Alpine Botany (2019) 129:175–183
https://doi.org/10.1007/s00035-019-00226-2

SHORT COMMUNICATION

Are mountaintops climate refugia for plants under global warming? A lesson from high-mountain oaks in tropical rainforest

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Received: 8 November 2018 / Accepted: 20 August 2019 / Published online: 27 August 2019

Abstract
Climate refugia are locations where plants are able to survive periods of regionally adverse climate. Such refugia may affect evolutionary processes and the maintenance of biodiversity. Numerous refugia have been identified in the context of Quaternary climate oscillations. With climate warming, there is an increasing need to apply insights from the past to characterize potential future refugia. Mountainous regions, due to the provision of spatially heterogeneous habitats, may contain high biodiversity, particularly important during climate oscillations. Here, we highlight the importance of mountaintops as climate refugia, using the example of high-mountain oaks which are distributed on the ranges of the Himalaya–Hengduan Mountains, and at high elevations in tropical rainforests. The occurrences of cold-adapted high-mountain oaks on mountaintops amidst tropical rainforest indicate that such locations are and will be climate refugia as global warming continues. We examine factors that predict the occurrence of future climate refugia on mountaintops using recognized historical refugia. Future research is needed to elucidate the fine-scale processes and particular geographic locations that buffer species against the rapidly changing climate to guide biodiversity conservation efforts under global warming scenarios.

Keywords Changing climate · Climate refugia · Mountaintops · Global warming · Biodiversity · Oak trees

Introduction

Species' geographic ranges repeatedly expanded and contracted, often with latitudinal-elevational shifts, in response to climate oscillations during the Quaternary (Hewitt 1996; Davis 1976; Davis and Shaw 2001; Huntley and Birks 1983). Locations where species persisted during climatic or environmental adverse conditions, particularly during glacial periods, have been called refugia (e.g., Willis and Whittaker 2000; Stewart et al. 2010). The refugia concept has evolved from its original definition in paleoecology as 'a restricted glacial population that underwent postglacial expansion' to a broader concept, which is currently used in biogeography, vegetation history, paleoecology, ecology, phylogeography, and global change biology (Gentili et al. 2015). Research on refugia is a growing discipline, with reviews on the definition of refugia (Bennett and Provan 2008), the evolutionary legacy of refugia (Hewitt 2000), the integration of different methods for identifying refugia (Gavin et al. 2014), and the

Hong-Hu Meng, Shi-Shun Zhou and Xiao-Long Jiang contributed equally to this work.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00035-019-00226-2) contains supplementary material, which is available to authorized users.

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evidence for refugia in the northern hemisphere (Petit et al. 2008).

Early researches using paleoecological data to study the distributions of warm-adapted northern temperate taxa suggested numerous refugia in the far south of the present-day distributions, such as the Iberian, Italian and Balkan Peninsulas of Europe, and southeast North America (Davis 1976; Huntley and Birks 1983; Knowles 2001; Petit et al. 2003). Recently, molecular phylogeography and species distribution modeling (Gavin et al. 2014) have indicated that "northern" refugia, close to ice sheet margins (McLachlan et al. 2005; Petit et al. 2008), and mountain refugia may be relatively stable over long periods (Opgenoorth et al. 2010). Certain species, particularly arctic and alpine plants, are characterized by their interglacial refugia, with small, localized populations growing in naturally open habitats during temperate interglacial stages (Birks and Willis 2008; Gentili et al. 2015). As anthropogenic climate change and human activities are already causing species extinctions, and more are expected, research and the identifying of potential refugia will become increasingly important (Willis and Whittaker 2000; Gavin et al. 2014).

Global climate change is having profound and diverse effects on organisms, causing shifts in their geographic ranges, and changing their seasonal phenology, community interactions, genetics, and extinction rate (Dillon et al. 2010). This is especially true for high-latitude populations and cold-adapted species, e.g., alpine, arctic-alpine, boreal, and cool-temperate plants (Pauli et al. 2012; Thuiller et al. 2005). To adapt to the changing climate, an increasing number of terrestrial species are undergoing latitudinal or elevational range shifts, expanding in newly favorable areas and declining in increasingly hostile parts of their former range (Kelly and Goulden 2008; Chen et al. 2011). However, plant community changes substantially lag behind the rapidly increasing climate warming (Alexander et al. 2018). Thus, if these range shifts cannot keep pace with the speed of warming, refugia may become critical for species survival. Therefore, biogeographers and conservationists need to assess potential sites which may serve as refugia under a warming climate, particularly for vulnerable, low-latitude populations of cold-adapted plants that are already inhabited "interglacial refugia".

Mountainous regions harbor extraordinary climatic and environmental diversity due to steep changes in elevation and aspect over short distances. Thus, mountains may provide habitats for many endemic and threatened species (Dullinger et al. 2012). In mountains, species can persist in a warming or cooling climate by relatively modest shifts up or down slopes, or between north and south-facing slopes. In the European Alps, species colonization events were more frequent on the warmer sides of temperate mountain peaks, and thermal differences caused by solar radiation determine plant diversity on temperate mountains (Winkler et al. 2016). Thus, high elevations may harbor critical refugia for maintaining biodiversity. Many studies have reported elevational range shifts in mountain plants during recent decades, and high-alpine species face increasing pressure from climatic change and novel super-competitors, including invasive species, which are expanding their ranges upwards (Kelly and Goulden 2008; Lenoir et al. 2008; Rumpf et al. 2018; Liang et al. 2018). Low-latitude populations of cold-adapted plants are known to harbor genetic diversity that fosters persistence in a future warmer climate (Abeli et al. 2018). However, little is known about the role of low-latitude mountaintops in tropical Asia, as potential climate refugia for plants under future climate warming. These regions harbor ancient relict species and populations that have survived numerous climate oscillations, and thus might serve as critical climate refugia also in the future.

To identify low-latitude areas where cold-adapted plants persisted allows to define the specific environmental features that are relevant for such refugia (Keppel et al. 2012), and to uncover the processes that have shaped current biogeographic patterns. Special physiological properties of alpine plants such as adaptive plasticity and the high efficiency of photosynthetic nitrogen at high elevations (Sun et al. 2015; Zhang et al. 2007; Zhou et al. 1994) have allowed alpine plants to adapt to environmental changes. Cold-adapted plants at high elevations are expected to "retreat" further into their current refugia as climate warming is accelerating. Which climatic parameters permit species persistence in such refugia, how such refugia are spatially organized, and whether climate refugia are suitable for dispersal and/or biotic interactions are key questions to understand how species will adapt to future climate change.

Here, we propose that certain high-elevation habitats could serve as climate refugia for cold-adapted plants in today's increasingly warm interglacial period. We focus on the case of high-mountain oaks (*Quercus* sect. *Ilex* following Denk et al. 2017, or *Quercu*s sect. *Heterobalanus* following Menitsky 1984). These oaks are mainly distributed in the Himalaya–Hengduan Mountains (HHM) and in tropical rainforest to their south (Fig. 1). We document the occurrence of cold-tolerant high-mountain oaks further south than previously described, on mountaintops in tropical rainforest surroundings. We use the present-day occurrences of oaks in the HHM and tropical rainforest to identify areas of previous or current climate suitability, to predict possible future refugia, and to define the climatic variables which are critical to such refugia at high elevations, to guide biodiversity conservation efforts under global warming.

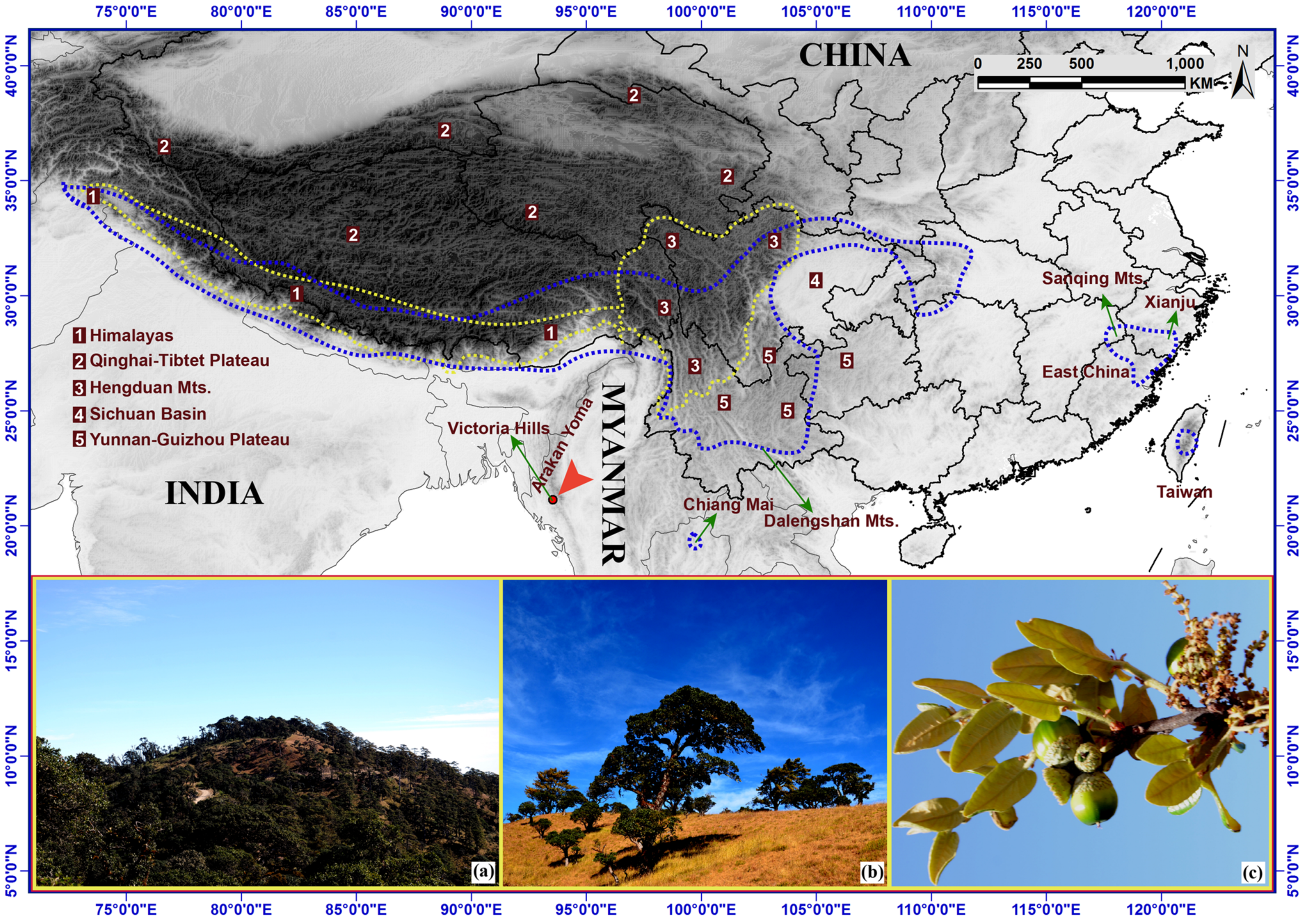

Fig. 1 The geographic distribution of high-mountain oaks and the locality of high-mountain oaks in Victoria Hills, Arakan Yoma, Myanmar. Blue dashed lines denote the geographic distribution of high-mountain oaks [adapted from Meng et al. (2017) and Zhou et al. (2003)]; yellow dashed lines denoted the Himalaya–Hengduan Mts., [adapted from Meng et al. (2017) and Liang et al. (2018)]; red dot and red pointer denote the locality of high-mountain oaks in Victoria Hills, Arakan Yoma, Myanmar. **a** The habitats of high-mountain oaks in tropical rainforests; **b** adult trees of high-mountain oaks on the mountain top of Victoria Hills; **c** a branch with fruits and inflorescence of high-mountain oaks

Materials and methods

Study system and field survey

High-mountain oaks are distributed in the mountain ranges of the HHM on sunny, and dry slopes between 2500 and 4300 m, and recently they were discovered also further south, at high elevation in the tropical rainforest of Myanmar. There are seven species in the section of high-mountain oaks in the HHM: *Quercus semecarpifolia*, *Q. guyavifolia*, *Quercus aquifolioides*, *Q. rehderiana*, *Q. spinosa*, *Q. monimotricha* and *Q. senescens* (Huang et al. 1999). Some of these species are broadly distributed across high elevation sites of East Asia (Fig. 1).

There are rich fossil records of high-mountain oaks from the late Eocene to the Pleistocene (Huang et al. 2016; Su et al. 2019; Zhou et al. 2003; Appendix S1), which suggest that these oaks have experienced numerous climate changes through the geological history. Combined molecular and fossil evidence indicate that high-mountain oaks originated in warm, mixed broadleaf forests; subsequently, with the HHM uplift and relevant climatic cooling, they became dominant species in the surrounding mountain ranges (Meng et al. 2017). Thus, the evolutionary history of high-mountain oaks and their current distribution involved their adaptation to cooler conditions.

During our field survey, a population of high-mountain oaks was discovered on tropical rainforests mountaintops in the Victoria Hills, Arakan Yoma, Myanmar (21°13′11″N, 93°55′54″E, alt. 2871 m; Fig. 1). The Victoria Hills in the Arakan Yoma ranges have a typical tropics (Ghazoul and Sheil 2010). The discovery of high-mountain oaks in this tropical area is unexpected, although a previous study reported high-mountain oaks in tropical Chiang Mai, in northern Thailand (Zhou et al. 2003). The topographic complexity of mountains in tropical regions is likely to have contributed to population isolation of oaks on mountaintops, which provide favorable habitats for relatively cold-adapted plants. In otherwise warm, mostly lowland regions, high mountain oaks are restricted to a few mountain summits and are consequently rare. In the subtropics, we observed three individuals of oaks on the summit of Sanqing Mountains, Jiangxi; and two individuals in Xianju, Zhejiang (Meng et al. 2017). This discovery suggests that mountaintops in the tropical rainforest may serve as climate refugia, at present and also in the future under global warming.

Species distribution model of high mountainous oaks using MaxEnt

Climatically suitable distributions for high-mountain oaks were estimated using a maximum entropy model performed by MaxEnt v3.3.3. Potential distributions were established for the present day, the Last Glacial Maximum (LGM, ca. 21,000 years before present), and the future, ca. 2070 (Phillips et al. 2006). Our input data to describe suitable distribution area included data from the tropical rain forests of Victoria Hills and previous records of high-mountain oaks (Meng et al. 2017), in total of 149 independent records of high-mountain oaks used to predict the climatically suitable distributions. Temperature and precipitation were important abiotic factors and consistent with previous species distribution model (SDM) analyses for oaks (Gugger et al. 2013; Jiang et al. 2016; Meng et al. 2017), we included eight climatic variables including temperature extremes and growing season precipitation in the modeling process (Appendix S2). These climate variables were obtained from the WorldClim database (available at: http://www.worldclim.org/) at 2.5 arcmin resolution for the present, LGM (CCSM3), and future (2070, RCP85, CCSM4) periods. The occurrence records of high-mountain oaks were randomly divided into training data (80%) and test data (20%), a maximum number of 10,000 background points was set and the mean value of ten replicate results with random seeds was applied as potential species distribution. Area under curve (AUC) from the receiver operating characteristics (Hanley and McNeil 1982), positively evaluated the model performance (AUC = 0.99). Analysis was performed using the 'dismo' package in R (Hijmans et al. 2005; R Core Team 2015). Potential distribution maps for high-mountain oaks were visualized using ArcGIS v.10.2 (Environmental Systems Research Institute, Inc., ESRI; Redlands, CA, USA).

Results and discussion

Inferring mountaintop climate refugia under global warming

Fossils of high-mountain oaks from the Eocene–Oligocene transition are few in number (Su et al. 2019), but become more abundant in the period over which the HHM was formed (Zhou et al. 2003), and the region's vegetation transitioned from warm to cold. Evidence from the fossil records and molecular analyses indicates that high-mountain oaks originated from tropical or subtropical forest habitats and colonized cold habitats during the HHM uplift (Meng et al. 2017). It is presumed that these oaks exploited the increase of favorable habitats areas and adapted to high-elevational conditions. Thus, oaks on the mountaintops of tropical rainforest are probably relicts from their early evolutionary history in the region, as well as from recent cool periods when oak forests may have been more continuous than they are today.

We combined our new occurrence records with previous records of high-mountain oaks to generate SDMs using MaxEnt (Gugger et al. 2013; Jiang et al. 2016; Meng et al. 2017) to explore the past, present and potential future climatically suitable regions of high-mountain oaks. In the SDMs, precipitation in the warmest quarter (bio18) and temperature seasonality (bio4) were the most important factors defining potential species distributions (see Appendix S2). Total precipitation in the warmest quarter (bio_18) and temperature seasonality (bio_4) were explaining 32.6% (SD 2.42) and 21.4% (SD 2.49) of the variation, respectively, in the distribution of high-mountain oaks. The remaining six environmental factors contributed 45.9% of the total variation (Appendix S2).

Comparing modelled distributions ranges in LGM, present, and future, we find that the overall geographic distribution ranges were relatively stable between the LGM and present, although the distribution center in the Hengduan Mountains shows signs of slight contraction, and the periphery may have slightly expanded to lower elevations and latitudes during the LGM (Fig. 2a, b). The results are consistent with single-species models for *Q. aquifolioide*s, *Q. spinosa* and *Q. rehderiana* (Feng et al. 2016; Du et al. 2016), and suggest that the geographic range of high-mountain oaks will move northwards at higher latitude and to higher elevation (Fig. 2c). This is consistent with the work of Liang et al. (2018), too. The SDMs suggest that oaks distribution areas have been little influenced much by cold periods during the LGM, and the habitats at high elevation along the mountain ranges are favorable sites for these species. Previous research has found that the geographic distribution of oaks during the LGM was not influenced as much as that of other co-occurring thermophilous plants (Meng et al. 2017). The newly recorded occurrence of high-mountain oaks at Arakan Yoma, maybe the lowest latitude distribution regions on record in tropical rainforest; the HHM may have provided more suitable habitats for the oaks under study during cold periods (Fig. 2a). The current low elevation presence of oaks in tropical rainforests may also represent not particularly favorable conditions (Fig. 2b).

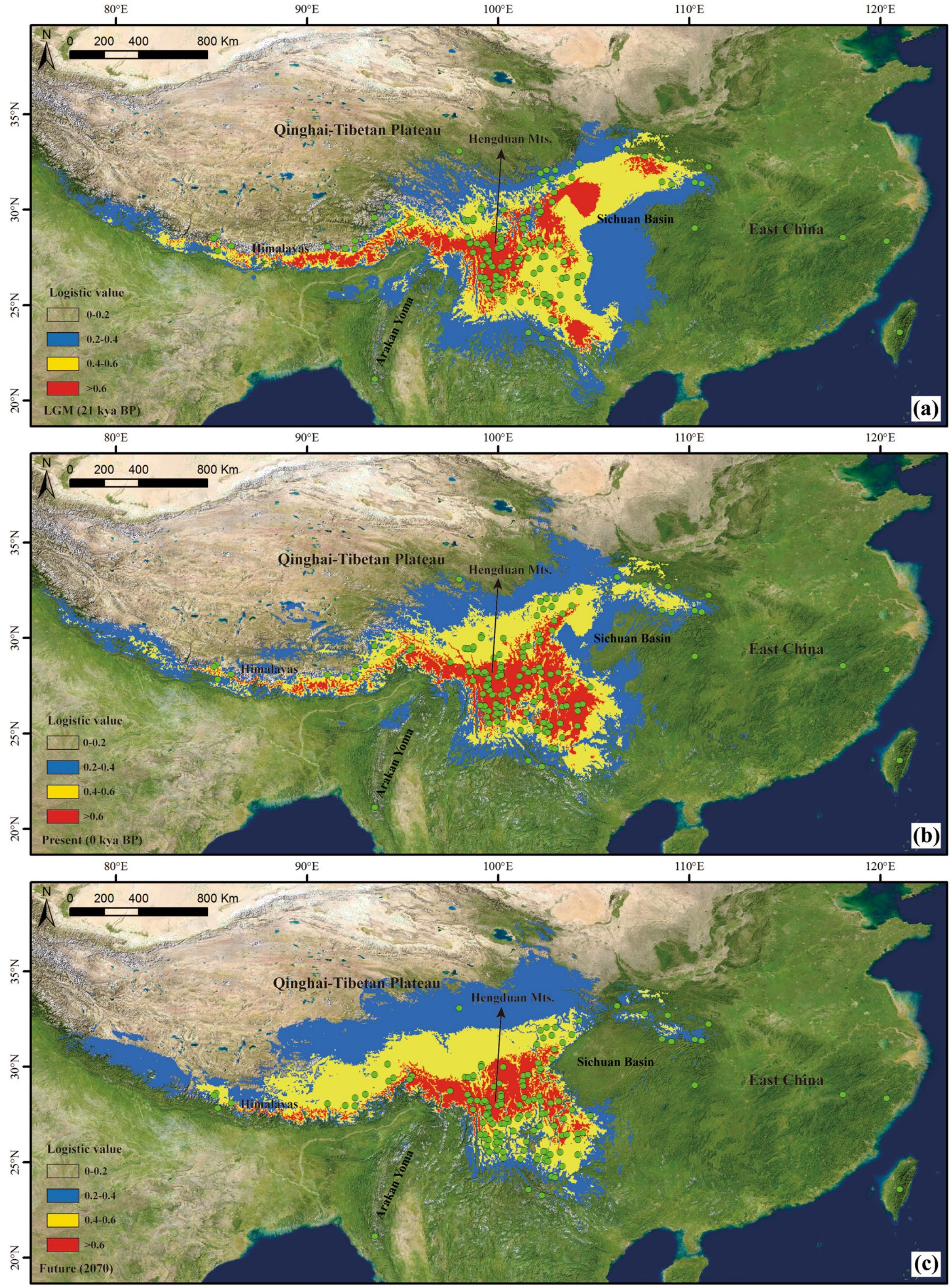

Fig. 2 MaxEnt models of the potential suitable areas of high-mountain oaks: **a** at the last glacial maximum (LGM; 21,000 years before present; BP); **b** under current conditions (1950–2000); **c** under future conditions (2070). Species distribution models were established with current bioclimatic variables on the basis of extant occurrence points (green dots) of the species

The models suggest that the distribution of oaks will shift northwards and to higher elevation in the future (Fig. 2c). Areas such as the edge of the Sichuan Basin, which is at low elevation, will also be unfavorable as the climate gets warmer (Fig. 2c). As temperatures have increased over geological time, oaks have been increasingly concentrated at high elevations. However, there are not such high elevations in subtropical and tropical regions as buffer zones such as high mountain ranges at the HHM, the cold-adapted plants always are distributed on the mountaintops as relicts (Fig. 3). Thus, mountaintops in lower latitude tropical regions are likely to serve as climate refugia under global warming (Fig. 3). As for species migrating under ongoing climate warming, trailing-edge populations (i.e. those currently in warmer climates) are the most likely to be genetically unique relicts of former glacial refugia (Hampe and Petit 2005) and will also be the first to suffer local extirpation (Razgour et al. 2013). Cooler mountaintops can buffer species against extreme heat stress during climate changes (Shoo et al. 2010), and so may represent a favorable habitat for cold-adapted plants, such as high-mountain oaks.

Different taxa will respond individually to environmental changes; however, some environmental parameters will affect a large number of taxa in a similar manner, and these factors are likely to be important for defining the spatial dimensions of refugia (Keppel et al. 2012). Precipitation in the warmest quarter and temperature seasonality contributed most to potential species distributions from the model, indicating that these climate factors are the main determinants of alpine plants range. The current distribution at high elevation of the HHM ranges (Fig. 3a) provide suitable buffer zones for high-mountain oaks. However, the oaks in tropical and subtropical regions are gathered on the mountaintops as relicts, examples include subtropical evergreen broad-leaved forest in the Dalengshan Mountains, Yunnan (Fig. 3b); and the Victoria Hills tropical rainforests in Arakan Yoma

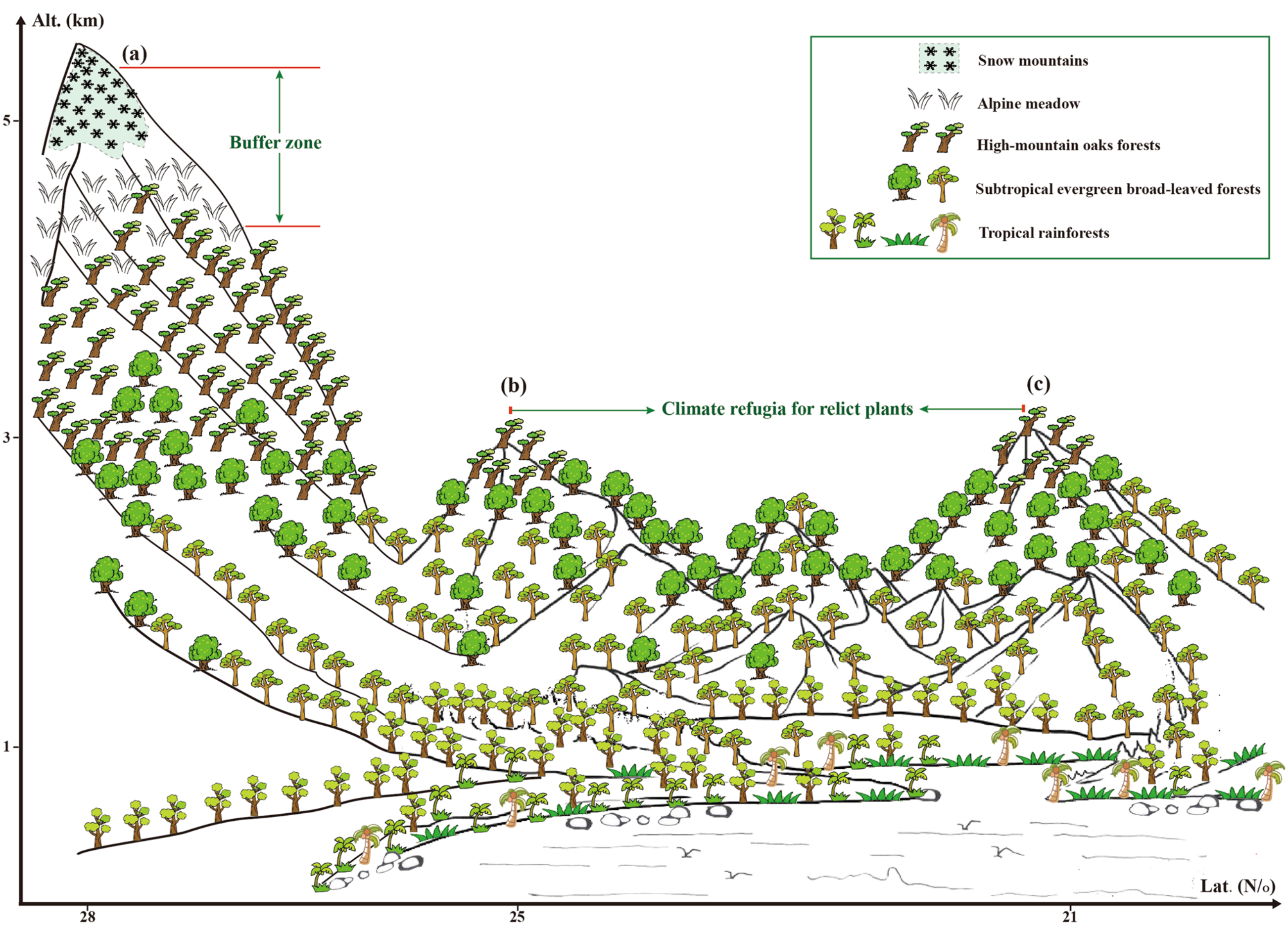

Fig. 3 Current geographic distribution of high-mountain oaks along the elevational-latitudinal gradients: **a** the locality at Hengduan Mountains, the highland near Tibetan Plateau, at which has enough high elevation as buffer zone for alpine forests; **b** the locality at Dalengshan Mountains, subtropical evergreen broad-leaved forest, at which has no high elevation; **c** the locality at Victoria Hills, Arakan Yoma, tropical rainforest, at which has no high elevation. The mountain tops of **b** and **c**, act as climate refugia for relict plants, are and always will be climates refugia under global warming, particularly in tropical and subtropical regions

(Fig. 3c). That is, the relict occurrence of oaks on mountaintops in tropical and subtropical regions may particularly suffer from the current pace of climate warming that may be faster than the ability of plants to adapt and evolve.

Alpine refugia in a changing climate

High elevations, such as the mountaintops in the tropical regions, are currently and will continue to be important climate refugia, whereas some lower elevation and latitude populations are at risk of extirpation, particularly for cold-tolerant plants in the tropics and subtropics (Fig. 3b, c). A better understanding of future climate refugia based on firm historical insights is needed for robust predictions. Mountaintops in tropical rainforest currently act as climate refugia for cold-adapted plants and need to be recognized and studied as part of ongoing efforts to understand biogeography and biodiversity of plants.

Although there is a rapidly growing literature on species migrations across elevation zones in temperate regions, in response to climate change, little is known about the importance of mountaintops as climate refugia in the tropics. We expect these regions to play a significant role in biogeography and conserving biodiversity under a changing climate. Mountaintops with complex topography and high elevation, particularly in the tropics, could provide the last heaven as climate refugia for populations against climate shifts and allow species to persist despite regionally unfavorable climate (Fig. 3).

Conservation organizations are currently working to identify potential climate refugia for modern populations which are at risk from ongoing climate change (Shoo et al. 2011; Groves et al. 2012; Olson et al. 2012). Climate warming and anthropogenic activities are expected to have a far-reaching influence on biodiversity (Meng et al. 2019; Song et al. 2019). However, refugia at high elevations in tropical and subtropical regions (Fig. 3) will be of great importance to harbor biodiversity in changing environments, particularly for the alpine and/or cold-adapted relicts. An understanding of future climate refugia should be used to guide the establishment of specific areas of conservation, and ultimately facilitate the long-term persistence and survival of cold-adapted plants in the face of accelerating changing climate.

Acknowledgements Prof. Jürg Stöcklin (Editor-in-Chief of Alpine Botany), Prof. Christian Parisod (Editor of Alpine Botany), and the three anonymous reviewers are gratefully acknowledged for their valuable suggestions and comments. This work is funded by Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences (Y4ZK111B01); and Youth Innovation Promotion Association, Chinese Academy of Sciences (2018432) to H.-H. Meng.

Author contributions HHM and JL conceived the study. HHM, SSZ, LL and YHT conducted field work. XLJ performed data analyses. HHM and PFG wrote the first draft of the manuscript. All of the authors contributed to and approved the final manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest in relation to this article.

Ethical statement The authors declare that observance ethical standards.

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