological knowledge, transboundary collaboration

1 | HOME AND INDIGENOUS KNOWLEDGE

Himalaya, the 'land of snow' (pronounced hee-MA-laya, the Sanskrit word is both singular and plural), stretches 2400 km across the heart of Asia, between the Indus and the Brahmaputra rivers. North of the valleys and snow peaks lies the vast expanse of the Tibetan Plateau, larger than the combined areas of France, Germany, UK and Spain. The highlands are home to more than 6 million Tibetans, along with at least 10 million people of Monpa, Lhoba, Nakhi, Qiang and Yi ethnicities inhabiting the mountainous regions at the eastern edge of the plateau (known as the Hengduan Mountains). South of Tibet, the

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Himalaya is home to more than 50 million people, representing diverse ethnic groups such as Chang-pas, Thakur, Gujjar, Bakkerwal, Gaddi, Bhutiya, Pahari, Khasas, Chettri, Lepcha, Tamang, Tharu, Sherpa, Ngalop, Nyishi, Apatani, Adi and Lama. These people live with a staggering amount of biodiversity: more than 10,000 species of vascular plants, 300 species of mammals and 1000 species of birds live along the Himalaya; on the eastern edge of the Tibetan Plateau, the Hengduan Mountains are home to at least 12,000 species of vascular plants, 230 mammals and 610 birds.

The immense biodiversity of the Tibetan Plateau and the Himalayan landscape is supported by water flowing from the third largest deposit of ice on earth (apart from the two poles). This ice mass is also the source of Asia's eight largest rivers, which sustain the livelihood of 1.5 billion people downstream. Under a drastically changing climate, local communities will suffer most of the environmental consequences of a melting Himalaya and a warming Tibetan Plateau (Lee et al., 2021; Pandit, 2017), including loss of traditional lifestyles and culturally significant, high-elevation adapted flora and fauna (Figure 1a), many of which biologists are only beginning to systematically document and study.

Biology in the Himalaya and Tibet underwent stages of exploitation and inventory to arrive at genomic insights. Colonial surveyors collected samples for imperial museums in the 19th century (e.g. Hooker, 1891; Kingdon-Ward, 1913). After nations achieved independence in the 20th century, taxonomists started documenting flora and fauna for their own Himalayan countries (e.g. Botanical Survey of India, 2022; Chinese Academy of Sciences, 2022). This period also coincided with the establishment of the majority of existing national parks and wildlife sanctuaries. In the 21st century, scientists started incorporating cellular and genomic tools in their investigations (Figure 1b). In the past decade, whole genomes of Tibetan barley (*Hordeum vulgare* L. var. *nudum*, ནས།) and yak (*Bos grunniens*, གཡག) have been assembled (Qiu et al., 2012; Zeng et al., 2015), and high elevation-adapted Tibetan pigs have been locally cloned (Global Times, 2021). In the past year alone, scientists have delineated the population history of Tibetan hotspring snakes (*Thermophis baileyi*) around the holy city of Lhasa (Yan et al., 2022), explored the metabolomics of differential gene expression of single plant-dimorphic flowers in alpine *Sinoswertia* gentians (Zhu et al., 2022) and identified a single gene *cortex* controlling pattern polymorphism of *Kallima* oakleaf butterflies across the Himalaya (Wang, Teng, et al., 2022).

This scientific narrative undercuts the experience of indigenous people across the Himalaya, especially their participation in present-day molecular ecological studies. For example, during the past decade, *Molecular Ecology* and *Molecular Ecology Resources* published 37 studies that sampled from the Tibetan Plateau but only one included a Tibetan co-author; a total of 13 studies drew on the

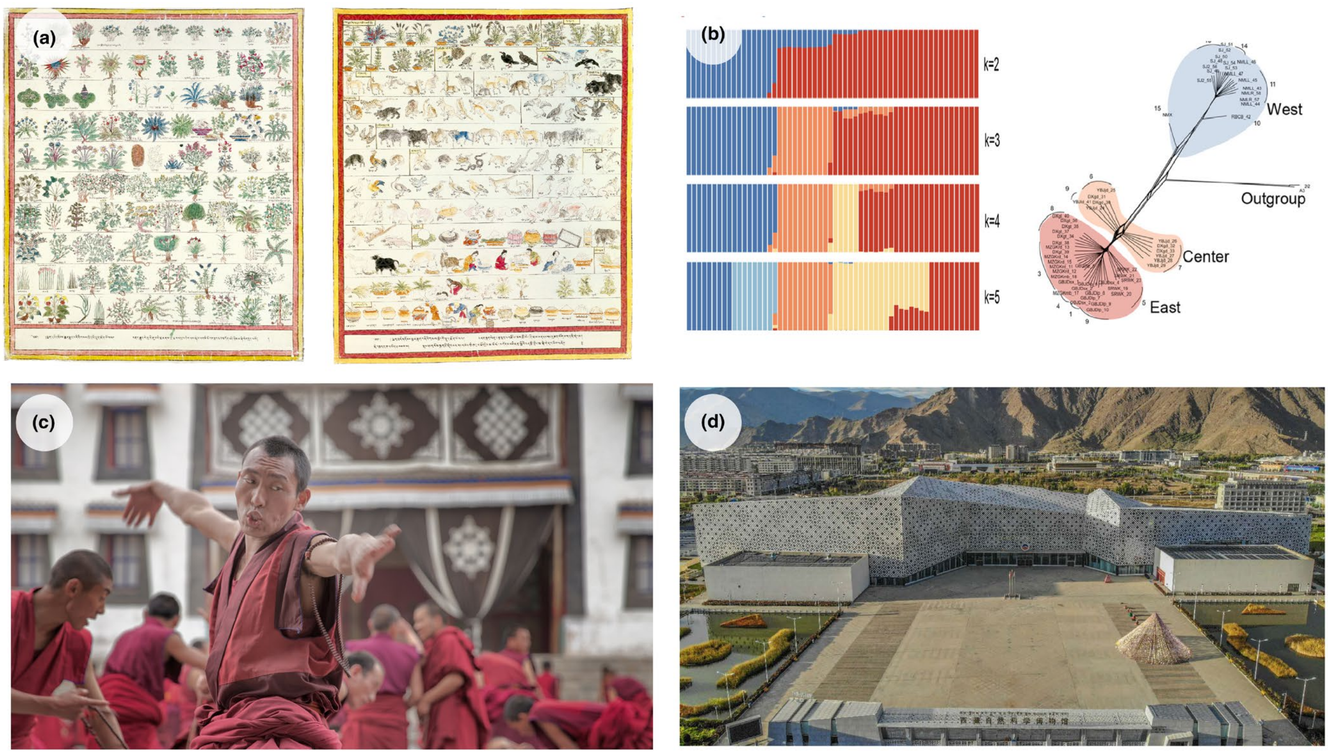

FIGURE 1 Continuity of indigenous knowledge into the genomic era. (a, b) Different perspectives of understandings of local biota: (a) as depicted in Tibetan *materia medica* by 17th century Sangye Gyamtso (སངས་རྒྱས་རྒྱ་མཚོ) and (b) as shown in modern day population genomics studies (adapted from figure 2 of Yan et al., 2022, with author permission). (c, d) Different means of knowledge transfer, as illustrated through a (c) debate in a monastery around Lhasa, the main method through which traditional teachings are examined (photo credit: Yuming Zhao) and (d) the new buildings of Tibet Museum of Natural Science, established in 2016 in Lhasa, TAR China (photo credit: Pingcuo Luosang).

Himalaya but none of the authors came from a Himalaya-based institution (Table S1).

Surveying a related discipline provided a glimmer of hope: in the same period, *Conservation Biology* and *Biological Conservation* published 43 papers on Tibet, four of which credited Tibetan authorship; of the 28 papers on the Himalaya, 12 involved Himalaya-based institutions, with six of their authors being in first/ corresponding positions (Table S2 and S3). Indigenous communities' positive contributions to conservation are being recognized worldwide. In Nyanpo Yutse (གཉན་པོ་གཡུ་རྩེ) national park at Golog Tibetan Autonomous Prefecture in China, decade-long ecological partnerships between scientists and Tibetan Buddhists strengthened local conservation capacity (Gao & Tashi, 2021); in Chamoli district of northern Uttarakhand in the Indian Himalaya, tribal belief in community planting of "sacred groves" has been adapted by NGOs and state forest departments as an important conservation practice (Kandari et al., 2014). Molecular ecology, *au fond*, addresses ecological interactions and evolutionary processes, and like conservation biology, the field can benefit from indigenous participation because they understand the pulse and texture of their land in culturally and ecologically intimate dimensions.

The perception of caterpillar fungus (དབྱར་རྩྭ་དགུན་འབུ), a symbiosis of *Thitarodes* moth larva and *Ophiocordyceps* fungus endemic to the Tibetan and Himalayan highland, is one of many examples of how traditional ecological knowledge (TEK) could provide a complementary understanding of ecological and evolutionary processes (see Box 1). To a broader extent, allopatric speciation and population isolation, two major themes of contemporary phylogeographical study on Himalayan-distributed biota, is deeply embedded in the Tibetan saying 'Each valley has its dialect; each lama has his religion' (ལུང་པ་རེ་རེར་སྐད་ལུགས་རེ་རེ། བླ་མ་རེ་རེར་ཆོས་ལུགས་རེ་རེ།). Tibetans arrive at these profound evolutionary insights from a familiarity with the landscape they inhabit. When integrated into global collaborations, TEK can provide holistic perspectives necessary to addressing major environmental challenges the region is facing.

BOX 1 Caterpillar fungus and traditional ecological knowledge.

Caterpillar fungus (དབྱར་རྩྭ་དགུན་འབུ in Tibetan, 冬虫夏草 in Chinese, meaning 'summer grass winter worm' in both languages) is a symbiosis of *Thitarodes* moth larva and *Ophiocordyceps* fungus endemic to the Tibetan and Himalayan highland. *Ophiocordyceps* parasitize soil-boring moth larvae in summer and release ascospores from caterpillar head capsules next spring. When excavated, parasitized larvae harden into mummified, caterpillar-shaped bundles of mycelium and stromata. The symbiont was first described, in its natural habitat, by Tibetan lama Nyamnyi Dorje (མཉམ་ཉིད་རྡོ་རྗེ) in the 15th century. It has since been collected by Tibetans for five centuries and sold across east and southeast Asia for ethnomedicinal purposes (Winkler, 2008). As commodities the dried-out symbionts are seen as homogenous products, but Tibetan collectors know that each valley produces a different breed of caterpillar fungi, and value their provenance and authenticity. Their insight was affirmed by work published in *Molecular Ecology* that showed that the symbiosis is a co-diversifying multispecies complex (Zhang et al., 2014), with distinguishable population genomic structure even within the same glacial valley (Wang & Pierce, 2023). These findings add nuance and complexity to the conservation planning of caterpillar fungi, particularly in predicting their range shift in face of climate change, but also provide opportunity to track and authenticate market produce with species-level molecular markers.

2 | BORDERS AND COLLABORATIONS

The sacred Himalayan landscape spans five countries: Pakistan, India, Nepal, Bhutan and China. They include the world's first, second and fifth most populous countries; each with its own history of indigenous land legislations. Today China and India share more than 2000 km of borders along the Himalaya, where historically, Tibetans and closely related indigenous groups traded and migrated (Goldstein, 1981; van Schaik, 2013). Himalayan populations in India, Nepal and Bhutan share more genetic markers with Tibetans than with their immediate geographical neighbours in south Asia (Tamang et al., 2018). In general, the Himalaya is not an effective biological dispersal barrier: 54% of over 550 butterfly species (83% of all genera) and 70% of over 1100 bird species (87% of all genera) found in the Tibet Autonomous Region (TAR, in China) are shared with the Indian Himalaya (Avibase, 2023; Birds of India Consortium, 2023; Kunte et al., 2023); 61% of all species (94% of all genera) of over 7850 angiosperms recorded in the Indian Himalaya, Nepal and Bhutan are also present in China (Rana et al., 2022; Flora of China, 2022). However, despite the presence of these species across multiple countries, among all Himalayan angiosperms only 40% have any molecular sequencing data available (Rana et al., 2022). Comprehensive biogeographical and phylogeographical taxon sampling in Himalaya-Tibet requires multi-national collaborations across indigenous lands.

Such international collaborations are indeed tasks of Himalayan proportions—but they are also opportunities for indigenous participation. Take the two largest Himalayan countries as examples: China and India have a huge potential to strengthen scientific collaborations (Bawa et al., 2010, 2020; Gupta & Dhawan, 2003) and have signed concrete memoranda of cooperation in science and technology (Embassy of India, 2015), including in the environmental sciences (Goodale et al., 2022), where some of the efforts come from a grass-root level (Feng & Garg, 2021). Even the culturally and economically important caterpillar fungus (see previous section) can now be identified with regional genetic markers because of a collaborative effort that involves scientists and communities from four Himalayan nations (Wang, Da, et al., 2022). Within their own borders, both China and India also actively invest in studying the roof of the world: Lhasa, the administrative capital of TAR, boasts a locally administered natural history museum and a seed bank, two regional research universities and a national-level field station; India has prioritized Himalayan ecosystem research with a suite of developmental programs (Kaur et al., 2022) and established world-class research institutions across the Himalaya (e.g. G. B. Pant National Institute). A more affirmative plan to recruit local communities and knowledge-holders into multi-national collaborations and *existing* research infrastructures that are tailored to administrative specificities of each Himalayan nation, will facilitate the transfer of expertise between the domain of genomic know-hows and that of TEK (Table 1). In particular, we note that despite differences in administrative details and indigenous legislations, all five Himalayan nations have signed and ratified the Nagoya Protocol (https://www.cbd.int/abs/doc/protocol/nagoya-protocol-en.pdf), which not only calls for fair and equitable sharing of benefits arising from genetic resources but highlights the importance of indigenous community participation in accessing traditional knowledge associated with genetic resources (Article 12). Effective participation from indigenous communities in the active research process (including collection, storage and publication of molecular and ecological data) can safeguard legally-binding international agreements such as Nagoya Protocol from deteriorating into bureaucratic lip service. India is already preparing a people's biodiversity register through formation of biodiversity management committees at village level throughout the country in order to document the bioresources and protect the intellectual property rights of indigenous people.

Moreover, indigenous-focused training and exchange programs across Himalayan nations could jumpstart broader international collaborations. Interestingly, scholarly exchanges have been an integral part of the centuries-old Tibetan monastic curriculum (Dreyfus, 2003), where monks travel across monasteries to defend their thesis before achieving the high monastic title of *Geshe* (དགེ་བཤེས). Innovating the practice into an international, scientific context would be a critical commitment to promote research at the Himalayan ecological interface by the world's two most populous nations (Figure 1c,d). Well-provisioned graduate student exchange programs, similar to the Erasmus Mundus Master Programme in Evolutionary Biology (MEME: https://www.evobio.eu/) across Europe, or training programs with strong focus on scientific expertise similar to the Summer Internship for Indigenous Peoples in Genomics program in North America, Australia and New Zealand (SING: https://singconsortium.org/) could provide diverse career and research pathways for indigenous molecular ecologists grounded in TEK while proficient in state-of-the-art sequencing and analytic techniques. For this next generation of molecular ecologists, researching and cataloguing the evolutionary history and genetic information of the Tibetan and Himalayan landscape is a race against the melting glacier. At the roof of the world, their scientific judgement and stewardship will have environmental impacts that percolate far beyond indigenous lands.

TABLE 1 Framework for facilitating the exchange of TEK and genomic knowledge. Columns list aspects of research, policy, and outreach effort that represent opportunities for incorporating TEK. Rows list environment and participants at the centre of research, policy, and outreach. To contextualize the examples, all references in the first two rows focus on caterpillar fungus ("focal species") and its habitat ("landscape"), while opportunities for participant engagement are drawn from a more global source.

		Research	Institution	Outreach
Environment	Focal species	Conserving focal species (Yan et al., 2017) Researching molecular mechanisms behind ethnobotanical use (Schwenzer et al., 2021)	Building local infrastructure for molecular sequencing and preservation of reference genetic resource (Wang, Da, et al., 2022)	Promoting use of common name in local language (Li, 2019) Documenting historical and current use (Czaja, 2019)
	Landscape	Elaborating on ecological implication of traditional land use (Hopping et al., 2018; Shen et al., 2012)	Negotiating land rights (Gurung, 2022; Wallrapp et al., 2019)	Incorporating ecological knowledge into youth media (e.g. board games, Takai & Kawano, 2018; comic books, Jun, 2021)
Participants	Communities	Promoting indigenous perspectives and values (e.g. traditional diet and way of life Guachamin-Rosero et al., 2022; Kimmerer, 2013)	Engaging civil society organizations as equal partners in land management (e.g. joint forest management, Singh et al., 2011) Recruiting local knowledge-holder (e.g. in environmental management Holifield & Williams, 2019)	Establishing digital knowledge commons for participatory biodiversity assessment and knowledge transfer (e.g. biodiversity database Ball-Damerow et al., 2019) Enrolling indigenous students in graduate programs (e.g. affirmative action Ding et al., 2017) Mentoring youth from indigenous communities (e.g. tribal mentoring program carr et al., 2017)
	Researchers	Acknowledging and collaborating with indigenous communities (Doering et al., 2022)	Emphasizing relation-building and benefit sharing (Carroll et al., 2022; Tone-Pah-Hote & Redvers, 2022)	Conducting equitable fieldwork training (Ramírez-Castañeda et al., 2022) Incorporating TEK in curriculum (middle-school: Kim & Dionne, 2014; undergraduate: Greenall & Bailey, 2022)

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interests.

DATA AVAILABILITY STATEMENT

Data analysed in our literature review are available in the supplementary material.

BENEFIT SHARING STATEMENT

Our team includes local and indigenous scientists; we are committed to increasing engagement with local and indigenous communities from the Himalaya and Qinghai-Tibetan Plateau, in both national and international settings.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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