

The role of the uplift of the Qinghai-Tibetan Plateau for the evolution of Tibetan biotas

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ABSTRACT

Biodiversity is unevenly distributed on Earth and hotspots of biodiversity are often associated with areas that have undergone orogenic activity during recent geological history (i.e. tens of millions of years). Understanding the underlying processes that have driven the accumulation of species in some areas and not in others may help guide prioritization in conservation and may facilitate forecasts on ecosystem services under future climate conditions. Consequently, the study of the origin and evolution of biodiversity in mountain systems has motivated growing scientific interest. Despite an increasing number of studies, the origin and evolution of diversity hotspots associated with the Qinghai-Tibetan Plateau (QTP) remains poorly understood. We review literature related to the diversification of organisms linked to the uplift of the QTP. To promote hypothesis-based research, we provide a geological and palaeoclimatic scenario for the region of the QTP and argue that further studies would benefit from providing a complete set of complementary analyses (molecular dating, biogeographic, and diversification rates analyses) to test for a link between organismic diversification and past geological and climatic changes in this region. In general, we found that the contribution of biological interchange between the QTP and other hotspots of biodiversity has not been sufficiently studied to date. Finally, we suggest that the biological consequences of the uplift of the QTP would be best understood using a meta-analysis approach, encompassing studies on a variety of organisms (plants and animals) from diverse habitats (forests, meadows, rivers), and thermal belts (montane, subalpine, alpine, nival). Since the species diversity in the QTP region is better documented for some organismic groups than for others, we suggest that baseline taxonomic work should be promoted.

Key words: biodiversity, biogeography, birds, diversification rates, flowering plants, freshwater diversity, mountain formation, molecular clocks, organismic evolution, Qinghai-Tibetan Plateau.

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I. INTRODUCTION

The heterogeneous distribution of the world's biodiversity is a well-known phenomenon that can be observed between adjacent ecoregions or biomes (Myers *et al.*, 2000; Olson *et al.*, 2001; Myers, 2003; Myers & Mittermeier, 2003; Kier *et al.*, 2005, 2009). Revealing the origin of such spatial patterns is a growing focus of ecology and biogeography. Reasons for this interest are manifold. Understanding the origin of biodiversity hotspots may, for example, help guide prioritization in conservation and may facilitate forecasts on the quality of ecosystem services under climate change. Revealing origins of regional biodiversity requires systematic knowledge of the native taxa, as well as the utilization of diverse analytical approaches to investigate the link between the evolution of organisms and changes in their environment. A large variety of studies have addressed these aspects for several biodiversity hotspots (Rull, 2008; Antonelli *et al.*, 2009; Hoorn *et al.*, 2010; Phillips, Hopper & Dixon, 2010; Hughes, Pennington & Antonelli, 2013), despite considerable controversy about which metric(s) to use to delineate these hotspots (Brummitt & Lughadha, 2003; Kareiva & Marvier, 2003; Possingham & Wilson, 2005). Yet processes leading to the accumulation of biodiversity are better understood for some hotspots than for others.

Higher biodiversity than expected based on area is known to be associated with mountains (Linder, 2008; Badgley, 2010; Sedano & Burns, 2010; Sandel *et al.*, 2011; Fjelds , Bowie & Rahbek, 2012; Hoorn *et al.*, 2013), and has been reported for the Caucasus, the Andes, the Himalayas, and the Tianshan (Myers *et al.*, 2000; Myers, 2003; Myers & Mittermeier, 2003; Kier *et al.*, 2005). Compared to the Andes (see Hoorn *et al.*, 2010), the evolution of biotas in the region of the Qinghai-Tibetan Plateau (QTP) remains insufficiently understood despite its outstanding geographic extent. With a mean elevation exceeding 4500 m above sea level (a.s.l.) and a surface area of 2.3 million km² (Herzschuh *et al.*, 2010), the QTP is the highest and largest plateau

in the world, and arguably the most prominent topological feature on Earth. Altitudes range from 1500 m a.s.l. in the north and 500 m a.s.l. at the foot of the Himalayas to 8848 m a.s.l. at Mount Everest/Qomolangma (all 14 peaks exceeding 8000 m a.s.l. on Earth are found in the region, see Fig. 1). Annual precipitation is unevenly distributed ranging from 100–300 mm at the centre of the Plateau to 3000 mm in Darjeeling (Indian Himalayas). The fringe of the QTP encompasses parts of four different hotspots of biodiversity (Fig. 1) which are listed among the main biodiversity hotspots of the Northern Hemisphere (Myers *et al.*, 2000; Myers, 2003; Myers & Mittermeier, 2003; Tang *et al.*, 2006) and are assumed to be particularly vulnerable to climate change (Zheng, 1996; Yao *et al.*, 2007). Several biomes occur in the QTP region (e.g. alpine tundra, montane forests, subtropical dry forests, and rainforests, see Ni & Herzschuh, 2011), and strong ecological gradients in temperature or precipitation might play an important role in providing a variety of terrestrial habitats (Fig. 2). In stream systems, the differences in altitude are also associated with unparalleled gradients in glacial influence, substrate, water temperature and oxygen saturation, rendering the stream biota highly specialised, but not very diverse (Hamerl k & Jacobsen, 2012). For example, at very high altitudes fishes and aquatic insects are impacted by glacial run-off (Hamerl k & Jacobsen, 2012) and/or reduced absolute oxygen levels (Jacobsen, 2008). For both terrestrial and aquatic ecosystems, high-altitude settings result in azonal habitats in this otherwise subtropical environment.

Most of the studies available to date associate the diversification of organisms on the QTP with Middle to Late Miocene uplift and simultaneous climate changes, for example in lizards (Guo & Wang, 2007; Guo *et al.*, 2011), frogs (Che *et al.*, 2010), butterflies (Leneveu, Chichvarkhin & Wahlberg, 2009), birds (Johansson *et al.*, 2007; P ckert *et al.*, 2012), and plants (Wang *et al.*, 2009, 2012a; Favre *et al.*, 2010; Jabbour & Renner, 2012; Barres *et al.*, 2013; Gao *et al.*, 2013; Zhou *et al.*, 2013; for a review see Wen *et al.*, 2014), or with corresponding changes

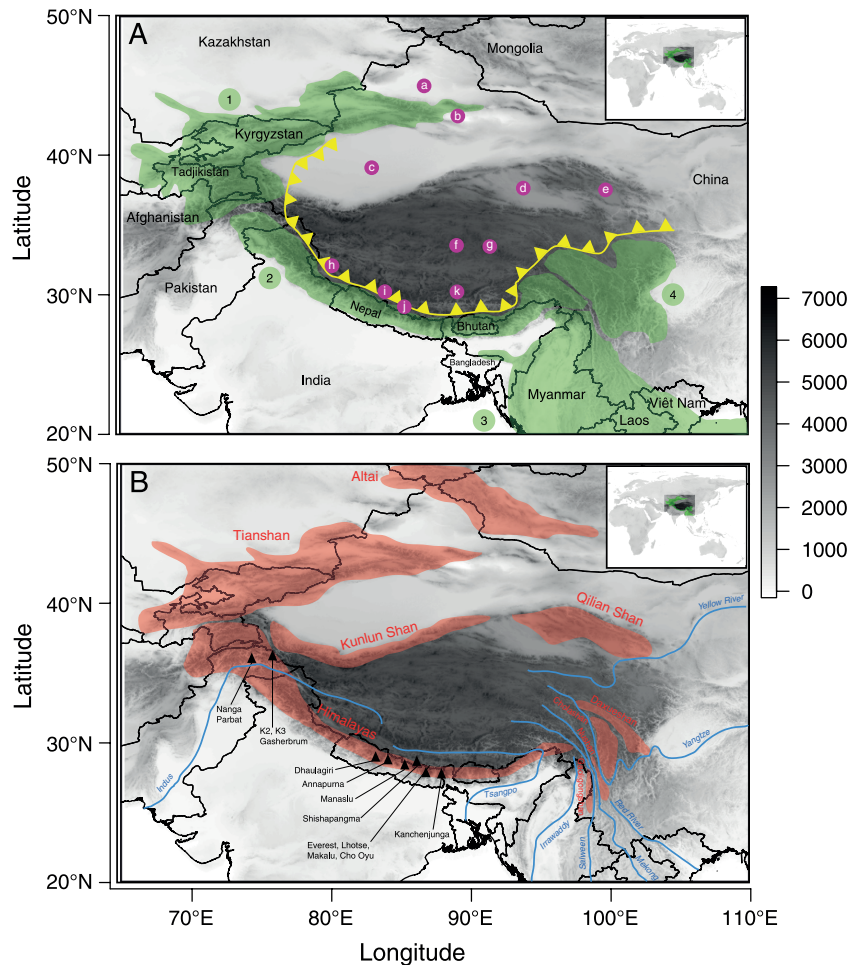


Fig. 1. Maps of the region of the Qinghai-Tibetan Plateau (QTP). (A) Four hotspots of biodiversity (green areas) surrounding the QTP: (1) mountains of Central Asia; (2) Himalayas; (3) Indo-Burma; (4) Hengduanshan. Sedimentary basins from which data contributed to estimate the palaeoelevation history of the QTP are shown by purple circles: (a) Junggar; (b) Turpan; (c) Tarim; (d) Qaidam; (e) Xining; (f) Nima; (g) Lunpola; (h) Zhada; (i) Thakkhola; (j) Gyirong; (k) Namling. The yellow line with triangles delineates a region receiving relatively low precipitation (600 mm/year or less). (B) Major mountain ranges (red areas), mountain summits exceeding 8000 m above sea level (black triangles) and main rivers in the region of the QTP. The grey scale indicates the average local altitude (m). These maps were created using WORLDCLIM data (Hijmans *et al.*, 2005).

in drainage systems, for example in freshwater fishes (e.g. He & Chen, 2006; Kang *et al.*, 2013) and freshwater crabs (e.g. Brandis, 2013). In the light of recent evidence, a significant part of the uplift of the QTP probably largely pre-dated the Miocene (Mulch & Chamberlain, 2006, see below). If mountain building did result in increased diversification rates, the lack of evidence for an earlier effect of the uplift on diversification might result from a natural delay of biological responses to environmental change, or from a warmer global climate that could have prevented a strong altitudinal zonation before and during the Middle Miocene climatic optimum (Fig. 3). The choice of study groups biased towards younger taxa or methodological difficulties (e.g. the lack of fossilised records) might have further obscured the patterns of diversification. Additionally, studies on organismic evolution often do not offer a global

perspective on biogeographic relationships between the QTP and other hotspots of biodiversity (a high proportion of taxonomic groups studied are endemics). It is clear, however, that biotic interchange contributed to the establishment of biodiversity hotspots, for example in the Andes (Cody *et al.*, 2010) or on either side of Wallace's Line (Lohman *et al.*, 2011; Richardson, Costion & Muellner, 2012). The role of immigration is often overlooked in studies on the QTP, which renders the estimation of the relative importance of *in-situ* diversification *versus* immigration followed by allopatric speciation impossible. Finally, to date, there is no consensus scenario on geological and climatic changes in the region of the QTP against which evolutionary scientists could test their hypotheses. Hence, this review aims to (i) provide such a geological and palaeoclimatic scenario to promote hypothesis-based research,

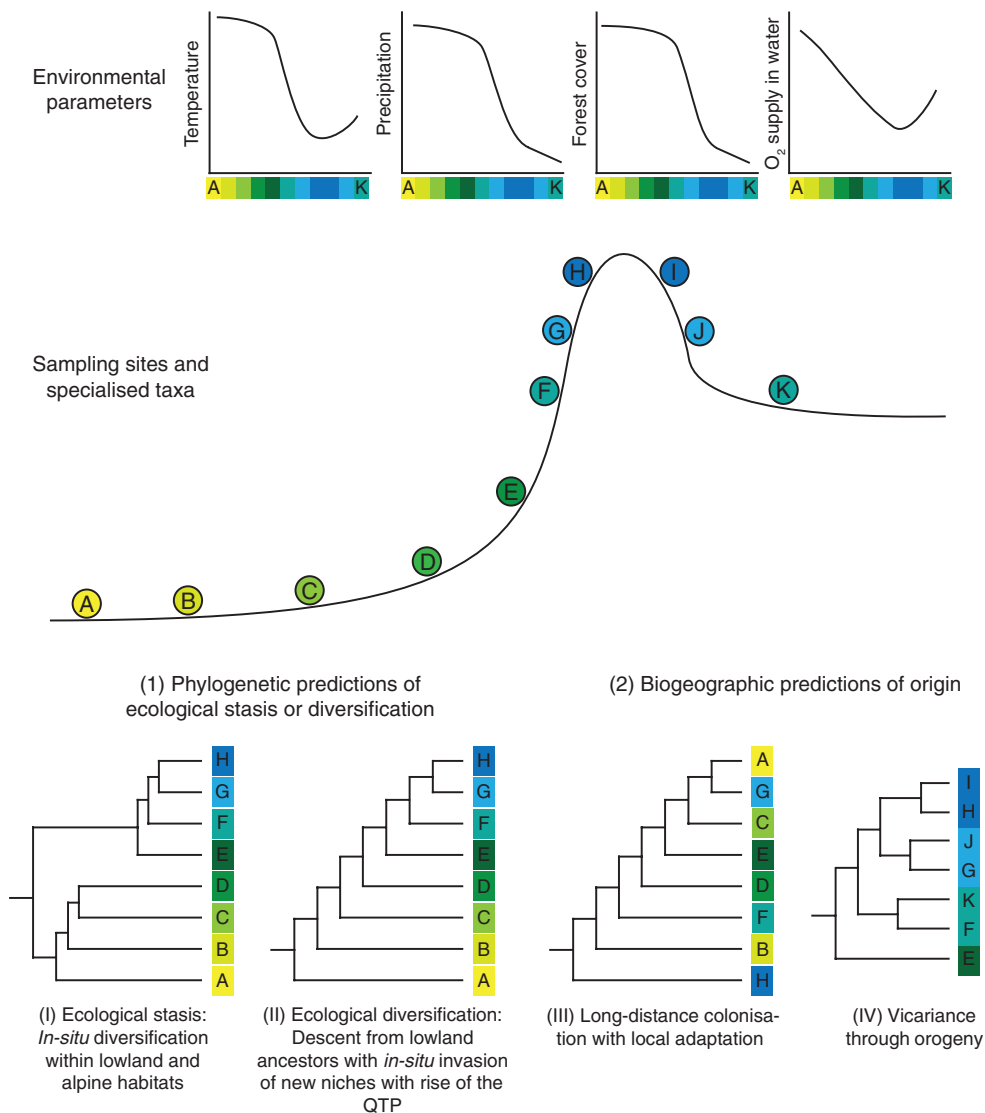


Fig. 2. Conceptual schematics of site location, environmental conditions at sampling sites, and phylogenetic predictions associated with different hypotheses on colonisation and ecological diversification. The upper diagrams show how selected environmental conditions may change with altitude along a cross section of the Qinghai-Tibetan Plateau (QTP) from south (site A) to north (site K). The central diagram shows the hypothetical distribution of ecologically specialised taxa along the cross section. Explicit environmental predictions and distribution of taxa allow the development of hypotheses on the biogeographic origin of biota and their trait and habitat evolution that can be studied in a classic hypothesis-testing framework using phylogenetic reconstructions and comparative methods or using model selection approaches (see Section III). The bottom diagrams show example predictions for scenarios of (1) ecological and trait diversification or stasis in a clade, and (2) biogeographic origin of clades. To compare taxa, ecological stasis or diversification can be linked to phylogenetic biome conservatism (*sensu* Crisp *et al.*, 2009) or biome shifts. Within distinct clades diversification can be linked to patterns of phylogenetic niche conservatism (*sensu* Crisp & Cook, 2012) with constraints on trait evolution or evolution of key innovations and/or adaptive diversification of traits (see methods in Section III.3). Specifically, on the basis of a dated multi-locus phylogeny, analysis of prevailing habitat preferences and character evolution provide a framework for testing if mountain and alpine species descended from alpine ancestors (phylogeny I: ecological stasis) or if they evolved from lowland ancestors *via in-situ* adaptation in novel azonal alpine habitats following the rise of the QTP (phylogeny II: ecological diversification). Analysis of phylogenetic relatedness among taxa can further reveal if the underlying processes occurred repeatedly. Ancestral area reconstructions (see methods in Section III.2) based on a multi-locus molecular phylogeny focussing on the regionally endemic alpine clades and carefully selected outgroups provide an independent test on the origin of the endemic alpine radiations of the QTP region. Repeated long-distance colonisation will lead to unrelated taxa occupying neighbouring biomes or ecological habitats (phylogeny III). Vicariance following the rise of a mountain range can lead to distribution of sister taxa north and south of the range (phylogeny IV).

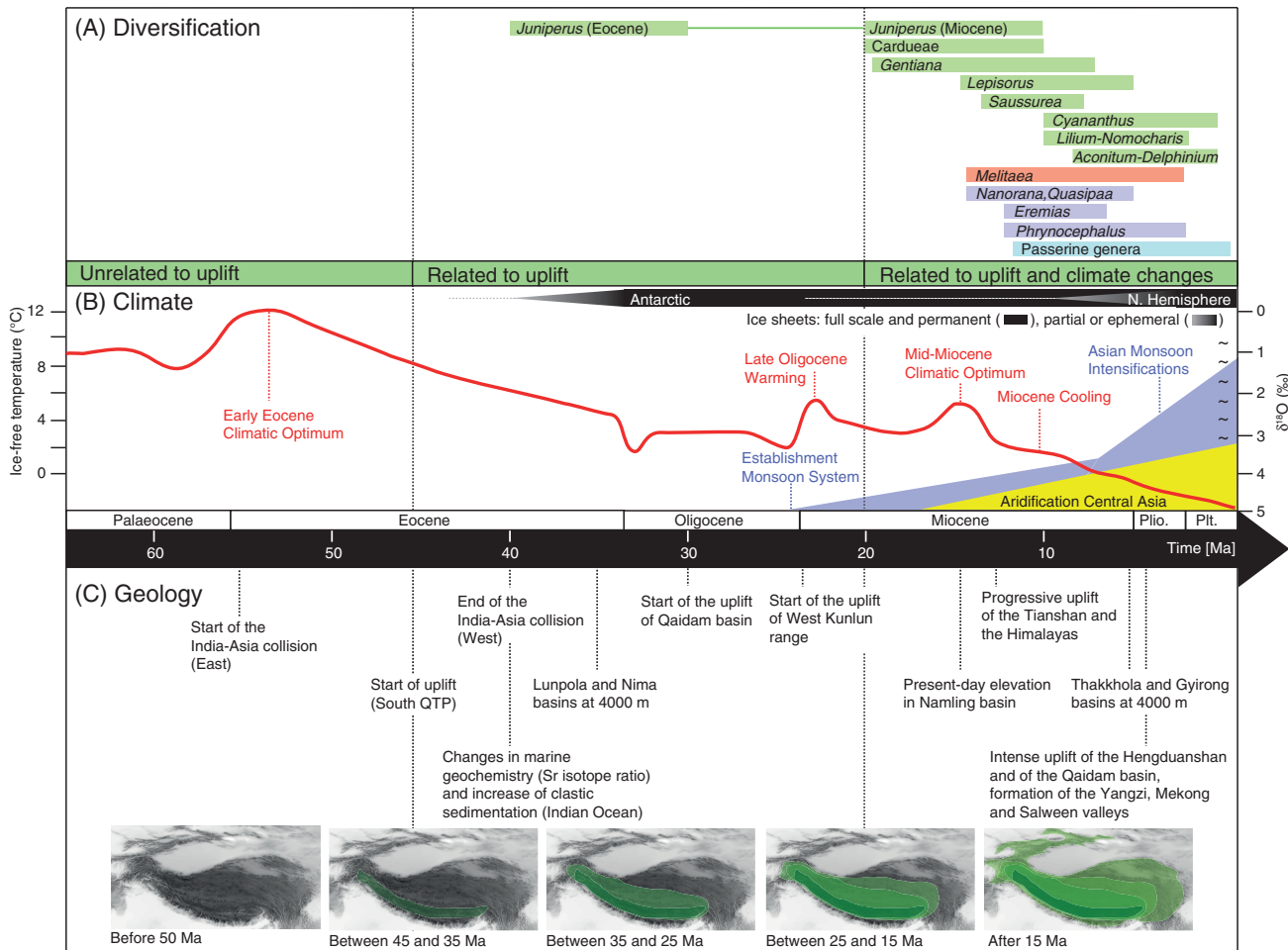


Fig. 3. Sequence of events for diversification (A), climate (B) and geology (C) in the region of the Qinghai-Tibetan Plateau (QTP). (A) Approximate timing of diversification for some selected groups of organisms: plants (green), insects (red), reptiles (purple) and birds (pale blue). (B) Climatic sequence of events including a global average $\delta^{18}\text{O}$ curve (right-hand axis) derived from benthic foraminifera which mirrors the major global temperature trends from Palaeocene to Pleistocene (red line); note that this average can only be interpreted in terms of absolute temperature (changes) for conditions of ice-free oceans during the Palaeocene and Eocene [modified from Zachos *et al.* (2001) and Zachos *et al.* (2008)]. Establishment of ice sheets of the Antarctic and of the Northern Hemisphere is indicated by grey to black bars on top. The onset and development of the monsoon and associated Central Asian aridification is symbolised by blue and yellow polygons. The climate oscillations during the Quaternary are represented by tildes (~). (C) Geological sequence of events related to the uplift of the QTP including a graphical representation of the extent of the uplift through time. Green shades indicate the portion of the QTP that had achieved altitudes comparable to present day for each given time (modified from Mulch & Chamberlain, 2006).

(ii) highlight available methods to test for possible correlations between organismic diversification *versus* geological and climatic events during the formation of the QTP, and (iii) review current knowledge on organismic evolution in the region of the QTP.

II. A GEOLOGICAL AND CLIMATIC SCENARIO TO PROMOTE HYPOTHESIS-DRIVEN RESEARCH

During the last decade, a growing number of phylogenetic and biogeographic studies have investigated the

link between organismic evolution and the uplift of the QTP and associated climate changes. In some of these studies, however, the timing of diversification of the study taxa tended to be compared with those geological or palaeoclimatic scenarios that simply supported the findings best, potentially conflicting with a more generally accepted geological sequence of events.

In order to promote hypothesis-driven research on the evolution of Tibetan biotas, we propose a likely scenario of geological and palaeoclimatic changes in the QTP (see Fig. 3). The task is admittedly difficult because the tectonic setting of this region is extremely complex (Zheng, Xiao & Zhao, 2013), and thus debates about

the geological and palaeoclimatic sequence of events related to the uplift of the QTP are still on-going. Nevertheless, understanding of the succession of these events has improved drastically during the last decade due to major contributions in the fields of geology, palaeoclimate reconstruction and palaeoclimate modelling (e.g. Zachos *et al.*, 2001; Zachos, Dickens & Zeebe, 2008; Tang *et al.*, 2013). In the following, we provide a geological scenario across five time slices: the Indian-Eurasian collision (*ca.* 55 to 40 Ma), the early uplift of the QTP (*ca.* 45 to 35 Ma), the extension of the uplift and the onset of the monsoon system (*ca.* 35 to 20 Ma), the uplift of high mountain ranges and aridification of Central Asia (*ca.* 20 to 10 Ma), and the final extension of the uplift (*ca.* 10 Ma to present). The locations of mountain ranges, sedimentary basins and river systems we refer to below are identified in Fig. 1.

(1) The collision (55 to 40 Ma)

The uplift of the QTP resulted from the collision of the Indian plate with Eurasia. Despite controversial studies suggesting a younger age for the collision (about 30 to 20 Ma or younger; Zheng *et al.*, 2000; Aitchison, Ali & Davis, 2007; Wan *et al.*, 2007), the collision is widely accepted to have started *ca.* 55 to 50 Ma (Klootwijk *et al.*, 1992; Yin & Harrison, 2000; Clift *et al.*, 2001; Dupont-Nivet *et al.*, 2010; Najman *et al.*, 2010; Zhang, Ding & Willems, 2012b; Chatterjee, Goswami & Scotese, 2013). Some recent studies have shown that the collision might have been asymmetric and more complex than previously assumed, involving two subduction zones: the collision started between 55 and 50 Ma in the east and progressed westward until its finalization about 40 Ma (Khan *et al.*, 2009; van Hinsbergen *et al.*, 2012; Bouilhol *et al.*, 2013). The uplift of the QTP is likely to have started during or shortly after the beginning of the collision (about 45 to 40 Ma; Li & Fang, 1999; Mulch & Chamberlain, 2006; Rowley & Currie, 2006). The migration speed of India northward was extremely fast (to a maximum of *ca.* 20 cm/year, Patriat & Achache, 1984; Klootwijk *et al.*, 1992; Chatterjee *et al.*, 2013), and the collision of India with the Eurasian continent represents one of the most spectacular examples of continental collisions during the Cenozoic. It is therefore very unlikely that the orogenic effect of the collision (the uplift) was delayed by several tens of millions of years (Yuan *et al.*, 2013).

(2) The early uplift of the QTP (45 to 35 Ma)

Contrasting opinions on the timing and dynamics of the uplift have been formulated and debated during the past 20 years (illustrated in Miao *et al.*, 2011). At the core of the discussion are questions related to when and how fast the QTP reached a significant average elevation. Today, under an admittedly cooler global climate than that of the Eocene, a mean elevation of

about 4000 m a.s.l. represents an important ecological threshold at the latitude of the QTP because it roughly corresponds to the tree line (Körner, 2007). Indeed, the upper tree line is generally found between 3700 and 4000 m a.s.l. with rare and isolated *Juniperus* forest patches occurring as high as 4900 m a.s.l. in south-eastern Tibet (Troll, 1948; Miehe & Miehe, 2000; Farjon, 2005; Miehe *et al.*, 2007). Also, fossils of three-toed horses (adapted to open habitats) found in the Zanda basin indicate that the tree line was at 4000 m a.s.l. or lower at least 4.6 Ma (Deng *et al.*, 2012). Earlier, during the Middle Miocene, forests probably thrived at altitudes of about 4600 m a.s.l. as suggested by palaeobotanical data from the Namling basin in southern Tibet (Spicer *et al.*, 2003). It seems likely that the tree line was at least at this height during the even warmer Palaeogene. In contrast to studies indicating a succession of orogenic phases interrupted by less active tectonic phases (Li & Fang, 1999; Wan *et al.*, 2007), strong evidence suggests a diachronous but constant uplift of the QTP (Rowley & Currie, 2006). As illustrated in Mulch & Chamberlain (2006), studies on palaeoaltimetry of the QTP show a progressive uplift from south to north. For example, estimates of the palaeoaltimetry ($^{18}\text{O}/^{16}\text{O}$ isotope-based ratios) of the Lunpola basin, in the centre of the QTP, indicate that this part of Tibet reached 4000 m a.s.l. at latest *ca.* 35 Ma (Rowley & Currie, 2006). A similar result was found in the Nima basin in Central Tibet (DeCelles *et al.*, 2007), whereas more northern localities were only half as high at that time (Cyr, Currie & Rowley, 2005). Nevertheless, palynological assemblages in lacustrine sediments from the Xining basin (north-eastern QTP) show the presence of high-altitude vegetation, confirming the occurrence of regional uplift as early as 38 Ma (Dupont-Nivet, Hoorn & Konert, 2008). In general, an early partial uplift of the QTP (*ca.* 40 to 35 Ma) is in agreement with the shift in ocean global geochemistry ($^{87}\text{Sr}/^{86}\text{Sr}$ isotope ratio) in marine carbonate records. Such changes in strontium isotope records in the sea are interpreted as an enhanced silicate weathering only possible if massive orogenic features were present in the region (Raymo & Ruddiman, 1992; Kump & Arthur, 1999). Also, a significant increase in clastic sedimentation offshore around south-eastern Asia corresponds to this timeframe (Potter & Szatmari, 2009). The fact that three independent proxies (isotope ratios of $^{18}\text{O}/^{16}\text{O}$, $^{87}\text{Sr}/^{86}\text{Sr}$, and clastic deposition) point towards a similar age for the early palaeoelevation of the southern part of the QTP is striking and strongly indicates that high-elevation orographic features (at least 4000 m a.s.l.) were already present in the region of the QTP as early as 40 to 35 Ma.

(3) The extension of the uplift and the onset of the monsoon system (35 to 20 Ma)

During the following epochs (Oligocene and Miocene) the uplift progressed particularly northward and

southward causing the extension of the QTP (Mulch & Chamberlain, 2006). Among other evidence, a magnetostratigraphic study of Tertiary sediments indicates that the start of the uplift of the north Qaidam (northern QTP) occurred at about 30 Ma (Sun *et al.*, 2005) or slightly earlier (Wang *et al.*, 2012b). Also located at the northern edge of the QTP, the initiation of the uplift of the West Kunlun range probably started 23 Ma due to upper crustal shortening and consequent crustal thickening (Jiang, Li & Li, 2013). The southern parts of the QTP likely reached an elevation comparable to present-day elevation by Mid to Late Miocene (between 15 and 5 Ma). Interestingly, two studies using independent proxies (oxygen isotopes and physiognomy of fossil leaves) agree that the region of the Namling basin (southern QTP) had reached such an altitude at about 15 Ma (Axelrod, 1998; Spicer *et al.*, 2003; Currie, Rowley & Tabor, 2005). However, these interpretations have been questioned based on comparisons of the fossil species of *Quercus* found in these localities with their nearest living relatives (Zhou, Yang & Xia, 2007). These authors compared the fossils' altitudinal ranges to those of the corresponding modern taxa and concluded that the basin was probably not elevated above 2500–3000 m a.s.l. during the Middle Miocene. Although the arguments of Zhou *et al.* (2007) seem reasonable at first glance, the authors did not take into account that the tree line in general as well as the altitudinal range of individual taxa may have been different from today due to the globally warmer climate during the Middle Miocene. Further studies suggest an elevation over 4000 m a.s.l. by the end of the Miocene in the Thakkhola basin and the Gyirong basin (Garzzone *et al.*, 2000; Rowley, Pierrehumbert & Currie, 2001), both located south of Lhasa. There is even evidence that the elevation of the Zhada basin, located near the southern margin of the QTP, reached a mean elevation of ca. 6000 m a.s.l. during the Miocene (Saylor *et al.*, 2009). Because the basin presently lies at an altitude of ca. 4500 m, the study of Saylor *et al.* (2009) indicates a potential 'collapse' of certain areas of the QTP due to crustal extensions or other (relaxing) tectonic processes.

The development of the Asian monsoon system is closely linked to the uplift history of the QTP and adjacent mountain ranges (Kutzbach, Prell & Ruddiman, 1993; Zhisheng *et al.*, 2001; Song *et al.*, 2010; Tang *et al.*, 2013). Because of its considerable size and altitude, the QTP progressively acted as an orographic barrier to atmospheric circulation in Asia and consequently contributed to major climatic changes in this region (Ruddiman & Kutzbach, 1991; Liu & Yin, 2002). Palaeoenvironmental records for the Palaeogene and Neogene suggest that these changes included the establishment of the monsoon system (Early Miocene; Sun & Wang, 2005; Guo *et al.*, 2008) and its progressive intensification (Zhisheng *et al.*, 2001; Liu &

Yin, 2002; Huntington, Blythe & Hodges, 2006; Wan *et al.*, 2007). In recent years a large number of studies have dealt with local or regional records of climatic changes, demonstrating that the intensities of the Indian monsoon and the East Asian monsoon varied on regional and temporal scales during the Cenozoic (e.g. Miao *et al.*, 2012; Xing *et al.*, 2012; Xu *et al.*, 2012; Yao *et al.*, 2012; Zhang *et al.*, 2012a; Jacques, Shi & Wang, 2013). For example, palaeobotanical data suggest that already during the Miocene the south-eastern margin of the QTP was under strong influence of both South Asian and East Asian monsoon and was dominated by a warm and humid climate and subtropical/tropical vegetation (Sun & Wang, 2005; Jacques *et al.*, 2011).

(4) The uplift of high mountain ranges and aridification of Central Asia (20 to 10 Ma)

The progressive extension of the uplift of the QTP (Mulch & Chamberlain, 2006) was associated with the orogeny of high mountain ranges such as the higher Himalayas and the Tianshan, both of which achieved a significant elevation during the Miocene (Valdiya, 1999; Tapponnier *et al.*, 2001; Wang *et al.*, 2008) and still constitute tectonically active areas. The original Tianshan belt formed in the Palaeozoic (Xiao *et al.*, 2004, 2009; Li *et al.*, 2006; Gao *et al.*, 2009; de Jong *et al.*, 2009; Lin *et al.*, 2009; Charvet *et al.*, 2011). The erosion processes have been active ever since (Hendrix, 2000; Charreau *et al.*, 2009; Yang *et al.*, 2013) and have deposited thick layers of sediments in adjacent basins (e.g. between 6 and 18 km of sediments in the Junggar basin; Novikov, 2013). The present-day Tianshan is a classic example of a reactivated intra-continental orogen: it was formed during the Miocene, in response to the collision of India with Eurasia (Wang *et al.*, 2010). Simultaneously, significant orogeny of the Himalayas (up to an elevation comparable to present day) is likely to have happened in the same timeframe (Tapponnier *et al.*, 2001; Wang *et al.*, 2008; Zhang *et al.*, 2013a), though the onset of the Himalayan orogeny (generating some punctual high altitudes) might have started slightly earlier (Chatterjee *et al.*, 2013 and references therein; Gébelin *et al.*, 2013).

The air circulation massively altered by the rise of the Tianshan and the Higher Himalayas, together with a worldwide cooling since the Middle Miocene climate optimum (Miao *et al.*, 2012), caused the progressive aridification of Central Asia (Guo *et al.*, 2001, 2004, 2008; Wu *et al.*, 2007, 2011; Tang *et al.*, 2011; Qiang *et al.*, 2011; Miao *et al.*, 2012). In a recent review, Lu & Guo (2014) specified that other factors such as changes in global ice volume and the final disappearance of the Tethys Sea in Asia (Late Miocene and Early Pliocene) also contributed to the aridification of Central Asia. Reduced precipitation in the Asian interior resulted in drastic shifts in the distribution of plant communities

(Sun & Wang, 2005; Zhang & Sun, 2011; Miao *et al.*, 2012) and major faunal turnovers (Meng & McKenna, 1998; Barry *et al.*, 2002; Badgley *et al.*, 2008). However, as many other complex physical mechanisms (such as thermal insulation of the Himalayas and heating effects of parts of the QTP on the troposphere) were involved in this development, it is still difficult to fully interpret the interplay between the temporally and spatially complex uplift history and the development of the monsoon system throughout the Cenozoic (e.g. Spicer *et al.*, 2003; Yao *et al.*, 2012; Tang *et al.*, 2013).

(5) The final extension of the uplift (10 Ma to present)

The QTP experienced further growth during the Late Miocene and the Pliocene (Li & Fang, 1999; Zheng *et al.*, 2000; Mulch & Chamberlain, 2006), particularly at its eastern edge (mostly the Chinese provinces of Qinghai, Sichuan and Yunnan). This area encompasses several mountain ranges composing the Hengduan-shan hotspot of biodiversity: the Daxueshan, the Gaoligongshan, the Cholan-shan and the Nushan. The palaeoelevation history of the QTP provided by Mulch & Chamberlain (2006) suggests that the orogeny of the Hengduan-shan occurred as a final propagation of the uplift after 10 Ma. An alternative view, recently supported by palaeobotanical and palaeoclimatic data, concludes that the Hengduan-shan underwent major uplift only after the Miocene, reaching peak elevation shortly before the Late Pliocene (Sun *et al.*, 2011 and references therein). Similarly, some lines of evidence indicate a rapid uplift in the region of the Qaidam basin at the same time (Zhang *et al.*, 2013b). Since the collision, the QTP has experienced shortening on its north–south axis. This shortening was accommodated by the formation of irregular surface features and by its deformation with a clockwise rotation in its eastern part (including the Hengduan-shan), a phenomenon which is still in progress as indicated by global positioning system (GPS) measurements (Zhang *et al.*, 2004; Cao *et al.*, 2009). As a result, parallel north–south oriented valleys surrounded by high peaks were formed in south-eastern Tibet and north-western Yunnan (e.g. the Yangzi, the Mekong, and the Salween valleys). Today, this region displays drastic altitudinal variations ranging from 1000 m a.s.l. (in deep valley floors) to numerous peaks above 6000 m a.s.l., and is one of the ecologically most diverse areas in the QTP region (López-Pujol *et al.*, 2011).

III. ARE GEOLOGICAL AND CLIMATIC CHANGES POTENTIAL DRIVERS OF BIOLOGICAL DIVERSIFICATION?

Evolution and diversification of organisms may be predominantly driven by abiotic factors (such as climatic

and tectonic events), biotic factors (e.g. inter- or intraspecific interactions like competition and predation; see e.g. Antonelli & Sanmartín, 2011), or a combination of both. Biotic and abiotic factors generally (but not always) have an effect on diversification at different temporal and geographical scales (Benton, 2009). Biotic factors, as described by the ‘Red Queen’ model, tend to act over relatively short periods of time (less than a million years) and more locally, whereas abiotic factors, as described by the ‘Court Jester’ model, tend to act over several millions of years and within a climate zone, a continent, or globally, and generate large-scale patterns (Benton, 2009). As the sequence of events related to the uplift of the QTP spans over several dozen million years, the impact of abiotic processes on the observable patterns likely outweighs that of biotic processes.

The effect of geological and climate dynamics on species diversification has been at the centre of debate for several years. A plethora of studies has suggested that the uplift of the QTP might have triggered evolutionary radiations, without formally inferring the temporal presence of the considered taxon in the region of the QTP, for example in plants (Wang, Yang & Liu, 2005; Fan *et al.*, 2009; Wang *et al.*, 2009; Favre *et al.*, 2010) and other organisms (Hou, Fu & Li, 2007; Guo *et al.*, 2011). Nevertheless, a growing number of studies provide both a temporal (molecular dating) and a spatial (biogeographic) framework (Liu *et al.*, 2006; Leneveu *et al.*, 2009; Mao *et al.*, 2010; Tu *et al.*, 2010; Jabbour & Renner, 2012; Sun *et al.*, 2012; Tietze & Borthakur, 2012; Barres *et al.*, 2013; Gao *et al.*, 2013; Tietze *et al.*, 2013; Lei, Qu & Song, 2014). In some studies the links between the timing of diversification and environmental conditions are more tangible. In river fishes of the genus *Schizothorax* and freshwater crabs of the genus *Himalayapotamon* the periods of diversification are associated with changes in the drainage systems caused by the Miocene uplift of the QTP (He & Chen, 2006; Brandis, 2013). The orogeny of high mountain ranges separating deep valleys may have created geographical barriers reducing gene flow between isolated populations and promoted allopatric divergence, as shown for plants (Xu *et al.*, 2010) and freshwater fishes (von Oheimb *et al.*, 2011). In addition to classic hypothesis-testing methods, model selection statistics can be applied to compare competing geological and/or climatic scenarios that potentially have triggered phylogenetic diversification, using time-calibrated molecular phylogenetic trees and high-resolution palaeoclimatic data. Model selection approaches can also be used to uncover the factors determining the range limits of selected taxa. This constitutes essential knowledge to understand shifts in geographic distribution induced by geological or climate change. We suggest an essential set of analyses, which taken together should provide a solid framework to evaluate hypotheses related to the influence of geological or climatic changes on organismic diversification (Fig. 2).

(1) The temporal framework

The temporal framework of diversification can be estimated by molecular clock analyses, for example using Bayesian approaches implemented in BEAST (Drummond & Rambaut, 2007; Drummond *et al.*, 2012) or MrBayes (Ronquist *et al.*, 2012). For these analyses, a reasonable density of sampled taxa is needed, because empirical and modelling studies have shown an effect of taxon sampling size on the robustness of phylogenetic hypotheses (e.g. due to long-branch attraction; Albert *et al.*, 2009) and thus on age estimates (Linder, Hardy & Rutschmann, 2005; Muellner, Vassiliades & Renner, 2007; Heath, Hedtke & Hillis, 2008; Milne, 2009). When studying the correlation between the uplift of the QTP and organismic evolution, the choice of the model systems is crucial. Ideally, the study group will allow for a good calibration in the molecular dating analysis, which is best achieved using reliable fossil evidence (Renner, 2005). This might represent a challenge, since the fossil record is scarce for most organismic groups. In some cases, the sampling of the focal group might be amended by phylogenetically related clades, to be able to include fossils available for the latter. In the absence of suitable fossils, secondary calibration is another viable alternative (Hedges & Kumar, 2004). Potential errors from the original analysis may, however, be propagated to the second analysis, and thus should be interpreted with the necessary care (Graur & Martin, 2004; Renner, 2005). In fact, a recent study on *Nothofagus* (in the fossil-rich Fagales) showed that sampling more outgroup species in order to include more external fossils was a better alternative than secondary calibration (Sauquet *et al.*, 2012). Finally, if the fossil record is too sparse and does not allow for any reliable calibration both in the ingroup and the outgroup, geological events such as the emergence of volcanic islands or the opening and closure of land bridges might serve as temporal constraints (Lerner *et al.*, 2011; Päckert *et al.*, 2012). This strategy, however, demands special care, as ancestral habitats (older than the respective island) might be submerged today, or the island might be a refugium for an older group, which once had a wider distribution before the appearance or the colonization of the island (Heads, 2011; Päckert *et al.*, 2013). Furthermore, events used as temporal constraints must be independent of the ones involved in a correlation test, to prevent circularity. Especially when only a few calibration points are available, the impact of the individual chosen priors is extremely high and might strongly bias the analysis. Solutions provide either choosing flat priors or estimating the prior itself during the analysis by placing hyperpriors (Heath, 2012).

(2) The spatial framework

Areas of origin as well as migration routes and directions can be deduced from biogeographic analyses.

Various analytical biogeographic methods are available to assess the likelihood of alternative biogeographic hypotheses (Cox & Moore, 2010; Lomolino *et al.*, 2010), including dispersal-variability analysis (DIVA) and dispersal-extinction-cladogenesis (DEC), with software such as RASP (Yu, Harris & He, 2012), Bayes-DIVA (Nylander *et al.*, 2008) and LAGRANGE (Ree & Smith, 2008). All these methods are based on a phylogenetic inference that allows reconstructing the biogeographic history of ancestral clades (Fig. 2). The latest methodological development allows overcoming computational limitations on the number of areas that can be specified in biogeographic analyses. This new approach employs a Bayesian framework and is implemented in BayArea (Landis *et al.*, 2013). Different methods for biogeographic analysis (Fitch parsimony, stochastic mapping, DIVA and DEC) may yield contrasting results, as was shown in a study on the plant family Gesneriaceae (Clark *et al.*, 2008). The results of this study highlight that parsimony methods are usually outcompeted by those based on likelihood due to the latter's power to incorporate prior knowledge (e.g. distances between distributional areas, and different geological settings during evolutionary history). Nevertheless, likelihood-based biogeographic analyses also have their own set of assumptions (e.g. the *a priori* specification of dispersal rates among areas) which might lead to potential bias. Therefore, applying and comparing a combination of the above-mentioned analyses is usually advisable.

Not many published studies on the QTP's flora and fauna have provided biogeographic analyses so far. Questions related to the origin of the taxa occurring in the region of the QTP thus remain unanswered. For example, the uplift of the North American Cordillera predates that of the QTP by several millions of years (Mix *et al.*, 2011), making it a potential source of pre-adapted lineages to colonise the QTP by long-distance dispersal or migration, possibly *via* the Bering Strait. Other regions of the world could have acted as source of biodiversity to colonise the QTP. A study by Li *et al.* (2012) indicates that a fern genus colonised the QTP from the Malay Archipelago. The rich passerine avifauna of the QTP might be the result of colonization of several lineages from adjacent regions: the ages of tropical and subtropical clades coincide with the colonization events of the Himalayan foothills by Indo-Burmese and Indo-Chinese ancestors, whereas Himalayan subalpine forests were colonised from northern Chinese and eastern Palearctic source populations (Johansson *et al.*, 2007; Päckert *et al.*, 2012). A similar pattern was originally assumed for the insect fauna of the Himalayan cloud forest, but recent studies have revealed that this pattern might be incorrect for non-flying ground beetles. Several groups of Carabidae, that were generally considered to be derived from a northern ancestral fauna, are in fact likely to

have radiated *in situ* in the Tibetan region (Schmidt & Hartmann, 2009; Schmidt *et al.*, 2012). Likewise, Condamine *et al.* (2012) found that temperate-adapted swallowtails (Lepidoptera: Papilionidae) diversified during warming periods in the Miocene in the area of the Himalaya and the Tibetan Plateau. These regions act as present-day alpine refugia. Under this scenario, the southern margin of the QTP might have acted as a centre of evolution (the southeastern QTP margin in some bird groups; Tietze *et al.*, 2013; Lei *et al.*, 2014). As illustrated here, two contrasting mechanisms can lead to similar biodiversity patterns. Adaptation and diversification could both have occurred *in situ*, or alternatively, multiple immigration events of pre-adapted lineages might have occurred on the QTP. If the latter process dominated the formation of the observed local biodiversity, it would not have predominantly resulted from increased diversification rates or longer diversification times in the QTP region, but rather from immigration. Future studies should recognise the potential of both processes, and the emerging questions should deal with discovering their relative frequency.

(3) Diversification rates

Rates of speciation and extinction often vary over time (e.g. Morlon, Potts & Plotkin, 2010; Stadler, 2011; Condamine, Rolland & Morlon, 2013), because they are modulated by extrinsic abiotic and biotic parameters. Studying the temporal variation of diversification rates allows addressing questions related to phenomena like rapid radiations (Baldwin & Sanderson, 1998; Hughes & Eastwood, 2006; Day, Cotton & Barraclough, 2008; Valente *et al.*, 2010), massive extinctions (Bininda-Emonds *et al.*, 2007), effects of past climate change (Condamine *et al.*, 2012, 2013), or temporal rate variations in general (Morlon, Parsons & Plotkin, 2011; Stadler, 2011). Moreover, it allows comparisons between geographical units (Ricklefs, Schwarzbach & Renner, 2006; Valente *et al.*, 2010; Goldberg, Lancaster & Ree, 2011) and between lineages (Phillimore *et al.*, 2006; Linder, 2008; Magallón & Castillo, 2009), and with respect to different traits (Maddison, Midford & Otto, 2007; FitzJohn, 2012; Goldberg & Igić, 2012).

Several programmes for the study of diversification rates derived from either extant or fossil data are currently available, like MEDUSA (Modeling Evolutionary Diversification Using Stepwise Akaike Information Criterion, Alfaro *et al.*, 2009), fossilMEDUSA, BayesRate (Silvestro, Schnitzler & Zizka, 2011), and PyRate (Silvestro *et al.*, 2014). In contrast to other methods that are mostly correlative, the approach by Condamine *et al.* (2013) allows for direct quantification of the effect of palaeoenvironments on diversification by describing speciation and extinction rates as likelihood-based functions of environmental variables. The study of diversification rates in association to traits or distribution is currently best implemented in BayesRate (Silvestro *et al.*,

2011), as the software includes considerable improvements with regard to previously available methods (Nee, May & Harvey, 1994; Rabosky, 2006, 2010; Rabosky & Lovette, 2008; Alfaro *et al.*, 2009). BayesRate allows accounting for uncertainties in divergence times and topology, as well as for incomplete taxon sampling, all of which are prominent sources of bias in molecular dating approaches. Most importantly, the program allows hypothesis-testing in a meta-analysis framework. By processing multiple datasets within one single analysis, the program allows a direct comparison of diversification rates between different taxonomic groups and/or geographical regions. The method was successfully used in a meta-analysis of four plant groups of the African Cape Floristic Region and revealed an overall rates difference between Cape and non-Cape clades (Schnitzler *et al.*, 2011). Another study detected an explosive radiation of the Andean clade of *Lupinus* (Silvestro *et al.*, 2011). Only a few studies have investigated diversification rates in the flora and fauna of the QTP so far (Leneveu *et al.*, 2009; Mao *et al.*, 2010; Jabbour & Renner, 2012; Kennedy *et al.*, 2012; Sun *et al.*, 2012; Wang *et al.*, 2012a). An increase in the diversification rate of the butterfly genus *Melitaea* (Lepidoptera: Nymphalidae) at around 15 Ma coincided with the progressive uplift of the QTP and adjacent mountain ranges and the evolutionary origin of butterfly lineages (*M. arcesia* and *M. fergana* group) in these areas (Leneveu *et al.*, 2009). Their study includes a good taxonomic sampling (about two-thirds of extant species) and excellent coverage of the genus' distribution range. Since the methods available to study diversification rates over time also allow comparing rates between geographical units, insights into large-scale organismic relations will be obtained by comparing taxonomic groups that have a wide distribution. Studies could test if differences in diversification rates occur between QTP lineages and non-QTP lineages, as well as QTP organisms and taxa from other mountain systems *versus* lowland taxa. The latter comparison will allow for results of much broader significance with respect to the evolution of hotspots of biodiversity associated with mountain formation.

IV. DISTRIBUTION, ECOLOGY, AND AGE OF TAXA

Identifying study taxa that could represent appropriate model systems to investigate the effect of geological and climate changes on organisms in the region of the QTP is a difficult task. In practice, studies preferably include taxa that are easily distinguishable in the field, those that are iconic or include economically important species. There is also a tendency to choose species-rich clades over single (relict) lineages. These trends in the choice of taxonomic groups, mainly driven by practical needs, might introduce bias in meta-analyses and therefore

we suggest that some rationale should be employed to aid the choice of taxa. Among the most important aspects to be considered are distribution, ecology, and (assumed) age of the studied organisms. In addition, it would be preferable to select groups with an extensive fossil record, to be able to interpret directly the evolutionary history of all lineages, as described in Fritz *et al.* (2013). Unfortunately, a continuous documentation of ancestral forms is rare, especially for terrestrial groups. It is very likely that the uplift of the QTP had different impacts on the evolution of different taxa; therefore a general understanding will be achieved only by combining datasets derived from a variety of organismic groups.

(1) Widespread *versus* endemic taxa

To test if the uplift of the QTP triggered diversification rates, it is necessary to compare QTP organisms with non-QTP organisms, either from other mountain systems or from lower elevations. Taxa to be investigated will therefore have a distribution range spanning way beyond the region of the Plateau, or display disjunctions. Some studies limited their investigation to endemic groups, or focused on Tibetan species of a taxon otherwise more broadly distributed (Wang, Liu & Miede, 2007; Yang & Wang, 2007; Zhang *et al.*, 2008, 2011; Yue *et al.*, 2009). Studying taxa restricted to the QTP region can nevertheless be a valuable approach to provide information on the biogeographic history of organisms within the QTP (Zhang *et al.*, 2011, 2012c; Zhou *et al.*, 2013). For example, a study on *Syncalathium* (Asteraceae) suggested possible migration routes from the north-eastern to the central and southern part of the QTP (Zhang *et al.*, 2011). Another study showed a clear pattern of allopatric speciation by geographic isolation for species of *Mollitrichosiphum* (Aphididae, Greenideinae) in China (Zhang *et al.*, 2012c). Several highly diverse plant genera mainly occurring in the QTP's highest biome (the alpine tundra) have a sub-worldwide distribution, among them *Primula*, *Saussurea*, *Rhododendron*, *Vaccinium*, *Rheum*, *Gentiana*, *Saxifraga* and *Pedicularis* (Wu, 1987). Some of these genera have already attracted the attention of scientists because they are likely to uncover valuable general evolutionary scenarios for alpine taxa (Wang *et al.*, 2005; Zhang *et al.*, 2009; Favre *et al.*, 2010; Sun *et al.*, 2012). Nevertheless, evolutionary consequences of the uplift of the QTP are not limited to alpine taxa, and concern a broader range of biomes of lower altitudes (mountain forests, monsoon forests and subtropical moist forests).

(2) Contrasting biome-dependent biogeographic histories

Comparing the biogeographic history of taxonomic units of different adjacent biomes might reveal

contrasting patterns, as shown for some groups of passerine birds. Tibetan endemics represent deep and ancient (Miocene/Pliocene) lineage splits within a passerine genus/family. For example, *Leptopoecile* in Aegithalidae (Päckert, Martens & Sun, 2010; Päckert *et al.*, 2012), and *Kozlowia* in 'true rosefinches', *Carpodacus* s. str. (Tietze *et al.*, 2013) are very plausibly the result of Mid to Late Miocene lineage divergence but of ambiguous biogeographic origin. By contrast, the Himalayan subalpine avifauna of the upper coniferous forest belt consists largely of Palaearctic faunal elements (Martens, 1984). Thus, the complex extant phylogeographic patterns observed today in several passerine genera can be traced back to successive colonization events under very different climate regimes and to repeated climate-driven vicariance in the QTP region (Voelker, 2010; Päckert *et al.*, 2012). Furthermore, the potential for diversification as a consequence of environmental change is likely to vary among taxa. While testing the link between the uplift of the QTP and the diversification of taxa, it is important to compare the evolutionary history of organisms with different ecological preferences to gather a realistic overview of the relevant processes. For example, forest and grassland organisms should be compared because the fragmentation of forests and the corresponding expansion of grasslands during the Miocene on the QTP (Zhisheng *et al.*, 2001) have potentially generated contrasting patterns of diversification. First, forest fragmentation might have supported allopatric speciation of organisms that are dependent upon the presence of trees, such as epiphytic plants or dispersal-limited organisms that are restricted to one or few forest types (e.g. micro-snails of the Ellobiidae or Diplommatinidae families). Second, the expansion of grasslands might have promoted particular adaptations (drought tolerance, ground-nesting) with or without subsequent diversification. For example, the passerine avifauna occurring in the Plateau habitats harbours a good number of local and regional endemics (Vaurie, 1972; Weigold, 2005) and most of them have strong morphological and behavioural adaptations to open alpine habitats such as ground-nesting. Genomics of the endemic ground-tit (*Parus humilis*) uncovered a number of physiological adaptations to the extreme high-elevation habitats of the QTP (in genes involved in energy metabolism, immune perception and hypoxia response) during 8–10 million years of lineage separation (Qu *et al.*, 2013). Habitat-driven morphological adaptations have been documented for forest-dwelling QTP species across large elevational gradients (Price, 2010; Kennedy *et al.*, 2012) and for alpine QTP species even across rather narrow gradients (Landmann & Winding, 1993). Likewise, a multicausal impact of both climate- and competition-mediated resource distributions provides an explanation for the north-westward decline of bird species richness along the southern QTP margin

(Price *et al.*, 2011) and for shifts in species assemblage structure across elevational gradients in the Himalayas (Gosh-Harihar, 2014). Another example can be found in fishes, where two highly specialised radiations dominate the fauna: the stone loach genus *Triplophysa* and the cyprinid snowtrout of the genus *Schizothorax* represent the most diverse groups on the QTP and dominate torrential mountain rivers in the QTP and Himalayas (He & Chen, 2006); their diversity peaks at mid-elevations (1700–2200 m.a.s.l.; Li *et al.*, 2009). Lake fish on the other hand seem to exhibit relatively low levels of diversity on the QTP and slopes compared to the lowland regions in China (Zhao *et al.*, 2006). Similar to these examples, other organisms of the QTP region might therefore best be approached based on biomes or larger and ecologically distinct geographical areas including similar biomes (Martens, Tietze & Päckert, 2011), e.g. the QTP itself (open habitats) and the forested margins of the Plateau (i.e. Himalayas and Hengduan Shan). Indeed, the eastern edge of the QTP is sometimes referred to as the ‘evolutionary front’ of China because of its high proportion of endemics probably resulting from the uninterrupted uplift of the region since the Late Neogene (López-Pujol *et al.*, 2011).

(3) The age of the study taxa

High diversification rates, which may be based on high speciation rates and/or low extinction rates, are expected in regions that are geologically dynamic, including regions with active orogeny (Linder, 2008; Badgley, 2010; Sedano & Burns, 2010; Sandel *et al.*, 2011; Fjeldså *et al.*, 2012; Hoorn *et al.*, 2013). Some taxa on mountains might be less affected by extinction due to climate change because climate zones are compressed there and habitat diversity could act as a safeguard against species loss (Sandel *et al.*, 2011). Those lineages could therefore be less vulnerable to climatic warming or cooling events. Since the region of the QTP is likely to have experienced a dynamic orogeny during at least the past 40 million years, it is surprising that the few studies including diversification rate analyses report a time for diversification as late as the Miocene for QTP organisms (Fig. 3), in ferns (Wang *et al.*, 2012a), gymnosperms (Mao *et al.*, 2010), angiosperms (Jabbour & Renner, 2012; Sun *et al.*, 2012), and butterflies (Leneveu *et al.*, 2009). The study on *Juniperus* (Mao *et al.*, 2010) also found higher diversification rates before the Oligocene, which was interpreted as a result of changes in global and local climates. The delay between the start of the uplift and the response of QTP lineages in terms of increased diversification rates might be the result of the time needed for the evolution of mountain habitats as environmentally distinct entities, for the adaptation of organisms to these habitats, or for colonization from remote areas (compare with Fig. 2). It could also indicate that increased diversification rates occurred after

the uplift had progressed sufficiently to alter global climates drastically. Possibly, cold-adapted montane biotas did not exist in the region of the QTP before the climate cooling from Mid-Miocene onwards (Fig. 3). If cold habitats were only present since about 13 Ma (in the cooling period that followed the Mid-Miocene), this would explain why not many lineages in those mountains today share common ancestors that trace back to *ca.* 40 Ma. The delay between the start of the uplift and the response of QTP lineages might also reflect a biased selection towards relatively young study taxa. Previous studies often investigated organismic evolution in the QTP at genus level. Given a *ca.* 40 million year timeframe for the uplift of the QTP, it might be more appropriate to perform studies at a higher taxonomic level, possibly including several related genera or families. More evidence needs to be gathered to assess whether the uplift had an impact on diversification, and which aspect of the orogeny and associated factors like climate change and evolution of the monsoon system was the driver.

V. CONCLUSIONS

(1) A number of studies have previously hypothesised that the uplift of the QTP triggered the diversification of many organisms. Yet only a few provided a full set of complementary analyses (molecular dating, biogeographic, and diversification rate analyses) to support this. In general, biogeographic analyses and diversification rate analyses related to the evolutionary history of the biotas of the QTP remain scarce in the literature and should be encouraged. These analyses largely depend on molecular clock dating, making use of the fossil record as source for setting temporal constraints. In addition, a synthesis of the fossil record through time for the region would be extremely important. This should include open data deposition in databases, like the palaeobiology database (<http://www.paleobiodb.org>). Future research should consider the great potential of palaeontological studies.

(2) Different patterns of diversification might be observed depending on the ecology of the studied taxa. It is therefore important to investigate organisms that are typical for each biome occurring in the region of the QTP. Moreover, the migration of taxa from other regions of the world might have contributed substantially to the establishment of high biodiversity levels in the QTP. To uncover the relative contribution of *in-situ* speciation *versus* colonisation, a variety of widespread taxa should be investigated within the framework of a meta-analysis approach. Since meta-analyses usually harvest published phylogenies reconstructed under different assumptions, methods and fossil calibrations, a standardised methodology could be an alternative, as

for example proposed by the SUPERSMART project (www.supersmart-project.org).

(3) Whereas the diversity of angiosperms and vertebrates is relatively well documented for the region of the QTP, the taxonomy of other highly diverse groups (e.g. molluscs or insects) remains understudied. For these groups a preliminary effort on taxonomy needs to be promoted.

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