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ORIGINAL ARTICLE

A global inventory of mountains for bio-geographical applications

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Abstract Mountains are hotspots of biodiversity. Yet, evaluating their importance in global biodiversity inventories requires the adoption of a pertinent definition of mountains. Here, we first compare the well-established WCMC and GMBA definitions, which both use geographical information systems. We show that the WCMC approach arrives at twice the global mountain area and much higher human population numbers than the GMBA one, which is explained by the inclusion of (mostly) low latitude hill country below 600 m elevation. We then present an inventory of the world's mountains based on the GMBA definition. In this inventory, each of the 1003 entries corresponds to a polygon drawn around a mountain or a mountain range and includes the name of the delineated object, the area of mountainous terrain it covers stratified into different bioclimatic belts (all at 2.5′ resolution), and demographic information. Taken together, the 1003 polygons cover 13.8 Mio km^2 of mountain terrain, of which 3.3 Mio km^2 are in the alpine and nival belts. This corresponds to 83.7% of the global mountain area sensu GMBA, and 94% of the alpine/nival area. The 386 Mio people inhabiting mountainous terrain within polygons represent 75% of the people globally inhabiting mountains sensu GMBA. This inventory offers a robust framework for the integration of mountain biota in regional and larger scale biodiversity assessments, for biogeography, bioclimatology, macroecology, and conservation research, and for the exploration of a multitude of socio-ecological and climate change-related research questions in mountain biota, including the potential pressure on alpine ecosystems.

Keywords Alpine · Biodiversity · Climate · Elevation · Montane · Map of life

Introduction

Mountains are remarkable in many ways, and in particular in the exceptional biodiversity they host. Likely because of the rapid change in climatic conditions with elevation across very short geographical distances and because of strong contrasts in life conditions with varying exposure and topography, mountains support an estimated one-third of terrestrial species diversity (Körner 2004) and host half of all 34 global biodiversity hotspots (Chape et al. 2008). The global alpine terrain alone hosts about twice the number of flowering plant species expected based solely on the area it covers (Körner et al. 2011). Additionally, because of the biogeographic isolation under which mountain ecosystems have evolved, these biomes also harbor high numbers of endemic species (Vetaas and Grytnes 2002; Barthlott et al. 2005; Tang et al. 2006). The richness of plant species

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observed in mountains is particularly important, in that a diverse vegetation is important for securing soils on steep slopes, thereby contributing to the protection of landscapes and populations against natural hazards and the impact of extreme events. Mountain vegetation further provides food, fiber, and fodder and mountains in their entirety supply clean water to half of humankind (Messerli and Ives 1997; Egan and Price 2016), attract tourists, and often host cultural heritage sites and landscapes of outstanding species richness and beauty. Because of their geodiversity, mountain ecosystems have served as refuge for organisms during past climatic changes and are predicted to provide protection for flora and fauna also under forthcoming climatic change (Scherrer and Körner 2011). Accordingly, mountain ecosystems represent areas of prime conservation value (Messerli and Ives 1997; Hamilton 2002; Harmon and Worboys 2004; Körner and Ohsawa 2006).

The global occurrence of mountains across all latitudes and the steep, small-scale environmental gradients that characterize them provides exciting research opportunities (Körner 2000). Additionally, as large environmental and biodiversity data sets become more readily available, new analyses become possible on a macro-ecological scale (Jetz et al. 2012). Because of their steep climatic gradients, mountains are also sentinels of change in a rapidly warming world (La Sorte and Jetz 2010; Pauli et al. 2012) and, thereby, offer unique 'experiments by nature' for studying the mechanisms driving the evolution and maintenance of biodiversity (Janzen 1967; Brown 1971; Körner 2000, 2001). Yet, comparative research in mountain biodiversity and conservation planning has been constrained by the lack of a standardized delineation and environmental characterization of the world's mountains. The spatial placement of inventories mobilized from the literature and the determination of expected species occurrences following expert-based bioclimatic associations have turned out to be particularly challenging (Jetz et al. 2012, http://www.mol.org). For the world's islands, both an existing inventory (Dahl 1991) and a more recent bioclimatic and physical characterization (Weigelt et al. 2013) have enabled fascinating research, including the comparative analyses of island flora and fauna and of their phylogenetic structure (Weigelt et al. 2016).

One major reason for the absence of an inventory of the mountains of the world is a long-lasting controversy about the arguably difficult definition of mountains (e.g., Smith and Mark 2003; Byers et al. 2013). This controversy results in part from the fact that different mountain definitions have been proposed for different contexts of use and even for different countries. Accordingly, a definition tailored for applications related to life conditions for humans, plants, and animals may not serve the purpose of applications related to hydrological (catchments) and climatological (atmospheric circulation) phenomena, mountaineering and tourism in general, mining, or political boundaries (Körner and Ohsawa 2006). Yet, regardless of the context of use, most people would agree that to define mountains, a distinction must be made between elevation (and its implications such as reduced barometric pressure and the associated reduction in atmospheric temperature), and steepness as a measure of inclination and gravitational forcing (Fig. 1). Among the geographic information system (GIS)-based approaches commonly applied to formulate a mountain definition, the one by Kapos et al. (2000) constrains mountains by a combination of elevation and ruggedness, whereas the one by Körner et al. (2011) constrains mountains by ruggedness of terrain only, irrespective of elevation. These two approaches define whether a point (a defined grid area) of the earth's surface is mountainous or not, but they do not define mountain territory as geographical regions. The former, herein called WCMC, was developed at the United Nations Environmental Programme World Conservation Monitoring Center (WCMC), used as part of the process of creating a map of the world's mountain forests (Blyth et al. 2002), and subsequently adopted by other international organisations. The latter, herein called GMBA, was developed by the Global Mountain Biodiversity Assessment network for mountain biodiversity and biogeography research (e.g., Paulsen and Körner 2014) and is being increasingly adopted in diverse scientific communities from natural sciences to the humanities (e.g., Green and Stein 2015).

In this paper, we offer a first version of a much needed inventory of the mountains of the world. This inventory rests on the GMBA definition of mountains, which, based on a quantitative comparison between the WCMC and GMBA definitions that we herein provide, appears as the most pertinent in a biogeographic context. Each entry corresponds to a polygon drawn around a single mountain or a mountain range and includes a local name as provided in major published maps and atlases, geographic coordinates, the total polygon area, and the area of mountainous terrain within polygon, subdivided into bioclimatic belts (sensu GMBA). Additionally, and to illustrate the broad utility of this inventory, we also report on human population densities in mountainous areas. The exact boundaries of any of the polygons have no bearing on the mountain statistics we provide (i.e., covered area of mountain terrain), as these strictly follow the GMBA definition of mountains.

Materials and methods

Summary of WCMC and GMBA mountain definitions

In the WCMC method, Kapos et al. (2000) define six classes of land area that belong to mountain terrain using the GTOPO30

Fig. 1 A mountain concept best differentiates between elevation as such *versus* topographic ruggedness. *Left* the village of Reine at sea level on the Norwegian Lofoten Islands, surrounded by very steep, but low elevation mountains. *Right* close to 2000 m asl plains in Wyoming (USA, Green River; photos by UM Weber). The landscape on the *left* resembles mountain terrain, the one on the *right* does not

digital elevation model, the WGS84 original projection, $2.5'$ pixels, and local elevation ranges in meters. All area above 2500 m asl is considered to be mountainous irrespective of ruggedness, whereas land below 300 m asl is non-mountainous by default, whatever its inclination. Land between 300 and 2500 m is attributed to mountain terrain based on ruggedness, with requirements of a minimum elevation contrast of 300 m over a horizontal distance of 7 km between 300 and 1000 m asl; $a \geq 5^\circ$ slope between the highest and lowest points within a grid cell or a minimum elevation contrast of 300 m over a horizontal distance of 7 km between 1000 and 1500 m; and $a \geq 2^\circ$ slope between the highest and lowest points within a grid cell between 1500 and 2500 m.

In the GMBA method, Körner et al. (2011) make no distinction by elevation, but apply a minimum 200 m elevational amplitude among $3 \times 3 = 9$ grid points of $30''$ in $2.5'$ pixels. For a $2.5'$ pixel to be defined as rugged (i.e., 'mountainous'), the difference between the lowest and highest of the 9 points must exceed 200 m. A $2.5'$ pixel in a grid corresponds to an area of 4.6 × 4.6 km near the equator. This size decreases as latitude increases. The maximum horizontal distance between any two of the 9 points within a $2.5'$ pixel that shows the largest vertical distance ranges from 0.9 to 3 km, depending on latitude and relief.

Following McVicar and Körner (2012), the term 'elevation' is used herein for the vertical distance of terrain from sea level, while 'altitude' applies to atmospheric conditions. Note also that the term 'ruggedness' does not imply 'steepness'. 'Steepness' is commonly defined as a feature of a single slope at a resolution of, for instance, 10–100 m, which is a scale that is far too small to be handled in a global geostatistics, even in a narrow geographical grid. Thus, both the WCMC and GMBA approaches use ruggedness of terrain instead as a measure of the vertical amplitude within a pre-defined space. This corresponds to the geometrical slope between the lowest and the highest grid point in a specific area.

Comparison of mountain definitions

Differences between the WCMC and GMBA mountain coverage were evaluated based on a comparison of the global area of land outside Antarctica defined as mountainous according to either approach. The values obtained for each definition were summed for eight mega-regions (mostly continents): North and South America, Africa, Europe, Asia, Australia, Oceania, and Greenland. The countries belonging to central America were attributed to North America. Herein, the terms "mountainous" and "mountain" are used for both the WCMC and the GMBA approaches despite the differences between the two definitions.

Delineation of mountain polygons (POLY)

Polygons were delineated by hand in ArcGIS10.0 (http://www.esri.com). The process started with the localization of mountains and mountain ranges in atlases and online resources. The sources selected in 2013 when the work started consisted in the world atlas of Knaurs (1999), a regional inventory of the mountains of Asia by Gurung (1999), and additional online maps at comparable resolution and occasionally in local language that were used in case of doubts (see supplementary material and https://ilias.unibe.ch/goto_ilias3_unibe_cat_1000515.html). A polygon was then drawn around a given mountain or mountain range if it (1) covered a minimum of 20 adjacent pixels of rugged terrain sensu GMBA on the GIS map (at a $2.5'$ resolution, this represents approximately 420 km^2 at the equator and smaller areas at higher latitudes; see above and Körner et al.

2011 for the definition of ruggedness), (2) had a name specified in the chosen resources (but see the discussion for a few exceptions), and (3) did not consist of scattered entities separated by extensive areas of lowland terrain. The drawings did not account for political borders or exact continental boundaries. The resulting polygons became either large if they included entire mountain ranges to which all the above criteria applied, or they remained small if they included only individual mountains. Although the primary objective was to include as much rugged terrain (sensu GMBA) as possible, the polygons inevitably included some non-rugged terrain and occasionally excluded less conspicuous, smaller scale rugged terrain that a strictly grid-based statistical procedure would identify as 'mountainous'. Based on primary feedback from GMBA network members and to simplify world-wide comparisons, we then also grouped individual polygons belonging to large mountain systems (e.g., all polygons belonging to the Rocky Mountains or to the Hindukush-Himalaya). When possible (e.g., Interior Mountains, Hindukush-Himalaya), individual polygons were simply aggregated, in which case the mountain area covered by the resulting large polygons was strictly the sum of the mountain area covered by the individual polygons. When large mountain systems obviously included inconspicuous mountain terrain that was not comprised in any individual polygon, the large polygons also included this additional mountain terrain. In these cases (e.g., Cordillera de Los Andes, Qilian Shan), the mountain area covered by the large polygons was more than the sum of the mountain area covered by the individual polygons. These very large, customized mountain polygons simply serve to facilitate the localization of larger, sub-continental mountain systems for specific applications. Accordingly, they are provided exclusively online (www.mountainbiodiversity.org, https://ilias.unibe.ch/goto_ilias3_unibe_cat_1000515.html) and are neither included in the final polygon count discussed in the result section nor in any of the calculations.

Climatic belts

Irrespective of the way mountains are defined, a global comparison of mountains should not employ elevation above sea level, because different life conditions can be encountered at identical elevations across latitudes, but also between front ranges and the interior of given mountain systems (mass elevation effect). Hence, the only way to arrive at meaningful comparisons is to apply climatic criteria, here referred to as climatic (thermal) belts.

Climatic belts were defined by first applying an algorithm that allows dividing mountain terrain in land above the potential climatic treeline (alpine, including what is often termed sub-nival and nival) and below (montane), and subsequently stratifying the land below the potential treeline in belts ranging from upper montane with recurrent freezing to frost-free tropical low montane and rugged lowland terrain (Körner et al. 2011; Körner 2012). Calculations were based on publicly available climatic data only (WorldClim, http://www.worldclim.org). The algorithm, developed and tested across all latitudes, predicts the potential climatic treeline at elevations where the seasonal mean temperature is 6.4 °C and the local growing season consists of at least 94 days, each with a mean temperature of $\geq$0.9 °C (Paulsen and Körner 2014). By additionally accounting for snowpack and drought, the algorithm provides a potential treeline, irrespective of whether trees are present at or absent from where they could still grow, which in turn implies that the reference line becomes independent of local peculiarities of tree distribution due to disturbances such as fire, logging, pastoralism, avalanches, erosion. The treeline algorithm was applied to the rugged terrain in both the GMBA and the POLY approaches.

Another climate classification frequently used in climate and climate change research, as well as in physical geography, hydrology, agriculture, and biology is that of Köppen–Geiger (Kottek et al. 2006), which distinguishes five climatic zones that are subsequently subdivided based on precipitation and air temperature. Because this classification is meaningful primarily on a global scale, as opposed to the regional scale at which the polygons are drawn, we applied it to the global mountainous terrain sensu GMBA only.

Estimation of total polygon area, area of mountainous terrain, and area by climatic belt

For each polygon, we quantified the total area and the area of mountainous terrain and stratified the latter by climatic belts. As those calculations strictly followed the GMBA definition of mountains, the exact shape and extent of any particular polygon were irrelevant. At the 2.5′ resolution applied (corresponding to 21 km^2 at low latitudes), the accuracy of such calculations is limited when an area of interest is small because edge effects become large relative to the size of the area. Hence, results are expected to be best for large polygons. Additional problems such as the elevational (and thus climatic) amplitude within a 2.5′ grid (e.g., a narrow valley passing through an otherwise predominantly high-elevation pixel) are intrinsic to gridded data.

Polygons were then assigned to mega-regions (see above) and both the total polygon area and the area of mountainous terrain, subdivided into climatic belts, were summarized for each of these mega-regions. The decision to ignore political borders and exact continental boundaries that was made when drawing the polygons was also followed when assigning them to mega-regions. Polygons ranging across the boundaries of two mega-regions (e.g., Greater Caucasus between Asia and Europe) or interfacing with two mega-regions (e.g., Serrania de San Blas in North America interfaces with a grid cell belonging to South America) were attributed twice (i.e., once to each mega-region). Accordingly, the number of polygons used for area calculations did not correspond exactly to the number of uniquely drawn objects.

Human population statistics

Anthropogenic pressure associated with human settlements in and below the montane belts, land use, land transformation, and other human activities may endanger mountain biota more than climate change in many regions of the world (Körner and Ohsawa 2006; Spehn et al. 2006). Here, we provide human population data for the GMBA mountain areas and for the individual mountain polygons to help draw inferences about human impact on mountain biota, including alpine terrain. To quantify human population in mountains, we used the FAO gridded global human population density data and overlaid it with the gridded GMBA and POLY mountain data. Similar quantifications were performed for the WCMC mountain area by Huddelston et al. (2003), with a new release by FAO Mountain Partnership in 2015 (FAO 2015). The FAO data consisted of LandScan (see http://web.ornl.gov/sci/landscan/landscan_documentation.shtml#01) and FAOSTAT data year 2000–2012 (provided by FAO/CDE, pers. com. A. Vita). LandScan data were adjusted by FAO for each country and standardized to the data available on FAOSTAT before being reallocated at pixel level following the LandScan distribution. Because we subdivided mountain terrain into thermal belts, the world's human population could also be assigned to climatic niches and to climatic envelopes in any non-mountainous terrain.

Results

Comparison of the WCMC and GMBA mountain definitions

The WCMC- and GMBA-based estimates of mountain terrain differ by a factor of about two (Table 1; Fig. 2). While neglecting the admittedly small fraction of often steep but low elevation mountains (<300 m asl, red in Fig. 2, left image in Fig. 1), WCMC includes vast areas of intra-mountain and foreland terrain as well as hill country. For instance, WCMC defines 94% of Switzerland as mountains, including almost all cropland and most urban areas that are commonly not considered mountainous, and approximately 7 of the 8.5 Mio Swiss people appear as mountain inhabitants (see below). The GMBA approach remains quite inclusive by attributing 66% of Switzerland to mountains. This in turn leads to an estimated 'mountain population' of approximately 2 Mio people living mainly in the large valleys inside the Alps but not in the metropolitan areas that are included by the WCMC definition. Similarly, almost all of Turkey is attributed to mountains in the WCMC approach, whereas the GMBA one excludes major cropland and urban areas in hill country (Fig. 2). Furthermore, WCMC in contrast to GMBA attributes flat fractions of high-elevation tablelands (>2500 m asl) such as the Mongolia highlands and, at higher elevation, the Tibetan plateau and the Andean Altiplano, to the mountain category. Regardless of the method adopted to delineate mountains, the area of land defined as mountainous is largest at around 600 m of elevation (cut off at 300 m asl in the WCMC approach) and approaches zero above 6000 m asl (Fig. 3).

Global mountain terrain as captured by mountain polygons and climatic belts

This first version of the GMBA mountain inventory consists of 1003 polygons (Fig. 4, see supplementary material), which can be visualized and queried for spatial an biodiversity information online at http://www.mountainbiodiversity.org/. Yet as 14 of these polygons appear in two mega-regions simultaneously (see above) calculations were performed with 1017 objects (c.f. supplementary material). The GMBA mountain polygons cover 19.3% or nearly 26 Mio km^2 of the global land area outside Antarctica and 83.7% of the total global mountain area estimate based on the GMBA mountain definition (Table 2). Specifically, the polygons capture between 85.8 and 88.8% of the terrain defined as mountainous (sensu GMBA) in Asia, Europe, North America, and Greenland, 91% of the mountainous terrain of South America, around 60% of the mountainous terrain of Africa and Australia, and around 37% of the mountainous terrain of Oceania (Table 2). With more than 14 Mio km^2 of polygon area, of which 7.6 Mio. km^2 fall in the mountain category, Asia hosts by far the greatest fraction of the global mountain terrain (Table 2). North America and South America follow with ca. 2.5 and 2 Mio km^2 of mountain terrain, respectively, and Africa and Europe with approximately 0.7 and 0.8 Mio km^2, respectively. Small fractions of less than 0.1 Mio km^2 are located in Australia, Greenland, and Oceania. Because of their smooth shape, the polygons inevitably consist of both mountainous and non-mountainous terrain. Currently, 53.3%, or 13.8 Mio km^2, of the total polygon area (26 Mio km^2) consists of mountain terrain sensu GMBA.

At the level of individual climatic belts, the largest areas of mountainous terrain are found in the lowest, 'no-freezing' belt in Africa and South America, in the lower montane belt in Asia, Australia, and Europe, in the upper montane belt in

Table 1 Global mountain terrain, separated by mega-regions, according to the WCMC and the GMBA definitions

Mega-region	Total land area [10^3 km^2]	WCMC mountain area [10^3 km^2] (% of total land area)	GMBA mountain area [10^3 km^2] (% of total land area)
Africa	29,900	4255 (14.2)	1191 (4.0)
Asia	44,385	17,386 (39.2)	8883 (20.0)
Australia	7677	357 (4.6)	126 (1.6)
Europe	9780	1862 (19.0)	916 (9.4)
Greenland	2120	836 (39.4)	92 (4.3)
North America	21,683	6300 (29.1)	2902 (13.4)
Oceania	424	209 (49.2)	175 (41.1)
South America	17,755	4034 (22.7)	2149 (12.2)
Total	133,724	35,238 (26.4)	16,434 (12.3)

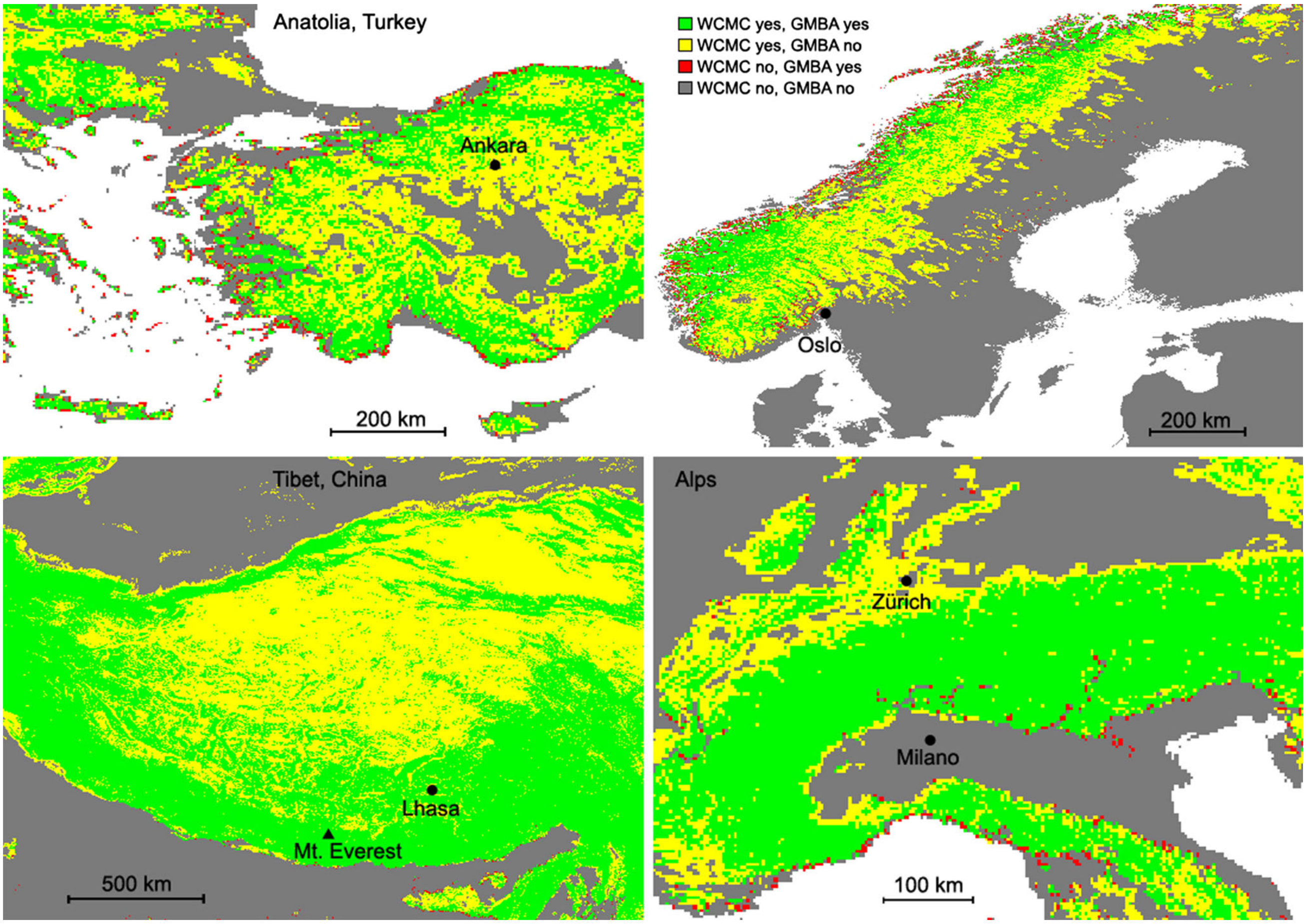

Fig. 2 Four examples showing the differences between the WCMC and the GMBA mountain definitions. **a** Asia Minor (Anatolia, Turkey), **b** Northern Scandinavia (the Norwegian coast), **c** the Tibetan Plateau, **d** the European Alps. Color code: *green* the WCMC and GMBA definition apply; *yellow* the WCMC definition only applies; *gray* neither the WCMC nor the GMBA definition apply; *red* only the GMBA definition applies (mountain areas <300 m asl)

North America and Oceania, and in the nival belt in Greenland (Table 3). Globally, 21.5% of mountain terrain occurs above the potential climatic treeline and 78.5% occurs below. This corresponds to 2.64 versus 9.62% of the entire terrestrial area outside Antarctica (Körner et al. 2011)

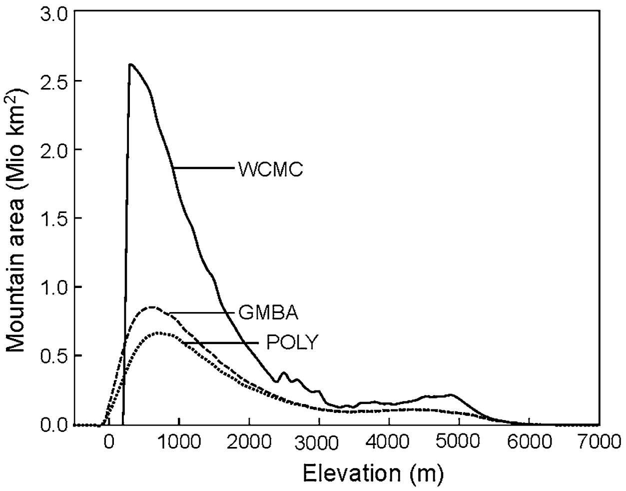

Fig. 3 The global mountain area at different elevations as assessed by WCMC (*solid line*), GMBA (*dashed line*), and POLY (*dotted line*). The cut edge on the *left* is due to the 300 m asl lower limit of terrain accepted as mountainous by WCMC, irrespective of ruggedness

Human populations in mountains

Mountain polygons as delineated here host a human population of 1.2 billion people, of which 386 million are actually living in mountains sensu GMBA. This corresponds to a density of 28 people km^{-2} in the mountainous terrain of polygons as compared to 67 people km^{-2} in the non-mountainous terrain (i.e., the mountain forelands). Of the 386 million 'mountain people', 233 million are inhabiting the mountains of Asia, between ca. 53 and 54 million are inhabiting the mountains of Africa and South America, respectively, and ca. 23 million are living in the mountains of each North America and Europe (Table 4). In comparison, the purely GIS-based WCMC and GMBA mountain definitions lead to an estimated 915 (FAO 2015) and 511 million people inhabiting mountains, respectively. Hence, when considering only the strictly mountainous terrain within polygons, the human population estimates reach 75.5% of those obtained at a global scale based on the GMBA definition.

At the 2.5′ resolution of our survey, about half of the people inhabiting mountains sensu GMBA are living in the entirely frost-free (tropical) lowest climatic belt (47% based on the GMBA definition and 44% based on POLY), roughly the other half (ca. 49% based on the GMBA definition and 50% based on POLY) are living in the lower (predominantly warm) montane belt, ca. 4 and 5% of all GMBA and POLY 'mountain people', respectively, are living in the uppermost climatic belt below the potential treeline (upper montane), and less than 1% are statistically expected to live in even colder rugged terrain (lower/upper alpine to nival), possibly at high latitude such as in North Siberia, Northern Scandinavia, and Alaska (Table 5). The latter percentage likely results from the inclusion of warmer terrain (e.g., mountain

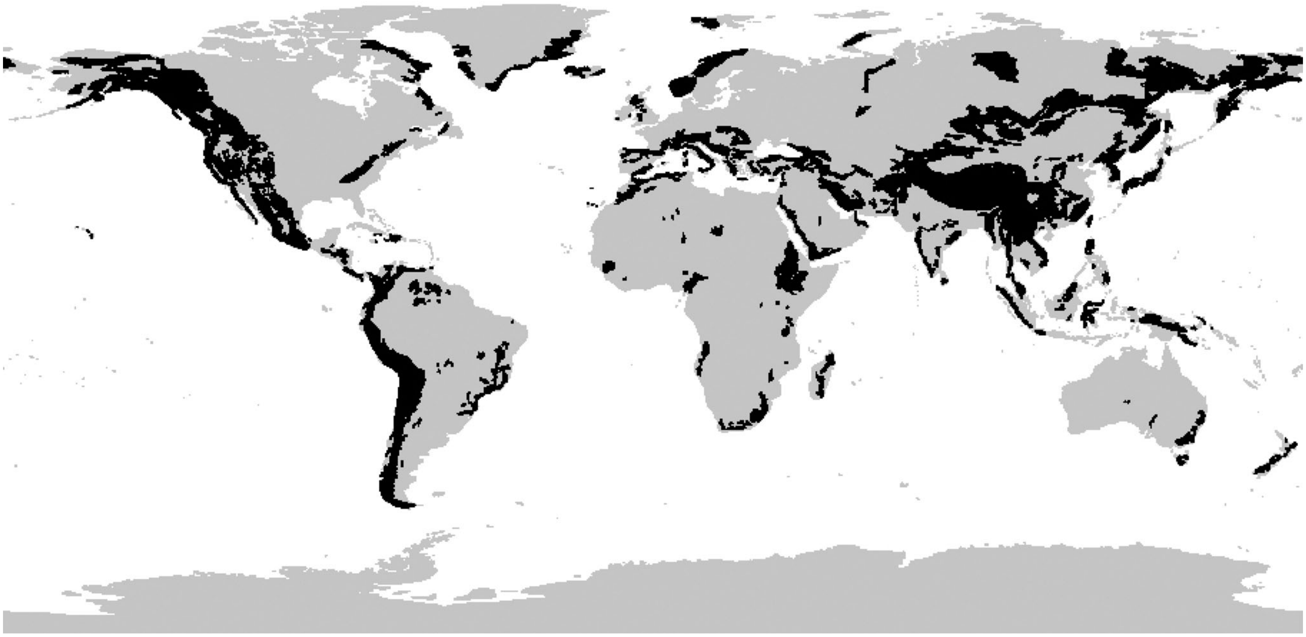

Fig. 4 The global distribution of mountain polygons. Statistics shown in Tables 2 and 3 represent all 1003 polygons. For certain applications, groups of polygons (e.g., the various polygons identified in the Rocky Mountains) can be merged to larger polygons (e.g., one large Rocky Mountains polygon). See electronic supplementary material and https://ilias.unibe.ch/goto_ilias3_unibe_cat_1000515.html for a detailed list of polygons

Table 2 Areal statistics of polygons (POLY, 2.5′, resolution) and area of mountain terrain within polygons for mega-regions outside Antarctica

Mega-region	Number of polygons	Total land area [10^3 km^2]	Total polygon area [10^3 km^2] (% of total land area)	Mountain area within polygons [10^3 km^2] (% of total polygon area)	Mountain area outside polygons [10^3 km^2]	Mountain area within polygons in % of global GMBA mountain area
Africa	70	29,900	1721 (5.8)	706 (41.0)	485	59.3
Asia	454	44,385	14,045 (31.6)	7600 (54.1)	1283	85.6
Australia	7	7677	181 (2.4)	74.8 (41.3)	50.9	59.5
Europe	58	9780	1464 (15.0)	785 (53.6)	131	85.7
Greenland	2	2120	217 (10.3)	81.8 (37.6)	10.4	88.8
North America	268	21,683	4756 (22.0)	2491 (52.3)	411	85.8
Oceania	60	424	96 (22.7)	64.8 (67.2)	110	37.1
South America	98	17,755	3342 (18.8)	1956 (58.5)	192.6	91.0
Total	1013	133,724	25,832 (19.3)	13,760 (53.3)	2674	83.7

The rugged area within polygons is defined by the GMBA mountain definition. For methodological reasons (see main text), the calculations are based on a total number of 1017 polygons

Table 3 Areal statistics for the world's mountain terrain within polygons (POLY, 2.5′ resolution) separated by major climatic belts and mega-regions

	Moutain area within polygons in km^2 (% of total mountain area within polygons per mega-region)						
Mega-region	Nival[a]	Upper alpine	Lower alpine	Upper montane	Lower montane	Warm[b]	No freezing[c]
Africa	43 (<0.01)	85 (0.01)	963 (0.1)	16,184 (2.3)	125,564 (17.8)	84,257 (11.9)	479,161 (67.8)
Asia	196,031 (2.6)	420,559 (5.5)	1,356,970 (17.9)	1,637,965 (21.6)	1,765,122 (23.2)	729,388 (9.6)	1,494,421 (19.7)
Australia	0	0	1010 (1.4)	22,078 (29.5)	38,521 (51.5)	11,386 (15.2)	1752 (2.3)
Europe	58,401 (7.4)	34,845 (4.4)	63,721 (8.1)	233,953 (29.8)	367,623 (46.9)	10,768 (1.4)	15,368 (2.0)
Greenland	71,000 (86.8)	7668 (9.4)	3030 (3.7)	146 (0.2)	0	0	0
North America	106,870 (4.3)	167,467 (6.7)	424,972 (17.1)	756,635 (30.4)	519,487 (20.9)	141,961 (5.7)	373,450 (15.0)
Oceania	450 (0.7)	241 (0.4)	3371 (5.2)	31,088 (48.0)	16,762 (25.9)	0	12,842 (19.8)
South America	27,952 (1.4)	70,351 (3.6)	292,615 (15.0)	372,769 (19.0)	298,660 (15.2)	62,824 (3.2)	831,109 (42.5)

The climatic belts follow the definitions by Körner et al. (2011) and are anchored at the potential climatic treeline

[a] Season length ≤10 days

[b] Warm mountain zone, but with possible freezing

[c] Mountain terrain with perpetual warm conditions, no freezing

valleys with steep vertical gradients) in otherwise predominantly 'cool' (i.e., high-elevation) pixels, which happens as an artefact of using a 2.5′ grid resolution. There is an over-proportional fraction of human 'mountain populations' in the ca. 16% of all mountains of the terrestrial surface outside Antarctica that are not covered by the polygons (125 million people). These are located in low elevation rangeland (tropical and subtropical) that still matches the ruggedness criterion, but is too inconspicuous to be captured by a mountain polygon.

When applying the Köppen–Geiger climate classification to all land outside Antarctica instead of the climatic belts described above, we estimate that 'mountain people' (sensu GMBA) represent 4.4% (133 million) of the 3 billion people living in equatorial low elevation life conditions, 9.2% (333 million) of the 3.6 billion people living in the warm temperate life zones with varying seasonality of moisture supply, and 5.5% (35million) of the 0.6 billion people living in cool temperate climates with cold winters (snow, Table 6). Densities vary from close to zero up to 77–114 km^{-2} in the warm temperate monsoon regions and are mostly below 20 people km^{-2} in the cooler parts of the world.

Discussion

Based on a quantitative comparison of mountain definitions that include ruggedness, elevation, and climate, we argue that the combination of ruggedness and climate is the most pertinent approach for biological questions, including

Table 4 Human population statistics for the world's mountain terrain (GMBA definition and POLY, 2.5′ resolution) separated by mega-regions

Mega-region[a]	Total human population [10^3]	Total human population in total polygon area [10^3]	Human population in mountain terrain [10^3] (% of total human population)[b]		Human population densities in mountains[c] (total[d])	
			GMBA	POLY	GMBA	POLY
Africa	1,230,000	151,900	83,100 (6.7)	52,700 (34.7)	69.8	74. (88.2)
Asia	4,497,000	734,100	302,200 (6.7)	233,000 (31.7)	34.0	30.6 (52.3)
Australia	22,530	597	264 (1.2)	73.4 (12.3)	2.1	1.0 (3.3)
Europe	541,300	69,178	29,360 (5.4)	23,300 (33.7)	32.1	29.7 (47.2)
North America	548,400	107,500	37,920 (6.9)	23,100 (21.6)	13.1	9.3 (22.6)
Oceania	8088	322	855 (10.6)	174 (53.9)	4.9	2.7 (3.3)
South America	451,100	135,400	57,490 (12.7)	53,800 (39.7)	26.8	27.4 (40.5)
Total	7,298,420	1,199,000	511,200 (7.0)	386,000 (32.2)	31.1	28.0 (46.4)

[a] Because of the low total human population in Greenland (approximately 56,000 inhabitants) and the resulting large uncertainty associated with the estimated total human population in total polygon area, Greenland is not shown in this table

[b] For POLY, the total human population corresponds to the total population in total polygon area

[c] The human population density in mountains is calculated by dividing the human population in mountain terrain by the mountain area as defined by GMBA (Table 1) and as estimated within polygons (Table 2)

[d] The total human population density is calculated by dividing the total human population in total polygon area by the total polygon area in each mega-region (Table 2)

Table 5 Human population statistics for the world's mountain terrain (GMBA definition and POLY, 2.5′ resolution) separated by major climatic belts

Climatic belt	Mountain area [10^3 km^2]		Human population in mountain terrain [10^3] (% of total population[a])		Human population densities in mountains[b] (total[c])	
	GMBA	POLY	GMBA	POLY	GMBA	POLY
Nival	526	461	236 (96.0)	236 (96.0)	0.4	0.5 (0.3)
Upper alpine	743	701	604 (71.3)	605 (72.5)	0.8	0.9 (0.8)
Lower alpine	2255	2147	2927 (59.2)	2900 (64.5)	1.3	1.4 (1.1)
Upper montane	3367	3071	18,485 (16.2)	17,809 (60.9)	5.5	5.8 (5.5)
Lower montane	3733	3132	132,800 (12.9)	113,500 (38.7)	35.6	36.2 (49.5)
Warm	1338	1041	107,830 (6.7)	81,890 (26.2)	80.6	78.7 (127)
No freezing	4473	3208	248,300 (5.5)	169,028 (30.3)	55.5	52.7 (87.0)
Total	16,435	13,760	511,164 (7.0)	385,960 (32.2)	31.1	28.0 (46.4)

[a] For POLY, the total human population corresponds to the total population in total polygon area

[b] The human population density in mountains is calculated by dividing the human population in mountain terrain by the mountain area

[c] The total human population density in polygons is calculated by dividing the total human population in total polygon by the total area within polygons

Table 6 Human population statistics for the world's mountain terrain (GMBA definition) separated into climate types (acronyms in brackets) as defined by Köppen and Geiger (Kottek et al. 2006)

Köppen–Geiger climate type	Total land area [10^3 km^2]	Mountain area [10^3 km^2] (% of total land area)	Total human population [10^3]	Human population in mountain terrain [10^3] (% of total population)	Human population densities	
					Total[a]	Mountain[b]
Equatorial fully humid rainforest (Af)	6720	1030 (15.3)	327,000	34,800 (10.6)	48.7	33.8
Equatorial monsoon (Am)	4620	408 (8.8)	418,000	23,900 (5.7)	90.6	58.5
Equatorial savannah with dry summer (As)	1110	55.9 (5.1)	82,700	2680 (3.2)	74.8	48.0
Equatorial savannah with dry winter (Aw)	22,000	1070 (4.8)	1,870,000	61,300 (3.3)	85.1	57.5
Hot arid steppe (BSh)	7390	222 (3.0)	178,000	4500 (2.5)	24.1	20.3
Cold arid steppe (BSk)	4640	1080 (23.2)	43,600	2370 (5.4)	9.4	2.2
Hot arid desert (BWh)	8960	116 (1.3)	102,000	2090 (2.0)	11.4	18.1
Cold arid desert (BWk)	1000	102 (10.2)	6170	933 (15.1)	6.2	9.2
Warm temperate perpetually humid with hot summer (Cfa)	10,100	739 (7.3)	1,070,000	84,000 (7.9)	105	114
Warm temperate perpetually humid with warm summer (Cfb)	4770	1200 (25.1)	398,000	43,400 (10.9)	83.4	36.1
Warm temperate perpetually humid with cool summer and cold winter (Cfc)	215	159 (73.8)	1780	1250 (70.4)	8.3	7.9
Warm temperate with dry and hot summer (Csa)	4490	657 (14.7)	425,000	34,300 (8.1)	94.8	52.2
Warm temperate with dry and warm summer (Csb)	1370	452 (32.9)	72,200	12,500 (17.3)	52.6	27.6
Warm temperate with dry and cool summer and cold winter (Csc)	48.3	34.1 (70.5)	46.3	39.2 (84.7)	1.0	1.2
Warm temperate with dry winter and hot summer (Cwa)	8130	1040 (12.8)	1,380,000	79,900 (5.8)	169	76.9
Warm temperate with dry winter and warm summer (Cwb)	2250	1120 (49.7)	248,000	74,800 (30.2)	110	66.9
Warm temperate with dry winter and cool summer and cold winter (Cwc)	124	79 (63.6)	5290	3250 (61.6)	42.6	41.2
Snow climate perpetually humid with hot summer (Dfa)	2120	18.9 (0.9)	67,400	362 (0.5)	31.8	19.1
Snow climate perpetually humid with warm summer (Dfb)	8730	571 (6.5)	215,000	8560 (4.0)	24.6	15.0
Snow climate perpetually humid with cool summer and cold winter (Dfc)	11,700	1280 (10.9)	13,300	1840 (13.8)	1.1	1.4
Snow climate perpetually humid, extremely continental (Dfd)	634	26 (4.1)	316	0.73 (0.2)	0.5	0
Snow climate with dry and hot summer (Dsa)	207	37.4 (18.1)	9570	964 (10.1)	46.3	25.8
Snow climate with dry and warm summer (Dsb)	465	250 (53.8)	8480	3620 (42.7)	18.2	14.5
Snow climate with dry and cool summer and cold winter (Dsc)	63.1	51.3 (81.2)	124	111 (89.7)	2	2.2
Snow climate with dry winter and hot summer (Dwa)	985	68.3 (6.9)	262,000	8310 (3.2)	266	122
Snow climate with dry winter and warm summer (Dwb)	1710	266 (15.6)	56,900	8820 (15.5)	33.4	33.2
Snow climate with dry winter and cool summer and cold winter (Dwc)	2650	906 (34.1)	9710	2840 (29.3)	3.7	3.1
Snow climate with dry winter, extremely continental (Dwd)	99.2	24.3 (24.5)	15.4	1.14 (7.4)	0.2	0
Bare ground with very short snow-free period (EFb)	1360	328 (24.2)	75.4	66.2 (87.8)	0.1	0.2

Table 6 continued

Köppen–Geiger climate type	Total land area [10^3 km^2]	Mountain area [10^3 km^2](% of total land area)	Total human population [10^3]	Human population in mountain terrain [10^3](% of total population)	Human population densities	
					Total[a]	Mountain[b]
Cold and dry desert (EFp)	6.49	5.45 (83.7)	38.1	37.9 (99.6)	5.9	7.0
Perpetual snow or ice (EFp)	2950	494 (16.7)	236	226 (96)	0.1	0.5
Tundra climate with drought in snow-free period (ETd)	3220	486 (15.1)	28,600	7560 (26.4)	8.9	15.5
Humid tundra climate (ETf)	8860	2070 (23.4)	3150	1910 (60.7)	0.4	0.9
Total	134,000	16,400 (12.3)	7,300,000	511,000	54.6	31.6

[a] The total human population density is calculated by dividing the total human population by the total land area

[b] The human population density in mountains is calculated by dividing the human population in mountain terrain by the mountain area as defined by GMBA

biodiversity assessments and forest inventories. The mountain inventory we then provide based on this approach facilitates the access to regionalized mountain statistics.

Global mountain statistics

Both GIS-based approaches (WCMC and GMBA) rely on specific assumptions and serve as ‘conventions’ that can help in establishing standardized protocols. The GMBA 200 m ruggedness threshold across the 9 neighbouring 30″ grid points for instance resulted from test runs, exploring the smallest elevation amplitude that still captures what might be considered a mountain rather than a hill. Tests runs for the Alps revealed that a 200 m ruggedness threshold causes a clear distinction between the Alps and the forelands, with almost all narrow, low elevation valleys within the Alps still belonging to the mountain category (because the valley floors are commonly <2 km wide). In Switzerland in general, the 200 m threshold allows for the Swiss plateau or Swiss midlands, with all major cities and cropland, to fall outside the GMBA mountain definition. By the WCMC criteria, this same area largely falls into the mountain category, as do all plateaus at high elevation (e.g., Tibetan Plateau, yellow area in Fig. 2, bottom left), whereas most coastal mountains are disregarded (e.g., Norway, red area in Fig. 2, top right). Hence, the major part of the discrepancy between the WCMC and GMBA approach is located far below 1000 m asl in the undulating, low elevation hill country, outside the mountains, with a peak near 300 m asl, and does presumably not result from the inclusion or exclusion of the high plateaus (the small hump near 5000 m asl in Fig. 3), because the really flat parts of those plateaus are quite small. These distinctions are important in view of the human population statistics, as many people considered to be ‘mountain people’ in the WCMC approach (FAO 2015) are living on land that causes a divergence in the WCMC and the GMBA estimates at very low elevation (see examples in Fig. 2).

It is worth noting that a very large fraction (the majority) of the world’s mountains falls in a low elevation category by all three mountain concepts, with comparatively high temperatures, particularly at low latitude. Furthermore, neither of the applied definitions uses low temperatures alone as a criterion for mountains, thereby preventing the attribution of vast Arctic and Antarctic lowland terrain to mountainous areas.

Mountain polygons

In contrast to a grid-based assessment of all terrestrial area, mountain polygons cannot provide an exhaustive representation of mountainous terrain. Mountain polygons are arbitrary shapes that inevitably include some low elevation or non-mountainous terrain and fail to account for certain (including isolated) mountains that would be recognized by a grid-based statistical procedure. Hence, only the mountainous terrain within polygons should be used to calculate mountain statistics, and not the total polygon area. With a coverage of approximately 13.8 Mio km^2, the polygons capture most of the 16.5 Mio km^2 of global mountain terrain estimated with the GMBA approach. This suggests that individual polygons and our inventory as a whole capture the existing mountain terrain sufficiently well for locating mountains and mountain ranges and for comparative purposes. The missing 2.7 Mio km^2 mostly consists of mountain terrain that is too scattered to be included in discrete polygons. Many of the missing, smaller mountains would probably not appear as distinct mountains on a physical world map and may also remain unnamed even though the absence of name is not always a matter of size. Larger rugged areas, for which no name could be found in atlases or online, were identified with codes for the purpose of this work. The largest discrepancies between GMBA and POLY were observed in Africa and Australia and may partly be attributed to the greater difficulties of delineating mountain terrain in areas where rugged terrain is more scattered or less conspicuous such as on the old Gondwana land shields.

The 1003 polygons of this first inventory are neither perfect nor comprehensive and refinements, including the use of a higher resolution Digital Elevation Model, will be needed in subsequent releases to achieve better coverage and higher accuracy. The three major criticisms to this first release are (1) the absence of some specific mountains or ranges, (2) the lumping of certain mountains, and (3) the inclusion of non-rugged terrain in individual polygons. The latter is intrinsic to the polygon delineation concept but does not affect the area of mountain terrain within polygons, which is strictly defined by GIS-based algorithms. The second criticism on lumping individual mountains is the most challenging to address, as the arguments for and against doing so can be numerous and controversial. User feedback will help improve this first version of the GMBA mountain inventory to possibly overcome the shortcomings that might result from the decisions we made in the delineation process.

Climatological stratification of mountain terrain

Since from a climatic point of view, it makes a considerable difference whether a mountain defined by ruggedness is in the Arctic, the temperate zone, or near the equator, a climatic stratification of land area is essential to identify ecologically comparable land cover units across the mountains of the world. Since available climatic layers (e.g., from WORLDCLIM) can be overlaid onto mountain topography, categorizations into any climatic belt are possible. For a climatic stratification to make sense and become globally useful, it should ideally capture conditions that reflect established biogeographic categories such as terrain above (alpine) and below (montane) the climatic treeline. As shown previously, the potential high-elevation tree limit is found at a globally common isotherm for the growing season (Körner 2012; Körner and Paulsen 2004; Körner et al. 2011) and, therefore, offers a bioclimatic reference, against which all other climatic belts in mountains can be positioned. Measures of temperature that include the dormant period in extratropical mountains, such as mean annual temperature (Jobbágy and Jackson 2000) or the mean temperature for the warmest month only—the often quoted 10 °C July isotherm for the northern temperate zone (Köppen 1919; Jarvis et al. 1989; Ohsawa 1990; Malyshev 1993), may fit either by chance or for certain latitudes or regions, but they do not capture global patterns (Hardy et al. 1998; Körner 1998).

Geophysical mountain statistics thus need to address two different issues: the first one is related to the structure of the elevated land surface, its ruggedness, and its exposure to the forces of gravity (the topographic nature of mountains), and the other one is related to the climatic life conditions (the climatic nature of mountains). At a given elevation, topography is independent of latitude, whereas climate is not. Topographically similar mountain terrain can be found in the Arctic and at the equator. Hence, a mountain concept that can be used for global comparisons must combine topography with a coherent climatological characterization as either one alone is insufficient and absolute elevation (m asl) alone is not ecologically meaningful either. Yet, there is a caveat, in that climatic data obtained from weather stations (2 m air temperature) do not represent the actual climatic conditions experienced within low stature vegetation and by soil biota (Scherrer and Körner 2011). Hence, assessing the actual life conditions of small plants, ground dwelling animals, and soil microbes will continue to require ground truth data.

Human populations in mountains

Given the significance of land use for biodiversity, it is interesting to estimate to which extent mountains are inhabited by humans. Using the combined ruggedness and climatic stratification of the world's mountains (sensu GMBA), we estimated human population densities in specific climatic belts within polygons and globally. Among the various observations we made, three were particularly surprising: (1) the comparatively high human population density in mountainous areas, given that much of the rugged terrain is very steep, very high, forested, or represents dangerous terrain; (2) the 53 million inhabitants in the relatively small mountain areas within polygons of Africa, indicating an over-proportional significance of mountain livelihoods; and (3) the approximately 23 million people inhabiting mountains in Europe, which indicate that the immediate forelands and the interior valleys are densely populated. Taken together, the human population data clearly evidence that by far the majority of 'mountain people' are inhabiting low elevation rugged terrain in tropical and warm temperate regions, and face challenges associated with steep slopes rather than with low temperatures. Above the inhabited areas, land use might nevertheless be very intense.

Because the fraction of mountainous land differs between mountain definitions, human population estimates for specific regions differ as well. Accordingly, the values we present differ substantially from estimates provided elsewhere (e.g., EEA report 2010; FAO 2015), which are based on the WCMC definition of mountains or variants of it. However, based on the estimates we obtain for human populations in Swiss mountains for example, we believe that the GMBA definition of mountains leads to meaningful results. Additional variation in the reported continent-based estimates may come from methodological assumptions specific to our calculations and from the division of the world we apply, which differs from the United Nations Statistics Division "M.49" standard used in FAO 2015 primarily, in that Australia is kept separate from Oceania, and Greenland is kept separate from North America.

In our opinion, the availability of human population data and the resulting climate co-defined livelihood statistics are a goldmine for the mountain biology and ecology community. These data open up the avenue for many interesting socio-ecological research questions, including the estimation of ecologically important regional demands for natural resources such as fire wood or grazing land, of current and future pressure on medicinal plants, and of pressure from hunting and tourism. Known caveats associated with these data include the fact that (1) the global statistics ignore political boundaries, which means that a regional match with national inventory data is not possible, (2) the 2.5′ grid (4.6 × 4.6 km at the equator) is quite coarse, which means that any rugged 2.5′ pixel can, and often does, include non-rugged land fractions suitable for settlement; (3) the data cannot reliably capture land use intensity, particularly pastoralism, which is not necessarily directly correlated with population densities; and (4) the data are likely imprecise in specific locations when none of the data sources is accurate. Specific drawbacks of the light-emission information used in generating the LandScan include their low reliability in certain locations such as high-elevation mountain resorts, where light emissions are often disproportionally high compared to the number of inhabitants. These caveats remain despite regional adjustments but the data still allow the estimation of potential human impact on mountain ecosystems and the identification of regions of high and low risk for biodiversity losses.

Conclusions

The field of mountain biodiversity research has long been suffering from the lack of a standardized inventory of the mountains of the world for robust comparisons of biogeographic characteristics and biodiversity data across mountain ranges and biomes. Here, we offer such an inventory in which each of the 1003 entries corresponds to a polygon drawn around a mountain or a mountain range sensu GMBA. With a total of 13.8 Mio km^2 of mountain terrain, the polygons cover 83.7% of the global mountain area estimated using the GMBA approach, which is a purely grid-based (geostatistical) survey of mountains on the terrestrial surface outside of Antarctica. With this coverage, we are confident that the inventory is representative and offers a useful tool for biodiversity researchers. However, to improve its representativeness and accuracy beyond applying a higher resolution Digital Elevation Model, we encourage users to explore and manipulate the GIS files available online (https://ilias.unibe.ch/goto_ilias3_unibe_cat_1000515.html) and provide their feedback and suggestions in view of the online release of subsequent versions. By offering for each polygon a subdivision of the mountainous terrain into climatic belts above and below the potential bioclimatic tree limit, we enable biodiversity experts to place their assessments in a meaningful climatological context, irrespective of elevation and latitude. The human population density data in turn are a useful resource for biodiversity risk assessment and conservation planning.

The polygon-based mountain inventory of the world described here is a unique information layer that is now available on the online 'Mountain Portal' of GMBA (www.mountainbiodiversity.org). Through collaboration with the Map of Life (http://mol.org) and EarthEnv projects (http://www.earthenv.org), the mountain polygon information can already be visualized together with an increasingly detailed set of additional topographic variable and a growing range of biodiversity information provided through Map of Life. Exploring the biodiversity information at the level of individual climate belt within polygons will become possible in the near future.

Defining mountains and life zones within mountains will remain a challenging task, given that different applications call for different definitions and assumptions. Here, we suggest that the most useful approach for biological questions, including biodiversity assessments and forest inventories, is the combination of a ruggedness term with a bioclimatic stratification. We further argue against approaches based on elevation above sea level, as life is driven by climate rather than by elevation. Organisms, including humans, that live at identical elevations can indeed be exposed to rather different climates across the globe. We hope that the mountain inventory we present and the additional information on climate and human populations we provide can serve as a reference for biodiversity assessment and comparative ecology of mountains.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Declaration of authorship CK and ES initiated the comparisons of mountain definitions. KR was responsible for the polygon delineation.

JP processed the polygons and population data in GIS and applied the various mountain definitions and climatic belt modeling. WJ established the conceptual links to the Map of Life project. CK drafted the text, with substantial contributions by KR, ES, and DP. All authors contributed to final editing.

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