The role of glacial gravel in community development of vascular plants on the glacier forelands of the Third Pole postprint

Authors: Wei Tianfeng, SHANGGUAN Donghui, TANG Xianglong, QIN Yu

Date: 2022-10-14T00:00:00+00:00

Abstract

On deglaciated terrain, glacial gravel constitutes the primary component of the natural habitat for vascular plant colonization and succession. However, knowledge regarding the role of glacial gravel in vascular plant growth remains limited. In this study, an unmanned aerial vehicle (UAV) was used to investigate plant family composition, species richness, fractional vegetation cover (FVC), and gravel cover (GC) along elevational gradients across three glacier forelands (Kekesayi, Jiangmanjiaer, and Koxkar Baxi) in the Third Pole region (encompassing the eastern Pamir Plateau and western Tianshan Mountains) of China. We then analyzed the spatial characteristics of vascular plants and explored the effects of glacial gravel on their development. Our findings indicated that FVC on these glacier forelands generally decreased with increasing elevation or decreasing distance from the current glacier terminus. At the glacier basin scale, the shady slope (Kekesayi) supported denser vegetation compared to the sunny slope (Jiangmanjiaer), while at the regional scale, the warm and humid deglaciated terrain (Koxkar Baxi) exhibited the highest FVC. Plant family composition and species richness on the glacier forelands decreased with rising elevation, except on the Jiangmanjiaer glacier foreland. The relationships between FVC and GC showed negative correlations, varying as power functions on the Kekesayi and Jiangmanjiaer glacier forelands of the eastern Pamir Plateau and as a linear function on the Koxkar Baxi glacier foreland of the western Tianshan Mountains. Glacial gravel was found to facilitate vegetation colonization and development during early succession until vascular plants adapted to cold and arid climatic conditions, but it became unfavorable for vascular plant expansion during later succession stages. These findings suggest that spatial differences in plant characteristics are closely connected to regional climatic and topographic conditions, as well as glacial grave

Full Text

Preamble

The Role of Glacial Gravel in Community Development of Vascular Plants on the Glacier Forelands of the Third Pole

WEI Tianfeng[1], **SHANGGUAN Donghui**[2],[3],[4], ***TANG Xianglong***[1], **QIN Yu**[2]

[1] School of Architecture and Urban Planning, Lanzhou Jiaotong University, Lanzhou 730070, China
[2] State Key Laboratory of Cryospheric Sciences, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou 730000, China
[3] University of Chinese Academy of Sciences, Beijing 100049, China
[4] China-Pakistan Joint Research Center on Earth Sciences, Chinese Academy of Sciences and Higher Education Commission Pakistan, Islamabad 45320, Pakistan

Abstract: On deglaciated terrain, glacial gravel constitutes the primary component of the natural habitat for vascular plant colonization and succession. However, knowledge regarding the role of glacial gravel in vascular plant growth remains limited. In this study, an unmanned aerial vehicle (UAV) was used to investigate plant family composition, species richness, fractional vegetation cover (FVC), and gravel cover (GC) along elevational gradients across three glacier forelands (Kekesayi, Jiangmanjiaer, and Koxkar Baxi) in the Third Pole region (encompassing the eastern Pamir Plateau and western Tianshan Mountains) of China. We then analyzed the spatial characteristics of vascular plants and explored the effects of glacial gravel on their development. Our findings indicated that FVC on these glacier forelands generally decreased with increasing elevation or decreasing distance from the current glacier terminus. At the glacier basin scale, the shady slope (Kekesayi) supported denser vegetation compared to the sunny slope (Jiangmanjiaer), while at the regional scale, the warm and humid deglaciated terrain (Koxkar Baxi) exhibited the highest FVC. Plant family composition and species richness on the glacier forelands decreased with rising elevation, except on the Jiangmanjiaer glacier foreland. The relationships between FVC and GC showed negative correlations, varying as power functions on the Kekesayi and Jiangmanjiaer glacier forelands of the eastern Pamir Plateau and as a linear function on the Koxkar Baxi glacier foreland of the western Tianshan Mountains. Glacial gravel was found to facilitate vegetation colonization and development during early succession until vascular plants adapted to cold and arid climatic conditions, but it became unfavorable for vascular plant expansion during later succession stages. These findings suggest that spatial differences in plant characteristics are closely connected to regional climatic and topographic conditions, as well as glacial gravel distribution.

Additionally, we concluded that aerial photographs can serve as a valuable tool for studying micro-environmental functions in vegetation colonization and succession on glacier forelands.

Keywords: vascular plants; fractional vegetation cover; glacial gravel; glacier foreland; unmanned aerial vehicle; Pamir Plateau; Tianshan Mountains

Citation: WEI Tianfeng, SHANGGUAN Donghui, TANG Xianglong, QIN Yu. 2022. The role of glacial gravel in community development of vascular plants on the glacier forelands of the Third Pole. *Journal of Arid Land*, 14(9): 1022–1037. https://doi.org/10.1007/s40333-022-0073-1

Corresponding authors: SHANGGUAN Donghui (E-mail: dhguan@lzb.ac.cn); TANG Xianglong (E-mail: tangxl@mail.lzjtu.cn)

Received 2022-05-07; revised 2022-08-05; accepted 2022-08-07

http://jal.xjegi.com; www.springer.com/40333

1 Introduction

China hosts a large number of mountain glaciers. According to the second Chinese Glacier Inventory (CGI) (Liu et al., 2015) and Randolph Glacier Inventory (RGI) 6.0 (RGI Consortium, 2017), the country's glaciers cover 5.18×10^{4} km^2, representing 7.3% of the world's total glacial area—the highest percentage outside the Arctic and Antarctic (70.58×10^{4} km^2). Due to global warming, glaciers worldwide have been retreating since the end of the Little Ice Age (approximately 1850) (Leclercq et al., 2011; IPCC, 2012), and China is no exception (Li et al., 1998; Liu et al., 2003; Shangguan et al., 2006; Zhang et al., 2016; Li et al., 2019). Uncovered surfaces following glacier retreat offer excellent opportunities to examine primary vegetation succession processes in the field. Consequently, numerous studies on succession dynamics and factors influencing vegetation development have been published, primarily focusing on the High Arctic, European mountainous areas, and North America (Raffl et al., 2006; He and Tang, 2008; Burga et al., 2010; Wietrzyk et al., 2018; Wei et al., 2021). In China, research on vegetation spatial distribution and succession has concentrated on several glacier forelands, including Yulong Snow Mountain, Tianshan Mountains, and Gongga Mountain (Li and Xiong, 1995; Chang et al., 2014; Wei et al., 2021). These works have provided valuable vegetation information on glacier forelands in the Third Pole region of China, though related studies remain scarce compared to those in the aforementioned regions.

All stages of plant community development on glacier forelands are governed by both biotic and abiotic factors, with abiotic control playing a more crucial role during early vegetation succession (Houle, 1997; Jumpponen et al., 1999). Glacial gravel, derived either supraglacially from nunataks and valley sides or from subglacial bed erosion (Boulton, 1978), is quite prevalent on glacier forelands and has attracted scientific interest because vegetation tends to grow in association with it. Previous publications (Rooney, 1997; Mong and Vetaas, 2006) indicate that glacial gravel plays a controversial role in vegetation colonization and development on glacier forelands. Some studies have noted that glacial gravel prevents herbivore disturbances (Rooney, 1997) and provides relatively safe sites for early colonization by pioneer plants (Stöcklin and Bäumler, 1996; Jumpponen et al., 1999; Niederfriniger Schlag and Erschbamer, 2000). Conversely, other studies have argued that potentially protective glacial gravel at microsites becomes an obstacle for seedling establishment by occupying available germination space (Mong and Vetaas, 2006). Therefore, further exploration of spatial vegetation characteristic changes and the impact of glacial gravel on vegetation colonization and development is urgently needed. To comprehensively address this scientific question, our investigation had to be expanded across several glacier forelands with various regional topographic and climatic conditions.

Glacier forelands are characterized by complex terrain, unique ecosystems, and harsh environments, making field investigation of vegetation dynamics challenging. Traditional ground sampling has been a valuable approach extensively applied in field surveys (Niederfriniger Schlag and Erschbamer, 2000; Mong and Vetaas, 2006; Raffl et al., 2006; Burga et al., 2010; Wietrzyk et al., 2018), but this methodology is time-consuming, labor-intensive, and requires trampling fragile habitats (Lee and Yeh, 2009; Martínez-López et al., 2014). Additionally, free satellite imagery is difficult to utilize for assessing vegetation characteristics on glacier forelands due to low resolution. In contrast, unmanned aerial vehicles (UAVs) provide an ideal solution through advantages such as increased field efficiency, effective avoidance of human disturbance, automatic acquisition of high-resolution images at the quadrat scale, and the ability to repeatedly observe the same area after setting flight lines (Sun et al., 2018). Furthermore, UAVs can easily acquire vegetation data in inaccessible areas, making the technique suitable for vegetation monitoring across various topographic conditions, including glacier forelands.

In this study, we investigated fractional vegetation cover (FVC), plant family composition, species richness, dominant species, and gravel cover (GC; defined as the ratio of the vertical projected area of glacial gravel to the total ground area) along chronosequences by integrating ground-based sampling and aerial photography across three glacier forelands in China's eastern Pamir Plateau and western Tianshan Mountains. We then analyzed variation characteristics of these vegetation indices during primary succession and examined the relationship between GC and FVC. This study aims to characterize spatial variations in vegetation characteristics (FVC, plant family composition, and species richness), examine spatial heterogeneity of vegetation under various regional topographic and climatic conditions, and assess the influence of glacial gravel on vegetation community development. The findings will assist investigators of primary vegetation succession and biodiversity and aid in regional ecological conservation and sustainability in the Third Pole region.

2.1 Study Area

The study area is situated in the Third Pole region, spanning the eastern Pamir Plateau and western Tianshan Mountains in Xinjiang Uygur Autonomous Region, China. We surveyed three glacier forelands: Kekesayi, Jiangmanjiaer, and Koxkar Baxi. Within each foreland, sampling sites were established along elevational gradients (Fig. 1 [Figure 1: see original paper]). Sites in the eastern Pamir Plateau were distributed across retreat areas of modern and paleo-glaciers (elevation ranges of 3843–4004 m a.s.l. for Kekesayi glacier and 3631–4241 m a.s.l. for Jiangmanjiaer glacier), whereas those in the western Tianshan Mountains were primarily located in deglaciated terrain of the modern glacier (elevation range of 2979–3099 m a.s.l. for Koxkar Baxi glacier).

The Kekesayi glacier (code number 5Y663D0087 from the Chinese Glacier Inventory) and Jiangmanjiaer glacier (code number 5Y663D0004 from the Chinese Glacier Inventory) are typical valley glaciers situated in the same glacier basin (Fig. 1b–d) beneath the ice caps of Muztagata Peak and Kongur Peak, respectively. The debris-covered Kekesayi glacier extends approximately 18.0 km over 86.50 km^2 from east to north, representing the largest glacier of Muztagata Peak (Shangguan et al., 2006; Seong et al., 2009a, b). The Jiangmanjiaer glacier spans 14.8 km over 45.08 km^2, making it the longest glacier on the southwestern slope of Kongur Peak (Wang et al., 2011). Field investigations of moraine ridges and previous publications on Quaternary glacial landforms revealed that both Muztagata Peak and Kongur Peak were covered by massive glaciers historically, extending into Kara Kol Lake during glacial maxima (Cui, 1960). However, remote sensing data indicate their frontal positions have shown almost no visual changes in the last four decades (Holzer et al., 2015). The two peaks are primarily controlled by upper-level westerly circulation and local circulation, with moisture transfer hindered by the “blocking effect” of surrounding high mountains (Yu et al., 2006), resulting in a cold and semi-arid continental climate. The Taxkorgan meteorological station, located approximately 50.0 km south of Muztagata Peak, is the sole station above 3000 m a.s.l. on the eastern Pamir Plateau. From 1957 to 2010, mean annual temperature was 3.4°C, mean summer temperature (June–August) was 15.1°C, and mean annual precipitation was 70.2 mm (Yan et al., 2013; Yang et al., 2014). Vegetation distribution along elevational gradients includes meadow (below 3500 m a.s.l.), desert vegetation (3500–4000 m a.s.l.), alpine grassland vegetation (above 4000 m a.s.l.), and alpine sparse vegetation (above 4500 m a.s.l.), with floristic composition consisting of *Ceratoides*, Graminoids, *Artemisia*, *Stipa*, etc. (Wang et al., 2016). However, vegetation characteristics differed markedly between the two glacier forelands (Fig. 2a [Figure 2: see original paper]–f).

The Koxkar Baxi glacier (code number 5Y674A0005 from the Chinese Glacier

Inventory) is situated on the southern slope of Tuomuer-Khan Tengri Mountain in the western Tianshan Mountains (Fig. 1). This typical continental glacier extends approximately 26.0 km over 83.60 km^2, with elevations ranging from 3020–6342 m a.s.l. (Zhang et al., 2007). It is debris-covered, and its terminus has been retreating at an average rate of 0.5–1.5 m/a since the 1980s (Xie et al., 2007). The region is most influenced by mid-latitude westerlies originating from the Atlantic Ocean, creating a sub-humid climate with mean annual precipitation of 669.4 mm at 3000 m a.s.l. (Li et al., 2012) and mean summer temperature (June–August) of 11.0°C at 3007 m a.s.l. (Han et al., 2008). Surrounding vegetation includes alpine meadow (2900–3600 m a.s.l.) and alpine cushion plants (3600–4250 m a.s.l.) (Sabit et al., 2016). Land near the glacier terminus is barren and covered by massive glacial gravel, though an alpine meadow occurs at 2979 m a.s.l. (Fig. 2g–i).

2.2 Unmanned Aerial Vehicle (UAV) Survey and Data Collection

The Mavic Pro (Fig. 3 [Figure 3: see original paper]), an electric rotary quadcopter manufactured by DJI Innovation Company (Shenzhen, China), was employed in this study. Equipped with a high-precision vision positioning system, it can precisely capture images with geodetic accuracy even under poor global navigation satellite system signal conditions. The integrated three-band FC220 digital camera features 12-megapixel resolution (4000$×$3000 pixels) and maintains horizontal orientation when stationary.

From September 26 to October 2, 2018, we selected 23 sampling sites along elevational gradients based on vegetation characteristics (FVC, plant height, and vegetation type) across the three glacier forelands. These sites exhibited obvious differences in plant community characteristics and could reflect real-world vegetation distribution patterns. At each site, the UAV was deployed from 2.0 m height to cover 40 m × 40 m quadrats (Fig. 3). Prior to each flight, waypoints were adjusted to follow glacier foreland topography. The UAV captured photographs vertically downward while flying autonomously between waypoints generated in flight planning software. During flight, the camera triggered every 3 seconds as the UAV traveled at 3.0 m/s, with all images stored in JPEG format for later processing. Camera white balance was set according to actual weather conditions, yielding at least 16 images per flight under normal circumstances. The high spatial resolution (0.07 cm) of all images facilitated extraction of necessary surface information.

No meteorological stations existed on the three glacier forelands, except for one automatic weather station on the Koxkar Baxi glacier foreland. Therefore, meteorological data (temperature and precipitation) were calculated through empirical formulas. On the Kekesayi and Jiangmanjiaer glacier forelands, the following equations were applied:

$$AP_{Pamir} = 605.0 + 13.7 \times \frac{A_i - 7010}{100}$$

$$AMT_{Pamir} = 0.70 - 0.71 \times \frac{A_i - 3250}{100}$$

where AP_{Pamir} and AMT_{Pamir} denote annual precipitation (mm) and annual mean temperature (°C) for the eastern Pamir Plateau, respectively; 13.7 and 605.0 represent the precipitation lapse rate (mm/100 m) and annual precipitation (mm) at 7010 m a.s.l., respectively (Duan et al., 2007); 0.71 and 0.70 represent the temperature lapse rate (°C/100 m) and annual mean temperature (°C) at 3250 m a.s.l., respectively (Luo, 1994; He et al., 2005); and A_i represents the elevation variable (m a.s.l.).

On the Koxkar Baxi glacier foreland, the equations used were:

$$AP_{Tianshan} = 669.4 + 49.8 \times \frac{A_i - 3000}{100}$$

$$AMT_{Tianshan} = 0.70 - 0.63 \times \frac{A_i - 2950}{100}$$

where $AP_{Tianshan}$ and $AMT_{Tianshan}$ reflect annual precipitation (mm) and annual mean temperature (°C) for the western Tianshan Mountains, respectively; 49.8 and 669.4 represent the precipitation lapse rate (mm/100 m) and annual precipitation (mm) at 3000 m a.s.l., respectively (Li et al., 2012); and 0.63 and 0.70 represent the temperature lapse rate (°C/100 m) and annual mean temperature (°C) at 2950 m a.s.l., respectively (measured data) (Han et al., 2008).

The calculated results are presented in Table 1 .

2.3 Evaluation of Fractional Vegetation Cover (FVC) and Gravel Cover (GC)

To accurately obtain ground-cover data such as FVC and GC, we removed low-quality images and processed high-quality ones using the traditional maximum likelihood classifier in ENVI software (Harris Geospatial Solutions, Boulder, CO, USA). Aerial photographs were positioned using Pix4D software (Pix4D Company, Lausanne, Switzerland) prior to classification. Image deformation was negligible due to low flight height (2.0 m) and relatively flat terrain. Individual photographs were classified independently using a supervised classification-based maximum likelihood method.

For this study, we divided photographs into three land cover types: vegetation, glacial gravel, and others (such as water bodies and barren land) (Fig. 3). Classification accuracy was assessed by comparing the sample class of the classified layer with the reference layer. Overall accuracy and Kappa coefficient were computed to evaluate classification accuracy using the error matrix (Muzein, 2006). Overall accuracy represents the sum of correctly classified values (diagonals) divided by the total number of randomly generated reference values in the error matrix (Lillesand and Kiefer, 2000). The Kappa coefficient, which measures the difference between actual agreement of the classified map and chance agreement of a random classifier compared to reference data, was calculated as:

$$\hat{K} = \frac{N\sum_{i=1}^{k} x_{ii} - \sum_{i=1}^{k}(x_{i+} \times x_{+i})}{N^2 - \sum_{i=1}^{k}(x_{i+} \times x_{+i})}$$

where $\hat{K}$ is the Kappa coefficient; N represents the total number of values; x_{ii} is the observed accuracy; and $(x_{i+} \times x_{+i})$ is the chance accuracy.

Results were tested with a Kappa coefficient exceeding 0.58, indicating acceptable data quality. Finally, we calculated FVC and GC based on classification results using:

$$FVC(\%) = \frac{\text{Pixel number}_v}{\text{Pixel number}_t} \times 100\%$$

$$GC(\%) = \frac{\text{Pixel number}_g}{\text{Pixel number}_t} \times 100\%$$

where FVC is fractional vegetation cover (%); GC is gravel cover (%); Pixel number$_v$ is the pixel count of vegetation; Pixel number$_g$ is the pixel count of glacial gravel; and Pixel number$_t$ is the total pixel count within each aerial image.

In this study, we regarded the mean FVC and mean GC calculated from 16 aerial photographs as reference data for each site. The flowchart for FVC and GC calculation is shown in Figure 4 [Figure 4: see original paper].

2.4 Calculations of Plant Family Composition, Dominant Species, and Species Richness

Plant families were identified from aerial photographs (see Wei et al. (2021) for details), with results validated by ground-based sampling. A total of 12 vascular plant families were identified (Table 2). Dominant species within each sampling site were determined by occurrence frequency and cover in the 16 aerial photographs, indicating that dominant species had the highest occurrence frequency and coverage. Species richness, a common vegetation index reflecting species diversity in a community or biotope (Karen et al., 2004), was obtained by visually identifying and counting species numbers from the 16 images at each site based on characteristic differences among species. Species richness was then calculated using:

$$D = \text{Species number appearing in unit area}$$

where D refers to the total number of species at each sampling site, i.e., the species count appearing in 16 aerial photographs.

2.5 Linear Mixed-Effects Model

We applied a linear mixed-effects model to assess changes in FVC as a function of GC (Meng et al., 2007). Fixed and random effects, as major model components, had to be determined prior to calculation. Since we first analyzed the effect of GC on FVC, GC was considered the fixed effect. At the glacier basin scale, aspect affected soil hydrothermal conditions by altering solar irradiation and subsequently modified vegetation patterns. At the regional scale, regional climate was a key element influencing vegetation development. This led to identification of regional climate and aspect as random effects. Analyses were conducted using the `lme` function in the `nlme` package in R v. 3.6.1 (https://cran.r-project.org/). Finally, we used `r.squaredGLMM` in the `MuMIn` package in R v. 3.6.1 to assess model accuracy, which provided two measures: R_m^2 and R_c^2. The first reports the R^2 of the model with only fixed effects, whereas the second represents the R^2 of the full model (including fixed and random effects). R^2 indicates model fitness. When R^2 is similar between models, it is most important that R_c^2 is only slightly different compared to R_m^2, implying that inclusion of random effects does not improve accuracy.

3.1 FVC Along Elevational Gradients

On the Jiangmanjiaer and Kekesayi glacier forelands of the eastern Pamir Plateau, FVC varied in an inverted "N-shaped" pattern with increasing elevation, though it exhibited general declining trends (Fig. 5 [Figure 5: see original paper]). FVC was highest in valley bottoms (old sites) and lowest near glacier termini (young sites). Specifically, on the Jiangmanjiaer glacier foreland, maximum and minimum FVC values were 91.9% (at 3631 m a.s.l.) and 4.8% (at 4241 m a.s.l.), respectively, whereas on the Kekesayi glacier foreland, they were 65.7% (at 3843 m a.s.l.) and 35.2% (at 3913 m a.s.l.), respectively. Furthermore, spatial variation in FVC on the Jiangmanjiaer glacier foreland was more dramatic (range of 87.1%) compared to the Kekesayi glacier foreland, which was more densely vegetated overall (Fig. 5).

On the Koxkar Baxi glacier foreland of the western Tianshan Mountains, FVC exhibited a linear decline trend with increasing elevation (Fig. 5c and f). Similar to spatial changes on the eastern Pamir Plateau forelands, maximum (86.9%) and minimum (0.0%) values occurred on the valley floor (old sites) and at the glacier terminus (young sites), respectively. FVC on the Koxkar Baxi glacier foreland showed a more pronounced growth trend with decreasing elevation compared to the two eastern Pamir Plateau forelands (Fig. 5).

3.2 Plant Family Composition Along Elevational Gradients

On the Kekesayi and Jiangmanjiaer glacier forelands, despite both being covered by cold-desert vegetation, plant family types and numbers displayed obvious differences along elevational gradients. On the Kekesayi glacier foreland, vegetation primarily comprised individuals from Gramineae, Compositae, Cyperaceae, Ephedraceae, Fabaceae, Rosaceae, Tamaricaceae, and Polygonaceae families. Cyperaceae was the dominant family, appearing at all sampling sites, whereas Tamaricaceae and Polygonaceae were the rarest, present only near valley bottoms (old sites; Table 2). From 4004 m a.s.l. to the glacier terminus (young sites), land was covered by abundant loose glacial gravel with sparse vegetation, where the simplest plant family composition occurred. The near valley bottom (3873 m a.s.l.) had the richest plant families, comprising 75.0% of all families. Plant family composition at the valley bottom (old sites) was simple and relatively stable, with four families present: Gramineae, Cyperaceae, Tamaricaceae, and Polygonaceae.

On the Jiangmanjiaer glacier foreland, plant families consisted of Gramineae, Compositae, Cyperaceae, Fabaceae, Caryophyllaceae, Rosaceae, Crassulaceae, and Chenopodiaceae. Gramineae was the leading family, occurring at all sampling sites (Table 2). Variation in plant family composition along elevational gradients was stochastic, with the richest composition appearing at 4149 m a.s.l. and the simplest composition occurring from 4241 m a.s.l. to the glacier terminus (young sites). Although each sampling site contained specific dominant species, *Artemisia minor* and *Carex moorcroftii* were dominant at all sampling sites on the Kekesayi and Jiangmanjiaer glacier forelands, respectively (Fig. 6a [Figure 6: see original paper] and b).

On the Koxkar Baxi glacier foreland, six plant families were recorded: Rosaceae, Gramineae, Cyperaceae, Polygonaceae, Crassulaceae, and Asteraceae. From 3049 m a.s.l. to the glacier terminus (young sites), no vegetation occurred on barren land covered by abundant glacial gravel. Plants first appeared at 3011 m a.s.l., where only Rosaceae plants were distributed sporadically around glacial gravel or in crevices (Fig. 2h). With decreasing elevation, plant family composition became increasingly abundant, culminating in a stable alpine meadow on the valley floor (2979 m a.s.l.) with the richest composition, including Gramineae, Cyperaceae, Polygonaceae, Crassulaceae, and Asteraceae (Fig.

2i; Table 2). *Kobresia pygmaea* and *Carex melanantha* were widely distributed below 2992 m a.s.l. (Fig. 6c).

3.3 Species Richness Along Elevational Gradients

On the Kekesayi and Koxkar Baxi glacier forelands, species richness initially increased then decreased with increasing elevation (Fig. 7 [Figure 7: see original paper]), with maxima occurring near valley bottoms (old sites) and minima near glacier termini (young sites). On the Jiangmanjiaer glacier foreland, species richness displayed a fluctuating pattern of initial decrease, subsequent increase, and final decrease with rising elevation, with extrema occurring at sites opposite to those on other forelands (Fig. 7).

Overall, species richness exhibited decreasing trends on the Kekesayi and Koxkar Baxi glacier forelands with increasing elevation, but showed an increasing trend on the Jiangmanjiaer glacier foreland with rising elevation (Fig. 7).

4.1 Community Development of Vascular Plants on the Three Glacier Forelands

During early plant community development stages, vascular plants on all glacier forelands shared similar characteristics of low FVC and species diversity (Burga et al., 2010; Schumann et al., 2016). However, landscapes began diverging during middle and late succession stages among forelands due to multiple factors such as natural disturbances, terrain age, regional climate, and topographic conditions (Tishkov, 1986; Jones and Roger, 2005; Raffl et al., 2006; Dolezal et al., 2008; Burga et al., 2010; Wietrzyk et al., 2018). This natural pattern also occurred on our three surveyed forelands. On newly exposed surfaces following glacier retreat, microorganisms first colonized barren land, and their dead organic matter subsequently facilitated pioneer plant colonization by providing initial soil and nutrient conditions. Accordingly, early plant community development stages exhibited the lowest FVC and species abundance, consistent with earlier studies on the Urumqi Glacier No. 1 foreland in northwestern China (Wei et al., 2021), Skaftafellsjökull glacier foreland in southern Iceland (Glausen and Tanner, 2019), and glacier forelands in the European Alps (Schumann et al., 2016). These colonized pioneer plants further promoted soil development and nutrient accumulation (Wietrzyk et al., 2018), after which vascular plants began expanding as succession proceeded. Spatial changes in vascular plant characteristics (FVC, plant family composition, and species diversity) showed evident differences under varying topographic (elevation and aspect) and climatic conditions.

Specifically, although FVC on the Kekesayi and Jiangmanjiaer glacier forelands within the same basin showed similar variation trends along elevational gradients, the shady slope (Kekesayi) was more densely vegetated compared to the sunny slope (Jiangmanjiaer). Moreover, the Kekesayi glacier foreland had formed small vegetation patches, whereas vegetation on the Jiangmanjiaer glacier foreland tended to grow individually, except in valley bottoms where grasslands occurred. This pattern aligns with previous literature (Ostendorf and Reynolds, 1998; Pearson et al., 1999; Schumann et al., 2016). Furthermore, plant species diversity on the Kekesayi glacier foreland was more abundant compared to the Jiangmanjiaer glacier foreland, indicating that aspect-induced changes in solar radiation may accelerate topsoil heat and moisture migration, subsequently altering spatial patterns of vegetation colonization and development. Our results are consistent with previous studies (Ostendorf and Reynolds, 1998; Schumann et al., 2016) showing that aspect affects communities by altering solar insolation and thus temperature and effective moisture, thereby impacting biodiversity and composition.

In addition to topographic factors, regional climate critically affected vegetation dynamics, though its effect has often been neglected except in studies by Robbins and Matthews (2010) and Schumann et al. (2016). Meteorological data (Table 1) revealed that climatic conditions on surveyed glacier forelands of the eastern Pamir Plateau were colder and drier than those on the western Tianshan Mountains foreland. This climatic difference was naturally reflected in ecosystem structure during later plant community development stages. Specifically, on the relatively warm and humid Koxkar Baxi glacier foreland, elevational vegetation zonality was obvious, with an alpine meadow emerging just 576 m from the glacier terminus at 2979 m a.s.l. (Fig. 2i). In contrast, the cold and dry eastern Pamir Plateau forelands supported sparse, scattered vascular plants that only progressed toward alpine grassland. This finding aligns with studies on glacier forelands in the eastern and western Alps (Schumann et al., 2016), though that study contended that vegetation differences between eastern and western Alps glacier forelands could not be explained by distinct climatic conditions alone, but rather by different species pools and treeline elevation (Schumann et al., 2016).

4.2 Effects of Glacial Gravel on Plant Colonization and Development on the Three Glacier Forelands

In the harsh glacier foreland environment, vegetation colonization and development were primarily dominated by multiple biotic and abiotic factors, making early succession colonization extremely difficult and allowing only a few pioneer plants to establish on barren lands (Dong et al., 2016). Our three surveyed forelands experienced similar conditions. Interestingly, these pioneer species typically grew on glacial gravel sides or in gaps, particularly common on newly exposed surfaces. Previous studies highlighted this occurrence as revealing plant adaptation to harsh environments, but provided only qualitative accounts of how glacial gravel aided vegetation colonization and growth (Thuiller et al., 2005;

Mondoni et al., 2015).

In this study, we quantitatively explored glacial gravel functions in vascular plant colonization and growth on glacier forelands. Throughout all plant community development stages, FVC was negatively related to GC (Fig. 5g–i; Table 3), though relationships varied depending on topographic and climatic conditions. Specifically, FVC on eastern Pamir Plateau forelands decreased as a power function with increasing GC, while on the western Tianshan Mountains foreland it decreased linearly. In addition to spatial relationships between vascular plants and glacial gravel (Figs. 2a and b, and 5g and h), we speculated that glacial gravel might facilitate early-stage vegetation colonization and development by providing suitable hydrothermal conditions and preventing herbivore damage, but might also impose potential restrictions on vegetation expansion during middle and late stages by reducing available space. Similar findings have been reported in earlier investigations (Stöcklin and Bäumler, 1996; Jumpponen et al., 1999; Niederfriniger Schlag and Erschbamer, 2000; Mong and Vetaas, 2006). According to Table 3, R_c^2 was significantly different from R_m^2 when analyzing FVC changes as a function of GC on eastern Pamir Plateau forelands, suggesting that aspect could improve model accuracy. This finding indicates that aspect effects on vegetation should not be neglected when analyzing glacial gravel's role in vegetation development at the basin scale. Additionally, R_c^2 was higher than R_m^2 when evaluating vegetation cover changes as a function of GC in both the eastern Pamir Plateau and western Tianshan Mountains (Table 3), implying that glacial gravel effects on vegetation distribution were mediated by regional climate at the regional scale.

4.3 Advantages and Limitations of UAV in Vegetation Investigation on Glacier Forelands

UAVs have been extensively employed in studying vegetation dynamics in recent years (Dunford et al., 2009; Chen et al., 2016; Mead and Arthur, 2020). However, their application for glacier foreland vegetation investigation is rarely reported, with exceptions including Eichel et al. (2017) and Wei et al. (2021). In this study, we investigated vegetation data (FVC, plant family composition, and species richness) on three glacier forelands using a UAV, demonstrating five benefits mentioned in Section 1. However, this advanced approach also had limitations, including time-consuming species identification in the laboratory, low-quality aerial photographs affecting species identification outcomes, and specific plants (creeping and low-growing plants, and plants matching ground colors) increasing difficulties in FVC extraction and species identification (Wei et al., 2021). Furthermore, UAV's inherent advantages in vegetation monitoring were further constrained by adverse field conditions, which was also evident in this study.

---

5 Conclusions

This study assessed spatial differences in vascular plant community development across three glacier forelands (Kekesayi, Jiangmanjiaer, and Koxkar Baxi) under various topographic and climatic conditions, and explored effects of glacial gravel on plant community development by integrating ground-based sampling and aerial photography. Findings indicated that vascular plant community characteristics exhibited different spatial changes along elevational gradients at different spatial scales. Specifically, at the glacier basin scale, the shady slope (Kekesayi) was more vegetated compared to the sunny slope (Jiangmanjiaer); at the regional scale, the relatively warm and humid Koxkar Baxi glacier foreland had the highest FVC. Meanwhile, vascular plant species diversity gradually decreased with increasing elevational gradients, except on the Jiangmanjiaer glacier foreland. Moreover, correlations between GC and FVC showed that glacial gravel's role in vascular plant colonization and development varied as community succession proceeded. Specifically, glacial gravel tended to play a positive role in early-stage plant colonization but a negative role in middle and late-stage plant community development. Numerous other factors, such as topography (elevation and aspect) and climate, also impacted this phenomenon. These findings provide strong implications for ecological restoration in harsh glacier environments.

Acknowledgements

This research was supported by the Strategic Priority Research Program of Chinese Academy of Sciences (XDA19070501), the National Natural Science Foundation of China (41671066), the Ministry of Science and Technology of the People's Republic of China (2018FY100502), the Young Scholars Science Foundation of Lanzhou Jiaotong University (1200061124), and the International Partnership Program of Chinese Academy of Sciences (131C11KYSB20160061). The authors are grateful to Mr. LIU Jun and Mr. LI Da for fieldwork assistance, Dr. YANG Shuping from Shihezi University, China for guidance in dominant species identification, and Dr. YANG Junhua for language editing of this manuscript.

References

Boulton G S. 1978. Boulder shapes and grain-size distributions of debris as indicators of transport paths through a glacier and till genesis. *Sedimentology*, 25(6): 773–799.

Burga C A, Krüsi B, Wernli M, et al. 2010. Plant succession and soil development on the foreland of the Morteratsch glacier (Pontresina, Switzerland): Straight forward or chaotic? *Flora*, 205(9): 561–576.

Chang L, He Y Q, Yang T B, et al. 2014. Analysis of herbaceous plant succession and dispersal mechanisms in deglaciated terrain on Mt. Yulong, China. *The Scientific World Journal*, 2014: 154539, doi: 10.1155/2014/154539.

Chen J J, Yi S H, Qin Y, et al. 2016. Improving estimates of fractional vegetation cover based on UAV in alpine grassland on the Qinghai–Tibetan Plateau. *International Journal of Remote Sensing*, 37(8): 1922–1936.

Cui Z J. 1960. Some characteristics of glaciers in the Muztag Ata-Kongur Tagh and their conditions for development and utilization. *Acta Geographica Sinica*, 26(1): 35–44. (in Chinese)

Dolezal J, Homma K, Takahashi K, et al. 2008. Primary succession following deglaciation at Koryto Glacier Valley, Kamchatka. *Arctic, Antarctic, and Alpine Research*, 40(2): 309–322.

Dong K, Tripathi B, Moroenyane I, et al. 2016. Soil fungal community development in a high Arctic glacier foreland follows a directional replacement model, with a mid-successional diversity maximum. *Scientific Reports*, 6: 26360, doi: 10.1038/srep26360.

Duan K Q, Yao T D, Wang N L, et al. 2007. Records of precipitation in the Muztag Ata Ice Core and its climate significance to glacier water resource. *Journal of Glaciology and Geocryology*, 29(5): 680–684. (in Chinese)

Dunford R, Michel K, Gagnage M, et al. 2009. Potential and constraints of Unmanned Aerial Vehicle technology for the characterization of Mediterranean riparian forest. *International Journal of Remote Sensing*, 30(19): 4915–4935.

Eichel J, Draebing D, Klingbeil L, et al. 2017. Solifluction meets vegetation: the role of biogeomorphic feedbacks for turf-banked solifluction lobe development. *Earth Surface Processes & Landforms*, 42(11): 1623–1635.

Glausen T G, Tanner L H. 2019. Successional trends and processes on a glacial foreland in Southern Iceland studied by repeated species counts. *Ecological Processes*, 8(1): 138–148.

Han H D, Liu S Y, Ding Y J, et al. 2008. Near-surface meteorological characteristics on the Koxkar Baxi Glacier, Tianshan. *Journal of Glaciology and Geocryology*, 30(6): 967–975. (in Chinese)

He L, Tang Y. 2008. Soil development along primary succession sequences on glacial gravels of Hailuogou Glacier, Gongga Mountain, Sichuan, China. *CATENA*, 72(2): 259–269.

He X B, Ding Y J, Liu S Y, et al. 2005. Observation and analyses of hydrological process of the Kaltamak Glacier in Muztag Ata. *Journal of Glaciology and Geocryology*, 27(2): 262–268. (in Chinese)

Holzer N, Vijay S, Yao T, et al. 2015. Four decades of glacier variations at Muztagh Ata (eastern Pamir): a multi-sensor study including Hexagon KH-9 and Pléiades data. *The Cryosphere*, 9(6): 2071–2088.

Houle G. 1997. No evidence for interspecific interactions between plants in the first stage of succession on coastal dunes in subarctic Quebec, Canada. *Canadian Journal of Botany*, 75(6): 902–915.

IPCC. 2012. *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation*. In: Field C B, Barros V, Stocker T F, et al. Cambridge: Cambridge University Press, 1–582.

Jones C C, Roger D M. 2005. Patterns of primary succession on the foreland of Coleman Glacier, Washington, USA. *Plant Ecology*, 180(1): 105–116.

Jumpponen A, Väre H, Mattson K G, et al. 1999. Characterization of "safe sites" for pioneers in primary succession on recently deglaciated terrain. *Journal of Ecology*, 87(1): 98–105.

Leclercq P W, Oerlemans J, Cogley J G. 2011. Estimating the glacier contribution to sea-level rise for the Period 1800–2005. *Surveys in Geophysics*, 32: 519–535.

Lee T, Yeh H. 2009. Applying remote sensing techniques to monitor shifting wetland vegetation: A case study of Danshui River estuary mangrove communities, Taiwan. *Ecological Engineering*, 35(4): 487–496.

Li J, Liu S Y, Han H D, et al. 2012. Evaluation of runoff from Koxkar Glacier Basin, Tianshan Mountains, China. *Climate Change Research*, 8(5): 350–356. (in Chinese)

Li X, Xiong S F. 1995. Vegetation primary succession on glacier foreland in Hailuogou, MT. Gongga. *Mountain Research*, 12(2): 109–115. (in Chinese)

Li Y J, Ding Y J, Shangguan D H, et al. 2019. Regional differences in global glacier retreat from 1980 to 2015. *Advances in Climate Change Research*, 10(4): 203–213.

Li Z, Sun W X, Zeng Q Z. 1998. Measurements of glacier variation in the Tibetan Plateau using Landsat data. *Remote Sensing of Environment*, 63(3): 258–264.

Lillesand T M, Kiefer R W. 2000. *Remote Sensing and Image Interpretation* (4th ed.). New York: John Willy Sons Inc., 1–736.

Liu S Y, Sun W X, Shen Y P, et al. 2003. Glacier changes since the Little Ice Age maximum in the western Qilian Shan, northwest China, and consequences of glacier runoff for water supply. *Journal of Glaciology*, 49(164): 117–124.

Liu S Y, Yao X J, Guo W Q, et al. 2015. The contemporary glaciers in China based on the Second Chinese Glacier Inventory. *Acta Geographica Sinica*, 70(1): 3–16. (in Chinese)

Luo Z Q. 1994. Preliminary study on the hydrological characteristics and calculation of the Gaizi River in Xinjiang. *Hunan Water Conservancy*, (6): 17–19. (in Chinese)

Martínez-López J, Carreño M F, Palazón-Ferrando J A, et al. 2014. Remote sensing of plant communities as a tool for assessing the condition of semiarid Mediterranean saline wetlands in agricultural catchments. *International Journal of Applied Earth Observation and Geoinformation*, 26(1): 193–204.

Mead L, Arthur M. 2020. Environmental condition in British moorlands: quantifying the life cycle of *Calluna vulgaris* using UAV aerial imagery. *International Journal of Remote Sensing*, 41(2): 573–583.

Meng Q M, Cieszewski C J, Madden M, et al. 2007. A linear mixed-effects model of biomass and volume of trees using Landsat ETM+ images. *Forest Ecology and Management*, 244(1–3): 93–101.

Mondoni A, Pedrini S, Bernareggi G, et al. 2015. Climate warming could increase recruitment success in glacier foreland plants. *Annals of Botany*, 116(6): 907–916.

Mong C E, Vetaas O R. 2006. Establishment of *Pinus wallichiana* on a Himalayan glacier foreland: Stochastic distribution or safe sites? *Arctic, Antarctic, and Alpine Research*, 38(4): 584–592.

Muzein B S. 2006. Remote sensing and GIS for land cover/land use change detection and analysis in the semi-natural ecosystems and agriculture landscapes of the Central Ethiopian Rift Valley. PhD Dissertation. Dresden: Techniche Universität Dresden.

Niederfriniger Schlag R, Erschbamer B. 2000. Germination and establishment of seedlings on a glacier foreland in the central Alps, Austria. *Arctic, Antarctic, and Alpine Research*, 32(3): 270–277.

Ostendorf B, Reynolds J F. 1998. A model of arctic tundra vegetation derived from topographic gradients. *Landscape Ecology*, 13(3): 187–201.

Pearson S M, Turner M G, Drake J B. 1999. Landscape change and habitat availability in the Southern Appalachian Highlands and Olympic Peninsula. *Ecological Application*, 9(4): 1288–1304.

Raffl C, Mallaun M, Mayer R, et al. 2006. Vegetation succession pattern and diversity changes in a Glacier Valley, Central Alps, Austria. *Arctic, Antarctic, and Alpine Research*, 38(3): 421–428.

RGI Consortium. 2017. Randolph Glacier Inventory - A Dataset of Global Glacier Outlines, Version 6. Boulder, Colorado USA. National Snow and Ice Data Center. [2021-07-20]. https://doi.org/10.7265/4m1f-gd79.

Robbins J A, Matthews J A. 2010. Regional variation in successional trajectories and rates of vegetation change on glacier forelands in south-central Norway. *Arctic, Antarctic, and Alpine Research*, 42(3): 351–361.

Rooney T P. 1997. Escaping herbivory: Refuge effects on the morphology and shoot demography of the clonal forest herb *Maianthemum canadense*. *Journal of the Torrey Botanical Society*, 124(4): 280–285.

Sabit M, Mamat Y, Nasirdin N. 2016. Landscape characteristics of the vertical natural zones of Tianshan Tomur Nature Reserve. *Journal of Glaciology and Geocryology*, 38(5): 1425–1431. (in Chinese)

Schumann K, Gewolf S, Tackenberg O. 2016. Factors affecting primary succession of glacier foreland vegetation in the European Alps. *Alpine Botany*, 126(2): 105–117.

Seong Y B, Owen L A, Yi C L, et al. 2009a. Quaternary glaciation of Muztag Ata and Kongur Shan: Evidence for glacier response to rapid climate changes throughout the late glacial and holocene in westernmost Tibet. *Bulletin of the Geological Society of America*, 121(3–4): 348–365.

Seong Y B, Owen L A, Yi C L, et al. 2009b. Geomorphology of anomalously high glaciated mountains at the northwestern end of Tibet: Muztag Ata and Kongur Shan. *Geomorphology*, 103(2): 227–250.

Shangguan D H, Liu S Y, Ding Y J, et al. 2006. Monitoring the glacier changes in the Muztag Ata and Konggur mountains, east Pamirs, based on Chinese Glacier Inventory and recent satellite imagery. *Annals of Glaciology*, 43(1): 79–85.

Stöcklin J, Bäumler E. 1996. Seed rain, seedling establishment and clonal growth strategies on a glacier foreland. *Journal of Vegetation Science*, 7(1): 45–56.

Sun Y, Yi S H, Hou F J. 2018. Unmanned aerial vehicle methods makes species composition monitoring easier in grasslands. *Ecological Indicator*, 95: 825–830.

Thuiller W, Lavorel S, Araújo M B, et al. 2005. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, 102(23): 8245–8250.

Tishkov A A. 1986. Primary succession in arctic tundra on the west coast of Spitsbergen (Svalbard). *Polar Geography and Geology*, 10(2): 148–156.

Wang J, Zhou S Z, Zhao J D, et al. 2011. Quaternary glacial geomorphology and glaciations of Kongur Mountain, eastern Pamir, China. *Science China Earth Sciences*, 54(4): 591–602.

Wang Y T, Dai Z G, Yang S J, et al. 2016. The distribution of marco polo sheep and their habitat vegetation dynamics in east pamir. *Acta Ecologica Sinica*, 36(1): 209–217. (in Chinese)

Wei T F, Shangguan D H, Yi S H, et al. 2021. Characteristics and controls of vegetation and diversity changes monitored with an unmanned aerial vehicle (UAV) in the foreland of the Urumqi Glacier No. 1, Tianshan, China. *Science of the Total Environment*, 771(1): 145433, doi: 10.1016/j.scitotenv.2021.145433.

Wietrzyk P, Rola K, Osyczka P, et al. 2018. The relationships between soil chemical properties and vegetation succession in the aspect of changes of distance from the glacier forehead and time elapsed after glacier retreat in the Irenebreen foreland (NW Svalbard). *Plant and Soil*, 428(1–2): 195–211.

Xie C W, Ding Y J, Chen C P, et al. 2007. Study on the change of Keqikaer Glacier during the last 30 years, Mt. Tuomuer, Western China. *Environmental Geology*, 51(7): 1165–1170.

Yan S Y, Guo H D, Liu G, et al. 2013. Mountain glacier displacement estimation using a DEM-assisted offset tracking method with ALOS/PALSAR data. *Remote Sensing Letters*, 4(5): 494–503.

Yang H N, Yan S Y, Liu G, et al. 2014. Fluctuations and movements of the Kuksai Glacier, western China, derived from Landsat image sequences. *Journal of Applied Remote Sensing*, 8(1): 084599, doi: 10.1117/1.JRS.8.084599.

Yu W S, Yao T D, Tian L D, et al. 2006. Relationships between δ^{18}O in summer precipitation and temperature and moisture trajectories at Muztagata, western China. *Science in China: Series D Earth Sciences*, 49(1): 27–35.

Zhang Y, Liu S Y, Ding Y J. 2007. Glacier meltwater and runoff modelling, Keqicar Baqi Glacier, southwestern Tien Shan, China. *Journal of Glaciology*, 53(180): 91–98.

Zhang Z, Liu S Y, Wei J F, et al. 2016. Mass change of glaciers in Muztag Ata-Kongur Tagh, Eastern Pamir, China from 1971/76 to 2013/14 as derived from remote sensing data. *PLoS ONE*, 11(1): e0147327, doi: 10.1371/journal.pone.0147327.

Note: Figure translations are in progress. See original paper for figures.

Source: ChinaXiv — Machine translation. Verify with original.