PERSPECTIVE
https://doi.org/10.1038/s41561-019-0513-5

nature geoscience

Manifestations and mechanisms of the Karakoram glacier Anomaly

Daniel Farinotti[1,2]*, Walter W. Immerzeel[3], Remco J. de Kok[3], Duncan J. Quincey[4] and Amaury Dehecq[1,2]

Global-scale glacier shrinkage is one of the most prominent signs of ongoing climatic change. However, important differences in glacier response exist at the regional scale, and evidence has accumulated that one particular region stands out: the Karakoram. In the past two decades, the region has shown balanced to slightly positive glacier budgets, an increase in glacier ice flow speeds, stable to partially advancing glacier termini and widespread glacier surge activity. This is in stark contrast to the rest of High Mountain Asia, where glacier retreat and slowdown dominate, and glacier surging is largely absent. Termed the Karakoram Anomaly, recent observations show that the anomalous glacier behaviour partially extends to the nearby Western Kun Lun and Pamir. Several complementary explanations have now been presented for the Anomaly's deeper causes, but our understanding is far from complete. Whether the Anomaly will continue to exist in the coming decades remains unclear, but its long-term persistence seems unlikely in light of the considerable warming anticipated by current projections of future climate.

The Karakoram is the mountain range spanning the borders of Pakistan, India and China, with extremities reaching into Afghanistan and Tajikistan (Fig. 1a). The region is geomorphologically very dynamic[1], with intense interactions between tectonic, fluvial and mass movement processes. The extremely steep and high topography, characteristic of the region, hosts some of the tallest mountains on Earth, and very dynamic glaciers (Box 1). According to current inventories[2], the region features roughly 13,700 glaciers, covering an area of about 22,800 km^2. The total volume of glacier ice is estimated to be on the order of 2,200 km^3, or about 30% of the total for High Mountain Asia[3].

Together with snowmelt, runoff from glaciers is the primary water source for the region's rivers[4], which include tributaries of both the Tarim and the Indus (Fig. 1a). This makes the Karakoram's glaciers of utmost importance in supplying water to millions of people downstream[5–7]. Glacier melt has been shown[8] to be of particular importance during periods of drought stress, and hence to contribute to social stability in an otherwise conflict-prone region. Against this background, characterizing the region's glacier evolution is of great relevance.

Peculiar behaviour of Karakoram glaciers was already suspected in early reports[9–12] of nineteenth-century explorers. It is difficult to ascertain, however, whether or not the reports were biased by the perception of an unusually dramatic landscape. Modern observations, instead, are more conclusive, and indeed indicate that—at least for the past decades—Karakoram's glaciers experienced a different evolution when compared with other regions on Earth. The most important difference is the regional glacier mass budget. At the worldwide scale, glaciers outside the Greenland and Antarctic ice sheets have lost an estimated[13] 9,625 ± 7,975 Gt (1 Gt = 10^{12} kg) between 1961 and 2016, or 480 ± 200 kg m^{-2} yr^{-1}. This is in direct contrast to what is reported for the central parts of the Karakoram, where most recent estimates[14] indicate a mass gain on the order of 120 ± 140 kg m^{-2} yr^{-1}. This slight glacier mass gain has probably contributed to an increase in ice flow velocities that is observable at the regional scale[15].

The frequent occurrence of glacier surges[16] is a second distinguishing characteristic of the Karakoram. Glacier surges are irregular phases of ten- to hundred-fold acceleration in glacier flow, typically lasting between a few months to several years[17]. Although surges occur in other regions on Earth as well (including Alaska and Svalbard, for example), they are absent for most other parts of High Mountain Asia[18]. In an overview from the 1930s[19], such behaviour was attributed to little-explained 'accidental changes', and was thought to be responsible for the high number of river floods caused by the outburst of glacier-dammed lakes. Today, various mechanisms have been proposed to explain the initiation and clustering of glacier surges (Box 2) but our understanding is incomplete. Similarly, it remains unclear whether the frequency of Karakoram glacier surges has changed over time, although indications exist[20] that surge activity might have increased after 1990.

The above peculiarities in glacier behaviour are often referred to as the Karakoram Anomaly, a term coined in the mid-2000s[21] when indications of anomalous glacier behaviour started to emerge (see Supplementary Section 1 for a brief history of how the idea of a Karakoram Anomaly developed). In the following, we detail the ways in which this Anomaly expresses itself, and review the mechanisms that have been proposed to explain it. We distinguish between early, partially speculative explanations, and more recent, holistic interpretations. We highlight the remaining gaps in the explanation chains, speculate about the Anomaly's implications and future evolution, and suggest avenues for future research.

Manifestations of the Karakoram Anomaly

Slight glacier mass gains and widespread surging activity are the two of the most prominent features of the Karakoram region. Evidence for the former has accumulated since satellite-based regional estimates of glacier surface elevation changes have become available[22–26]. Although patterns of glacier changes are spatially variable (Fig. 2), there is now general agreement that the Karakoram experienced balanced glacier budgets, or even marginal glacier mass

---

[1]Laboratory of Hydraulics, Hydrology and Glaciology (VAW), ETH Zurich, Zurich, Switzerland. [2]Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland. [3]Department of Physical Geography, Faculty of Geosciences, Utrecht University, Utrecht, the Netherlands. [4]School of Geography, University of Leeds, Leeds, UK. *e-mail: daniel.farinotti@ethz.ch

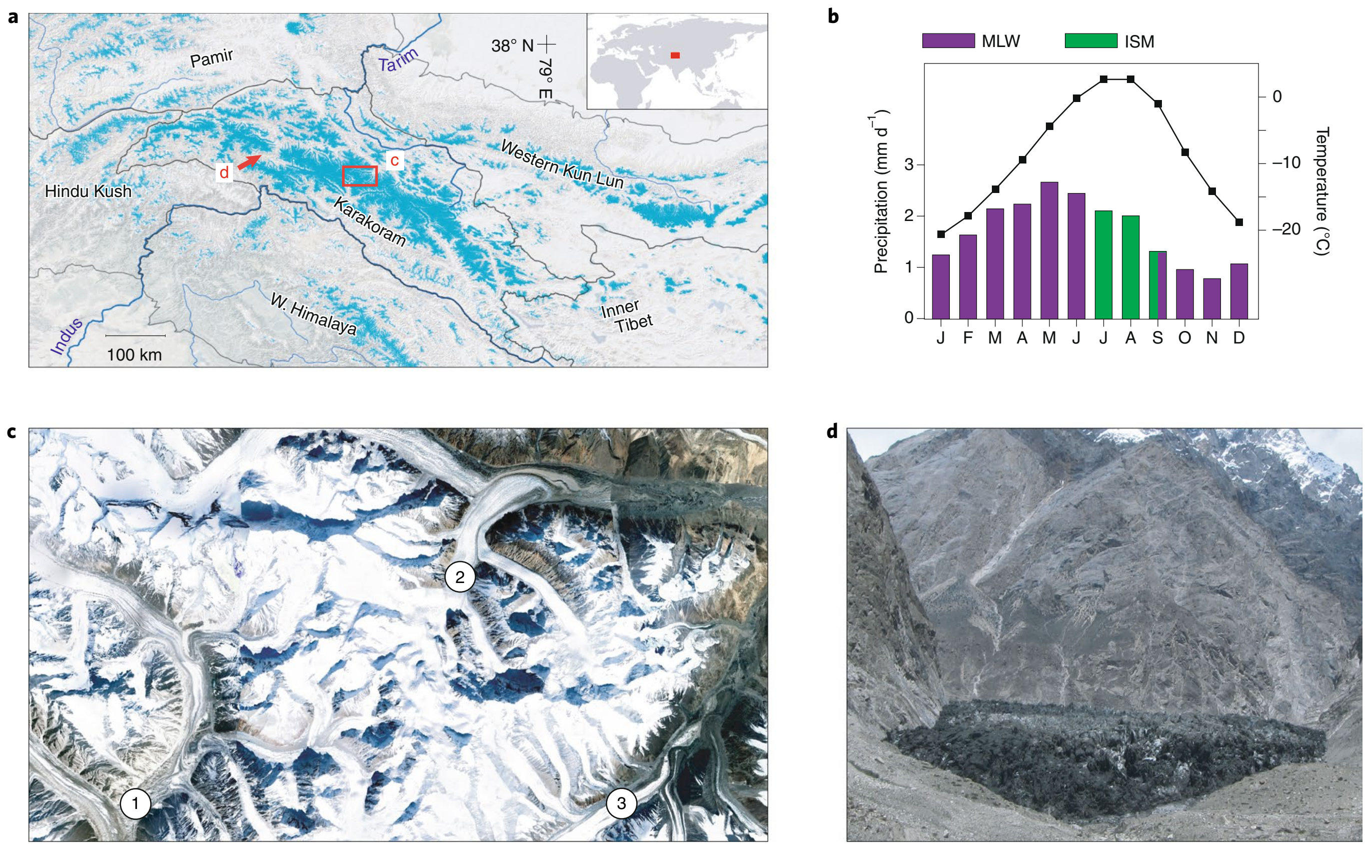

Fig. 1 | Distribution of Karakoram glaciers and climate characteristics. **a**, Glacier coverage and regions per the Randolph Glacier Inventory[2] version 6. **b**, Regional average temperature (plotted on the right *y* axis) and precipitation (plotted on the left *y* axis) for the period 1989–2007. The data are based on ERA-Interim[100] and are redrawn from ref. [101]. The influences of mid-latitude westerlies (MLW) and the Indian summer monsoon (ISM) are shown, based on the classification by ref. [90]. **c**, Satellite image with looped and folded moraines, providing indications of past surges at Panmah (1), South Skamri (2) and Sarpo Langgo (3) glaciers. **d**, Terminus of Shishper Glacier in May 2019, showing clear signs of recent advance. Credit: Base map from Esri, USGS, NOAA and glacier data from ref. [2] (**a**); reproduced with permission from ref. [101], John Wiley and Sons (**b**); Google Earth (**c**); courtesy of Rina Saeed Khan (**d**)

gains, in the early twenty-first century[13,14,27]. The most recent studies[14,26,28], however, indicate that the signal of positive glacier budgets is not centred over the Karakoram itself, but rather over its eastern part and Western Kun Lun (circles in Fig. 2; see also the uncertainties shown in Supplementary Fig. 1). The western part of the Karakoram, which shows balanced mass budgets, is thus understood to be a region of transition between negative mass balances in the Pamir and slightly positive mass balances in Western Kun Lun. Interestingly, regional-scale surface elevation changes show neither significant differences between debris-covered and clean-ice glaciers[22,29] nor between surge-type glaciers and glaciers that do not surge[24].

The slightly positive mass budgets in parts of the Karakoram and Western Kun Lun are also indirectly confirmed by long-term trends in glacier ice flow velocities (arrows in Fig. 2; uncertainties are shown in Supplementary Fig. 1). Even if glacier-specific velocity changes are difficult to interpret because of large seasonal and interannual variability[16,30], analyses over the period 2000–2016 show velocity changes on the order of 0 to +20% per decade[15,31]. Regional averages for the Karakoram and Western Kun Lun are on the order of +3.6 ± 1.2% and +4.0 ± 2.1% per decade, respectively[15]. This trend in ice flow velocities was shown to be unrelated to the region's surging glaciers[15], and thus interpreted as an indication of increased ice deformation and sliding due to glacier thickening. The thickening is, in turn, consistent with the positive glacier mass budgets. The findings of accelerating glacier flow are in contrast to what has been observed in other parts of High Mountain Asia, where ice flow slowdown dominates[15,32].

The dynamic adjustments to positive mass budgets are also manifested in the majority of the region's glaciers, which show stable or advancing termini[33,34]. Albeit not resulting in significant net changes in glacier area[35], these changes are again in contrast to the rest of High Mountain Asia, where glacier terminus retreat and area loss largely prevails[36,37]. It must be noted, however, that the detection and interpretation of changes in the region's glacier extents are complicated by the widespread debris coverage[33]. The debris-covered area itself remained virtually unchanged over the past four decades in the upper Hispar and Shimsha valleys[38], and increased by about 11% in the central Karakoram over the 2001–2010 period[35] (see fig. 1 in refs. [35,38] for definitions of regions). This further corroborates the balanced (slightly negative) mass budgets reported for the central (eastern) part of the Karakoram[14], given that positive and negative mass budgets would be expected to result in reductions and extensions of the debris-covered area, respectively.

Many terminus advances and changes in velocity may also be ascribed to glacier surges. The phenomenon is uncommon elsewhere in High Mountain Asia but is widespread in the Karakoram[16] and the nearby regions[31,39,40]. It has been suggested that this clustering of surge-type glaciers might be related to particular climatic and geometric conditions that lead to periodic enthalpy imbalances[18], but the specific controls on surging remain poorly understood. This is also because data on englacial and subglacial conditions,

Box 1 | Peculiarities of Karakoram glaciers

Glaciers in the Karakoram are unusually large compared with other regions of High Mountain Asia[2], and have exceptional elevation ranges (images below). The extremely high altitudes, exceeding 8,000 m a.s.l. at times, cause precipitation to occur as snow during most of the year, giving rise to a year-round accumulation regime[43]. The characteristic steep mountain walls confining the accumulation area of many glaciers cause orographic concentration of snow (Turkestan- and Mustagh-type glaciers[43]) and are source of extensive debris[1]. The latter covers the ablation zones of many glaciers in the region (right and centre images below). The debris cover, in turn, makes the glacier response to external forcing nonlinear[102], and results in large portions of glaciers that persist at lower elevations than debris-free glaciers responding to the same climate forcing[103]. Widespread surging activity gives rise to some peculiar geomorphic features, such as lobed medial moraines, strandlines, ice foliation and rugged, strongly crevassed glacier surfaces[20].

The geomorphology of the Upper Hunza Valley, characterized by perspectives looking north-eastward over the terminus lake of Pasu Glacier (left; 36.45° N, 74.87° E), north-north-eastward over the debris-covered tongue of Ghulkin Glacier (middle; 36.42° N, 74.83° E) and westward into the clean-ice accumulation zone of the Ghulkin Glacier (right).

which are thought to be pivotal in controlling surge cycles (Box 2), are almost entirely lacking for the region[16]. The frequency of surge events seems to have increased in recent decades[20], potentially correlating with a period of warming atmospheric temperatures[40] and increasing precipitation[20]. No definitive connection between surge activity and changes in external forcing has been established yet[41], and it is still difficult to discern whether the reported increase in surge frequency is related to a real environmental trend, or to an improved ability to detect surges through advances in observational techniques.

A further open question is for how long the observed anomalous behaviour might have persisted. Early works based on sparse field observations suggest a retreat of the Karakoram glaciers between 1940 and the 1960s[42], with periods of slight advances in the late 1970s and 1990s[43]. Meta-analysis of reports for glacier changes across High Mountain Asia, however, indicates that no significant change occurred since the 1960s[37]. The only field-based mass balance estimate available for the twentieth century in the region[44] (Siachen Glacier) is negative, but very uncertain[45]. Satellite-based estimates, on the other hand, reach back to 1973, and suggest that nearly balanced glacier budgets might have persisted since then for the Karakoram[46,47], Western Kun Lun[48,49] and the eastern Pamir[50,51]. The uncertainties of these estimates are also large, and the temporal resolution of such estimates is low—typically only providing information for the period 1973–2000, or for 1973 onwards. All of this makes it difficult to establish temporal variations in the Anomaly's magnitude and extent.

Box 2 | Classical surging mechanisms

Two main mechanisms have been proposed to explain glacier surging[104]: thermal and hydrological control. Both attribute the ultimate cause of the acceleration in ice motion to an increase in subglacial water pressure and the resulting enhancement of sliding at the glacier base.

- In thermally controlled surges, changes in basal temperature promote a positive feedback between ice deformation, basal melt, pore water pressure and sliding. This mechanism is comparatively slow, and leads to seasonally independent surge initiation and termination phases that are several years long.
- In hydrologically controlled surges, the increases in sliding velocities are directly caused by a change in the efficiency, and therefore water pressure, of the subglacial drainage system. This mechanism is much faster than thermal control, and results in phases of winter initiation and summer termination, both comprising days to weeks in duration.

Recent work[94] proposed a unifying theory that recognizes the importance of both heat and water, casting surges as an imbalance in enthalpy. This imbalance occurs only within narrow climatic and geometric envelopes[18], both of which can be found in the Karakoram and neighbouring regions.

Early explanations of anomalous behaviour

Although it was known that debris-covered glaciers were widespread in other parts of High Mountain Asia as well, the substantial debris cover that characterizes the glaciers of the Karakoram was often invoked in early explanations for a potentially anomalous behaviour of the region's glaciers[52,53]. The debris cover was not only suggested to significantly suppress ice melt in the ablation zones, thus preventing glacier wastage and retreat, but was also suspected[21] to make it

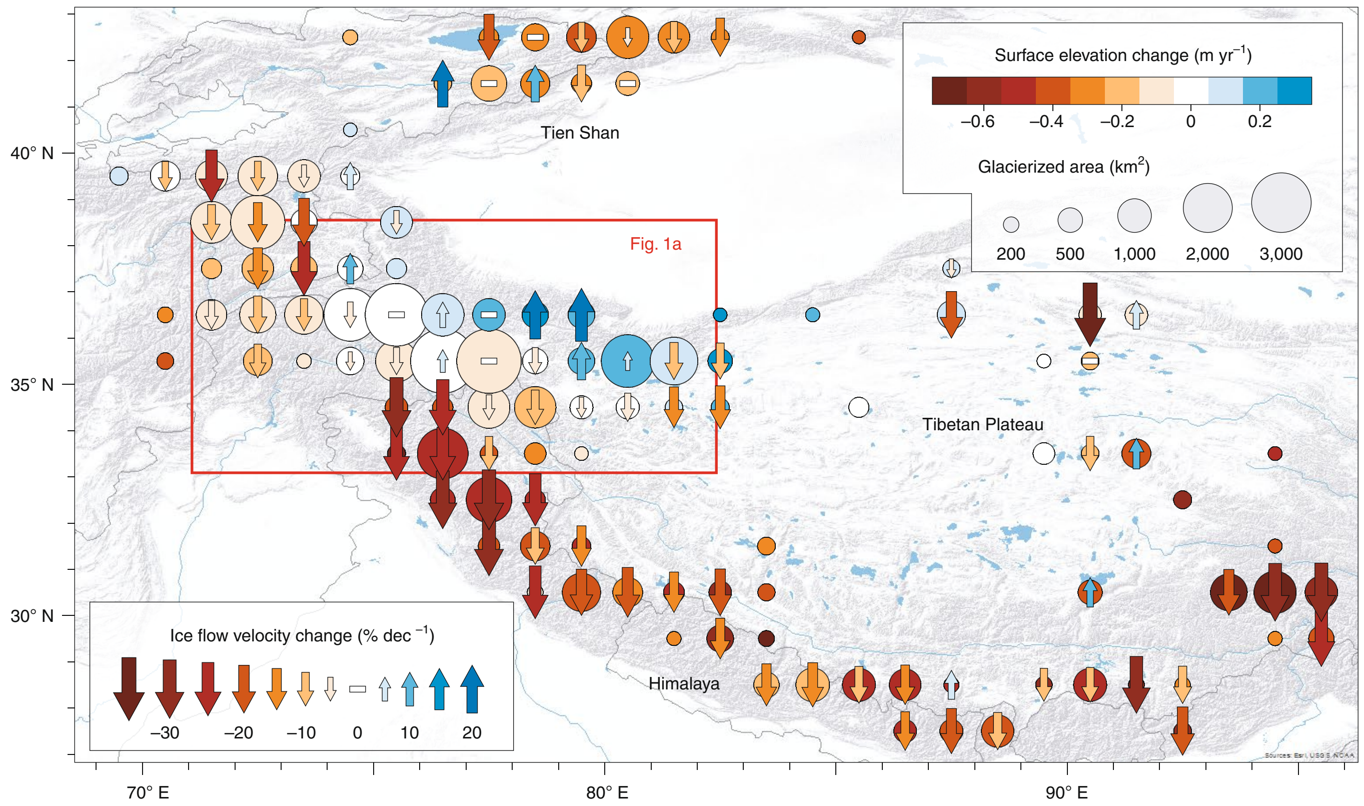

Fig. 2 | Recent glacier changes in High Mountain Asia. The rate of glacier surface-elevation change[28] is shown together with changes in ice flow velocity[15] for the period 2000–2016. The size of the circles is proportional to glacier area. Data are aggregated on a 1° × 1° grid, and uncertainties are shown in Supplementary Fig. 1. The red box indicates the area shown in Fig. 1a, and includes the Karakoram. Base map from Esri, USGS, NOAA.

difficult to detect glacier changes. The morphology of the glaciers in the Karakoram remained one of the main explanations when the idea of a Karakoram Anomaly was proposed in the mid-2000s: the confinement of the main glacier trunks by characteristically high and steep headwalls (Box 1) was suggested to cause an "elevation effect"[43], that is, an orographic enhancement of high-altitude precipitation and a related downslope concentration of snowfall driven by avalanches. Combined with a year-round accumulation regime, the effect would cause limited sensitivity to warming, as a rise in temperature would only result in a small decrease in the accumulation area.

Indications of a climatic control for the Karakoram's peculiar glacier behaviour emerged in the early 2000s. Archer and Fowler[54,55] analysed trends in temperature and precipitation for meteorological stations in the region for the period 1961–2000, and identified significant increases in winter, summer and annual precipitation[54], as well as a lowering of summer mean and minimum temperatures[55]. These observations were independently supported[56,57] by data obtained from tree rings, which indicated that the western Himalaya saw pre-monsoon (March–May) cooling in the latter part of the twentieth century[56]. For the Karakoram, the twentieth century was shown to have been the wettest over the past millennium[57]. The combined decrease in summer temperatures and increase in precipitation were suggested to be consistent with positive glacier mass balances in the region, an interpretation further supported by the simultaneous decrease in summer river flows[54]. This line of argument was echoed and amplified by a number of subsequent studies[20,22,33,58,59], making it the generally accepted hypothesis for the Karakoram Anomaly by about 2010.

The deeper causes of the observed temperature and precipitation changes, however, remained elusive. A preliminary analysis[54] identified a significant positive (negative) correlation between winter (summer) precipitation and the North Atlantic Oscillation, whereas later investigations[60] showed that the westerly jet stream over central Asia—a key mechanism of regional moisture transport during winter (Box 3)—had strengthened and shifted to both lower elevations and lower latitudes between 1979 and 2001. These observations remain central to present-day understanding of the potential drivers of change (see the next section).

Box 3 | Karakoram climate

In contrast to the neighbouring Himalaya, which are under the influence of the Indian monsoon, the Karakoram's climate[54] is predominantly influenced by westerly weather systems and the Tibetan anticyclone. Most of the annual precipitation falls in spring and winter, during which the westerly influence dominates (Fig. 1b). The Mediterranean and Caspian seas are the main sources of moisture under such conditions. The monsoon makes sporadic incursions during summer, with the volumes of precipitation rapidly decreasing from the southeast to the northwest. Moisture from the Arabian Sea is brought to the region when low-pressure systems develop over Pakistan. In such cases, precipitation decreases sharply northward due to orographic shielding.

Concerning the widespread occurrence of glacier surges, it was recognized very early that substantial basal sliding must be involved to maintain high rates of glacier flow. For example, Finsterwalder[61] suggested (on the basis of a set of observations collected during the 1930s) that the glaciers of the Nanga Parbat area mainly move

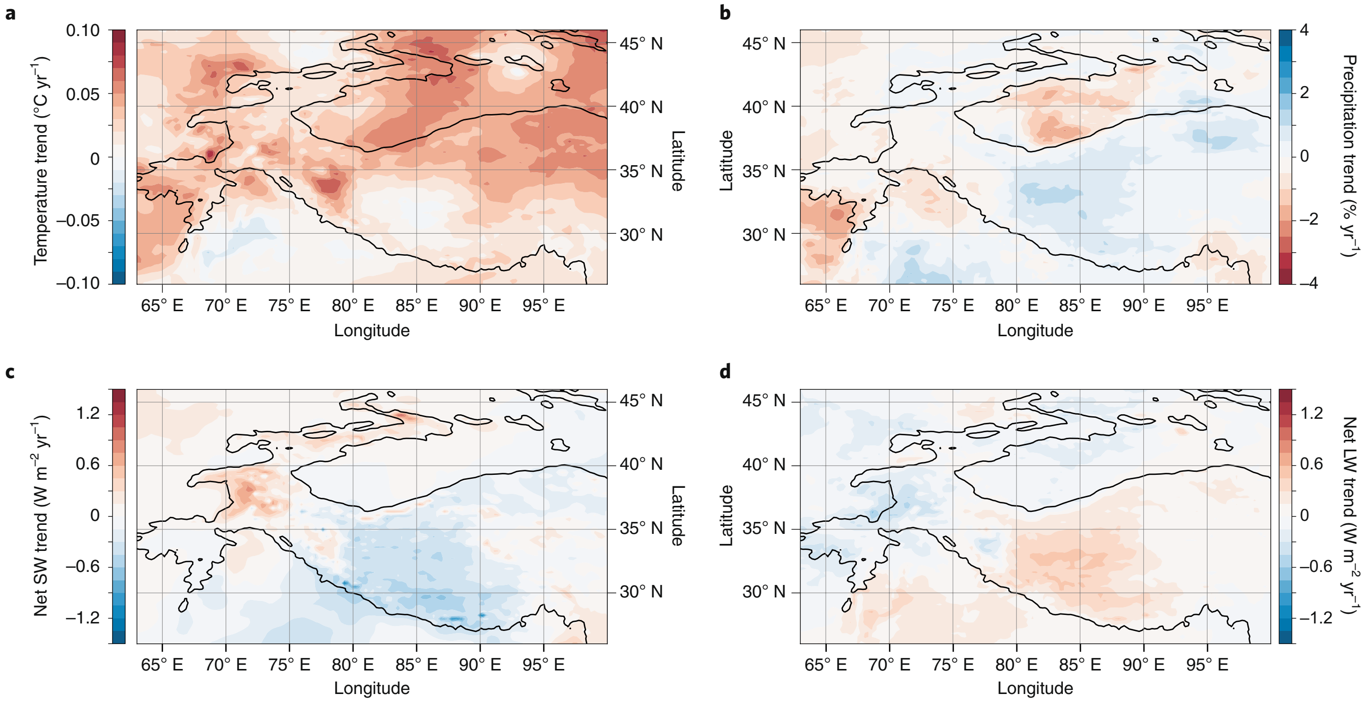

Fig. 3 | Potential meteoclimatic drivers of the Karakoram Anomaly. a–d, The spatial distributions of linear trends in summer (JJA) temperature (**a**), annual precipitation (**b**), summer net shortwave (SW) radiation (**c**) and summer net longwave (LW) radiation (**d**) are shown for 1980–2018. The representations are based on ERA5 data[92]. Trend significances and a comparison with the high-resolution climate model results from ref. [76] are provided in Supplementary Figs. 2 and 3, respectively. A 2,000-m contour line (black) is provided for orientation.

through 'blockschollen-motion', that is, sliding-dominated plug-flow, primarily resisted by drag at the glacier margins. The important contribution of basal sliding to the total motion of both surge-type and non-surging glaciers in the Karakoram was confirmed repeatedly by both ground-based[62–66] and remotely sensed observations[67]. Whether and why such high sliding rates are peculiar to the region, however, remain largely unknown.

To explain surge initiation, the literature generally focuses on two main mechanisms that invoke changes in either thermal or hydrological conditions as the trigger (Box 2). Which of the two is predominant for the Karakoram has been a matter of debate[68]. Quincey et al.[59] argued in favour of thermal control, noticing that surges develop over several years and that no seasonality can be discerned in their initiation. In contrast, Copland et al.[20] advocated for hydrological control, as the active phases of Karakoram surges seem to be short-lived and separated by decades-long phases of quiescence. To explain the increase in surging activity after the 2000s, Hewitt[68] speculated about the role of changes in climate, stating that "response to climate change seems the only explanation for [the] events at [four tributaries of] Panmah Glacier [Central Karakoram]". However, demonstrating such a climatic control is difficult, and evidence remains scant.

Current understanding of the Anomaly's drivers

Whilst a climatic control on surging activity is debated, the positive glacier budgets in and around the Karakoram must be associated with a meteorological forcing. Compared with other parts of High Mountain Asia, the forcing must either favour more accumulation, less ablation, or a combination of both. Several potential explanations can be found in the literature, including increased snowfall in the accumulation zones or a suite of factors—such as increased cloud cover and a higher surface albedo—that reduce the net energy available for the melting of snow and ice.

The Karakoram's general meteorological characteristics are well established[69–71] (Box 3). In winter, when the westerly jet is located south of the Karakoram, mid-latitude cyclones (or westerlies) control the region's weather[72,73]. Their associated fronts interact with the extreme topography and can provide heavy mountain precipitation[74]. An increase in the strength and frequency of such westerlies-dominated precipitation has been identified[75] for the period 1979–2010, and seems to have led to a slight increase in the region's winter snowfall[76]. This is in contrast to other regions in High Mountain Asia, where snowfall trends are mostly negative[69]. The contrasting trends in the geopotential heights between different parts of High Mountain Asia (Fig. 2 in ref. [76]) have been suggested to be responsible for the changes in westerlies-driven precipitation events[70,75,76], but the underlying mechanisms are still unclear. The precipitation changes, in turn, have been proposed to exert a strong control on regional glacier mass balances[69,70,77]. It has to be noted, however, that precipitation trends are uncertain and mostly non-significant[78], and that no increase in Karakoram's total precipitation is evident in recent meteorological reanalyses (Fig. 3b and Supplementary Fig. 2b,d).

In summer, the interplay between the monsoon and mid-latitude westerlies is complex, and results in a high interannual precipitation variability[69]. This variability has been associated[70,71] with modulations of the Karakoram/Western Tibetan Vortex, an atmospheric structure that extends from the near surface to almost the height of the tropopause[70]. Temperatures also show variability, and for the latter part of the twentieth century, an increase in diurnal temperature ranges has been inferred from both weather stations[55,79] and tree-rings[56]. This increase has been related to large-scale deforestation, which caused a lowering of the soil's thermal inertia due to reduced water infiltration[56]. A concomitant cooling of summer temperatures was observed despite a general warming trend in regional air temperatures[79]. The cooling was particularly pronounced in the period 1960–1980[55,79], and has been attributed

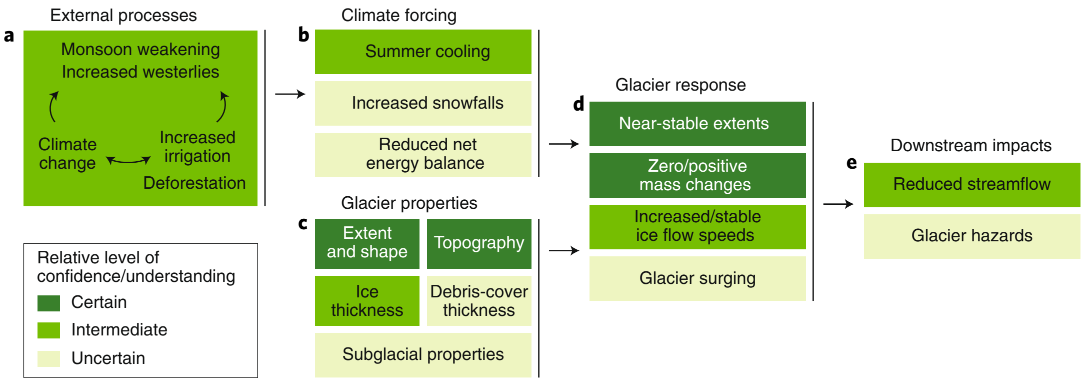

Fig. 4 | Schematic of the process chain leading to anomalous glacier evolution. a, External processes. **b**, Climate forcing. **c**, Glacier properties. **d**, Glacier response. **e**, Downstream impacts. For every element, a relative level of confidence in its characterization or understanding is indicated by the colour shading. The confidence level is based on the authors' expert judgement and literature review.

to a weakening of the monsoon[70,71]. It is this summer cooling that has been suggested[55,70] to be a particularly important driver of the balanced glacier budget of the Karakoram in recent decades. It should be noted, however, that tree-ring chronologies at one high-elevation site[80] did not provide any indication of Karakoram temperatures being out of phase with other regions in High Mountain Asia over centennial timescales.

Changes in glacier accumulation and ablation have also been suggested[81] to be linked to increased evaporation in Northwest China during the twentieth century. This increased evaporation—caused by a dramatic surge in irrigation after 1960[82]—has caused a rise in atmospheric moisture, which in turn seems to have resulted in more frequent summer snowfalls in Western Kun Lun and the Pamir. This elevated atmospheric moisture also increased cloudiness and reduced incoming shortwave radiation[81] (Fig. 3c), thus reducing ice and snow ablation. Support for this hypothesis is being found in both observational records and modelling studies[76,83], but cannot be considered conclusive yet.

Although often assessed independently, the weakened monsoon and irrigation hypotheses are in fact inherently interconnected. The weakening of the monsoon has been suggested to be a partial consequence of changes in irrigation itself[84,85]: increased irrigation causes changes in near-surface heat fluxes, which leads to a cooling of both the surface and the lower troposphere; the troposphere cooling, in turn, decreases the geopotential height over the irrigated regions, thus affecting atmospheric circulation including the westerly jet and the monsoon[84]. Such changes in large-scale circulation would partly explain regional differences in glacier response, and the different glacier budgets in the Karakoram with respect to other regions of High Mountain Asia.

Regional differences in glacier response are also affected by spatial variations in climate sensitivity[86]. The response of glacier mass balance to a given change in temperature, for example, was shown to vary[87], and to correlate well with the observed mass budgets. These differences can be explained by regional variations in the glaciers' energy balance. Both field-based[88,89] and model-based[90] investigations, in fact, indicate that net shortwave radiation is more important in driving glacier melt in the Karakoram than it is in other parts of High Mountain Asia. As the shortwave radiation budget is decisively controlled by surface albedo and cloudiness, this partly explains why glaciers in the Karakoram might be particularly susceptible to changes in albedo-enhancing summer snowfalls. The increase in summer snowfall and the decrease in net shortwave radiation observed in the Karakoram over the past few decades (Fig. 3c) might thus have favoured positive glacier budgets, whereas the increases in both temperature and net longwave radiation in other parts of High Mountain Asia (Fig. 3a,d) favoured glacier mass loss.

Knowledge gaps, implications and a look into the future

The Karakoram's balanced to slightly positive glacier mass budgets are the strongest argument for anomalous behaviour, both at the scale of High Mountain Asia and the world. Moreover, enough evidence now exists to show that these close-to-balance glacier budgets extend into the neighbouring Western Kun Lun and Pamir. To justify being named an Anomaly, however, qualitatively different glacier behaviour must be distinguished from regional characteristics. Large, low-elevation and debris-covered glacier termini; strong verticality resulting in pronounced avalanche-driven snow accumulation; and even the high number of surge-type glaciers might, in fact, be considered as characteristic of the region rather than anomalous[91].

Figure 4 provides an overview of the process chain related to the Anomaly, with a focus on the evolution observed during past decades. In a nutshell, the interplay between land cover, atmospheric processes and climate change (Fig. 4a) is suggested to have led to summer cooling, increased snowfall and reduced net energy available for glacier melt (Fig. 4b). In conjunction with specific glacier properties (Fig. 4c), a combination of these effects resulted in glacier advance, constant to slightly accelerating glacier ice flow and insignificant changes in both total glacier area and debris cover (Fig. 4d). This, in turn, reduced downstream flows and affected glacier-related hazards on some occasions (Fig. 4e). The mechanisms that control the region's peculiar glacier behaviour (including glacier surging, for example) are, however, far from being completely understood. Based on our expert judgement and the reviewed literature, we assigned a relative level of confidence to the degree to which individual elements of Fig. 4 are characterized or understood.

The lack of long-term observations, for instance, causes uncertainties in the estimated trends for factors that drive glacier change. In the Karakoram and nearby regions, this is particularly true for meteorological parameters (Fig. 4b). Air-temperature trends obtained from high-resolution climate models[76], for example, show large differences when compared with climate reanalysis products[92] (Supplementary Fig. 2a,c). Precipitation trends show better agreement, although the trends themselves are less certain (Supplementary Fig. 2b,d). High-altitude precipitation is particularly poorly quantified, both in terms of temporal and spatial variability, as well as elevation dependency. Together with the difficulty in characterizing snow transport by wind and avalanches, this makes the estimates of glacier accumulation highly uncertain. The identification of trends is also complicated by the region's high interannual climate variability. The latter results in low statistical significance (Supplementary Fig. 3) and slow trend emergence, which both complicate attributive studies. The use of climate model ensembles, rather than individual products, can increase the robustness of such studies, but cannot overcome the lack of ground-truth information. This lack affects the level of confidence with which drivers of the Karakoram's glacier budgets can be identified.

The present-day understanding of the mechanisms that control the region's glacier behaviour is often based on model simulations that use simplified parameterizations to represent important glaciological (Fig. 4c) or atmospheric (Fig. 4a) processes[93]. Both introduce uncertainties that are difficult to quantify. The continuous development towards models with higher spatial resolution and complexity is unlikely to resolve this. Although some driving processes might indeed be better represented in higher-resolution models, a strong need remains for direct observations that support model calibration and validation. Crucially, such observations need to cover the time spans pertinent to glacier changes, and need to be representative in terms of both resolution and spatial coverage. Such observations also hold the key to increasing the understanding of individual processes and process chains, which in turn is the prerequisite for improving model parameterizations. Bridging the gap between in situ observations and model simulations remains one of the major challenges when aiming to gain further insights into the Anomaly's deeper causes.

While surface parameters such as glacier extent, topography and temporal evolution (top of Fig. 4c and d) are observed with increasing accuracy due to advances in remote-sensing techniques, detailed information on subsurface characteristics such as the thermal regimes, hydrological systems and subglacial lithology of glaciers (bottom of Fig. 4c and d) remain out of reach. This hampers a robust analysis of the physical processes that control local glacier behaviour. For the Karakoram, this is particularly relevant in the context of the region's surging activity. Important advances in the conceptual understanding of surge occurrences are being made[18,94] but a definitive explanation for why surge-type glaciers are clustered in the Karakoram is still missing, and surge behaviour is far from being predictable. Indications that the spatial distribution of surge-type glaciers is strongly controlled by climate now exist[18], but a better characterization of englacial and subglacial properties would certainly add to that understanding. Better constraining the controls on regional surge activities seems particularly important in light of recent indications that environmental changes may influence catastrophic, surge-like glacier collapses[95,96] (Fig. 4e).

One unanswered question is for how long the Anomaly is likely to persist in the future. If the global climate continues to warm, as anticipated by current projections[97], it seems unlikely that it will persist in the longer term—especially not in the form of positive glacier budgets[7,98]. Changes in precipitation will affect future glacier evolution as well. Here, a key uncertainty is how the monsoon system and westerly jet will respond to ongoing warming, and to other forcings such as land-use changes. At present, irrigation is suggested to influence the region's climate through the control of heat exchanges and moisture fluxes[84,85]. Irrigated areas, however, cannot continue to expand limitlessly as space is scarce and water resources are limited, and may even shrink if groundwater levels drop beyond economically viable depths. If recent hypotheses on regional-scale mechanisms[81] are accepted, such land-use changes could result in decreased precipitation, possibly affecting the region's glaciers via reduced accumulation.

The anomalous glacier behaviour in the Karakoram and its neighbouring regions is not only a curiosity in an epoch dominated by glacier retreat. The glaciers' importance for regional water supplies[7,8] (Fig. 4e), and the cultural and religious value attributed to glaciers by the local communities and their traditional practices[99] make some of the unanswered scientific questions of great societal relevance. Future glacier evolution, and the effect on both water supplies and glacier-related hazards, are of particular concern in this geopolitically complex region where communities have limited resilience to environmental stress. Establishing the mechanisms that are driving the Karakoram Anomaly, their relative importance and how they are likely to evolve in coming decades therefore remains a key challenge for climatic and cryospheric researchers alike.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41561-019-0513-5.

Received: 7 May 2019; Accepted: 20 November 2019;

References

1. Hewitt, K. Rock avalanches that travel onto glaciers and related developments, Karakoram Himalaya, Inner Asia. *Geomorphology* **103**, 66–79 (2009).
2. RGI Consortium. *Randolph Glacier Inventory—A Dataset of Global Glacier Outlines: Version 6. 0* (Global Land Ice Measurements from Space, 2017); https://doi.org/10.7265/N5-RGI-60
3. Farinotti, D. et al. A consensus estimate for the ice thickness distribution of all glaciers on Earth. *Nat. Geosci.* **12**, 168–173 (2019).
4. Armstrong, R. L. et al. Runoff from glacier ice and seasonal snow in High Asia: separating melt water sources in river flow. *Reg. Environ. Change* **19**, 1249–1261 (2019).
5. Akhtar, M., Ahmad, N. & Booij, M. J. The impact of climate change on the water resources of Hindukush-Karakorum-Himalaya region under different glacier coverage scenarios. *J. Hydrol.* **355**, 148–163 (2008).
6. Immerzeel, W., van Beek, L. & Bierkens, M. Climate change will affect the Asian water towers. *Science* **328**, 1382–1385 (2010).
7. Huss, M. & Hock, R. Global-scale hydrological response to future glacier mass loss. *Nat. Clim. Change* **8**, 135–140 (2018).
8. Pritchard, H. D. Asia's shrinking glaciers protect large populations from drought stress. *Nature* **569**, 649–654 (2019).
9. Schlagintweit, H., Schlagintweit, A. & Schlagintweit, R. *Results of a Scientific Mission to India and High Asia Undertaken Between the Years 1854 and 1858* (Trubner, 1861).
10. Godwin-Austen, H. H. The glaciers of the Muztagh Range. *Proc. R. Geogr. Soc.* **34**, 19–56 (1864).
11. Shaw, R. *Visits to High Tartary, Yarkand, and Kashghar: Formerly Chinese Tartary* (John Murray, 1871).
12. Hayden, H. H. Notes on certain glaciers in Northwest Kashmir. *Rec. Geol. Surv. India* **35**, 127–137 (1907).
13. Zemp, M. et al. Global glacier mass balances and their contributions to sea-level rise from 1961 to 2016. *Nature* **568**, 382–386 (2019).
14. Berthier, E. & Brun, F. Karakoram glacier mass balances between 2008 and 2016: persistence of the anomaly and influence of a large rock avalanche on Siachen Glacier. *J. Glaciol.* **65**, 494–507 (2019).
15. Dehecq, A. et al. Twenty-first century glacier slowdown driven by mass loss in High Mountain Asia. *Nat. Geosci.* **12**, 22–27 (2019).
16. Quincey, D. J., Glasser, N. F., Cook, S. J. & Luckman, A. Heterogeneity in Karakoram glacier surges. *J. Geophys. Res. Earth Surf.* **120**, 1288–1300 (2015).
17. Meier, M. F. & Post, A. What are glacier surges? *Can. J. Earth Sci.* **6**, 807–817 (1969).
18. Sevestre, H. & Benn, D. Climatic and geometric controls on the global distribution of surge-type glaciers: implications for a unifying model of surging. *J. Glaciol.* **61**, 646–662 (2015).
19. Mason, K. *The Glaciers of the Karakoram and Neighbourhood* (Geological Survey of India, 1930).
20. Copland, L. et al. Expanded and recently increased glacier surging in the Karakoram. *Arct. Antarct. Alp. Res.* **43**, 503–516 (2011).
21. Hewitt, K. The Karakoram anomaly? Glacier expansion and the 'elevation effect', Karakoram Himalaya. *Mt. Res. Dev.* **25**, 332–340 (2005).
22. Gardelle, J., Berthier, E. & Arnaud, Y. Slight mass gain of Karakoram glaciers in the early twenty-first century. *Nat. Geosci.* **5**, 322–325 (2012).
23. Kääb, A., Berthier, E., Nuth, C., Gardelle, J. & Arnaud, Y. Contrasting patterns of early twenty-first-century glacier mass change in the Himalayas. *Nature* **488**, 495–498 (2012).
24. Gardelle, J., Berthier, E., Arnaud, Y. & Kääb, A. Region-wide glacier mass balances over the Pamir-Karakoram-Himalaya during 1999–2011. *Cryosphere* **7**, 1263–1286 (2013).
25. Gardner, A. S. et al. A reconciled estimate of glacier contributions to sea level rise: 2003 to 2009. *Science* **340**, 852–857 (2013).
26. Kääb, A., Treichler, D., Nuth, C. & Berthier, E. Brief communication: contending estimates of 2003–2008 glacier mass balance over the Pamir-Karakoram-Himalaya. *Cryosphere* **9**, 557–564 (2015).

27. Azam, M. F. et al. Review of the status and mass changes of Himalayan-Karakoram glaciers. *J. Glaciol.* **64**, 61–74 (2018).
28. Brun, F., Berthier, E., Wagnon, P., Kääb, A. & Treichler, D. A spatially resolved estimate of High Mountain Asia glacier mass balances from 2000 to 2016. *Nat. Geosci.* **10**, 668–673 (2017).
29. Brun, F. et al. Heterogeneous influence of glacier morphology on the mass balance variability in High Mountain Asia. *J. Geophys. Res. Earth Surf.* **124**, 1331–1345 (2019).
30. Scherler, D. & Strecker, M. R. Large surface velocity fluctuations of Biafo Glacier, central Karakoram, at high spatial and temporal resolution from optical satellite images. *J. Glaciol.* **58**, 569–580 (2012).
31. Lv, M. et al. Characterizing the behaviour of surge- and non-surge-type glaciers in the Kingata Mountains, eastern Pamir, from 1999 to 2016. *Cryosphere* **13**, 219–236 (2019).
32. Heid, T. & Kääb, A. Repeat optical satellite images reveal widespread and long term decrease in land-terminating glacier speeds. *Cryosphere* **6**, 467–478 (2012).
33. Scherler, D., Bookhagen, B. & Strecker, M. R. Spatially variable response of Himalayan glaciers to climate change affected by debris cover. *Nat. Geosci.* **4**, 156–159 (2011).
34. Rankl, M., Kienholz, C. & Braun, M. Glacier changes in the Karakoram region mapped by multimission satellite imagery. *Cryosphere* **8**, 977–989 (2014).
35. Minora, U. et al. Glacier area stability in the Central Karakoram National Park (Pakistan) in 2001–2010: the "Karakoram Anomaly" in the spotlight. *Progr. Phys. Geogr. Earth Environ.* **40**, 629–660 (2016).
36. Bolch, T. et al. The state and fate of Himalayan Glaciers. *Science* **336**, 310–314 (2012).
37. Cogley, J. G. Glacier shrinkage across High Mountain Asia. *Ann. Glaciol.* **57**, 41–49 (2016).
38. Herreid, S. et al. Satellite observations show no net change in the percentage of supraglacial debris-covered area in northern Pakistan from 1977 to 2014. *J. Glaciol.* **61**, 524–536 (2015).
39. Goerlich, F. & Paul, F. Surging glaciers everywhere? An updated inventory of surging glaciers for the Pamir Mountains derived from the analysis of multi-temporal optical satellite data. In *EGU General Assembly Conference Abstracts* Vol. 21, 5747-2 (EGU, 2019).
40. Chudley, T. R. & Willis, I. C. Glacier surges in the north-west West Kunlun Shan inferred from 1972 to 2017 Landsat imagery. *J. Glaciol.* **65**, 1–12 (2019).
41. Bhambri, R., Hewitt, K., Kawishwar, P. & Pratap, B. Surge-type and surge-modified glaciers in the Karakoram. *Sci. Rep.* **7**, 15391 (2017).
42. Mayewski, P. A. & Jeschke, P. A. Himalayan and Trans-Himalayan glacier fluctuations since AD 1812. *Arct. Alp. Res.* **11**, 267–287 (1979).
43. Hewitt, K. Glacier change, concentration, and elevation effects in the Karakoram Himalaya, upper Indus basin. *Mt. Res. Dev.* **31**, 188–200 (2011).
44. Bhutiyani, M. R. Mass-balance studies on Siachen glacier in the Nubra valley, Karakoram Himalaya, India. *J. Glaciol.* **45**, 112–118 (1999).
45. Zaman, Q. & Liu, J. Mass balance of Siachen Glacier, Nubra valley, Karakoram Himalaya: facts or flaws? *J. Glaciol.* **61**, 1012–1014 (2015).
46. Zhou, Y., Li, Z., Li, J., Zhao, R. & Ding, X. Slight glacier mass loss in the Karakoram region during the 1970s to 2000 revealed by KH-9 images and SRTM DEM. *J. Glaciol.* **63**, 331–342 (2017).
47. Bolch, T., Pieczonka, T., Mukherjee, K. & Shea, J. Brief communication: Glaciers in the Hunza catchment (Karakoram) have been nearly in balance since the 1970s. *Cryosphere* **11**, 531–539 (2017).
48. Zhou, Y., Li, Z., Li, J., Zhao, R. & Ding, X. Glacier mass balance in the Qinghai-Tibet Plateau and its surroundings from the mid-1970s to 2000 based on Hexagon KH-9 and SRTM DEMs. *Remote Sens. Environ.* **210**, 96–112 (2018).
49. Wang, Y. et al. Glacier anomaly over the western Kunlun Mountains, Northwestern Tibetan Plateau, since the 1970s. *J. Glaciol.* **64**, 624–636 (2018).
50. Holzer, N. et al. Four decades of glacier variations at Muztagh Ata (eastern Pamir): a multi-sensor study including Hexagon KH-9 and Pleiades data. *Cryosphere* **9**, 2071–2088 (2015).
51. Zhou, Y., Li, Z., Li, J., Zhao, R. & Ding, X. Geodetic glacier mass balance (1975–1999) in the central Pamir using the SRTM DEM and KH-9 imagery. *J. Glaciol.* **65**, 309–320 (2019).
52. von Wissmann, H. & Flohn, H. *Today's Glacierization and Snow Line in High Asia, with Hints on the Glaciation During the Last Ice Age* (in German) Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse No. 14 (Akademie der Wissenschaften und der Literatur, 1960).
53. Kick, W. in *Glacier Fluctuations and Climate Change* (ed. Oerlemans, J.) 129–142 (Kluwer, 1989).
54. Archer, D. R. & Fowler, H. J. Spatial and temporal variations in precipitation in the Upper Indus Basin, global teleconnections and hydrological implications. *Hydrol. Earth Syst. Sci.* **8**, 47–61 (2004).
55. Fowler, H. J. & Archer, D. R. Conflicting signals of climatic change in the upper Indus basin. *J. Clim.* **19**, 4276–4293 (2006).
56. Yadav, R. R., Park, W.-K., Singh, J. & Dubey, B. Do the western Himalayas defy global warming? *Geophys. Res. Lett.* **31**, L17201 (2004).
57. Treydte, K. S. et al. The twentieth century was the wettest period in northern Pakistan over the past millennium. *Nature* **440**, 1179–1182 (2006).
58. Quincey, D. J. et al. Ice velocity and climate variations for Baltoro Glacier, Pakistan. *J. Glaciol.* **55**, 1061–1071 (2009).
59. Quincey, D. J. et al. Karakoram glacier surge dynamic. *Geophys. Res. Lett.* **38**, L18504 (2011).
60. Archer, C. L. & Caldeira, K. Historical trends in the jet streams. *Geophys. Res. Lett.* **35**, L08803 (2008).
61. Finsterwalder, R. The glaciers of Nanga Parbat, glaciological works of the German Himalaya-expedition and their results (in German). *Z. Gletsch. Glazialgeol.* **25**, 57–107 (1937).
62. Batura Glacier Investigation Group. The Batura Glacier in the Karakoram mountains and its variations. *Sci. Sin.* **22**, 958–974 (1979).
63. Hewitt, K., Wake, C. P., Young, G. J. & David, C. Hydrological investigations at Biafo Glacier, Karakoram Range, Himalaya; an important source of water for the Indus River. *Ann. Glaciol.* **13**, 103–108 (1989).
64. Gardner, J. S. & Hewitt, K. A surge of Bualtar Glacier, Karakoram Range, Pakistan: a possible landslide trigger. *J. Glaciol.* **36**, 159–162 (1990).
65. Wake, C. P. & Searle, M. P. Rapid advance of Pumarikish Glacier, Hispar Glacier Basin, Karakoram Himalaya. *J. Glaciol.* **39**, 204–206 (1993).
66. Mayer, C., Lambrecht, A., Beló, M., Smiraglia, C. & Diolaiuti, G. Glaciological characteristics of the ablation zone of Baltoro glacier, Karakoram, Pakistan. *Ann. Glaciol.* **43**, 123–131 (2006).
67. Copland, L. et al. Glacier velocities across the central Karakoram. *Ann. Glaciol.* **50**, 41–49 (2009).
68. Hewitt, K. Tributary glacier surges: an exceptional concentration at Panmah Glacier, Karakoram Himalaya. *J. Glaciol.* **53**, 181–188 (2007).
69. Kapnick, S. B., Delworth, T. L., Ashfaq, M., Malyshev, S. & Milly, P. C. D. Snowfall less sensitive to warming in Karakoram than in Himalayas due to a unique seasonal cycle. *Nat. Geosci.* **7**, 834–840 (2014).
70. Forsythe, N., Fowler, H. J., Li, X.-F., Blenkinsop, S. & Pritchard, D. Karakoram temperature and glacial melt driven by regional atmospheric circulation variability. *Nat. Clim. Change* **7**, 664–670 (2017).
71. Li, X.-F., Fowler, H. J., Forsythe, N., Blenkinsop, S. & Pritchard, D. The Karakoram/Western Tibetan vortex: seasonal and year-to-year variability. *Clim. Dynam.* **51**, 3883–3906 (2018).
72. Maussion, F. et al. Precipitation seasonality and variability over the Tibetan Plateau as resolved by the High Asia Reanalysis. *J. Clim.* **27**, 1910–1927 (2013).
73. Curio, J., Maussion, F. & Scherer, D. A 12-year high-resolution climatology of atmospheric water transport over the Tibetan Plateau. *Earth Syst. Dynam.* **6**, 109–124 (2015).
74. Cannon, F., Carvalho, L. M. V., Jones, C. & Norris, J. Winter westerly disturbance dynamics and precipitation in the western Himalaya and Karakoram: a wave-tracking approach. *Theor. Appl. Climatol.* **125**, 27–44 (2016).
75. Cannon, F., Carvalho, L. M. V., Jones, C. & Bookhagen, B. Multi-annual variations in winter westerly disturbance activity affecting the Himalaya. *Clim. Dynam.* **44**, 441–455 (2015).
76. Norris, J., Carvalho, L. M. V., Jones, C. & Cannon, F. Deciphering the contrasting climatic trends between the central Himalaya and Karakoram with 36 years of WRF simulations. *Clim. Dynam.* **52**, 159–180 (2019).
77. Mölg, T., Maussion, F. & Scherer, D. Mid-latitude westerlies as a driver of glacier variability in monsoonal High Asia. *Nat. Clim. Change* **4**, 68–73 (2014).
78. Palazzi, E., von Hardenberg, J. & Provenzale, A. Precipitation in the Hindu-Kush Karakoram Himalaya: observations and future scenarios. *J. Geophys. Res. Atmos.* **118**, 85–100 (2013).
79. Hasson, S., Böhner, J. & Lucarini, V. Prevailing climatic trends and runoff response from Hindukush-Karakoram-Himalaya, upper Indus Basin. *Earth Syst. Dynam.* **8**, 337–355 (2017).
80. Asad, F. et al. Are Karakoram temperatures out of phase compared to hemispheric trends? *Clim. Dynam.* **48**, 3381–3390 (2017).
81. de Kok, R. J., Tuinenburg, O. A., Bonekamp, P. N. J. & Immerzeel, W. W. Irrigation as a potential driver for anomalous glacier behavior in High Mountain Asia. *Geophys. Res. Lett.* **45**, 2047–2054 (2018).
82. Cook, B. I., Shukla, S. P., Puma, M. J. & Nazarenko, L. S. Irrigation as an historical climate forcing. *Clim. Dynam.* **44**, 1715–1730 (2015).
83. Bashir, F., Zeng, X., Gupta, H. & Hazenberg, P. A hydrometeorological perspective on the Karakoram anomaly using unique valley-based synoptic weather observations. *Geophys. Res. Lett.* **44**, 10470–10478 (2017).
84. Lee, E., Sacks, W. J., Chase, T. N. & Foley, J. A. Simulated impacts of irrigation on the atmospheric circulation over Asia. *J. Geophys. Res. Atmos.* **116**, D08114 (2011).
85. Singh, D. et al. Distinct influences of land cover and land management on seasonal climate. *J. Geophys. Res. Atmos.* **123**, 12017–12039 (2018).

86. Wang, R., Liu, S., Shangguan, D., Radić, V. & Zhang, Y. Spatial heterogeneity in glacier mass-balance sensitivity across High Mountain Asia. *Water* **11**, 776 (2019).
87. Sakai, A. & Fujita, K. Contrasting glacier responses to recent climate change in high-mountain Asia. *Sci. Rep.* **7**, 13717 (2017).
88. Untersteiner, N. Glacial-meteorological analyses in the Karakoram (in German with English abstract). *Arch. Meteorol. Geophys. Bioklimatol. Ser. B* **8**, 1–30 (1957).
89. Mihalcea, C. et al. Ice ablation and meteorological conditions on the debris-covered area of Baltoro glacier, Karakoram, Pakistan. *Ann. Glaciol.* **43**, 292–300 (2006).
90. Bonekamp, P. N., de Kok, R. J., Collier, E. & Immerzel, W. W. Contrasting meteorological drivers of the glacier mass balance between the Karakoram and central Himalaya. *Front. Earth Sci.* **7**, 107 (2019).
91. Hewitt, K. *Glaciers of the Karakoram Himalaya* (Springer, 2014).
92. *ERA5: Fifth Generation of ECMWF Atmospheric Reanalyses of the Global Climate* (Copernicus Climate Change Service, 2017); https://cds.climate.copernicus.eu/cdsapp#!/home
93. Shea, J. M., Immerzeel, W. W., Wagnon, P., Vincent, C. & Bajracharya, S. Modelling glacier change in the Everest region, Nepal Himalaya. *Cryosphere* **9**, 1105–1128 (2015).
94. Benn, D. I., Fowler, A. C., Hewitt, I. & Sevestre, H. A general theory of glacier surges. *J. Glaciol.* **65**, 701–716 (2019).
95. Kääb, A. et al. Massive collapse of two glaciers in western Tibet in 2016 after surge-like instability. *Nat. Geosci.* **11**, 114–120 (2018).
96. Gilbert, A. et al. Mechanisms leading to the 2016 giant twin glacier collapses, Aru Range, Tibet. *Cryosphere* **12**, 2883–2900 (2018).
97. Dimri, A. P., Kumar, D., Choudhary, A. & Maharana, P. Future changes over the Himalayas: mean temperature. *Glob. Planet. Change* **162**, 235–251 (2018).
98. Kraaijenbrink, P., Lutz, A., Bierkens, M. & Immerzeel, W. Impact of a global temperature rise of 1.5 degrees Celsius on Asia's glaciers. *Nature* **549**, 257–260 (2017).
99. Quincey, D. et al. The changing water cycle: the need for an integrated assessment of the resilience to changes in water supply in High-Mountain Asia. *WIREs Water* **5**, e1258 (2018).
100. Dee, D. et al. The ERA-Interim reanalysis: configuration and performance of the data assimilation system. *Q. J. R. Meteorol. Soc.* **137**, 553–597 (2011).
101. Kumar, P. et al. Response of Karakoram-Himalayan glaciers to climate variability and climatic change: a regional climate model assessment. *Geophys. Res. Lett.* **42**, 1818–1825 (2015).
102. Benn, D. I. et al. Response of debris-covered glaciers in the Mount Everest region to recent warming, and implications for outburst flood hazards. *Earth Sci. Rev.* **114**, 156–174 (2012).
103. Anderson, L. S. & Anderson, R. S. Modeling debris-covered glaciers: response to steady debris deposition. *Cryosphere* **10**, 1105–1124 (2016).
104. Harrison, W. D. & Post, A. S. How much do we really know about glacier surging? *Ann. Glaciol.* **36**, 1–6 (2003).

Methods

The trend analyses displayed in Fig. 3 are based on the ERA5 climate reanalysis dataset[92]. ERA5 provides global-scale meteorological information at a horizontal resolution of ~31 km for the period 1979 to present. The information stems from an ensemble of ten model members, for which we consider only the ensemble mean (the ERA5 standard product). Trends were calculated independently for each grid cell through linear fitting of the accumulated annual or summer values.

Data availability

The data shown in the individual figures are available in the publications cited.

Code availability

The code used to produce Figs. 2 and 3 is available from the corresponding author on request.

Acknowledgements

We thank F. Brun for providing the data underlying Fig. 2 and Supplementary Fig. 1, and J. Norris for providing the data for Supplementary Fig. 3.

Author contributions

D.F. initiated the study, designed the figures and led the writing, to which all authors contributed. W.W.I. and D.Q. provided materials for Fig. 1 and Box 1. A.D. provided materials for Figs. 1 and 2. The analyses shown in Fig. 3 and Supplementary Figs. 2 and 3 were performed by R.d.K. R.d.K. and W.W.I. conceived Fig. 4, with additions from A.D., D.F. and D.Q.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41561-019-0513-5.

Correspondence should be addressed to D.F.

Peer review information Primary Handling Editor: Heike Langenberg.