Vegetation structural shift tells environmental changes on the Tibetan Plateau over 40 years

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https://doi.org/10.1016/j.scib.2023.07.035
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**Article Info**

**Abstract**

Structural information of grassland changes on the Tibetan Plateau is essential for understanding alterations in critical ecosystem functioning and their underlying drivers that may reflect environmental changes. However, such information at the regional scale is still lacking due to methodological limitations. Beyond remote sensing indicators only recognizing vegetation productivity, we utilized multi-variate data fusion and deep learning to characterize formation-based plant community structure in alpine grasslands at the regional scale of the Tibetan Plateau for the first time and compared it with the earlier version of Vegetation Map of China for historical changes. Over the past 40 years, we revealed that (1) the proportion of alpine meadows in alpine grasslands increased from 50% to 69%, well-reflecting the warming and wetting trend; (2) dominances of Kobresia pygmaea and Stipa purpurea formations in alpine meadows and steppes were strengthened to 76% and 92%, respectively; (3) the climate factor mainly drove the distribution of Stipa purpurea formation, but not the recent distribution of Kobresia pygmaea.

**Keywords:**
Vegetation structural shift
Climate change
The Tibetan Plateau
Vegetation map
1. Introduction

Plant communities in grasslands on the Tibetan Plateau have developed unique characteristics adapting to the alpine environment [1], including short or mat- or rosette-like shape, well-developed root systems that parallelly spread to the ground, and short growing periods [2]. With a high altitude and a continental plateau climate, the Tibetan Plateau has a wide vegetation distribution, displaying a clear zonality [3]. Among various vegetation types, alpine grassland is dominant on the Tibetan Plateau, accounting for $1.5 \times 10^8 \text{ km}^2$ or 67% of the entire Tibetan Plateau area [4,5], and alpine grassland mainly includes alpine meadows and alpine steppes [6], which are the focuses of this study. Grasslands (herbaceous vegetation) mainly consist of dry and mesophytic herbaceous plant species [7], including steppes, meadows, and scrubs [8,9]. According to temperature, grasslands can be divided into alpine and temperate types, and alpine grasslands can be further divided into alpine desert, alpine steppe, and alpine meadow [8]. Species numbers are around 4–28 [10] and 3–32 [11] in alpine steppes and alpine meadows, respectively. Total coverage of alpine steppe varies from 14% to 43% on average [11], while it varies from 80% to 90% in alpine meadows [12]. Alpine steppes in this region are dominated by *Stipa purpurea* and *Carex moorcroftii* [10], whereas the dominant plant species in alpine meadows are usually *Kobresia* species such as *K. pygmaea*, *K. capillifolia*, and *K. tibetica* [13].

Formation is an important hierarchical unit in plant community classification, mainly based on the establishing or co-establishing species. In other words, the same formation shares the same establishment or co-establishing species, distinguishing one type of formation from others [9,14]. Spatial-temporal distribution pattern of the plant community structure in the Tibetan Plateau grasslands, especially at the formation level, is essential for understanding changes in critical functions, e.g., biodiversity maintenance, ecological barrier, livestock production, and livelihood support for pastoralists. However, the cognition of such spatial-temporal changing trend is highly constrained by methodological limitations for characterizing the large-scale structure of plant communities in the Tibetan Plateau grasslands. On the one hand, previous studies for plant community structure in alpine grasslands are dominantly based on ground surveys covering only small areas [15–17], which are insufficient to represent the Tibetan Plateau at the regional scale with complex topography and high spatial heterogeneity. On the other hand, though as a useful way to obtain the large-scale vegetation information, the satellite remote sensing is incapable of distinguishing plant formations or plant community structure.

Vegetation mapping is an effective method to characterize the structure of plant communities and their spatial distribution patterns at a large scale. From 1980 to 2008, plant ecologists had completed a vegetation map of China (1:1,000,000) to depict the vegetation distribution for the mid-1980s [18,19]. This vegetation map for the mid-1980s had played important roles in biodiversity conservation, ecosystem management and restoration, as well as government decision making [20–25]. Combining field surveys, expertise, and literature review to merely obtain the potential vegetation distribution [26], this traditional vegetation mapping method is time-consuming, costly, and difficult to update [27] to cater for shifting situations when vegetation change after a long period of time.

Due to these methodological limitations, much information over the current plant community structure, plant community structure’s changing trends over the past 40 years, and driving mechanisms in alpine grasslands on the Tibetan Plateau is still extremely scarce, thus constraining the conservation and utilization of grassland resources and functions. For example, based on remote sensing data, a general trend of “greening” has been widely recognized for vegetation on the Tibetan Plateau [28–31]. However, the ecological effects and production values of this reported “greening” trend on the Tibetan Plateau are still vague [32–34]. To decipher these issues, it is required to understand large-scale changes in plant community structure, which can directly reflect ecosystem processes and functions.

To fill this above-mentioned gap, we developed a method combining ground survey, expert identification, and large-scale information acquisition, which has made the large-scale characterization of plant community structure become possible [27,35,36]. Briefly, based on digital ground vegetation survey, high temporal resolution multi-source remote sensing data and cloud computing technology, we adopted deep learning to construct a model to capture relationships between plant community structure and environment habitat and further expand these relationships to the regional scale on the Tibetan Plateau for a mapping system of plant community structure at the formation level. This enabled us to analyze the current spatial distribution of plant community structure, compare this current pattern with the vegetation map for the mid-1980s to obtain 40 years’ temporal changes, and decipher driving mechanisms underlying the spatial–temporal changes in plant community structure in the Tibetan Plateau grasslands.

2. Methods and data

A regional-scale vegetation mapping method based on a combination of digital ground vegetation survey, time-series multi-source remote sensing data, and deep learning was proposed (Fig. S1 online). Firstly, a ground survey in grid format was conducted in the study area, and expert identification was applied to obtain accurate formation of quadrats and multi-source remote sensing data covering the study area. Next, based on the latitude and longitude of ground quadrats, a cloud computing platform was used to extract time-series multi-source plant characteristics and habitat data of the plots including spectral, structural, and functional plant characteristics as well as the habitat features such as topography and water and thermal conditions of each grassland formation. Each adopted feature in this study contained time series information in order to better characterize the changes of plants and their growing environment in a year so as to establish the formation–habitat data set. A deep learning network framework was constructed, where the formation–habitat data set was trained to develop a habitat information-based formation identification model. Finally, the model was applied to the multi-source plant
features and habitat data of the entire Tibetan Plateau to realize formation identification. The constructed deep learning model for formation identification through this method was equivalent to an automatic expert model, obtaining the advantage of identifying habitat features that consisted of hundreds of variables so as to make full use of spatial and temporal information in multi-source data.

2.1. Ground survey data

The ground survey was conducted during the vegetation growth period of 2019–2020, led by nearly 100 experts from University of Chinese Academy of Sciences, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, and Qinghai University, etc. A total of 24,661 datasets was obtained, and the distribution of these plots in Fig. 1 covers most regions on the Tibetan Plateau.

In the vegetation survey, the selected plots were at least 500 m off the road, and each plot was a square of 100 m × 100 m. The habitat conditions, plant communities, and utilization patterns within the plots were relatively consistent. Every two plots were 10 km away from each other, and each plot contained five 0.5 m × 0.5 m quadrats, which were set up by the five-point method (four quadrats were located at the four vertices of a site and one at the center) with a spacing of 50 m between each quadrat. The relationship between the plots and the quadrats is shown in Fig. S2 (online). The information such as plant dominant species name, dominant species photo, quadrat photo, quadrat coordinates, vegetation cover, and vegetation height of each quadrat was recorded by digital survey software. All species in the plots were identified and recorded. Simultaneously, the habitat photos of the plots were recorded, and plant specimens of dominant species were collected from the plots for experts to identify plant species and determine their formation type.

2.2. Time series multi-source plant characteristics and habitat feature data

Google Earth Engine (GEE) cloud computing platform, which combines a multi-petabyte catalog of satellite imagery and geospatial datasets with planetary-scale analysis capabilities [37,38]. In this study, it was used for acquiring and processing time-series multi-source plant characteristics and habitat feature data. A variety of remote sensing products and geospatial datasets were integrated to provide a comprehensive set of the plant characteristics and habitat features including spectral information, as well as environment-related data (i.e., Terraclimate actual evapotranspiration, Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) elevation, slope and aspect [39]), vegetation-related remote sensing indices (i.e., Moderate-resolution Imaging Spectroradiometer (MODIS) enhanced vegetation index, normalized difference vegetation index [40], gross primary productivity, net photosynthesis [41], leaf area index, fraction of photosynthetically active radiation [42], and clumping index [43]), and climate-related remote sensing data (i.e., MODIS land surface temperature [44], Terraclimate precipitation accumulation, and soil moisture [45]) (Table S1 online). Time series features were extracted to distinguish plant formations with different phenological profiles. The spatial resolution of these datasets ranged from 30 m to 2.5'. We uniformly resampled them to 250 m and reorganized them into one large dataset, which was learned and processed by the deep neural network mentioned in Section 2.3.
2.3. Deep neural networks for formation identification

Deep neural network is a feedforward artificial neural network composed of interconnected nodes, or neurons [46]. In this study, it was used for identifying grassland formations by establishing the relationship between grassland formation and the data of time-series multi-source plant characteristics and habitat feature. Our deep neural network was built on the TensorFlow framework [47], providing an advanced and complete set of foundational elements based on application requirements. Considering that grassland formation features are complex and numerous (255), we designed a deep neural network with strong feature learning capability for digging features from a large quantity of redundant data. The designed deep neural network consisted of 8 fully connected layers, and the number of nodes in each layer was 4096, 2048, 1024, ... 64, and 32, respectively (Fig. S3 online). The activation function of the hidden layer was chosen using a linear rectifier function (ReLU), which has the advantages of being robust to noise and avoiding gradient disappearance and gradient explosion problems. Besides the fully connected hidden layer, batch normalization [48] layers were incorporated between each fully connected layer. This inclusion ensured that the distribution of input data in each layer remained relatively stable, thereby accelerating the learning speed of the model. Moreover, it reduced the model’s sensitivity to parameters within the network, thereby enhancing the stability of network learning. Preceding the output layer, a Dropout layer was employed to mitigate overfitting. During training, this layer randomly dropped units (along with their connections) from the neural network [49]. Furthermore, due to big variations in the number of sample sizes from different formations, a customized loss function, known as focal loss, was utilized instead of the commonly used cross-entropy loss function. Focal loss down weighted the loss assigned to well-classified examples, thus improving the training effectiveness for categories with a limited number of samples [50]. Finally, the Adam optimizer was used and the learning rate of the network was set to become smaller with time to enhance the training speed and improve the training results [51].

Our deep neural network was accelerated using the CUDA toolkit [52] and ran on an RTX 2070 Super GPU. The training process was conducted when the network was trained by a training dataset with ground survey samples as labels, together with the data of time-series multi-source plant characteristics and habitat feature. The training continued for 500 epochs until the accuracy and loss reached a stable state. For accuracy assessment, ground survey data were randomly split into two parts: 80% for network training and model construction, and 20% as the independent test set. During the training and model construction, and 20% as the independent test set. During the training, the loss assigned to well-classified examples, thus improving the training effectiveness for categories with a limited number of samples [50]. Finally, the Adam optimizer was used and the learning rate of the network was set to become smaller with time to enhance the training speed and improve the training results [51].

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3. Results

3.1. Spatial pattern of plant community structure on the Tibetan Plateau

3.1.1. Grassland types and major formations

Based on the developed vegetation map (Fig. 2), the alpine grassland area on the Tibetan Plateau reaches 1,415,800 km², accounting for 55% of the total area and 93% of the grassland area on the Tibetan Plateau. Among these alpine grasslands, alpine steppes cover a total area of 439,000 km², accounting for 31% of the alpine grassland area, while alpine meadows cover a total area of 976,800 km², accounting for 69% of the alpine grassland area. Compared to the alpine grassland, the distribution of temperate grassland is much less, covering only 107,600 km², accounting for 4% of the total area and 7% of the grassland area on the Tibetan Plateau.

The top five dominant formations on the Tibetan Plateau cover a total area of 1,308,200 km², accounting for 92% of the alpine grassland area. Regarding the order of area from highest to lowest, they are K. pygmaea meadow, S. purpurea steppe, K. humilis meadow, E. nutans meadow, and K. capillifolia meadow.

Alpine meadows on the Tibetan Plateau are the most widely occupied by the K. pygmaea formation, covering 742,900 km² and accounting for 76% of the total area of alpine meadows; the K. humilis meadow covers 80,600 km² and accounts for 8% of the total area of alpine meadows; and the E. nutans meadow, covers 69,000 km² and accounts for 7% of the total area of alpine meadows; the K. capillifolia meadow, covers 13,900 km² and accounts for 0.5% of the total area of alpine meadows. The S. purpurea steppe dominates alpine steppes covering 407,700 km² and accounting for 92% of the total area of alpine steppes.

3.1.2. Spatial patterns of grassland types and major formations under various climatic zones

During 2010–2018, the zone with 100–400 mm annual precipitation was the largest on the Tibetan Plateau, reaching 1,124,400 km² and accounting for 46.8% of the Tibetan Plateau area; the zone with > 500 mm annual precipitation was the second largest, reaching 833,400 km² and accounting for 32.1% of the Tibetan Plateau area (Table 1; Supplementary materials online).

The zone with 400–500 mm annual precipitation was 244,200 km² for the average July temperature ≤ 9 °C and 167,800 km² for the average July temperature > 9 °C, totally accounting for 15.9% of...
the Tibetan Plateau area. The area of zone with ≤ 100 mm annual precipitation was the least on the Tibetan Plateau (5.1%), which was 2900 km² for the average July temperature ≤ 9 °C or 118,000 km² for the average July temperature > 9 °C.

Regarding distribution of grassland types and major formations in climate zones, except for drought conditions (the annual precipitation ≤ 100 mm), the alpine grassland area for the average July temperature > 9 °C is smaller than that for the average July temperature ≤ 9 °C (Supplementary materials online).

In all climate zones, proportions of alpine meadows in alpine grasslands are consistently higher than that of alpine steppes (Fig. 2). In zones with 100–500 mm annual precipitation (100–400 and 400–500 mm) and the average July temperature > 9 °C, proportions of alpine steppes in alpine grasslands are the highest (41%–44%), while proportions of alpine meadows are < 60% (56%–59%). In the rest zones, proportions of alpine meadows in alpine grasslands generally exceed 70% (69%–76%), and even reach 90% when the annual precipitation ≤ 100 mm.

**Table 1**

<table>
<thead>
<tr>
<th>Climate zone</th>
<th>Climate zone area (km²)</th>
<th>Changing rate (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Climate zone</td>
<td>1979–1990</td>
<td>2010–2018</td>
</tr>
<tr>
<td>$P_{avg}$ (mm)</td>
<td>$T_{avg}$ (°C)</td>
<td></td>
</tr>
<tr>
<td>≤ 100</td>
<td>≤ 9</td>
<td>271,473</td>
</tr>
<tr>
<td>≤ 100</td>
<td>&gt; 9</td>
<td>237,458</td>
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<td>49,279</td>
</tr>
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<td>≤ 9</td>
<td>447,960</td>
</tr>
<tr>
<td>&gt; 500</td>
<td>&gt; 9</td>
<td>254,326</td>
</tr>
</tbody>
</table>
Proportions of the *K. pygmaea* formation in alpine meadows are relatively stable in all climate zones (Fig. 3). However, they slightly decrease with decreasing precipitation, from 77% to 83% (> 400 mm annual precipitation) to 73% (100–400 mm annual precipitation). Similarly, proportions of the *S. purpurea* formation in alpine steppes are also relatively stable in all climate zones, with a slightly increasing trend with decreasing precipitation, ranging from 87% (> 500 mm annual precipitation) to 91%–93% (400–500 mm annual precipitation) and to 91%–96% (100–400 mm annual precipitation). Distributions of *K. pygmaea* and *S. purpurea* formations are almost negligible in zones with ≤ 100 mm annual precipitation.

### 3.2. Historical changes in climate zone areas

For historical changes over the past 40 years, features of formation-based plant community structure during 2010–2018 were compared with the Vegetation Map of China with the proportional scale of 1:1,000,000 [18,19] reflecting the vegetation status during 1979–1990. To begin with, we compared climate zone changes during two temporal spans, namely 2010–2018 and 1979–1990 (Table 1), which well reflected the warming and wetting trends on the Tibetan Plateau (Supplementary materials online).

In addition, compared to 1979–1990, the average precipitation increased in zones with annual precipitation ≤ 400 mm in 2010–2018, but average July temperature tended to be stable with annual precipitation of 100–400 mm or increased with annual precipitation ≤ 100 mm. In zones with annual precipitation of 100–400 mm, their average annual precipitation increased by 15.7%–32.9% (34.9–75.49 mm) for average July temperature > and ≤ 9 °C, while their average July temperature largely remained unchanged (<5%). In zones with annual precipitation ≤ 100 mm, their average annual precipitation increased by 16.5%–32.9% (10.1–23.02 mm) for average July temperature > and ≤ 9 °C, while their average July temperature increased by 11.8%–20.8% (0.62–2.94 °C). However, in zones with precipitation > 400 mm, their annual precipitation slightly decreased or remained unchanged (–3.7%–0.8%, –31.82–3.79 mm), while their average July temperature tended to decrease by –0.6%–3.5% (–0.04–0.47 °C) if average July temperature > 9 °C or increase by 9.6%–11.6% (0.58–0.68 °C) if average July temperature ≤ 9 °C (Table 2).

### 3.3. Historical changes in formation-based plant community structure

For historical changes over the past 40 years, features of formation-based plant community structure during 2010–2018 were compared with the Vegetation Map of China with the proportional scale of 1:1,000,000 [18,19] reflecting the vegetation status during 1979–1990. To begin with, we compared climate zone changes during two temporal spans, namely 2010–2018 and 1979–1990 (Table 1), which well reflected the warming and wetting trends on the Tibetan Plateau (Supplementary materials online).

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### Fig. 3. Dominance of specific formations in alpine steppes and meadows. (a) The distribution of five most dominant formations in 1979–1990. (b) The distribution of five most dominant formations in 2010–2018. (c) Proportions of *Kobresia pygmaea* in alpine meadows. (d) Proportions of *Stipa purpurea* in alpine steppes.

Table 2

<table>
<thead>
<tr>
<th>Climate zone</th>
<th>Changing value</th>
<th>Changing rate (%)</th>
</tr>
</thead>
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<tr>
<td>$P_{avg}$ (mm)</td>
<td>$T_{avg}$ (°C)</td>
<td>$P_{avg}$ (mm)</td>
</tr>
<tr>
<td>≤100</td>
<td>≤9</td>
<td>23.02</td>
</tr>
<tr>
<td>&gt;100</td>
<td>&gt;9</td>
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<tr>
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<td>75.49</td>
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<tr>
<td>100 &lt; $P_{avg}$ ≤400</td>
<td>&gt;9</td>
<td>34.90</td>
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<tr>
<td>400 &lt; $P_{avg}$ ≤500</td>
<td>≤9</td>
<td>3.79</td>
</tr>
<tr>
<td>400 &lt; $P_{avg}$ ≤500</td>
<td>&gt;9</td>
<td>-4.50</td>
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<td>-0.25</td>
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<tr>
<td>&gt;500</td>
<td>&gt;9</td>
<td>-31.82</td>
</tr>
</tbody>
</table>

were compared with the Vegetation Map of China with the proportional scale of 1:1,000,000 [18,19]. Such comparison provides indicative information for historical changes of formation-based plant community structure in the Tibetan Plateau grasslands over the past 40 years.

Compared to 1979–1990, the alpine grassland area on the Tibetan Plateau increased from 1,245,100 to 1,415,800 km² in our newly developed vegetation map representing the status in 2010–2018, with an increasing percentage of 14% (170,700 km²). However, changes of alpine grassland area were inconsistent in various climate zones. Increases of alpine grassland area were weakened with decreases of average July temperature and annual precipitation, and areas of some specific zones even decreased. Specifically, with annual precipitation > 400 mm, the alpine grassland area increased by 309%–868% (110,200–139,100 km²) in zones for average July temperature > and < 9 °C, respectively; while proportions of alpine meadows decreased to 76% and 74% in 2010–2018 for average July temperature > and < 9 °C, respectively. With annual precipitation of 400–500 mm, alpine grasslands were dominated by alpine meadows in 1979–1990, reaching 80% and 83% of alpine grasslands when the average July temperature was > and < 9 °C, respectively; while proportions of alpine meadows reduced to 59% and 69% in 2010–2018 when the average July temperature was > and < 9 °C, respectively.

3.3.1. Increased proportions of alpine meadows in alpine grasslands

Compared with 1979–1990, the proportion of alpine meadows in alpine grasslands increased from 50% to 69% in our newly developed vegetation map representing the status in 2010–2018 (Fig. 2). Accordingly, the proportion of alpine steppes decreased from 50% to 31%. Moreover, high heterogeneity in various climate zones was observed for changes in the proportion of alpine meadows or alpine steppes. With annual precipitation ≤400 mm, alpine grasslands were dominated by alpine steppes in 1979–1990, while they were dominated by alpine meadow in 2010–2018. With annual precipitation > 400 mm, the dominance of alpine meadows decreased from 1979 to 1990 to 2010–2018.

In zones with annual precipitation of 100–400 mm, alpine grasslands were dominated by alpine steppes in 1979–1990, accounting for up to 75% and 65% of alpine grasslands when the average July temperature was > and ≤9 °C, respectively; while alpine meadows turned to dominate in 2010–2018, increasing to 56% and 74% of alpine grasslands when the average July temperature was > and ≤9 °C, respectively. In zones with annual precipitation ≤100 mm, alpine grasslands were also dominated by alpine steppes in 1979–1990 when the average July temperature was > and ≤9 °C, accounting for up to 86% and 94% of alpine grasslands, respectively; while alpine meadows became dominant in 2010–2018, increasing to 90% and 98% of alpine grasslands when the average July temperature was > and ≤9 °C, respectively.

3.3.2. Intensified dominance of specific formations in alpine steppes and meadows

Compared with 1979–1990, proportions of S. purpurea formation increased from 60% to 92% of alpine steppes in 2010–2018, and proportions of K. pygmaea formation in alpine meadows increased from 71% to 76% (Fig. 3). In 1979 to 1990, proportions of dominant formations in alpine meadows or alpine steppes greatly varied in different climate zones. In alpine steppes, proportions of S. purpurea formation increased with the decreasing precipitation. Specifically, in zones with July temperature > 9 °C, proportions of S. purpurea formation were 3% with annual precipitation > 500 mm, 49% with annual precipitation of 400–500 mm, 85% with annual precipitation of 100–400 mm, and 76% with annual precipitation ≤ 100 mm. In zones with July temperature ≤ 9 °C, its proportions were 48% with annual precipitation > 500 mm, 75% with annual precipitation of 400–500 mm, 64% with annual precipitation of 100–400 mm, and 82% with annual precipitation ≤ 100 mm.

Except the condition with annual precipitation ≤ 100 mm, proportions of K. pygmaea formation in alpine meadows were lower in zones for average July temperature > 9 °C than ≤ 9 °C, and tended to increase with the decreasing precipitation. Specifically, in zones with July temperature > 9 °C, proportions of K. pygmaea formation were 32% with annual precipitation > 500 mm, 65% with annual precipitation of 400–500 mm, and 56% with annual precipitation of 100–400 mm. In zones with July temperature ≤ 9 °C, its proportions were much higher, i.e., 70% with annual precipitation > 500 mm, 77% with annual precipitation of 400–500 mm, and 83% with annual precipitation of 100–400 mm. With annual precipitation ≤ 100 mm, proportions of Kobresia pygmaea formation were 11% and 42% when average July temperature in July was > and ≤ 9 °C, respectively. However, regarding its area, K. pygmaea formation was almost absent with annual precipitation ≤ 100 mm.

In the vegetation map developed in this study as described in Section 3.1.2, proportions of major formations in alpine meadows or alpine steppes for 2010–2018 were highly consistent in different
climate zones. The *K. pygmaea* formation accounted for 73%–83% of the alpine meadow area in all climate zones, though tended to decrease slightly with decreasing precipitation. Similarly, *S. purpurea* formation accounted for 87%–96% of the alpine steppe area in all climate zones, with a slightly increasing trend with decreasing precipitation. With annual precipitation ≤ 100 mm, distributions of *K. pygmaea* and *S. purpurea* formations were minimal or almost absent.

4. Discussion

Beyond remote sensing indicators (e.g., normalized difference vegetation index (NDVI) [56], leaf area index (LAI), and net primary productivity (NPP)) which only recognize vegetation productivity, we utilized multivariate data fusion and deep learning to characterize formation-based plant community structure in alpine grasslands at the regional scale of the Tibetan Plateau for the first time. This exploration would benefit future large-scale vegetation-related studies, e.g., providing a basis for more accurate evaluations of soil carbon input from plants, whose stability or adaption to environmental disturbance, is important for soil carbon stability. Also, its comparison with the earlier version of Vegetation Map of China (1:1,000,000) enabled us to explore historical changes of grassland vegetation structure. Alpine grasslands on the Tibetan Plateau have changed dramatically over the past 40 years [54] with a clear greening trend at the regional scale based on vegetation productivity by remote sensing technologies [54,57,58]. However, due to methodological issues, characterizing structural information of plant communities at large scales in the Tibetan Plateau grasslands had been previously impossible [54]. Integrating ground survey, remote sensing data, and artificial intelligence, this study is the first attempt to investigate changes in formation-based plant community structure in the Tibetan Plateau grasslands over the past 40 years. Our study found that underlying mechanisms of grassland changes over the past 40 years were formation dependent and varied by vegetation classification levels (e.g., grassland type and formation).

4.1. Climate factors dominated grassland type distribution pattern and its change over 40 years

From the perspective of grassland type, climate factors dominated its recent distribution pattern on the Tibetan Plateau, and led to the increased proportion of alpine meadows in alpine grasslands over the past 40 years. As revealed in this study, the alpine grassland area during 2010–2018 was higher in climate zones with lower growing season temperature (average July temperature ≤ 9 °C) than with lower growing season temperature (average July temperature > 9 °C). Moreover, the proportion of alpine meadows in alpine grasslands increased from 50% during 1979–1990 to 65% during 2010–2018, well-reflecting the warming and wetting trend of climate changes. Vegetations on the Tibetan Plateau have been reported to highly depend on specific climatic conditions and therefore sensitive to climate changes [59]. Consistently, local ground studies also observed shifts from alpine steppes to alpine meadows under warming and wetting [60], driven by enhanced hydrothermal conditions [60,61]. With decreasing precipitation and temperature, the plant community structure was simplified in alpine grasslands and shifted from alpine meadows to alpine steppes [60,62–65]. By increasing the dominance of warm-adapted plant species but decreasing or even eliminating that of cold-adapted species, warming altered the pattern of plant community structure on the Tibetan Plateau [66]. Climate factors also well explained the heterogeneity in proportion changes of alpine meadows in various climate zones (Fig. S4 online). Over the past 40 years, the dominated type of alpine grasslands shifted from alpine steppes to alpine meadows with annual precipitation ≤ 400 mm, while the proportion of alpine meadows decreased with annual precipitation > 400 mm, though still being dominated. Compared to 1979–1990, the average precipitation increased in climate zones with precipitation ≤ 400 mm during 2010–2018, but the average July temperature tended to remain unchanged (with annual precipitation of 100–400 mm) or increase (with annual precipitation ≤ 100 mm). In those climate zones, enhanced hydrothermal conditions may lead to the shift of dominated grassland type from alpine steppe to alpine meadows [60,61]. Consistently, shifts from alpine steppes to alpine meadows mostly occurred in areas with increased precipitation and more frequently in areas with increased temperature. In contrast, the average precipitation in climate zones with precipitation > 400 mm tended to slightly decrease, likely responsible for the decreased proportion of alpine meadows in alpine grasslands, though keeping dominated. Moreover, the shift from alpine meadows to alpine steppes may also imply intensified grazing pressure [67].

4.2. Various drivers for historical changes of *S. Purpurea* and *K. Pygmaea* formations over 40 years

At the formation level, information of plant community structure changes provides a new perspective to understand drivers of grassland changes and its spatial heterogeneity, likely reconciling the controversy in relative contributions of climate change and human activities to alpine grassland changes on the Tibetan Plateau [68,69]. Climate factors may drive the increased dominance of *S. purpurea* formation in alpine steppes over the past 40 years as its proportions of *S. purpurea* formation tended to increase with decreasing precipitation in all climate zones during both 1979–1990 and 2010–2018. As a xerophyte [70,71], the expansion of *S. purpurea* well reflects the climate change trend in these zones. The vegetation status during 1979–1990 represents the condition with less grazing intensity. Thus, the consistent trends for *S. purpurea* formation during 1979–1990 and 2010–2018 indicate the major impact of climate factors on it. However, climate factors may not be responsible for the increased dominance of *K. pygmaea* formation in alpine meadows. Its proportions tended to increase with decreasing precipitation in all climate zones during 1979–1990, while an opposite trend was observed during 2010–2018. This phenomenon implied that the proportion of *K. pygmaea* formation may be determined by factors other than climate elements in the new era. Using the growing season precipitation as the dominant factor to determine the distribution of *K. pygmaea* formation, the maximum entropy model predicted that the distribution area of *K. pygmaea* was 434,900 km² [72], dramatically different from what was obtained by our newly developed vegetation map (742,900 km²). Such discordance also indicated that the distribution of *K. pygmaea* was not climatically dominated in recent decades. Rather, grazing pressure or even overgrazing may contribute to the widespread distribution of *K. pygmaea* formation on the Tibetan Plateau during 2010–2018. Consistently, local ground investigations found that Gramineae grass-*K. humilis* formation would succeed to *K. humilis* formation when subjected to a certain degree of grazing, and continue (e.g., 4–5 years) to succeed to *K. pygmaea* formation under higher grazing pressure or even overgrazing [73,74]. In this way, structural information of plant community is critical for explaining the heterogeneity of alpine grassland changes on the Tibetan Plateau [54] since their driving mechanisms vary by formations.

4.3. Technology innovation and limitation

In this study, we developed a method integrating with ground survey, remote sensing data, and artificial intelligence to characterize formation-based plant community structure in alpine...
grasslands at the regional scale. Traditional vegetation mapping highly relies on ground surveys and expert knowledge, and it is hard to update rapidly and duly. Ground survey combined with expert judgment is useful to recognize formations, which is only suitable at small scales or needs enormous datasets at large scales [26,27]. Compared with these methods, this study introduced time series data based on cloud computing, though greatly increasing the workload of computation. These time-varying features are particularly useful to distinguish different plant formations that are similar at one point in time but with different growth and habitat profiles, and to distinguish different grassland types that are “on the same spectrum”. In addition to the improvement of the classification accuracy, our method is also time-efficient and scalable, allowing rapid updating of the vegetation map when more ground data points are added [75]. Thus, we have already created a website to achieve crowd acquisition (https://imap.ucas.ac.cn).

However, this method also has some limitations or uncertainties. The accuracy of deep learning highly depends on the representativeness of different formation types based on training samples, which might be still insufficient for some formation types. However, the crowd acquisition may supplement more data for improving its accuracy. Moreover, soil factors could be important for influencing plant community structure. In this study, only soil moisture data were available at the regional level with similar temporal and spatial resolutions to those of adopted data. Unfortunately, the most of other soil physical and chemical properties were not included in the deep learning model of this study because they were hard to obtain at the regional level with comparable temporal and spatial resolutions. Furthermore, we adopted the updated classification system as in the revised scheme of vegetation classification system of China [7], different from the classification system of Vegetation Map of China (1:1,000,000) [55]. This made the comparison between two Vegetations becoming challenging and time-consuming. Two vegetation map classification systems were developed by the same team and their differences are previously discussed in details [7].

5. Summary

Our study for the first time explored the structural information of plant community changes, providing a new perspective to understand drivers of grassland changes and their spatial heterogeneity at the regional scale of the Tibetan Plateau. Climatic factors mainly drove increased proportion of alpine meadows in alpine grasslands over the past 40 years and the intensified dominance of S. purpurea formation in alpine steppes. However, increased dominance of K. pygmaeae formation in alpine meadows was not driven by climate factors alone and human activities such as grazing may be critical. Thus, underlying mechanisms of grassland changes over the past 40 years were formation dependent, because responses and adaptations of various formations to climate change and human activities differed. This first exploration for structural information of plant community changes at the regional scale of the Tibetan Plateau would innovate large-scale vegetation study paradigm, going beyond remote sensing indicators alone.

Conflict of interest

The authors declare that they have no conflict of interest.

Acknowledgments

This work was supported by the Second Tibetan Plateau Scientific Expedition and Research Program (2019QZXK0304-02), Joint Chinese Academy of Sciences (CAS)-Max Planck Society (MPG) Research Project (HZXM20225001MI), the Strategic Priority Research Program A of Chinese Academy of Sciences (XDA20050104), the National Natural Science Foundation of China (42041005), CAS Light of West China Program, and the Fundamental Research Funds for the Central Universities.

Appendix A. Supplementary materials

Supplementary materials to this article can be found online at https://doi.org/10.1016/scib.2023.07.035.

References

[9] Chen ZZ, Wang YF, Wang SP, et al. Preliminary studies on the classification of vegetation of China [7], different from the classification system of Vegetation Map of China (1:1,000,000) [55]. This made the comparison between two Vegetations becoming challenging and time-consuming. Two vegetation map classification systems were developed by the same team and their differences are previously discussed in details [7].