Interaction of climate change, potentially toxic elements (PTEs), and topography on plant diversity and ecosystem functions in a high-altitude region of the Tibetan Plateau

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Abstract

Mining activities that shape geographical patterns of biodiversity in individual regions are increasingly understood, but the complex interactions on broad scales and in changing environments are still unclear. In this study, we developed a series of empirical models that simulate the changes in biodiversity and ecosystem functions in mine-affected regions along elevation gradients (1500-3600 m a.s.l) in the metal-rich Qilian Mountains (~800 km) on the northeastern Tibetan Plateau (China). Our results confirmed the crucial role of potentially toxic elements (PTEs) dispersal, topography, and climatic heterogeneity in the diversification of plant community composition. On average, 54% of the changes in ecosystem functions were explained by the interactions among topography, climate, and PTEs. However, merely 30% of the changes were correlated with a single driver. Plant species composition (explained variables = 94.8%) changed more in lowland than in highland areas. The changes in species composition (explained variables = 94.8%) in the PTE-polluted habitats located in the warm low-elevation deserts and grasslands were greater than those occurring in the alpine deserts and grasslands. The ecosystem functions (soil characteristics, nutrient migration, and plant biomass) experienced greater changes in the humid low-elevation grasslands and alpine deserts. The effect of topography (i.e., slope and aspect) was less important than that of climatic heterogeneity (MAT, win10, and ET0) in predicting ecosystem functions of PTE-polluted habitats. Our results suggest that the processes driven by climate or other factors can result in high-altitude PTE-affected habitat expansions or contractions.

Introduction

In recent decades, human activities have caused a significant loss of global biodiversity due to their impact on climate and vegetation[1,2]. In some "hotspots", vegetation diversity variations have led to major changes in ecosystem function, stability, and serviceability[3,4]. The establishment of global conservation priorities and an understanding of the alteration processes in different environments have become necessary to focus the limited economic resources on those areas with the highest protection value and that are most threatened by environmental changes[5,6]. As demonstrated by several studies, long-term metal mining and processing have disturbed mountain ecosystems and altered the succession of plant communities in many regions. For example, in the mountains of Eastern Europe (Alps)[7], North America (Appalachian Mountains)[8], and South Africa[9], as well as in other mineral-rich mountain ranges, extensive mining has triggered the spread of potentially toxic elements (PTEs, such as Cd, Zn, Cu, Pb, Ni, Hg, and Cr), which profoundly alter the local environment for the growth of plant species[10,11,12]. However, some researchers argued that the effect of PTEs on vegetation succession was shown to affect plant species richness within limited small areas[12,13]. Other studies on habitats and abiotic factors have demonstrated that regional level variations (e.g., climate patterns and topographic heterogeneity) may lead to greater changes in community succession processes[14-16]. For example, the effects of PTE transport can overlap with rapidly changing climatic conditions along elevation gradients, causing variations in plant diversity and ecosystem function[17,18]and, eventually, concealing the effects of PTEs on succession[19,20,21]. Understanding the potential additive and interactive effects of climate, topography, and PTEs on biodiversity and ecosystem functions (ESFs) at multiple spatial scales is therefore crucial to comprehending the ecological consequences of abandoned mines worldwide[10,20,22].

Although some authors have been highlighted the influence of PTEs transport in small-scale experiments or in study regions with narrow climatic gradients[8,9,23], most mining ecosystems still lack long-term biophysical and ecological data sets for assessments of possible ecosystem responses. Ideally, the prediction of climate-related ecological changes requires the simultaneous consideration of multiple climate drivers and the assessment of the mid- to long-term temporal changes to capture the complex, interacting responses[24]. "Space-for-time" substitutions, also known as ergodic gradient studies, allows for quantitative predictions to be realized in the absence of long-term data sets or a detailed mechanistic knowledge of possible responses to climatic changes[25,26]. This approach uses multiple sites across environmental gradients (i.e., the elevation gradient) to predict the time trajectory in ecological changes, which is considered to be causally correlated with the changes across the gradient[24]. Studies employing this approach have been applied in paleoenvironmental investigations of pollen[27], altitude changes in bird distribution[28] and biodiversity changes in land use[29].

The objective of this study was to quantify the combined impact of climate, mountain topography, and PTEs on plant biodiversity and ecosystem functions through a broad survey of the multiregional mining sites of the Qilian Mountain metallogenic belt in the northeastern Tibetan Plateau (China) (Supplementary materials Fig. 1, Table 1). Within an elevation gradient rising from 700 to 5,808 m above sea level (a.s.l.) and an extension of approximately 800 km, the Qilian Mountains are a metal-rich mountain range that covers several major natural ecosystems of temperate regions, from low-elevation desert to mountain, mountain shrub-steppe, and alpine grassland, including high-elevation desert ecosystems. Based on the "space-for-time" method, a multimodel framework was proposed to assess the statistical distribution of ecological responses arising from exposure to one or more metal stressors along different elevation gradients (1500-3600 m a.s.l) and determine which elevation zone (or climate condition) has habitats that are more vulnerable to PTE threats. The importance of a series of environmental covariates correlated with ecological risks, PTE transport, and species richness patterns was quantified. For instance, elevation and ecological risk caused by PTE transport were found to be significantly correlated in all the elevation gradients ($r = 0.68$). Climate variables such as the mean annual precipitation (MAP, $r = -0.92$), mean annual temperature (MAT, $r = 0.79$), transpiration rate (ET0, $r = 0.45$), and wind speed (win10, $r = -0.83$) were found to be correlated with elevation. Among the topographic factors, both slope ($r = 0.41$) and aspect ($r = 0.40$) were correlated with the distribution of the ecological risk related to mines. Afterward, we selected four variables to characterize the intensity of PTEs (ecological risk index, mining years, closure period, and the relative proportion of mining area/plant/factory in the surrounding landscape) and calculated their normalized indicators (PTE intensity). Finally, we compared the statistical support of generalized additive models (GAMs), including the individual and interactive effects of PTEs, climate, and topography, on biodiversity and ecosystem functions.

Patterns of species richness and turnover rate along the elevation gradients.

Our results suggest that PTEs, with the interaction of topographic heterogeneity and climate change, have profoundly affected the biodiversity trends around metal mines along the elevation gradients of the Qilian Mountains. In the habitats classified as "natural" (i.e., not contaminated or lightly contaminated), the plant richness showed a unimodal distribution with increasing elevation (Fig. 1a, explained deviance =

38%, $P < 0.005$). Compared to the natural habitats, the presence of PTEs in soil caused an increase in plant richness (Fig. 1a, explained deviance = 58%, $P < 0.005$) and a decrease in plant evenness (Fig. 1b, explained deviance = 76%, $P < 0.005$). For the variations in plant richness, evenness, and cover, the models involving Climate × PTEs or Topography × PTEs described the data better than the models of climate, PTEs, or topography alone or the models involving additive effects (Supplementary materials Tables 2, 3, 4). Nevertheless, the deposition of PTEs in the soil altered the plant diversity distribution unevenly along the elevation gradient. Compared to the natural habitats, the plant species richness in PTE-polluted habitats located in the low-elevation desert (1578-2183 m a.s.l) and lowland grassland (2365-3079 m a.s.l) showed significant changes, with maximum increases of 25% and 18%, respectively. However, the evenness in the PTE-polluted habitats in the same elevation zone decreased by 44% and 45%, respectively (Fig. 1b and Supplementary Materials Fig. 7). Unlike the obvious changes in plant richness between the natural habitats and PTE-polluted habitats, the change in plant coverage between these two areas was relatively small (Fig. 1c, explained deviance = 95%, $P < 0.005$).

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Alongside changes in species richness, the species composition of plant communities changed with the presence of PTEs and the interaction of topographic heterogeneity and climate change. Nonmetric multidimensional scaling (NMDS) demonstrated the spatial changes in plant communities shaped by PTE deposition in different study sites ($n = 64$) of the mountain range (average turnover rate = 0.51, range = 0.16 - 1.00) (Fig. 1d). The turnover rate reflected the high similarity in the plant composition at the mine sites on the same elevation gradient (PERMANOVA, $R^2 = 47\%$, $P = 0.01$). The results showed that PTE deposition changed the plant species composition of PTE-polluted habitats in most classified groups compared with that in the natural habitats ($F = 9.06$, $df = 2696$, $P = 0.027$, Fig. 1d). Throughout the four studied climate zones along the elevation gradient (mountain desert steppe, mountain grasslands, desert grassland, and mountain shrub-steppe), we found that the turnover rates in the PTE-polluted habitats showed greater changes in plant composition in the low-elevation mountain desert steppe (ANOVA, $P = 0.052$) and mountain grassland (ANOVA, $P < 0.01$) (Fig. 2).

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Changes in the ecosystem functions along the elevation gradients.

Since most prior studies have largely focused on the influence of PTE transport on biodiversity in polluted areas with a single natural habitat[30,31], the correlation between ecological functions and PTE transport has never been fully analyzed at multiple spatial scales (i.e., across climate zones). However, in the natural habitats of the Qilian Mountains, most soil and plant-mediated functions varied linearly along the elevation gradients. For the natural ecosystem functions mediated by plants and soil, climate and topography jointly predicted the changes in habitat and ecosystem functions (Fig. 3). On average, these factors explained 65% (± 23% (s.d.), ranging from 20% to 99%; Supplementary materials Table 4) of the changes in the ecosystem functions for the natural habitats over all the elevation gradients. Most soil- and plant-mediated functions peaked at lower, and middle elevations (2370-3051 m a.s.l), where the highest MAP (353.91˜445.93 mm year^{-1}), and relatively low MAT (4.42˜6.02) were recorded (Fig. 4). In contrast, pH, electrical conductivity (EC), and total salt content declined with elevation, whereas alkaline N peaked at lower-middle elevations (Fig. 4). For the natural ecosystem functions, the effect of topography (i.e., slope and aspect) was less important than that of climatic heterogeneity (MAT, win10, and ET0) in predicting ecosystem functions (Fig. 3). For the plant-mediated ecosystem functions, the absolute effect strength values were, on average, higher for climate change (i.e., ET0, MAT, and win10), whereas the soil-mediated ecosystem functions were strongly explained by both topography (i.e., slope and elevation) and climate change (i.e., MAT, win10, and ET0) (linear mixed effect model, $P < 0.05$).

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The majority of the ecosystem functions (explanatory variable = 92% +- 5% (SD), $P < 0.005$) were altered by the presence of PTEs, with the interaction of topographic heterogeneity and climate change (Fig. 5a). In most cases, the presence of PTEs varied with both the climate and topography of the study sites in different climate zones (Supplementary materials Table 2). The two-way interaction models (PTEs-topography and PTEs-climate) for different elevations explained most of the 21 ecosystem functional variables (explanatory variable = 39% +- 20% (s.d.), $P < 0.005$, explanatory variable = 47% +- 26% (s.d.), $P < 0.005$) (Supplementary materials Table 2). In the three-way interaction models (climate-PTEs-topography), both climatic and topographic variables were input, causing the explained variation in ecosystem functions to increase to 53% +- 26% (s.d.) and indicating that the interactive model supported the empirical data more strongly (Supplementary materials Table 2). The climate zones in which the strongest effects of PTE intensity on ecosystem functions were observed varied for different response variables (Fig. 4). For example, the C/N content of the plants in the PTE-polluted habitats decreased as the elevation increased, which occurred especially in the mine areas of the warm and relatively humid low-elevation mountain grasslands (2370-2500 m a.s.l) (residual effect = 0.21, $R^2 = 0.57$, $P < 0.005$). The NDVI of the PTE-polluted habitats in the arid low-elevation mountain desert steppe (1000-1500 m a.s.l) changed significantly, as explained by the local climate (residual effect = -0.21, $R^2 = 0.90$, $P < 0.005$; Supplementary materials Tables 2, 3). The large degree of support for the climate-PTEs-topography interaction models across ecosystem functions was robust to different PTEs criteria (Supplementary Note 1, Supplementary materials Tables 5, 6 and Supplementary Materials Figs. 8, 9) and allowed us to consider potentially confounding environmental variables that systematically change with elevation (Supplementary Note 1 and Supplementary materials Tables 5, 6). As plant species and ecosystem functions may respond more strongly to certain factors related to the ecological risk induced by PTE transport, we tested whether the uncertainty of ecological risk was affecting the prediction of the response variables. Our results showed that most of the models equally supported the prediction of the response variables with or without considering the uncertainty of ecological risks. Furthermore, we also tested three models incorporating only a subset of the original data, and the results supported the complete three-way interaction models (climate-PTEs-topography) in most cases (explanatory variable = 63% +- 23% (s.d.), $P < 0.005$; Supplementary Materials Figs. 2-4 and Supplementary Materials Tables 6, 7, 8).

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The multivariate index of ecosystem multifunctionality.

To quantify the overall differences in ecosystem functions, we calculated the multivariate index of multifunctionality of the average change in ecosystem functions in the PTE-polluted habitats compared to the natural habitats (Fig. 6). The multivariate index of multifunctionality was best explained by the climate-PTEs-topography interaction model (Supplementary Materials Table 9, $R^2 = 0.86$). However, the patterns of dissimilarity in the multivariate index of multifunctionality could not fully explain the dissimilarity structure of the species communities (Fig. 1d and Fig. 6), indicating that the relationship between species composition and ecosystem functioning in actual ecosystems was more complex than expected. Across the elevation zones, the models showed that the changes in ecosystem multifunctionality (i.e., the average changes in the ecosystem functions of the PTE-polluted habitats compared with those of the natural habitats) decreased with PTE intensity (Fig. 5b (1)). However, as we took both climate and topographic factors into account, the opposite trend of ecosystem multifunctionality with m-PTE intensity (m-PTE is a complex variable taking all PTEs, topography, and climate variables into account) was observed (Fig. 5b (2)). This finding indicated that the changes in ecosystem multifunctionality would deviate from the actual situations if climate factors and topographic variables were not included as explanatory variables. In detail, in the four studied climate zones of the Qilian Mountains, the impact of climate and other factors on ecosystem multifunctionality was higher in PTE-polluted habitats of the relatively humid mountain grasslands and alpine deserts than in the arid low-elevation desert steppes (Fig. 5c). Moreover, stronger changes were observed for the soil-mediated ESFs than for the plant-mediated ESFs (Supplementary Materials Fig. 5 a-d), and a higher change in the soil-mediated ESFs occurred in the lowland mine areas (both desert and grassland) (Supplementary Materials Fig. 5 e, f).

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The results of our study demonstrate the importance of fully considering climatic and topographic impacts while assessing the changes in plant diversity caused by mining activities in different elevation zones of mountain ranges. We highlighted that the presence of PTEs can unevenly affect plant diversity trends along elevation gradients. First, compared with natural habitats, the plant turnover in PTE-polluted habitats at mid-elevation sites may be greater than that at sites in any other climate zone of the Qilian Mountains. Indeed, at mid and low elevations, species habitats have a higher spatial coincidence, with many species cooccurring in narrow geographical ranges[38,32,33]. Moreover, extreme climatic conditions (e.g., hurricanes and heavy precipitation) have a greater impact on the habitats of mid- and low-elevation species, where plant richness is higher and more sensitive to PTE sediments. Second, speciation increases in the habitat mosaic of topographically complex areas[34,35,]. Interestingly, we found that in the mountains with very high peaks and more rugged terrain, changes in the PTE deposition in the topsoil were more likely to promote the upslope/downslope movement of rare species, leading to their disruptive selection and displacement[39,45](Supplementary Material Fig. 9). Similar phenomena have occurred historically in other contexts[32,36], for instance, when vegetation belts moved upslope during warm and wet interglacial periods, leading to the fragmentation of populations and genetic divergence. As temperatures dropped again in glacial episodes, vegetation belts moved downslope, forcing secondary contact of populations and leading to founder effects[32,36]. Third, the succession mechanisms of plants showed significant differences in different PTE-polluted habitats. In the mine areas of the lowland grasslands, several toxic and harmful herbaceous plants (i.e.,*Stellera chamaejasme* , *Potentilla multicaulis,* and*Pedicularis* Linn) occupied the niche of the PTE-polluted areas in the humid mountain grasslands (Supplementary Materials Fig. 7 and Table 8). Species evenness showed greater changes, especially in the sites containing more ultramafic rocks (such as AR, an asbestos plant, XTS, and multimetal mines), where ultrahigh magnesium content and low phosphorus availability act as powerful and selective plant filters[11]. In contrast, in the mine areas located in the arid mountain desert, the large and medium shrubs restricted the dispersal of PTEs and protected the nearby small shrubs and grasses with high fertility, leading to the establishment of new plant communities. In general, compared with the vulnerable ecosystems in low-elevation dry deserts and warm grasslands, the mine areas located in alpine deserts and cold humid grasslands may have a stronger resistance to disturbance and may possibly support more rapid restoration processes.

Despite the lack of time-series data for the Qilian Mountains, the "space-for-time-approach" could explain the changes in biodiversity and ecosystem functions caused by mining activities[37]. Based on the long-term effect of mining activities over the broad elevation gradients of the mountain range, the models we proposed demonstrated, from a holistic perspective, the importance of climate change on the impact of metal pollution on different spatial and temporal scales. Although previous studies have considered the critical importance of local adaptation along natural elevation gradients, they only explored the potential effects of zinc (Zn) and climate change (20 and 24) on certain species (*Ischnura elegans*)[23]. Our models, instead, took into account the majority of the potential drivers (12 variables) that shape the contemporary patterns of biodiversity and generated predictions, which we tested with independent data. More particularly, the models showed that the impact on biodiversity and ecosystem functions depends largely on the original climatic environment and geological conditions. In vulnerable mining ecosystems, the processes driven by climatic or other factors may present contrary effects on species richness and vegetation cover, which may conceal the actual succession effects and habitat expansion or contraction at landscape level due to the presence of PTEs. From a long-term perspective, at larger spatial scales (hundreds of kilometers) encompassing a range of ecosystems and climate types, the importance of topography declines, while broad-scale climatic variations become substantially more important[38]. Given that most mining areas in the Qilian Mountains, as well as in other mountain ranges, have been closed for only some decades and that the community succession in PTE-polluted habitats cannot usually reach a stable level after decades or even hundreds of years[39], our findings have worrying implications for the impacts of global climate change. As a consequence, we strongly suggest considering the role of global climate change when developing management strategies for plant diversity conservation in the mine areas of high-altitude mountain ranges.

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Author contributions J.Z.L and H.W.L designed the concept for ecological research of mine areas in Qilian Mountains. M.L.B. and L. H. developed the mathematical theory. J.Z.L and A.G. processed the data of plant diversity. J.Z.L, H.W.L., T.C.Y., P.P.T., S.S. F., Q.Y., Q.W.N., Y.Y.Y., C.Y., M.T., W.F., Y.X.X and F.P.Y. established study sites and collected data. J.Z.L., S.S.F, M.T., Y.Y.Y., Q.W.N. and C.Y. conducted the chemical analysis of the plant and soil samples. T.C.Y., P.P. T and Q.Y. processed the topography and climate data of the Qilian Mountains. All authors contributed to the subsequent drafts.

Competing interests The authors declare no competing interests.

Supplementary data

Figs and tables supporting the main text can be found in the files of supporting information

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Methods

Study Area. All data were collected from July 2019 to March 2020 on the Qilian Mountains (94deg10'E-103deg04'E, 35deg50'N-39deg19'N), a mountain on the northeastern border of the Tibetan Plateau (China)[40,41]. The environmental characteristics of the Qilian Mountains vary significantly with the elevation gradients (maximum elevation range of 5806 m). The vertical precipitation distribution shows a quasi-linear manner with elevation. The main rainy season is normally from April to September, with average annual precipitation from 150 to 800 mm[42,43]. The eastern part is affected by the southeast monsoon and is relatively humid, with more precipitation than the western part. The mean annual temperature (MAT) decreases with elevation, starting at 8degC in the foothills and decreasing to 2 degC in the alpine meadows.

The Qilian Mountains are rich in minerals (i.e., asbestos, pyrite, chromite, copper, lead, and zinc)[44]. They mainly consisted of Cu-Ni, Cu-Ni-Pt deposits (mafic igneous rocks) related to volcanic magma, massive Zn-Pb-Cu and Zn-Cu sulfide deposits related to marine volcanic rocks and intrusive rocks (ophiolite), and several types of skarn-quartz vein tungsten (Cu, Mo) deposits[45]. Large-scale mining commenced in the 1980s and ceased at the beginning of the 21st century. Up to now, only several large mines are still in operation (over 1500 m. a.s.l). Owing to a long history of mining activities, natural habitats in the lowland and sub-montane zones of the Qilian Mountain were largely damaged. Some regions are protected as a national nature reserve of the Qilian Mountains (97deg25'-103deg46' E, 36deg43'-39deg36' N).

Experimental Design and Sample collection . We investigated eight abandoned mine areas of the Qilian Mountains spanned an elevational gradient of 1500 to 3,600 m a.s.l, on the basis of mineralization types, distribution of major minerals, periods of mining exploitation, habitat types, as well as elevations (Supplementary Materials Fig. 7). We excluded mine areas in climate zones like alpine and subalpine meadows ([?] 4000 m) because the mineral resources and the PTE-polluted habitats are mostly distributed in the lower elevation zones. The eight abandoned mine areas occurred in the four major natural habitats of the Qilian Mountains:

(1) Low-elevation deserts (arid and semi-arid desert, 1578-2183 m a.s.l), containing JYG, metal industry (salt desert, halophyte); SN, multi-metal industrial park (shrub desert, bushes);

(2) Low-elevation grasslands (semi-arid grasslands, 2365-3079 m a.s.l), containing HB, Chrome chemical factory (flat grasslands, vegetations); AR, an asbestos factory (mountain grasslands, shrubs and grass); XF, Chrome chemical factory (field, vegetations);

(3) High-elevation deserts (alpine desert steppes, 3043-3203 m a.s.l), only XTS, Solder iron mountain (dry/cold desert, shrubs and grass);

(4) High-elevation grasslands (semi-damp grasslands, 3427-3618 m a.s.l), containing HX, multimetal mine (mountain grasslands, shrubs and grass); SBG, multimetal mine (mountain grasslands, shrubs and grass).

Among the eight abandoned mine areas, we established sixty-four study sites (Supplementary Materials Fig. 7). A total number of 48 PTE-polluted habitats and 16 natural habitats (e.g., not contaminated or lightly contaminated) were selected. This arrangement was aimed at comparing the plant species diversity and the ecosystem functions of the habitats. All the study sites (n=64) were chosen from the core zones of the corresponding habitats to eliminate the disturbance of the transition zones. From 1 to 6 study plots (50 x 50 m^2) per study sites (n=48, the PTE-polluted habitats) were arranged with a total number of 174 plots to reflect a within-habitat-type elevation gradient showing the fine-scale changes in biodiversity at changing environments. The soil and plant samples were collected from each plot. The soil samples were properly packed in plastic bags (500 g per piece), and plant samples (more than 3 individuals) were packed and stored in a low temperature (-4degC). Six topsoil samples (0-20 cm) were collected from the Qilian Mountains Natural Reserve where the ecological system had never been affected by mining activities. Then, the samples were taken back to the laboratory of the Physical and Chemical Center of the Institute of Geography, Chinese Academy of Sciences for further analysis.

PTEs, topography and climate data. *PTEs.* The PTEs was calculated to characterize the strength of potentially toxic elements by using four evaluation criteria (1) ecological risk index, (2) mining years, (3) closure years, (4) the relative proportion of mining area/plant/factory in the surrounding landscape[46, 47,48]. The four criteria were calculated as follows:

(1) Ecological risk index (RI), introduced by Hakanson (1980)[49], was calculated as the sum of the E_i values for each trace metal element according to the following equation:

$$Ri = \sum E_i$$

$$E_i = T_i \frac{C_i}{B_i}$$

where E_i is the single risk index for the trace metal element i , dimensionless; T_i is the toxic-response factor for a given metal (1 for Zn, 5 for Cu, 5 for Ni, 5 for Pb, 2 for Cr, 30 for Cd); dimensionless; $C_i$is the concentration of metals in soils, mg kg^{-1};B_i is the background value for metals, mg kg^{-1}.

(2) The mining years, from the beginning of mining activities to closure (open ~ shutdown). This indicator shows when the toxic elements started affecting the surrounding environment during the mining process and how long the process lasted.

(3) Closure years, from the mine shutdown to 2020 (shutdown ~ 2020). This indicator reflects the long-term effects of potentially toxic elements on ecosystems after pollution cessation.

(4) The relative proportion of mining area/plant/factory in the surrounding landscape, which is the relative proportion of natural habitats and mine areas. This indicator reflects the relationship between mine areas and the disturbed ecosystem areas around mine areas.

All four criteria of the PTEs were standardized before averaging them to final composite PTEs. According to the following equation:

$y = (y_i - \bar{y}\ )/(\text{maximum}(y\ ) - \text{minimum}(y\ ))$

where y is the measured value of each component. The produced PTEs value is between 0 (lowest PTE intensity) and 1 (highest PTE intensity).

Climate data . The 1980-2018 climate data were collected from 8 weather stations close to the eight studied mine areas of the Qilian Mountains. In each mine area, the mean annual climate (MAC) data were calculated to characterize the climate change among different elevation gradients. Data included monthly surface evapotranspiration (ET0), average temperature, average precipitation, and average wind speed (win10) (http://www.cma.gov.cn/).

Topography data . Coordinates and elevation of the 64 study sites were recorded by hand-held GPS (China, Yili-X28). Data on the slope and aspect were extracted from the 90 m × 90 m Digital Elevation Model (DEM) of Gansu and Qinghai province (SRTM 90 m Digital Elevation Data; http://www.gscloud.cn/). ArcGIS 10.2 was used to edit and filter the 90 m resolution DEM data with the Qilian Mountains' boundary and acquired the study area map.

Species diversity and indicators of ecosystem functions.*Species richness, evenness, and richness.* For each study site (n = 64), the total number of species (cumulative) was recorded and vascular plant species richness was calculated (Supplementary Materials Fig. 7). In each study site, 1 to 6 study plots (50 × 50 m^2) were arranged depending on local terrain and plant distribution, with a total number of 174 plots. For each plot, 5 subplots with 25 sampling points (1 × 1 m^2) in total were set up with the standard sampling method. Data on species coverage, richness, and evenness of dominant herbaceous species in each point were recorded and their mean values were calculated for further analysis[50,51].

Soil physical and chemical properties (pH, N, P, K, EC and soil TOC). Soil samples were taken from soil pits on a horizon basis, and in 10-cm intervals, using a standard soil auger. The samples were sieved (2-mm mesh), and roots and plant materials were removed. Field samples were dried at room temperature for 72 h, and ground for further analysis. For all study sites, results were standardized and averaged to 0-40 cm depth. Subsequently, chemical analyses were carried out in the Physical and Chemical Analysis Center of the Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences (Beijing, China). Soil pH was determined with an inoLab Level 1 pH meter in suspension with 1:1.25 (w/v) soil, deionized water, and 0.01 M $CaCl_2$. Total organic carbon (TOC) was measured by wet oxidation with $K_2Cr_2O_7$and the absorbance at 590 nm was measured with Spectrophotometer (Liqui TOC II, Elementar, Germany). Thereafter, total nitrogen (N) was measured by a dry combustion automated C: N analyzer (Vario EL, Elementa). Available P extracted by 0.002 N H_2SO_4solutions was measured with the Truog method, while available K was determined with NH_4OAc using gas chromatography-flame photometry.

Soil water content. We extracted the monthly global 0.5deg x 0.5deg soil moisture data from 1980 to 2004 for our studied sites in the Qilian Mountains from the 1948-2004 dataset originally calculated by Fan et al. (2004)[52]. Afterward, the average value of annual soil moisture was calculated for each of the 64 studied sites.

Plant biomass. We determined plant biomass per study site by summing up the biomass of shrubs and herbs. Shrub biomass was estimated in subplots of 5 x 20 m in the center of each study site and then extrapolated to the scale of study sites. Herbaceous biomass was determined by removing all plant biomass of the herbaceous layer in four representative subplots of 0.25 x 0.25 m per study site when the herbaceous biomass was maximal. Herbaceous samples were dried in a drying oven at 65 degC for 72 h and then weighed.

Root fine biomass. At each plot, 10 to 15 soil cores (inner diameter 3.5 cm) were taken randomly down to a depth of 40 cm. Soil samples were kept in plastic bags and stored below 4 degC. In the laboratory, samples were soaked and washed via a sieve of 200 µm mesh size. All root fragments were extracted by hand with tweezers (root lengths [?] 0.2 cm was ignored). Root fractions were dried at 70 °C for 48 h, and weight and fine root biomass were expressed as mg ha^{-1}.

Plant physiological properties (C/N, C/P, K, and TOC). All plant physical and chemical properties analyses were carried out in the Physical and Chemical Analysis Center of the Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences (Shandong, China). Total organic carbon (TOC) was measured by wet oxidation with $K_2Cr_2O_7$and the absorbance at 590 nm was measured with Spectrophotometer (Liqui TOC II, Elementar, Germany). Total nitrogen (N) was measured with the Kjeldahl method. Available P extracted by 0.002 N H_2SO_4 solutions was measured with the Truog method while available K was determined with NH_4OAc using gas chromatography-flame photometry.

Plant bio-concentration factor (BCF) . Metal (Al, Fe, Mg, Cd, Cr, Cu, Ni, Pb, Sr, Zn, Mn, and Ba) concentration of both soil and plant samples was determined by using a mixture of acids (HCl-HNO_3-HF-$HClO_4$) to digest and the extraction solution was analyzed through ICP-OES (Optima 5300DV, PerkinElmer, USA). A quality assurance/quality check (QA/QC) program was established to ensure the accuracy of the results of metal concentrations in all samples. Furthermore, three samples from sixty-four studied sites were taken for inter-laboratory analysis to further ensure the validity of the data. Finally, the bio-concentration factor (BCF) of plants was calculated as follows[53,54].

$$\mathrm{BCF}_{\mathrm{metal\ j}} = \frac{1}{n}\sum_{i=1}^{n}\frac{\mathrm{CPT}}{\mathrm{CE}} \qquad (i = 1,\ 2,\ \ldots n)$$

where *CPT* and *CE* are the concentration (mg kg^{-1}) of metal j in plant tissue and soil, respectively, i is the *i-th* plant in the plot, and$n$ is the total number of plants in the plot. Then, the factor analysis method was used to calculate the normalized *BCF* values.

Normalized Difference Vegetation Index (NDVI). NDVI dataset for the 64 study sites was extracted from Landsat 5 and 8 series (horizontal resolution of 30 × 30 m) and MYD13Q1 (horizontal resolution of 250 × 250 m). Cloud pollution was a prominent feature for the remote sensing data extraction, limiting the accuracy of environmental indices computation. To solve this problem, we first identified all pixels marked as 3 of MYD13Q1 quality and then deleted them along with eight surrounding pixels[55]. Using a "Whitaker smoother" based on three iterations of 6,000λ, we calculated the overall average NDVI from 1980 to 2018 and extracted the pixel values corresponding to the study sites.

Leaf Area Index (LAI) . We measured the LAI at 25 points per study site and calculated the mean value from these measures. The leaf area was measured at ground level using a plant canopy analyzer in combination with a remote 'above-canopy' sensor (LAI 2200, LI-COR Bioscience). The above canopy reading was measured at ground level in an open area or forest gap as close to the site as possible, and LAI values were calculated using the program FV-2200 (LI-COR Bioscience).

Statistical Analysis. Generalized additive models (GAMs) was employed to analyze the correlation between species biodiversity (richness, evenness, and cover) or ecosystem function (response variables) and elevation (continuous predictor)[56]. All the ecosystem function indicators were transformed into z-axes before the analysis. Considering the consistency of data analysis, pollution types were added into the model as a binary factor variable (natural habitats versus PTE-polluted habitats). The binary factor variable was based on our main statistical analyses (i.e., the tests of seven major PTEs, climate, and topography models described below) on models in which the potential toxic element intensity was integrated as a continuous predictor variable (that is, the *PTEs*). Poisson or Gaussian distributions were applied in the case of species richness and ecosystem functions and the basic dimension of the smoothing function was set to 4 to 6. Here, pollution type was added to the GAMs as an interaction factor to determine the correlations of response variables and elevation between PTE-polluted and natural habitats. If the interaction term was not significant ($P > 0.05$), the corresponding term was removed from the model but the additive effect of elevation and PTE dispersal was anyway tested (i.e., we tested for differences in the intercept between natural and PTE-polluted habitats). If the effect of PTE dispersal was not significant, the corresponding term was removed from the prediction variable and the response variable was modeled only by elevation, assuming that the mean distributions of response variables in the natural and PTE-polluted habitats were the same. Otherwise, we assumed the null model to be best supported by the data, and the response variable was modeled only by the intercept (i.e., the average values of the data).

To assess the effects on biodiversity and ecosystem functions determined by PTE dispersal and interacted by climate and topography, we evaluated the support for seven different hypotheses with linear models within a multimodel inference approach[57]. Multimodel inference takes both uncertainty in parameter estimation and uncertainty in model selection into account. Moreover, the multimodel inference is good at dealing with related predictor variables. In the model, strongly correlated predictors with the same explanatory power reduce support for the multimodel. The seven hypotheses or models we tested were:

(1) PTEs only (PTEs model); (2) PTEs + Climate (additive model); (3) PTEs + Topography (additive model); (4) PTEs + Climate + Topology (additive model); (5) PTEs × Climate (interaction model); (6) PTEs × Topography (interaction model); (7) PTEs × Climate × Topography (interaction model).

In the PTEs model (1), we assumed that the PTE impact alone could fully explain the variations of biodiversity and ecosystem functions. In the additive model (2) to (4), we assumed that PTEs, topography, and/or climate had additive effects. The best model was then selected and at least one PTEs, one climate, and/or one topography variable were included. In the interaction model (5) and (6), we tested the hypothesis that climate (or topography) could influence the impact of PTEs on biodiversity and ecosystem functions. The interaction terms of PTEs-climate (or PTEs-topography) were added in the GAMs. The best model (with the lowest value of Akaike information criterion with correction for small sample sizes (AIC_C)) was selected and at least one interaction term of PTEs-climate variables (or PTEs-topography variables) was included. In the interaction model (7), instead of testing the interaction terms of the three indicators, we run the model which involved both the interaction terms of PTEs-climate and those of PTEs-topography. The best model was selected (with the lowestAIC_C value) and at least one PTEs-topography and one PTEs-climate interaction terms were included.

For each response variable (plant richness, evenness, coverage, and ecosystem functions), we calculated the support for each of the above-mentioned models by calculating the AIC-based model weight (also known as '*AIC* weight' or 'model probability')[58]. The lower the *AIC* value was, the better the fitting effect was. Meanwhile, we calculated the R^2 value of the optimal model to represent the relative importance and significance of each prediction variable. For multimodel averaging analyses, the R package MuMIn (https://CRAN.R-project.org/package=MuMIn) was used. To analysis the robustness of the model, we analyzed the uncertainty of ecological risk and the influence on the stability of the model from other environmental variables (slope direction, atmospheric pressure, etc.) that could change the modeled results[61].

To visualize and analyze the relative importance of PTEs, climate, and topography on species turnover (β-diversity), we calculated a dissimilarity matrix of plant diversity based on the Sørensen dissimilarity index. The nonmetric multidimensional scaling (NMDS) using Meta MDS function of the vegan R-package was used to ordinate the dissimilarity matrices in two-dimensional ordination space. For all biodiversity datasets, stress levels were low, which justified using this approach. The effect of PTEs, climate, and topography on the dissimilarity of plant communities was examined through the permutational multivariate analysis of variance (PERMANOVA) method (the function adonis in the vegan package). We started with the most complex model and deleted the least important predictor variables in sequence to obtain the optimal model for each of the seven assumptions.

To quantify the overall differences in ecosystem functions of multiple mine areas of the study area, we calculated two measures of ecosystem multifunctionality: (a) a multivariate index of multifunctionality, and (b) a measure of the average change of ecosystem functions in PTE-polluted, compared to the natural habitats.

The multivariate index of multifunctionality (a) was calculated by removing the default values in pairs and obtaining the Euclidean dissimilarity matrix based on the z-transformed ecosystem functions. Classical multidimensional scaling was used to visualize the dissimilarity matrix in the sorting space, while PERMANOVA was used to determine the significance of climate, PTEs, and topography on multidimensional scaling axis 1 and 2 scores.

We quantified the dissimilarity in ecosystem functions of PTE-polluted habitats to the average conditions in the natural habitats (b) by modeling ecosystem functions in natural ecosystems in a GAM with elevation as a predictor variable. Before analysis, all the ecosystem functions were transformed into z-axes. We then modeled the average dissimilarity in ecosystem functions as a function of PTE intensity and m-PTE intensity, and compared differences in PTE intensity among elevation zones by using simple ordinary linear models and AIC-based model inference. The values of m-PTEs were the multi-dimensional factors (axis1) obtained from multidimensional scaling of a total of 12 variables of climate, PTEs, and topography variables in the final model. This analysis was done for all 20 ecosystem functions and separately for the soil- and plant-mediated ecosystem functions.

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