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Long-term change in stream diatom assemblages in the Nepalese Himalaya

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Abstract Mountain ecosystems are sensitive to global change, but long-term data assessing effects for running waters are scarce. We, therefore, investigated changes in diatom diversity and assemblage composition using five surveys between 1992–2023 in streams across a 2345 m altitudinal gradient in the Himalaya. Taxon richness tended to decline at high altitudes while peaking in the later years of the study. Among 75 species found, most were cosmopolitan - including the most abundant species which occurred across altitude. *Navicula nielsfogedii* and *Gomphosinica chubichuensis* had restricted distributions geographically and altitudinally and are potentially indicators of warming. The former increased through time at lower altitudes while the latter was restricted to the highest altitudes where it had declined by 2023. *Gllvm models* suggested that time, season and altitude affected abundance and assemblage composition. Few species were more abundant at higher or lower altitudes, while many had wide altitudinal ranges and equal prevalence between seasons. Composition, nevertheless, changed with increasing altitude reflecting changes in vegetation cover and stream chemistry and occurred through taxonomic turnover rather than nestedness. Compositional changes through time in both seasons were observed in most streams but were least pronounced above 3500 m except in a glacier-fed stream.

Keywords Climate change, streams, diatoms, mountains, Himalaya, Nepal

Statements and Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

65 **Introduction**

66 Climate change has pronounced effects on high altitude regions. In the Himalayan
67 mountains, for example, warming has been greater than the global average (Singh et
68 al., 2016; Negi et al., 2021) with mean temperature projected to increase by up to 5.8
69 °C over the next century (Bajracharya et al., 2007). Negative impacts on the water
70 cycle, increasing hazards such as glacier lake outbursts, avalanches, floods, and
71 constraints on water availability will affect the entire region (IPCC, 2022). Even small
72 changes in the Himalayan climate will affect aquatic ecosystems and lead to
73 biodiversity losses, threatening ecosystem function and impact the delivery of
74 resources – potentially interacting with uneven distribution of water resources and
75 growing resource demands, and affecting many millions of people in down-stream
76 areas (Eriksson et al., 2009; Kattel 2022). Local communities in high mountain
77 valleys already experience changes related to a warming climate including receding
78 and thinning glaciers, changing patterns in precipitation and temperature (Tuladhar et
79 al., 2021), and upward shifts in plant distributions (Lamsal et al., 2017a).

80 Climate change affects all biological communities including microbial and algal
81 communities in surface water, groundwater and terrestrial ecosystems (Retter et al.,
82 2021; Parray et al., 2022). In sub-arctic, arctic and alpine freshwaters, warming and
83 glacial retreat have affected the structure and function of microbial communities
84 (Wilhelm et al., 2013), diatoms (Smol et al., 2005; Thies et al., 2013; Fell et al., 2018)
85 and invertebrates (Cauvy-Fraunié et al., 2016; Khamis et al., 2016; Niedrist & Füreder
86 2018; Jacobsen et al., 2024; see also review by Slemmons et al., 2013). In the
87 Himalaya, climatic effects on freshwater biodiversity and species distribution are
88 expected across the large altitudinal gradient as a result of changes in hydrological
89 conditions, stream habitat character and catchment vegetation (Hotaling et al., 2017;
90 Sharma et al., 2022). Modeling of river invertebrates, including in the Langtang
91 Valley in Nepal, has predicted range-shifts along the altitudinal gradient, with an
92 increase in warm-adapted and a loss in cold-adapted species (Li et al., 2016). In lakes
93 of the Indian Himalaya, lake phytoplankton and macrophyte diversity has declined
94 (Jeelani et al., 2008) while diatom sediment records have changed concurrently with
95 global warming (Diwate et al., 2024).

96 Diatoms are important components of benthic communities and food webs in
97 freshwater systems. This is especially the case at high altitude and latitude where
98 harsh environmental conditions include low temperatures, reduced nutrient
99 availability, distinct seasonal change, ice cover, highly variable flows and unstable

stream substrata (Jüttner et al., 2010; Clitherow et al., 2013). These same pristine, cold freshwaters in mountain headwaters often support unique assemblages and rare species (Taxböck et al., 2017; Jyrkänkallio-Mikkola et al., 2018). Warming effects on these refugia, therefore, pose risks to cool stenothermal diatoms from range contraction and eventual extinction (Bahls, 2017). Simulating climate change effects on different river types predicted a homogenization of assemblages (Tornés et al., 2022), and studies in the Arctic and the European Alps showed that climate warming had already altered current assemblages (Kahlert et al., 2020; Kuefner et al., 2020).

Moreover, altitude is a determining factor structuring mountain diatom assemblages (He et al., 2020; Kim & Lee, 2017) due to strong environmental gradients (pH, conductivity, nutrient concentrations, flow, substratum, catchment vegetation) which determine species distribution, and turnover in metacommunities is strongly influenced by environmental filtering (Kurthen et al., 2020). Any climate-mediated effects on temperature or discharge at particular altitudes could therefore affect diatom distribution in both lotic and lentic environments. Stream diatoms are known to be effective predictors of climatic conditions (Pajunen et al., 2015, 2016) while richness and abundance are determined by a covariance of climate and water chemistry (Passy et al., 2018). In a global dataset, diatom assemblage composition was significantly related to annual temperature (Soininen et al., 2016). Similarly in lakes, surface water temperature was a significant factor in addition to gradients in water chemistry in explaining species distribution (Weckström et al., 1997). Weckström et al. (2006) used high-resolution sediment diatom records to document short-term temperature variability over multiple centuries and Lotter et al. (1997) developed lake-temperature models for different biota, including diatoms, and showed that a temperature effect is independent of other factors.

Alongside global warming, freshwater biodiversity in the Himalaya is affected by other pressures including demand for resources and pollution. These changes are exemplified in the Langtang Valley, Langtang National Park, Nepal. Major environmental issues affecting the Park biodiversity include warming, changes in catchment character resulting in forest fires during the dry season, degradation of high altitude habitats, resource exploitation by local people and pressures from tourism (LNP, 2020). The Park's terrestrial vegetation is already changing with a significant increase in the Normalized Difference Vegetation Index (NDVI) at the treeline ecotone found between 2000–2017 and 16.45% of its area greening, suggesting an upslope vegetational shift as predicted for the wider Himalayan region (Lamsal et al.,

2017b; Baniya et al., 2021). Mean annual temperatures have risen while the numbers of cold days per year and average annual river flow between 1993–2006 have declined (Gautam, 2014). Temperatures and precipitation, particularly rainfall, are projected to increase further and contribute to snow and ice melt while the Park’s glaciated area is predicted to decline by 32% by 2035. River flows are projected to rise due to increasing rain runoff and base flow while glacier runoff will eventually decrease as glaciers retreat (Immerzeel et al., 2012). This will alter stream temperature, increase flow velocity and reduce stream bed stability with likely impacts on altitudinal species distributions, colonization and growth of benthic algae (Biggs et al., 1998; Yang et al., 2025).

Despite these ongoing environmental changes, long-term studies of the impacts are rare both locally in the Langtang National Park and more generally across the Himalayan mountains (Bartwal & Nautiyal, 2025). We, therefore, designed this study as the first study of its type to (i) assess long-term changes in stream diatoms due to warming in the Himalayan region and (ii) assess long-term change in two different seasons and across a large altitudinal gradient. Specifically, we investigated how diatoms in thirteen streams changed over a 31year period between 1992 and 2023 across an altitudinal range of 2345 m in two seasons. We tested whether warming affected assemblages across the entirety of this large altitudinal gradient, and in particular, whether species distribution, assemblage composition and diversity changed (1) over time in both autumn and spring, (2) between autumn and spring in two consecutive years, and (3) across altitude in autumn and spring.

Methods and Materials

Study area

The high mountain Langtang Valley is in the 1710 km² Langtang National Park of the Nepalese Himalaya, an area established as Nepal’s first high mountain National Park in 1976. Located at the meeting point between the Eastern and Western Himalayan Biotic Provenance, it is home to a large number of rare and threatened plants including endemic species, and has a wide range of vegetation types across a large altitudinal gradient. It is located c. 80 km north of the capital Kathmandu in the Gosaikunda Rural Municipality of the Rasuwa district and borders the Tibet Autonomous Region (TAR) of China in the north. The 13 streams investigated are tributaries to the Langtang River fed by the Langtang Glacier at 4500 m a.s.l. It joins

the Trisuli River at 1400 m a.s.l., itself a major tributary of the Gandaki River and eventually the Ganges. The study sites were located across an altitudinal range of 2345 m, between 1465-3810 m a.s.l. (Fig.1). The type and cover of vegetation changes considerably with altitude with subtropical montane broadleaf woodlands dominating < 2000 m, changing to montane conifer forests at mid altitudes, and to sub-alpine dwarf shrub and grassland, and alpine tundra at the highest altitudes. A considerable portion of the catchment at higher altitudes is alpine tundra and glaciated, with glaciers and permafrost covering 46 km² of the valley (Bajracharya et al., 2014). The region has a pronounced monsoon climate with a warm rainy season from June – September, and a dry season from October – April. Human settlements in the National Park are limited to a few small settlements with cultivated land, which has not significantly changed over time. Crops are restricted to small areas used for barley, buckwheat and potatoes and there is a small number of livestock (Tuladhar et al., 2021). The area is heavily dependent on tourism and large number of visitors, including an increasing number of domestic tourists in recent years, arrive during the main trekking seasons in the autumn and spring.

Fourteen streams in the Langtang Valley were first investigated for diatoms in November 1992 (post-monsoon, Ormerod et al., 1994), and in April 1993 (pre-monsoon, Jüttner unpubl. data), and in November 2000 (Jüttner et al., 2010a; site labels ‘Helan’). To assess long-term change in diatom assemblages across altitude and in two seasons, thirteen of the fourteen streams were reinvestigated in November 2022 and in April 2023, with the site labels used in Ormerod et al. (1994). T7 was not studied recently as it had dried up, and T10 and C33 were only studied in autumn 2022 because they had dried up in spring 2023.

Field and laboratory procedures

Site locations were determined and found again during later surveys using maps, GPS and site descriptions. In each stream, diatoms were collected from ca. 10 pebble to cobble-sized stones in riffle sections using toothbrushes, scrapes combined in one sample per stream and preserved using alcohol. In the laboratory diatoms were processed using hot peroxide oxidation to remove organic cell content. Silica valves were mounted on permanent glass slides using Naphrax®. Assemblages were studied and a minimum of 500 valves were counted under light microscopy at 1000× magnification using a NIKON E600 microscope (DIC, 100× objective, N.A. 1.40). To ensure consistency in identification across time, all samples were reinvestigated.

Diatoms were identified to species level using Jüttner et al. (2000, 2004, 2010b, 2017) Kociolek et al. (2015), and Lange-Bertalot et al. (2017), following nomenclature in Guiry & Guiry (2026), and using <https://www.ipni.org/> for the names of species authorities. Relative abundances were calculated prior to statistical analysis. The diatom slides are kept in the diatom collections of Amgueddfa Cymru – Museum Wales, Cardiff, UK (NMW), the Natural History Museum, London, UK (BM), and at Kathmandu University, Department of Environmental Science, Dhulikhel, Nepal. Field measurements (pH, conductivity) were carried out using portable meters (LUTRON) and water samples were collected for analysis of ions, hardness and alkalinity following APHA (2012) protocols.

Data analysis

Catchment boundaries for each stream site were delineated using a digital elevation model (DEM, Copernicus Global Digital Elevation Model GLO-30, resolution of ~ 30 m, ESA 2021). For vegetation coverage, satellite imagery was used to determine the mean NDVI calculated from surface reflectance. In 1992, NDVI was calculated at 30 m resolution using a single Landsat 5 scene with minimal cloud cover from 21 September. There was greater cloud cover in 2023 and images and NDVI were calculated using a median mosaic of 8 scenes captured in September (for further details see Jacobsen et al., 2024 and references therein).

Changes in assemblage composition and the abundance of the 18 most common and abundant taxa were modelled using generalised linear latent variable models, using the *gllvm* package (Niku et al., 2019) in R version 4.5.1 (R Core Team, 2025). This approach allows inference at both the community and individual taxon level. Following Niku et al. (2019), we selected the number of latent variables by minimising the small-sample Akaike Information Criterion, settling upon two variables, and used a log-link function with negative binomial errors based on residuals from the model. The models were fitted with year, season and altitude as covariates, and the overall statistical significance of each of these tested using likelihood ratio tests, based on the analysis of deviance (Niku et al., 2019).

In addition, changes in assemblage composition over time and season were visualised using non-metric multi-dimensional scaling (NMDS) based on Bray-Curtis similarity after down-weighting of rare species (weight 0.1) and square-root transformation of relative abundance data. NMDS of sites based on environmental

measurements (altitude, vegetation cover, water chemistry) was carried out using Euclidean distance after normalising variables (PRIMER7, Clarke & Gorley, 2015).

We estimated the extent to which altitude could account for beta-diversity, and its turnover and nestedness components, among the sampling locations using R's *betapart* package (Baselga et al., 2023). Following Gutiérrez-Cánovas et al. (2013), we regressed matrices of overall beta-diversity, and its turnover and nestedness components (based on Sorensen dissimilarities, Simpson dissimilarities and the difference between the Sorensen and Simpson respectively), onto the altitudinal differences between sites using multiple regression on distance matrices from the *ecodist* package (Goslee & Urban, 2007; Lichstein, 2007). Taxon richness and Simpson's evenness were calculated in R (R Core Team, 2025).

Results

Species diversity, distribution across altitude, season and time

At all altitudes, taxon richness and evenness were highly variable between years. Although the overall difference across altitude was marginally significant ($p = 0.0557$), richness tended to be higher at low and mid altitudes (1465–2747 m) than at altitudes above 3000 m, and ranged overall between 14–26 species. There was no relationship between altitude and evenness (Fig. 2). Taxon richness and evenness were not significantly different between seasons and years. However, mean richness was higher in autumn 2022 and spring 2023 with the difference over time being larger in autumn than in spring (Fig. 3).

Seventy-five species were found during five surveys in autumn and spring between 1992–2023. Most species belonged to the Achnanthales, Fragilariales and Cymbellales, with *Fragilaria* Lyngb., *Gomphonema* Ehrenb. and *Achnanthidium* Kütz. being the most species rich genera, while species in the Naviculales, Bacillariales and Thalassiophysales were less numerous and often rare (Table 1, Guiry & Guiry 2026). Most species are known to have a cosmopolitan distribution, but some have a more restricted distribution, were described from the Himalayan region and occurred at a small number of sites. They include *Gomphonema incognitum* Reichardt, Jüttner & Cox (found regularly in 3 streams), *G. himalayaense* Jüttner and *G. nepalense* Reichardt, Jüttner & Cox (found regularly in 5 streams), *Gomphosinica chubichuensis* (I.Jüttner & E. J. Cox) Kociolek et al., (Fig. 4a) which only occurred

above 3200 m and dominated a glacier-fed stream during all autumn surveys, *Odontidium himalongissimum* Jüttner, D.M.Williams & E.J.Cox (rarely found at low abundance) and *O. longiovalum* Jüttner, D.M.Williams & E.J.Cox (abundant at one high-altitude stream but rarely found elsewhere; Jüttner et al., 2000; Jüttner et al., 2004, Jüttner et al., 2017, 2018). *Navicula nielsfogedii* J.C.Taylor & Cocquyt (Fig. 4b), known from the Himalaya and south-east Asia (Chudaev et al., 2020), was found mostly at the lowest altitudes (≤ 2519 m). Few cosmopolitan species were common in all streams. Those occurring across the entire altitudinal range included *Achnanthidium minutissimum* (Kützing) Czarnecki, *Achnanthidium* cf. *sibiricum* Kulikovskiy et al., *Odontidium mesodon* (Kützing) Kützing and *Hannaea arcus* var. *recta* (Cleve) M.Idei, the four most abundant taxa which often dominated assemblages, and *Reimeria sinuata* (Gregory) Kociolek & Stoermer and an unidentified *Eunotia* species.

Change in assemblage composition across altitude, over season and time

Generalized linear latent variable models showed that time ($D = 40.85$, $df = 18$, $p = 0.0016$), season ($D = 66.68$, $df = 18$, $p < 0.0001$) and altitude ($D = 135.26$, $df = 18$, $p < 0.0001$) appeared to affect species abundance and assemblage composition (Fig. 5). Only one species, *G. chubichuensis*, was restricted to high altitude streams, although *Encyonema brevicapitatum* Krammer, *Delicata delicatula* (Kützing) Krammer (mostly restricted to streams at 2500–3500 m), and *A. cf. sibiricum* were more abundant at higher altitudes. In contrast, *N. nielsfogedii*, *G. nepalense*, *Achnanthidium subhudsonis* (Hustedt) H.Kobayasi, *Adlafia bryophila* (J.B.Petersen) Lange-Bert. and *Gomphonema parvulum* (Kützing) Kützing were predominantly found at lower altitudes (Fig. 6).

While most species were equally prevalent during both seasons, some were more abundant in autumn or spring (Fig. 5). *Navicula nielsfogedii* typically occurred in the autumn and was rare in spring. Although *G. chubichuensis* was abundant in both seasons in a glacier-fed stream at the highest altitude (CC, 3810 m), it always dominated assemblages in autumn (59–89%) and, when present, was more abundant in autumn at two other high-altitude streams (C31, C33). *Hannaea arcus* var. *recta*, *G. parvulum* and *A. bryophila* were also more abundant during autumn. There was less evidence for species being more abundant in spring except for *A. minutissimum*. *Gomphonema nepalense* dominated in one stream during both spring surveys (43–62%, Fig. 6). Few species changed significantly over time. *Navicula nielsfogedii* and

an unidentified *Eunotia* species became more abundant while *A. subhudsonis* and *R. sinuata* declined (Fig. 5). *Cocconeis lineata* Ehrenberg declined at three streams $\geq$ 2747 m but increased at the lowest altitude (T1, 1456 m). *Encyonema brevicapitatum* and *Encyonema minutum* (Hilse) D.G.Mann declined over time in some but not in all streams. *Gomphosinica chubichuensis* dominated the glacier-fed stream at the highest altitude (CC, 3810 m) in all autumn surveys. Its abundance was $> 80\%$ in autumn 1992 and 2000 when the stream contained large amounts of ice but its abundance was lower (59%) in 2022 when the stream contained less ice. In spring when the stream was ice-free *G. chubichensis* was much less abundant (1993: 21%, 2023: 24%, Fig. 6). Similarity between sites in autumn 1992 and 2022 and in spring 1993 and 2023 was not correlated with altitude (Fig. 7).

Overall beta-diversity correlated with altitude, i.e. the greater the differences in altitude, the greater the difference in assemblage composition ($R^2 = 0.09$, $F = 192.36$, $p = 0.0001$). This was driven by a turnover of taxa ($R^2 = 0.08$, $F = 159.34$, $p = 0.0001$) rather than a pattern of nestedness ($R^2 < 0.01$, $F = 0.83$, $p = 0.69$). With some exceptions, streams at 1465–1660 m differed from those at mid altitudes due to the presence of taxa that occurred predominantly at low altitudes, while streams at mid altitudes (2044–3570 m) were characterized by taxa that were abundant across a wide altitudinal range and taxa that typically occurred at mid to high altitudes. Streams $\geq$ 3660 m were distinct due to the abundance of one high-altitude species, *G. chubichuensis*, and mid- to high-altitude species which occurred alongside those with a wide altitudinal range (Fig. 6). In autumn 2022, *A. minutissimum* and *A. cf. sibiricum* declined at the highest altitudes but increased at mid-altitudes (Fig. 6).

Across gradients of altitude and vegetation cover, measured in autumn 1992 and 2022, assemblages changed over time in both seasons (Figs 8a, b) but long-term change in assemblage composition varied between streams (Figs 9a, b). In autumn, assemblages changed clearly over time in six streams, with smaller changes observed in further three streams; in spring, assemblages changed in seven streams, with small changes observed in further two streams. Above 3500 m, long-term change was small or not observed except in spring at C31 (3790 m) and in both seasons at CC, the glacier-fed stream at the highest elevation. Long-term change was also small or not observed in a shaded woodland stream at low altitude (T2, 1660 m) and in a stream fed by a spring (C29, at 3663 m, Figs 9a, b).

Assemblage composition in relation to environmental factors

Environmental conditions changed across altitude, between seasons and over time (Figs 10, 11b, Appendix, Tables 1, 2). Vegetation cover decreased with altitude with catchment vegetation changing from subtropical broadleaf woodland at the lowest to alpine tundra at the highest altitudes. Between 1992 and 2022, NDVI increased over time in 12 of the 13 stream catchments. Stream chemistry, measured in 2022/23, changed with altitude and differed between seasons. Si concentrations decreased with altitude, and alkalinity, total hardness, Ca^{2+} , and NO_3^- concentrations were often larger at higher altitudes. Total hardness, alkalinity, Na^+ and NO_3^- concentrations were higher during spring. Environmental change correlated with change in diatom assemblage composition with altitude, Ca^{2+} , hardness, alkalinity, NDVI and Si being the most important variables (Fig. 11b). With few exceptions, assemblages differed between autumn and spring in 1992/93 and in 2022/23; at altitudes ≥ 3663 m assemblage were more dissimilar to those at mid-altitudes in 2022/23 than in 1992/93 (Fig. 11a, b). Taxa most strongly correlated with environmental change across altitude included *N. nielsfogedii*, *Gomphonema minutum* (C.Agardh) C.Agardh, *G. parvulum*, and *A. bryophila*, typical at the lowest altitude up to 2519 m, and *G. chubichuensis* and *O. mesodon* at high altitudes. Similarity between sites in autumn 1992 and 2022 was not correlated with 2022:1992 ratio in vegetation cover (Fig. 12).

Discussion

Taxonomic diversity and richness

Global warming changes diatom assemblages in both marine and freshwater habitats (Bopp et al., 2005; Rühland et al., 2015) due to increasing temperature and/or other factors including pH, nutrients, dissolved organic matter, hydrological and catchment changes that are ultimately controlled and altered by climate change (Anderson, 2000; Rantala et al., 2017). In Asia, diatoms are increasingly used to study environmental change and the impacts of warming in mountain areas (e.g. Li et al., 2021). Although assemblages at high altitudes in the Himalaya including those in the Langtang Valley contain many species with a wide geographical range, they are distinct from alpine regions elsewhere. Compared with diatoms in the European Alps, only 21% taxa were shared in Himalayan streams, because some species were restricted to the Himalaya while European species indicating severe anthropogenic impacts were absent (Cantonati et al., 2001). The eastern and western Himalayas are floristically distinct, also for diatoms, but with few exceptions species with regional distribution were not

abundant in streams of the Langtang Valley. Most taxa belonged to the Fragilariaceae, Achnanthidiaceae and Cymbellaceae, while taxa in the Naviculaceae and Bacillariaceae, typical in low-altitude habitats with higher nutrient concentrations, were rarer and less abundant. The most common and abundant species, including *A. minutissimum*, *A. cf. sibiricum*, *H. arcus* var. *recta*, and *O. mesodon*, have often been reported from mountain areas elsewhere in the world (e.g. Rimet et al., 2007; Kim & Lee, 2017; Pardhi et al., 2023 and references therein).

Some taxonomic revisions are required to adequately document the diatom flora in the Langtang Valley, and for this study several taxa remained unidentified or were treated as an aggregate. *Achnanthidium cf. sibiricum*, often more abundant at higher altitudes, is morphologically similar to *Achnanthidium sibiricum* Kulikovskiy, Lange-Bertalot, Witkowski & Khursevich described from Lake Baikal (Kulikovskiy et al., 2011), *Achnanthidium pseudopusillum* Genkal & Gabyshev described from northern Siberia (Genkal & Gabyshev, 2025), and *Achnanthidium nanum* (F.Meister) Novais & Jüttner (Novais et al., 2015) described from the European Alps. It is uncertain whether these species, all reported from clean, often cold, waters with low-medium conductivity, are distinct or whether they are conspecific. In the Langtang Valley streams, *A. cf. sibiricum* often co-occured with *A. minutissimum*. In the European Alps, *Achnanthidium lineare* W.Smith, a similar taxon, possibly conspecific with *A. cf. sibiricum*, was typical in streams of glaciated catchments and more sensitive to higher nutrient concentrations than *A. minutissimum* (Bert et al., 2024). The distribution of these taxa was similar in the Langtang Valley. Taxa in the genus *Hannaea* are widely distributed in the northern hemisphere with several species being described recently from mountain areas in Tibet, Mongolia and Tajikistan (Liu et al., 2019). *Hannaea arcus*, regarded as well adapted to high flow conditions, was an indicator species in streams located in areas with higher glacier cover in the European Alps (Bert et al., 2024). *Hannaea* is frequently found in the Himalaya but requires taxonomic revision. As recorded here, *H. arcus* var. *recta* may represent an aggregate of two taxa that could not consistently be separated with light or scanning electron microscopy, exhibiting high morphological variability within populations.

While cosmopolitan taxa dominated the Langtang Valley streams, two species with a regional distribution, *G. chubichensis* and *N. nielsfogedii* (Jüttner et al., 2000, 2017; Chudaev et al., 2020), were abundant. These are potentially good indicator species for climate change at high and low altitudes, respectively. *Gomphosinica chubichuensis* dominated in the glacier-fed stream at the highest altitude in autumn when large

amounts of ice were present in 1992 and 2000 but was less abundant when the amount of ice had declined in 2022 or the stream was ice-free during spring suggesting that it has a competitive advantage at low temperatures and during ice cover. Shrinking glaciers and meltwater influence produced lower beta-diversity in both diatoms and stream macroinvertebrates, due to reduced habitat heterogeneity and potential decline or extinction of endemic cold-water species (Brown et al., 2007; Fell et al., 2018). In the western United States, a number of cold-water stenothermal diatom taxa, some of which are endemics or alpine species with disjunct populations, are predicted to be at risk of extinction due to continued rise in temperature (Bahls, 2018).

Cold-stenothermic species confined to rivers with high percentage of glacier cover might decline because of increasing geographical and genetic isolation. Glacier shrinkage, reduced glacier stream connectivity and loss in cold-water habitats will likely reduce habitat variability and beta-diversity with lower species turnover between high-altitude freshwater habitats. In addition, dispersal limitation and a lack of suitable species pools nearby constrain colonization, particularly in mountain areas (Brederveld et al., 2011). Species of *Gomphosinica* could be at risk since all currently known species occur in high-altitude, mountainous regions including *Gomphosinica chubichuensis*, first described as *Gomphonema chubichuensis* Jüttner & Cox from the high-altitude stream (CC) in the Langtang Valley (Jüttner et al., 2000). Seven new species of *Gomphosinica* have been described from high altitude areas in China (Kunlun Mountains, Xinjiang Province) and the USA (Glacier National Park, Montana), and a new combination, *Gomphosinica hedinii* (Hustedt) Kociolek, You, Wang & Liu, is a species originally described from Southern Tibet (Kociolek et al., 2015). More recently, four more species in this genus have been described from other high-altitude areas in Yunnan Province and Tibet, China (Cheng et al., 2018; Yang et al., 2019; Xie et al., 2025). In a study of 206 streams between 1994–2000 in the Himalaya of Nepal and India, *G. chubichuensis* was only abundant in streams between 2500–4000 m altitude (Jüttner et al., 2010). A change in the altitudinal range and frequency of occurrence of this species in the region might indicate changing conditions in high altitude freshwater habitats due to warming. At low altitudes warming could be indicated by abundance changes in *N. nielsfogedii*. In the Langtang Valley streams, this taxon was typical at altitudes ≤ 2561 m in the autumn, similar to its distribution in the wider Himalayan region where it frequently occurred between 200–1700 m (Jüttner et al., 2010). More recently, this species became more abundant in 2000 and 2022 than in 1992. *Navicula nielsfogedii* has a wider regional distribution

and occurs at altitudes between 12–1625 m in Southeast Asia (Chudaev et al., 2020). In a sediment record spanning the last 100 years from the low-altitude Douhu Lake in China, a species identified as *Navicula heimansioides* Lange-Bertalot has increased since 1985, with this change believed to be caused by warming (Li et al., 2019). *Navicula heimansioides* and *N. nielsfogedii* are similar and the latter was previously misidentified as *N. heimansioides* (Jüttner et al., 2010; Chudaev et al., 2020). It is therefore possible that the *Navicula* from Douhu lake actually represents *N. nielsfogedii*, and its recent increase would confirm that the species indicates warming in the respective habitats.

Species varied in their elevational range. While *G. chubichuensis*, adapted to specific conditions at high altitudes, had a small elevational range, most high altitude species have a wide elevational range, while species that prefer lower altitudes were abundant across a smaller elevational range. Based on our limited dataset, which lacked streams < 1465 m, this appears to confirm Rapoport's elevational rule that postulates larger elevational ranges in high altitude species which tolerate the highly variable conditions at higher altitudes (Stevens, 1992). A detailed analysis of range-elevation relations for Himalayan diatoms is not available but previous observations suggest a lack of a consistent pattern. Some species occurred over the entire altitude range, while others were confined to low, mid or high altitudes (Jüttner et al., 2010). Teittinen et al. (2016) found no relationship between altitude range and altitude for diatoms in subarctic streams. For vascular plants in Nepal, tropical species supported Rapoport's rule (when boundary effects were controlled for), while temperate species did not (Feng et al., 2016), and, in Taiwan, responses varied between plant groups (Zhang et al., 2010).

Patterns in diatom diversity varied across studies, with richness declining or increasing with altitude, peaking at mid-altitudes, showing no or a clear elevational trend, with local environmental factors being more important than altitude in, or jointly, determining taxa distribution (Teittinen et al., 2016; He et al., 2019; Sahin & Barinova, 2022). Overall, change in diatom richness in the Langtang Valley was not formally significant across altitude but was often higher at lower altitudes and sites with elevated Si concentrations reflecting observations elsewhere in the Himalaya (Jüttner et al., 2010), while richness at the high altitudes tended to be lower, similar to observations in alpine streams elsewhere (Bert et al., 2024). At high altitudes and in glaciated catchments, low temperature, turbidity, variability in flow and ice-cover can limit algal growth and reduce diversity (Hieber et al., 2001). In the European Alps,

taxonomic richness, the number of Red List diatom taxa, and Shannon diversity increased with decrease in glacier cover, while nestedness declined (Fell et al., 2018). Richness of marine phytobenthos in Sweden did not increase across a temperature gradient between 0.6–9.3 °C (Hillebrand et al., 2010). In the Himalaya, richness did not increase significantly over time, but mean richness was higher in 2022 and 2023. Macroinvertebrate richness increased over time in the same streams with the largest relative increase at the two highest altitude streams. Additional macroinvertebrate families were found in 2022 but, in contrast, no additional diatom taxa were found over time. Over time in both seasons, there was no correlation between diatom assemblage similarity and altitude, or with difference in vegetation cover, nor was there any pronounced effect on macroinvertebrate richness between 2900–3500 m (Jacobsen et al., 2024), suggesting that restricting monitoring to a single climate sensitive zone (CSZ, Shah et al., 2015) might be insufficient in the Langtang Valley.

Assemblage change across altitude, season and time

Diatom assemblage composition reflects geology and gradients in hydrochemistry, habitat and catchment characteristics that vary across altitude and regions (Rimet et al., 2007; Jüttner et al., 2010; Muñoz-López & Rivera-Rondón, 2022). Continued warming will lead to a significant change in the cryosphere at high altitudes. Changes in thermal and chemical conditions, organic and suspended matter, turbidity, streambed stability and hydrology, including increased groundwater contribution, will affect biological communities (Brown et al., 2007; Brighenti et al., 2019). Diatom beta-diversity in the Langtang Valley correlated with altitude and was due to a turnover of taxa. Nestedness did not contribute significantly in contrast to phytoplankton beta-diversity in a high-elevation river catchment in Tibet where nestedness was important particularly at sites with harsh environmental conditions at the highest (temperature) and lowest (salinity) altitudes (Jia et al., 2024). With rising temperatures species from lower elevations might expand upwards and initially replace species at mid altitudes. With few exceptions assemblages in the Langtang Valley became more dissimilar over time at altitudes up to 3458 m. Some species with a wide altitudinal range (*R. sinuata*, *A. subhudsonis*) became less abundant over time and in autumn, were replaced by the low-altitude species *N. nielsfogedii*. At higher altitudes assemblages have changed little except in the glacier-fed stream (CC). High-altitude assemblages tended to be less diverse and were most distinct. Similar pattern were found in both subarctic and tropical streams where assemblage similarity

decreased significantly with elevational distance, headwater streams were highly unique and had high species turnover, but were also less diverse than higher order streams (Teittinen et al., 2016; Jyrkänkallio-Mikkola et al., 2018). A clear change in assemblages in the glacier-fed stream in the Langtang Valley indicates that glacial cold-water habitats might currently be more affected by warming due to retreating glaciers. Homogenisation of alpine streams will lead to a decline of uniquely adapted species (Cauvy-Fraunié & Dangles, 2019). Habitat heterogeneity is important for maintaining a high regional diversity and ecologically unique communities, and emphasizes the need to focus conservation and monitoring on high-altitude freshwaters (Robinson & Kawecka, 2005; Benito et al., 2020).

In the Langtang Valley, streams at mid-altitudes differed from those at higher and lower elevations due to species loss of high and low-altitude species. While some taxa were more abundant at certain altitudes, only *G. chubichuensis* was restricted to a narrow range at high altitudes resulting in specialised assemblages as reported from glaciated catchments elsewhere (Kochoska et al., 2025). Many species were abundant across a wide altitude range. This is in contrast to the Clementsian and Quasi-Clementsian metacommunity structuring found in streams of the Cangshan Mountain, Yunnan, China, suggesting that groups of species in the assemblages responded in a similar way to changes in the environment with niche-based grouped species sorting and species pools replacing each other (Presley et al., 2010; Kurthen et al., 2020). There is evidence of diatom response to warming elsewhere. Many lake studies showed a significant shift in assemblages linked to global warming (Rühland et al., 2008). For example, Sorvari et al. (2002) found that assemblage composition and richness changed in remote high latitude lakes in Finland and correlated with a change in spring temperature reflecting post-19th century Arctic warming. In marine phytobenthos, Hillebrand et al., (2010) found a significant increase in species turnover, altered species composition and indicator species with increasing temperature. In mountain streams in Spain, assemblages differed slightly between two time periods (2003-2008/2016-2020) but not significantly (González-Paz et al., 2021). Global warming will inevitably lead to changes in diatom species distribution with models predicting a large decline in cold-water taxa, an even larger increase in warm-water taxa, a significant increase in species richness, but a significant decline in beta-diversity (Pound et al., 2020).

Conclusions

Changes in diatom assemblages in high altitude Himalayan streams across time, season and altitude suggest that diatoms responded to climatic warming and seasonal variation in temperature, and to altitudinal change in the environment such as gradients in water chemistry and vegetation cover. This was reflected by changes in species abundance with beta-diversity driven by a turnover of taxa rather than a pattern of nestedness. Diatom assemblage composition changed in most streams over time but long-term change was rarer at higher altitudes. A small number of taxa changed significantly in abundance over time, however, one species known from warmer stream habitats in the Himalaya increased in abundance and range at lower altitudes, and a species typical at high altitudes became less abundant when ice cover declined in a glacier-fed stream. The diatom collections at Amgueddfa Cymru – Museum Wales, Cardiff, the Natural History Museum, London, UK, and at Kathmandu University, Nepal, contain many samples collected from a variety of freshwater habitats in Nepal during the last 30 years and across large altitude gradients. These collections could be used in future studies to investigate further how warming has affected diatom assemblages in streams, lakes and springs in the Himalayan region.

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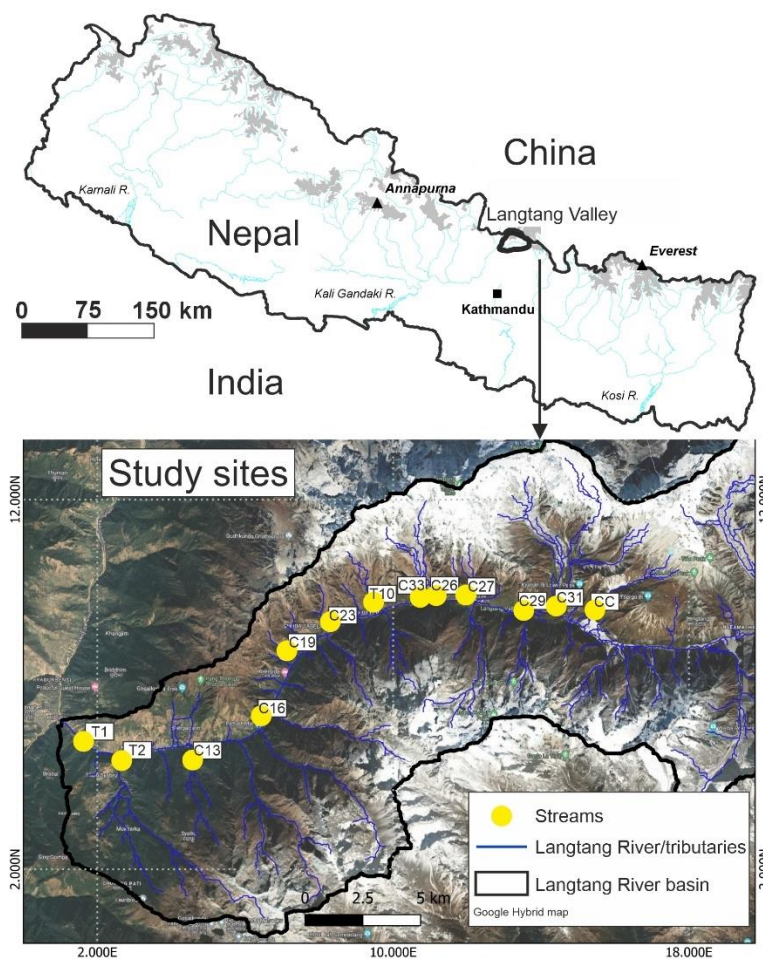
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Figures

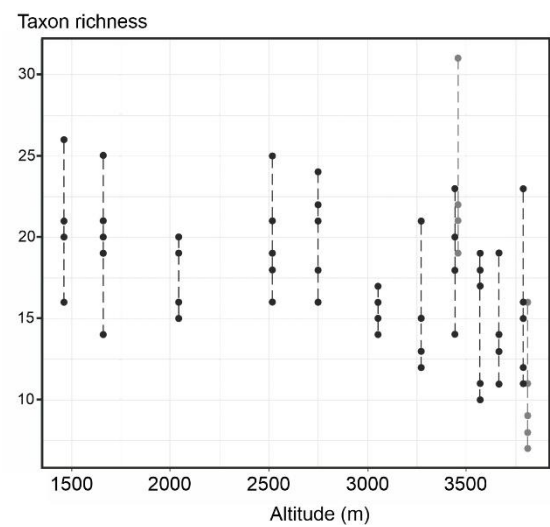
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Fig. 1.

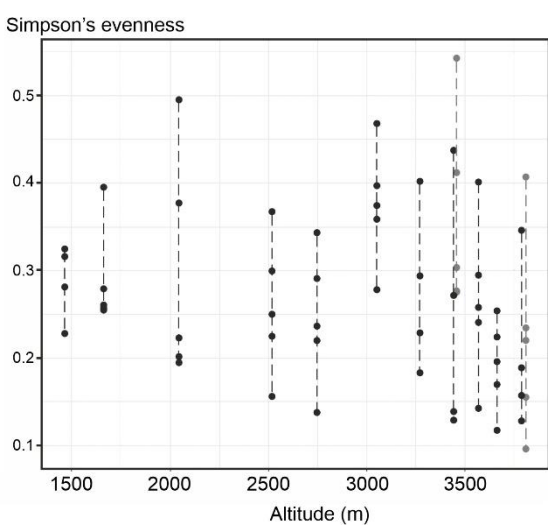


1107 Fig. 1. Study area: location of 13 streams, tributaries to the Langtang River, in the
1108 Langtang Valley, Langtang National Park, Nepal.

Fig. 2a.



b.



1109 Fig. 2. Variation in taxon richness (a) and Simpson's evenness (b) of diatom
1110 assemblages in 13 streams of the Langtang Valley, Nepal, across a 2345 m altitudinal

gradient. Dashes link values found during five surveys at the same sites. Grey is used to optically separate values found at sites located at similar altitudes.

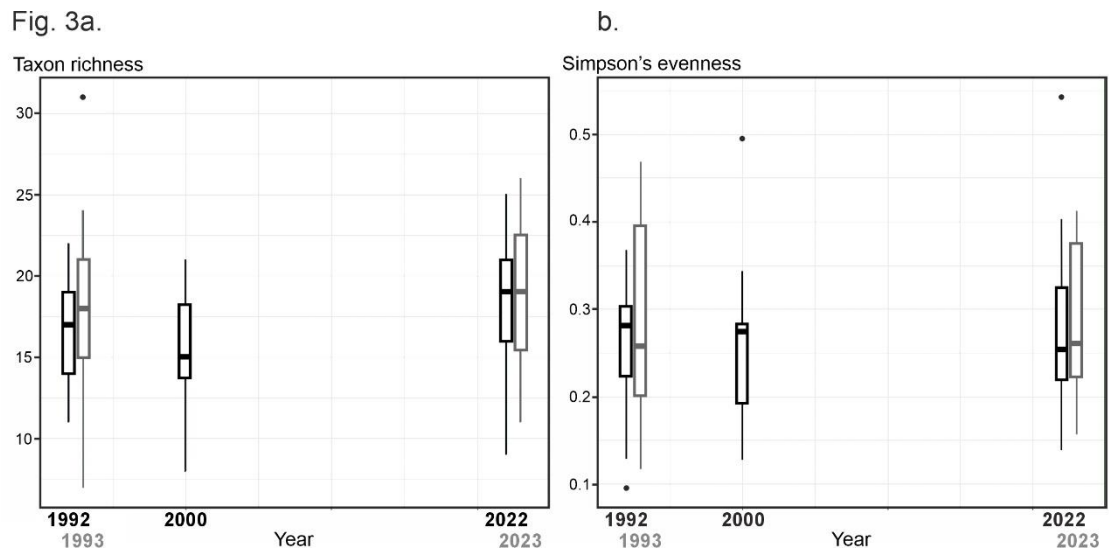


Fig. 3. Mean taxon richness (a) and Simpson's evenness (b) of diatom assemblages in 13 streams of the Langtang Valley, Nepal, in 1992, 1993, 2000, 2022 and 2023.

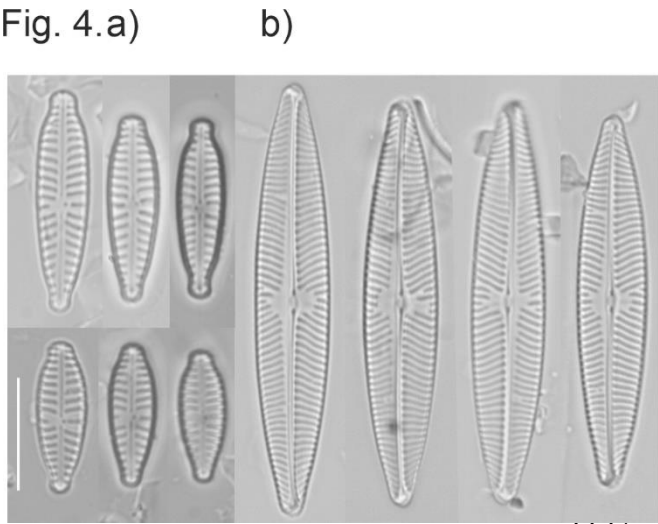


Fig. 4. *Gomphosinica chubichuensis* (a), *Navicula nielsfogedii* (b), scale bar = 10 μ m.

Fig. 5.

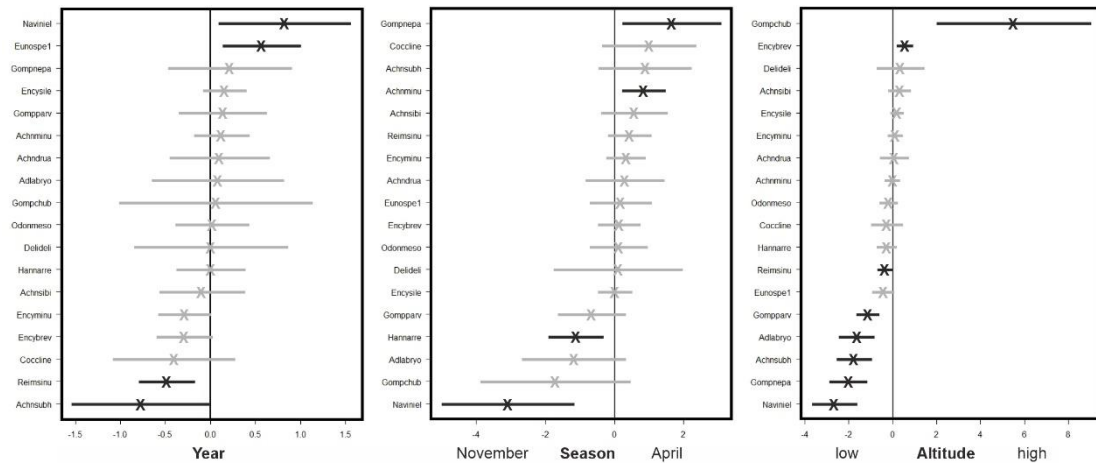


Fig. 5. Generalised linear latent variable models (GLLVM) using log link and negative binomial errors for 18 common diatom species in streams of the Langtang Valley, Nepal; coefficient estimates and confidence intervals indicating change in species abundance over time, season and altitude (black lines = significant change).

Fig.6.

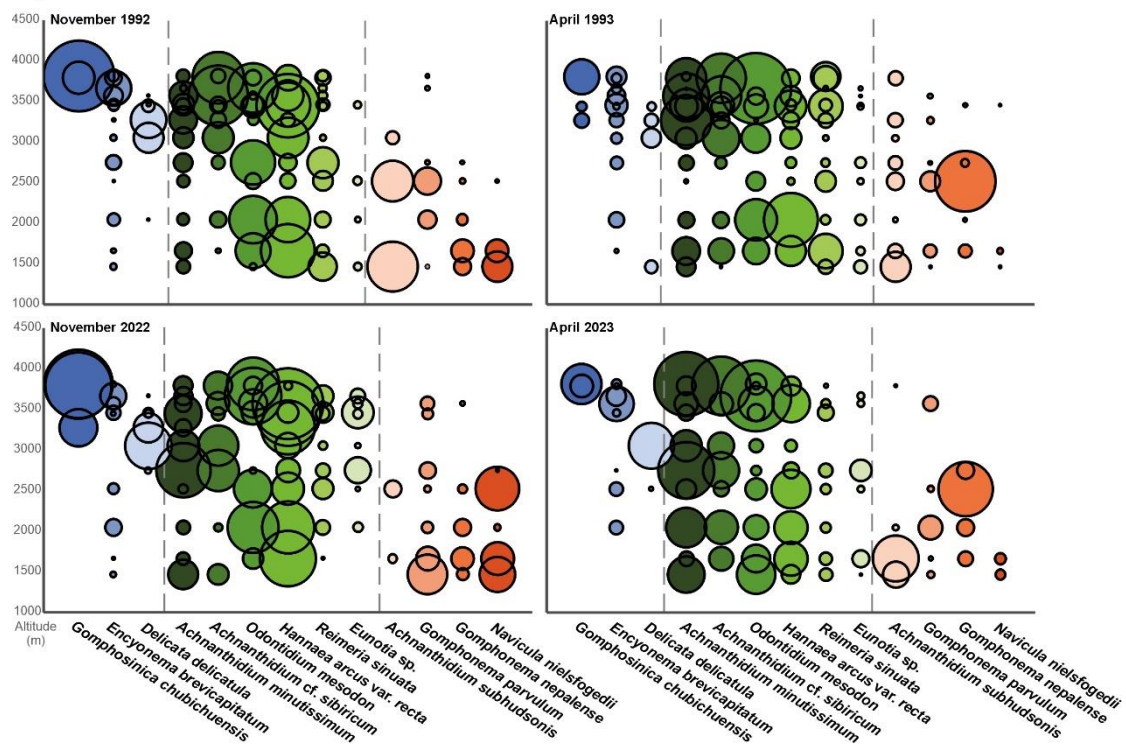
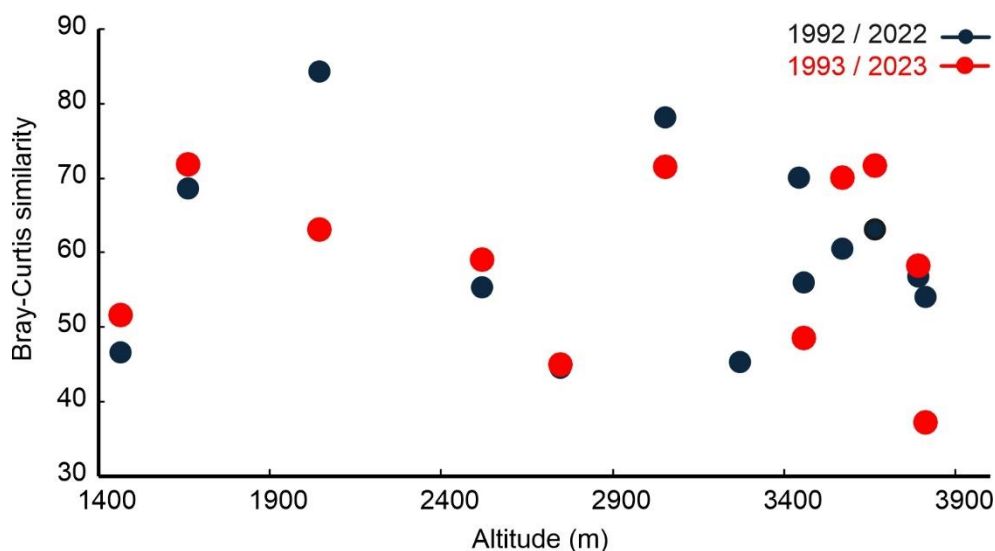


Fig. 6. Abundance of diatom species in 13 streams of the Langtang Valley, Nepal, across a 2345 m altitudinal range in autumn 1992 and 2022, and in spring 1993 and 2023.

1147 Fig. 7.

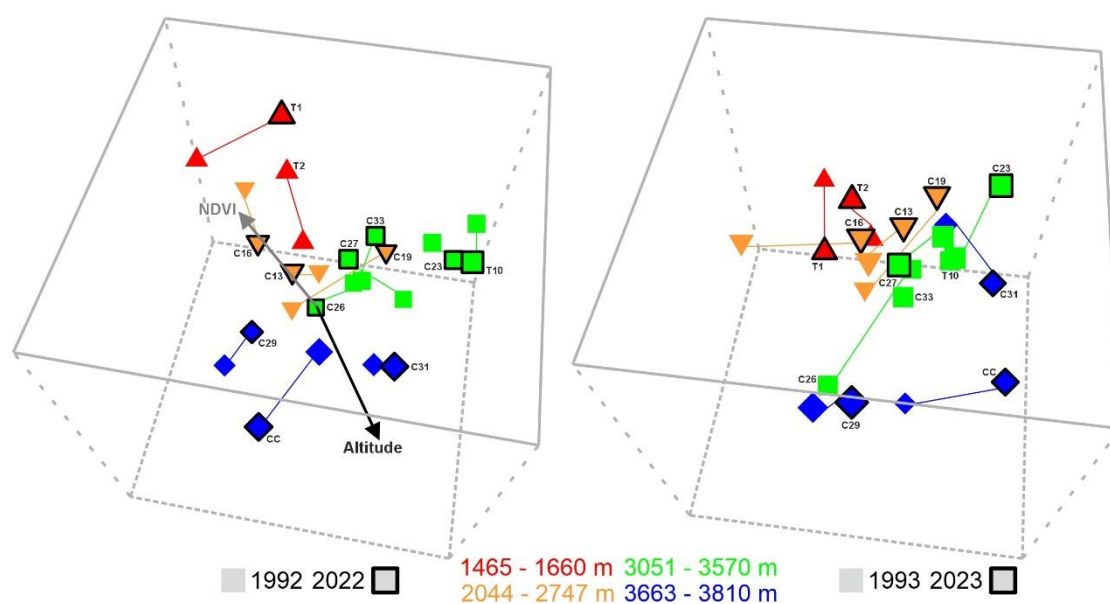


1148

1149 Fig. 7. Relationship between Bray-Curtis similarity of diatom assemblages over time
1150 and altitude.

1151 Fig. 8.
a)

b)



1152

1153 Fig. 8. Long-term change in diatom assemblages in 13 streams of the Langtang
1154 Valley, Nepal, a) autumn 1992, 2022 and overlay of environmental gradients in
1155 altitude and NDVI, NMDS, 3D stress: 0.1, b) spring 1993, 2023, NMDS, 3D stress:
1156 0.11.

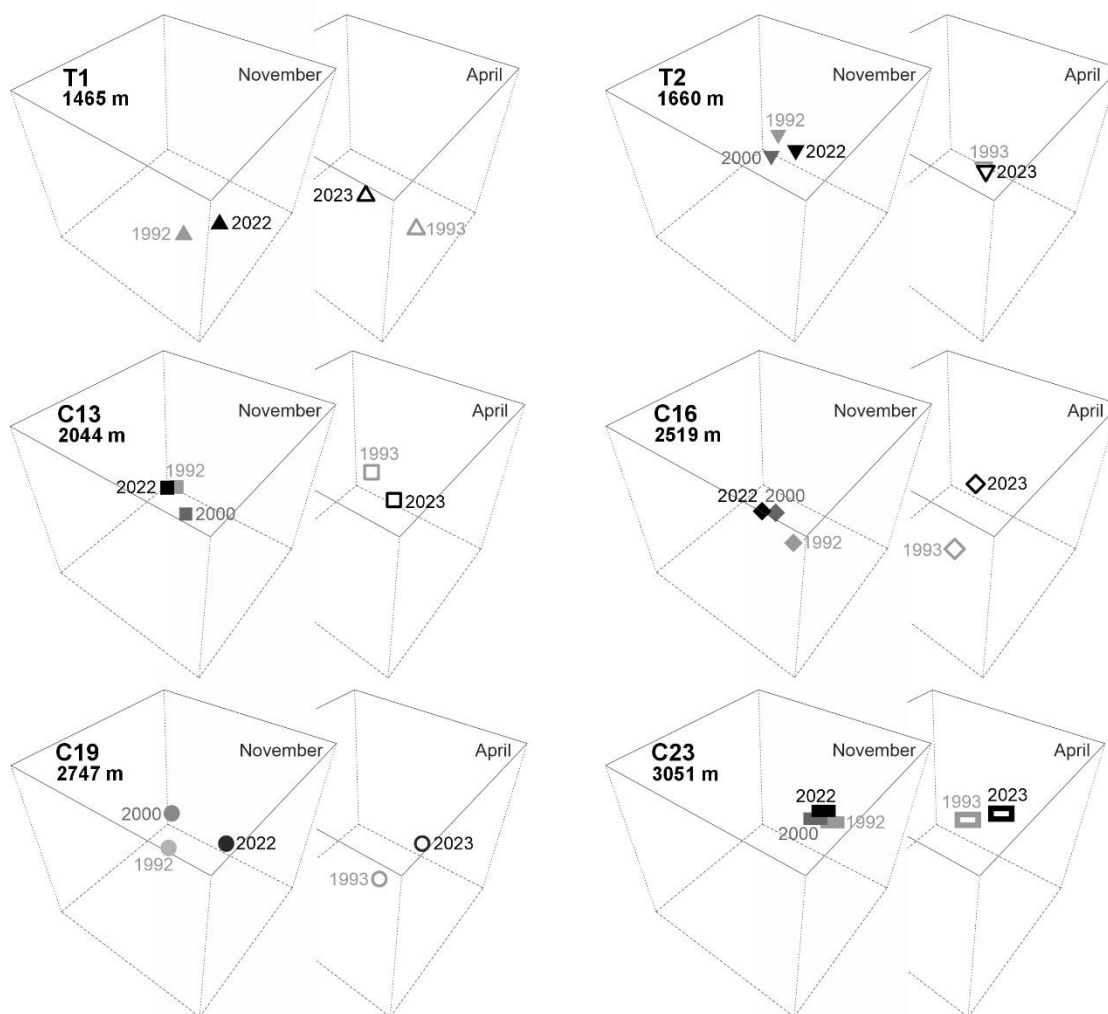
1157

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1160

Fig.9a.

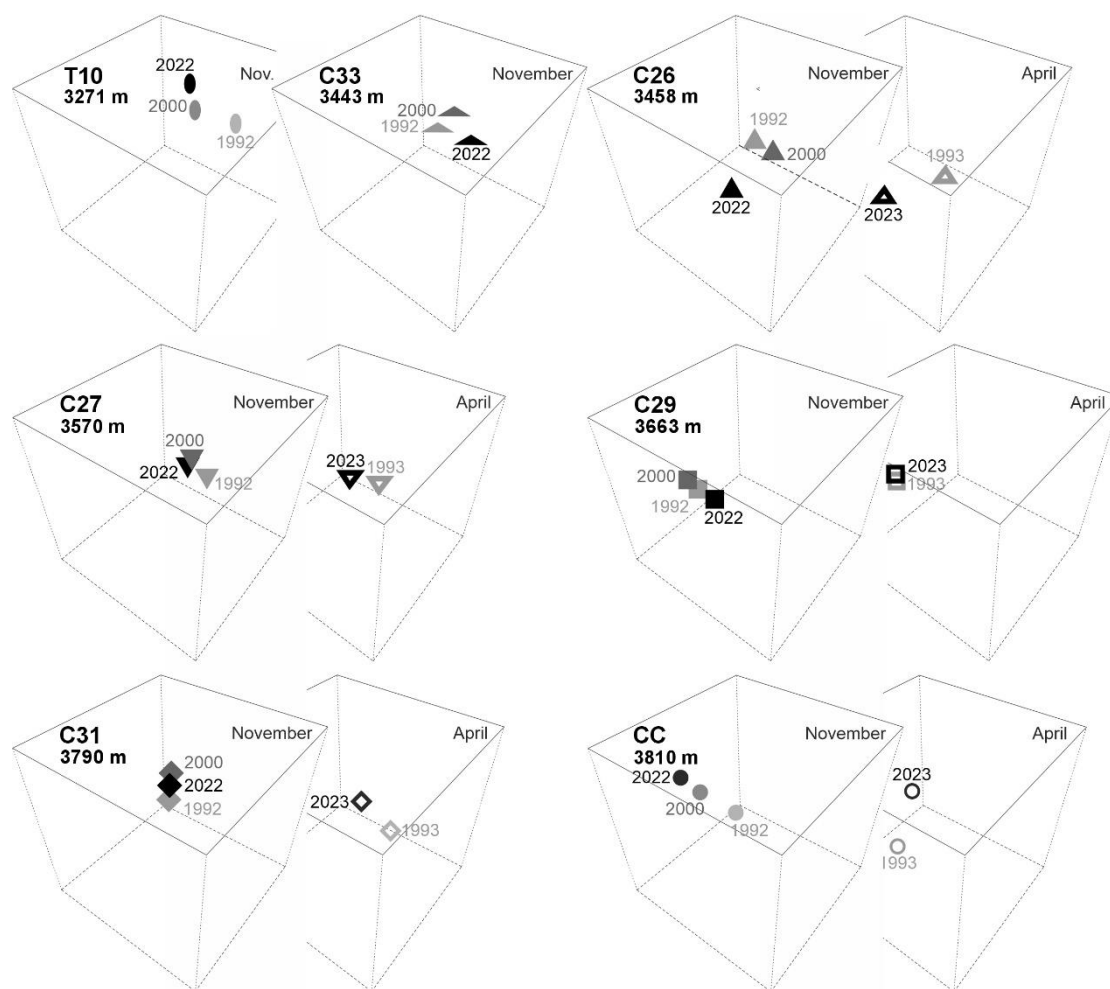


1161 Fig. 9a. Change in diatom assemblages in 13 streams of the Langtang Valley, Nepal,
 1162 each pair of graphs represents one stream with changes in assemblage composition
 1163 over time in autumn (left, 1992→2000→2022) and spring (right, 1993→2023),
 1164 streams located between 1465–3051 m a.s.l, NMDS, 3D stress: 0.13.

1165

1166

1167 Fig.9b.

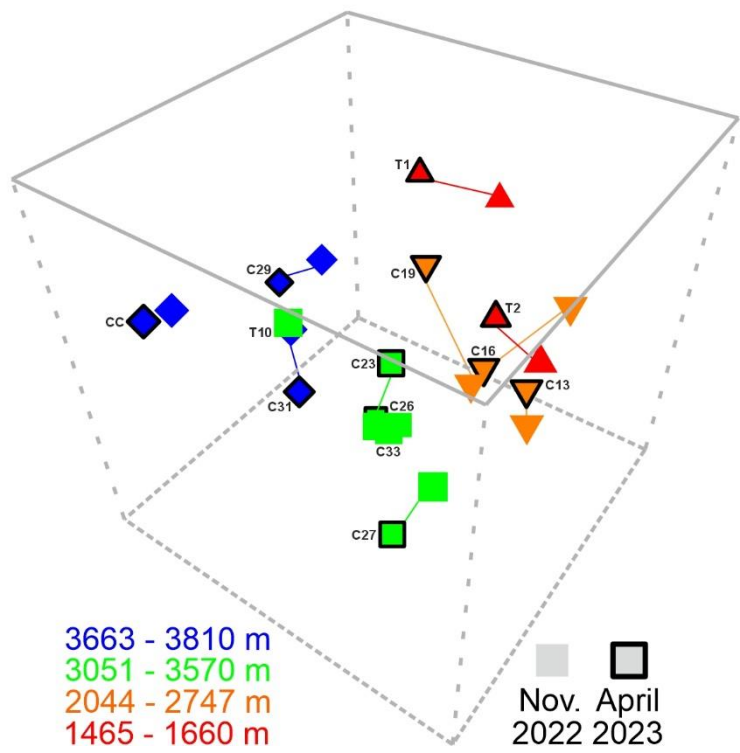


1168 Fig. 9b. Change in diatom assemblages in 13 streams of the Langtang Valley, Nepal,
 1169 each pair of graphs represents one stream with changes in assemblage composition
 1170 over time in autumn (left, 1992→2000→2022) and spring (right, 1993→2023),
 1171 streams located between 3271–3810 m a.s.l., NMDS, 3D stress: 0.13.

1172

1173

1174 Fig. 10.

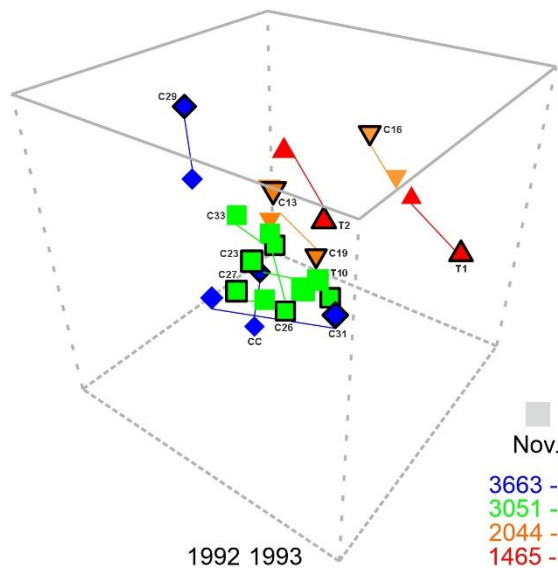


1175

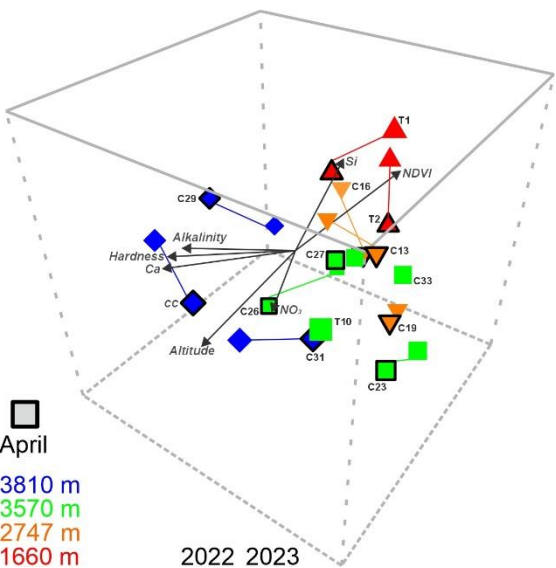
1176 Fig. 10. Seasonal change in environmental conditions across altitude in 13 streams of
1177 the Langtang Valley, Nepal, NMDS, 3D stress: 0.05.

1178

1179 Fig. 11.
a)



b)



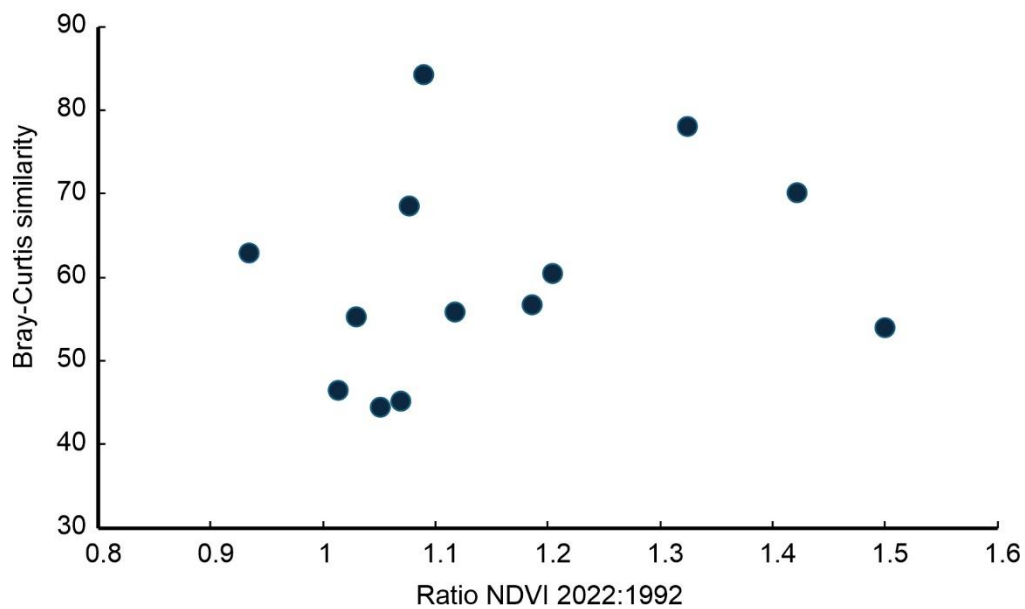
1180 Fig. 11a and b. Seasonal change in diatom assemblages across altitude in 13 streams
1181 of the Langtang Valley, Nepal; a) autumn 1992 and spring 1993, b) autumn 2022 and
1182 spring 2023 and overlay of environmental gradients in altitude, NDVI and water

1183 chemistry (Si [dissolved], alkalinity [as CaCO₃], total hardness [as CaCO₃], calcium,
1184 nitrate), NMDS, 3D stress 0.12.

1185

1186

1187 Fig. 12.



1188 Fig. 12. Relationship between Bray-Curtis similarity of diatom assemblages in
1189 autumn 1992 and 2022 and changes in vegetation cover over time.

1190

1191

1192 Table 1. Orders, families, genera and species in streams of the Langtang Valley,
 1193 Nepal.

Achnanthales P.C.Silva			
Achnanthidiaceae D.G.Mann	<i>Achnanthidium</i> Kütz. 5	<i>Karayevia</i> Round & Bukht. ex Round 1	<i>Planothidium</i> Round & Bukht. ex Round 4
Cocconeidaceae Kütz.	<i>Cocconeis</i> Ehrenb. 3		
Fragilariales P.C.Silva			
Fragilariaceae Kütz.			
<i>Fragilaria</i> Lyngb. 9	<i>Odontidium</i> Kütz. 3		
Staurosiraceae Medlin	<i>Staurosira</i> Ehrenb. 1	<i>Staurosirella</i> D.M.Williams & Round 3	<i>Pseudostaurosira</i> D.M.Williams & Round 1
Ulnariaceae E.J.Cox	<i>Hannaea</i> R.M.Patrick 1	<i>Ulnaria</i> (Kütz.) Compère 2	
Cymbellales D.G.Mann			
Cymbellaceae Kütz.	<i>Cymbella</i> C.Agardh 4	<i>Delicata</i> Krammer 1	<i>Didymosphenia</i> Mart.Schmidt 1
Encyonemataceae Kulikovskiy, Mironov, Maltsev & Kociolek	<i>Encyonema</i> Kütz. 4		
Gomphonemataceae Kütz.	<i>Gomphonema</i> Ehrenb. 8	<i>Gomphosinica</i> Kociolek, Q.-M.You, Q.- X.Wang & Q.Liu 1	<i>Reimeria</i> Kociolek & Stoermer 1
Naviculales Bessey			
Naviculaceae Kütz.	<i>Adlafia</i> Gerd Moser, Lange-Bert. & Metzeltin 1	<i>Navicula</i> Bory 3	
Sellaphoraceae Mereschk.	<i>Sellaphora</i> Mereschk. 3		
Bacillariales Hendey	Bacillariaceae Ehrenb.	<i>Denticula</i> Kütz. 1	<i>Nitzschia</i> Hassall 3
Thalassiophysales D.G.Mann	Catenulaceae Mereschk.	<i>Amphora</i> Ehrenb. ex Kütz. 3	

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Appendix

Table 1. Normalized difference vegetation index (NDVI) of 13 stream catchments in the Langtang Valley, Nepal, in 1992 and 2022.

Streams	Altitude (m)	NDVI	
		1992	2022
T1	1465	0.75	0.76
T2	1660	0.65	0.70
C13	2044	0.67	0.73
C16	2519	0.69	0.71
C19	2747	0.59	0.62
C23	3051	0.37	0.49
T10	3271	0.29	0.31
C33	3443	0.38	0.54
C26	3458	0.60	0.67
C27	3570	0.54	0.65
C29	3663	0.45	0.42
C31	3790	0.27	0.32
CC	3810	0.24	0.36

Table 2. Water chemistry in 13 streams of the Langtang Valley, Nepal, in November 2022 and April 2023 (conductivity $\mu\text{S}/\text{cm}$; ion concentrations mg/L ; total hardness, alkalinity as CaCO_3).

Conductivity	2022	2023
T1	91	104
T2	41	45
C13	46	18
C16	46	53
C19	57	72
C23	33	53
T10	70	-
C33	51	-
C26	59	61
C27	33	22
C29	95	105
C31	86	75
CC	93	93
Total hardness		
T1	30	46
T2	12	22
C13	12	12
C16	14	20
C19	20	28
C23	22	22
T10	38	-
C33	20	-
C26	22	26
C27	16	20
C29	36	46

C31	36	38
CC	44	46
Alkalinity		
T1	24	38
T2	8	14
C13	6	10
C16	6	10
C19	6	24
C23	16	22
T10	28	-
C33	14	-
C26	18	24
C27	6	12
C29	28	38
C31	20	18
CC	34	36
Ca		
T1	8.4	12.8
T2	3.8	4.8
C13	4.4	2.4
C16	4.6	4.8
C19	6.3	8.8
C23	7.6	7.2
T10	14.1	-
C33	6.6	-
C26	6.5	6.4
C27	5.3	3.2
C29	12.1	13.6
C31	12.2	11.2
CC	15.6	15.4
Na		
T1	3.3	7.1
T2	2.1	6.6
C13	1.7	4.8
C16	2.6	6.0
C19	2.2	5.8
C23	1.5	5.6
T10	1.1	-
C33	2.2	-
C26	3.7	7.3
C27	1.2	4.1
C29	4.0	9.8
C31	1.9	5.0
CC	1.7	5.6
Si (dissolved)		
T1	40.2	35.2
T2	25.5	25.4
C13	22.9	28.3
C16	29.3	25.4
C19	24.9	31.2

C23	12.8	23.11207
T10	10.2	-
C33	12.1	-
C26	21.7	12.7
C27	8.3	6.9
C29	24.9	24.2
C31	15.9	9.2
CC	14.0	14.4
NO₃⁻		
T1	0.43	0.81
T2	0.54	0.57
C13	0.27	0.83
C16	0.20	0.76
C19	0.53	1.10
C23	0.73	1.20
T10	0.71	-
C33	0.56	-
C26	1.91	2.78
C27	0.53	2.19
C29	0.68	0.96
C31	0.46	1.38
CC	0.58	1.10

Table 3. Diatom species richness and evenness in 13 streams of the Langtang Valley, Nepal.

Richness	N	Mean	SD	Median	SE
1992	13	16.77	3.49	17	0.97
1993	13	18.00	6.01	18	1.67
2000	12	15.25	3.77	15	1.09
2022	13	18.31	4.57	19	1.27
2023	11	18.73	5.14	19	1.55
Evenness	N	Mean	SD	Median	SE
1992	13	0.26	0.08	0.27	0.02
1993	13	0.28	0.12	0.27	0.03
2000	12	0.26	0.10	0.27	0.03
2022	13	0.28	0.11	0.25	0.03
2023	11	0.29	0.09	0.27	0.03

Table 4. Fitted simple linear mixed-effects models to test for effects of year, season and altitude on diatom species richness and evenness in streams of the Langtang Valley, Nepal.

	Value	Std. Error	DF	t-value	p-value
Richness					
Intercept	-68.52221	67.57261	47	-1.014053	0.3157
Year	0.04599	0.03363	47	1.367471	0.1780
Season	1.31250	0.94825	47	1.384125	0.1729
Altitude	-0.00229	0.00107	11	-2.138588	0.0557
Evenness					
Intercept	-0.4605413	1.8010644	47	-0.2557051	0.7993
Year	0.0003906	0.0008971	47	0.4354423	0.6652
Season	0.0141851	0.0252865	47	0.5609752	0.5775

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Altitude	-0.0000185	0.0000191	11	-0.9704567	0.3527
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