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RESEARCH

Contrasting range changes of *Bergenia* (Saxifragaceae) species under future climate change in the Himalaya and Hengduan Mountains Region

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Abstract

The Himalaya and Hengduan Mountains (HDM) are recognized as two global biodiversity hotspots, harboring the world's richest alpine flora. However, to what extent the distribution of alpine plants here is affected by climate change remains largely unknown. *Bergenia* (Saxifragaceae) are perennial medicinal herbs mainly distributed in the Himalaya-HDM region. In this study, we used bioclimatic data for current and future climate scenarios to assess the impact of climate change on the potential distribution of three *Bergenia* (Saxifragaceae) species. Our results revealed that the geographical distribution of the studied *Bergenia* species is primarily influenced by precipitation and elevation. By 2090, the three *Bergenia* species are expected to show contrasting range changes. The western Himalayan alpine species *Bergenia stracheyi* is expected to expand its range with 21.93 and 17.36% under the optimistic (SSP1-2.6) and moderate (SSP2-4.5) climate change scenario, respectively, while its distribution will shrink by 5.26% under the pessimistic scenario (SSP5-8.5). The Himalayan mid-elevation species *B. ciliata* is expected to expand its range from 142.42 to 157.14%. In contrast, the distribution range of the east Himalaya-HDM alpine species *B. purpurascens* is expected to shrink with 34.88 to 47.24%, with most of the habitats in the southeast chains of the HDM at lower elevation summits being lost. In addition, all three *Bergenia* species are projected to shift their ranges to higher elevations in response to temperature increases. Overall, we conclude that alpine plants may be more vulnerable to climate change than their congeners at lower elevations, supporting the "nowhere to go" hypothesis.

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1 Introduction

Climate change is expected to have a profound impact on the distribution of species, most likely shifting species towards higher latitudes and elevations in response to warming temperatures. However, the rate at which species undergo these shifts varies greatly (Chen et al. 2011a, b; Román-Palacios and Wiens 2020). Mountain regions are known for their high levels of biodiversity and endemism (López-Pujol et al. 2011; Rahbek et al. 2019; Ding et al. 2020), with endemism often increasing with elevation (Steinbauer et al. 2016). However, plants at high elevations in mountain systems are particularly vulnerable to climate change due to limited space for dispersal and establishment (Dullinger et al. 2012). This vulnerability is referred to as the "nowhere to go" hypothesis (Loarie et al. 2009).

Comparisons of historical and recent plant surveys in the European Alps have shown a significant upward shift in the elevation ranges (including highest, optimum, and average ranges) of plant species during the last century, coupled with an increase in species richness at high elevations (Walther et al. 2005; Lenoir et al. 2008; Pauli et al. 2012; Rumpf et al. 2018). Therefore, alpine plant species face the dual pressure of climate change and competition with species from lower elevations (Walther et al. 2005; Rumpf et al. 2018). Plant species with narrow distribution ranges at high elevations are considered particularly vulnerable to climate change (Dullinger et al. 2012; Wani et al. 2022). However, it still needs to be understood whether alpine plant species are more vulnerable to climate change than their congeners at lower elevations.

The Tibetan Plateau and the adjacent mountain regions constitute the highest and most expansive upland area on Earth and are often referred to as the third pole (Liu et al. 2022). Over the past few decades, the rate of temperature increase on the Tibetan Plateau has exceeded that of the Northern Hemisphere and other regions at the same latitudinal zone (Liu and Chen 2000; Yao et al. 2012). In contrast with plants in the European Alps, climate change has more complicated effects on the flowering phenology and species distribution of plants on the Tibetan Plateau (Gaira et al. 2011; Gaira and Dhar 2020; Wang et al. 2022b; Zu et al. 2023ab). Climate change has advanced the flowering phenology of some plants, while delaying that of others (Gaira et al. 2011; Gaira and Dhar 2020; Zu et al. 2023a). Some plants have shifted upwards, while some other plants have shifted downwards (Wang et al. 2022b; Zu et al. 2023b).

The Himalaya and the Hengduan Mountains Region (HDM), two neighboring mountain ranges that are part of the Tibetan Plateau sensu lato (Liu et al. 2022), are recognized as global biodiversity hotspots (Myers et al. 2000; Mittermeier et al. 2011). These mountain ranges harbor the world's richest alpine flora and numerous endemic species (López-Pujol et al. 2011; Li et al. 2014; Sun et al. 2017; Ding et al. 2020). More specifically, the HDM has about 3000 species of alpine seed plants (Li et al. 2014), accounting for approximately 30% of all alpine plant species worldwide. The HDM primarily consists of north–south mountain ranges and rivers, serving as a corridor for plant migration along elevation and latitude in response to climate change (Muellner-Riehl 2019; Wang et al. 2020). The Himalaya extends from northwest to southeast, featuring the cold and dry Tibetan Plateau in the north and the hot and moist Indian subcontinental plain in the south. It is believed that the distribution of most alpine plants is restricted to this region (Huang et al. 2008; Muellner-Riehl 2019). However, we still do not know how climate change affects the geographical distribution of plant species in these two regions and whether all species will respond in similar way to climate change remains limited. Given the pronounced differences in topography and the high level of endemic plant diversity in these alpine mountains, they serve as an ideal study system for investigating the vulnerability of plant species with different elevations and geographical ranges to climate change and for testing the "nowhere to go" hypothesis.

The genus *Bergenia* Moench (Saxifragaceae) consists of perennial plants that are distributed across the Himalaya-HDM and adjacent regions. The genus comprises ten species, eight of which are native to China. *Bergenia purpurascens* (Hook.f. & Thomson) Engl. and *B. scopulosa* T. P. Wang are traditional Chinese medicinal plants. Additionally, *B. stracheyi* (Hook. f. et Thoms.) Engl. and *B. ciliata* (Haw.) Sternb. are medicinal plants that occur primarily in the Himalaya (Pan and Soltis 2001; Hou et al. 2021; Shrestha et al. 2022). Plants of the genus *Bergenia* contain bergenin, a trihydroxybenzoic acid glycoside that is used to treat respiratory diseases and stomach disorders (Li et al. 2006; Rafi et al. 2021). Most *Bergenia* species have a narrow distribution with few occurrence records except for *B. stracheyi*, *B. ciliata*, and *B. purpurascens*. *Bergenia stracheyi* is found in the western Himalaya, *B. ciliata* in the Himalaya, and *B. purpurascens* is mainly distributed in the HDM, extending to the eastern Himalaya (Fig. 1). Both *B. stracheyi* and *B. purpurascens* are typical alpine plants, with *B. purpurascens* occurring at significantly higher elevations than *B. stracheyi*. On the other hand, *B. ciliata* is found at significantly lower elevations compared to its two congeners (Fig. S1). Unfortunately, populations of the three *Bergenia* species have experienced dramatic declines in recent decades due to overexploitation for medicinal purposes (Tiwari et al. 2015).

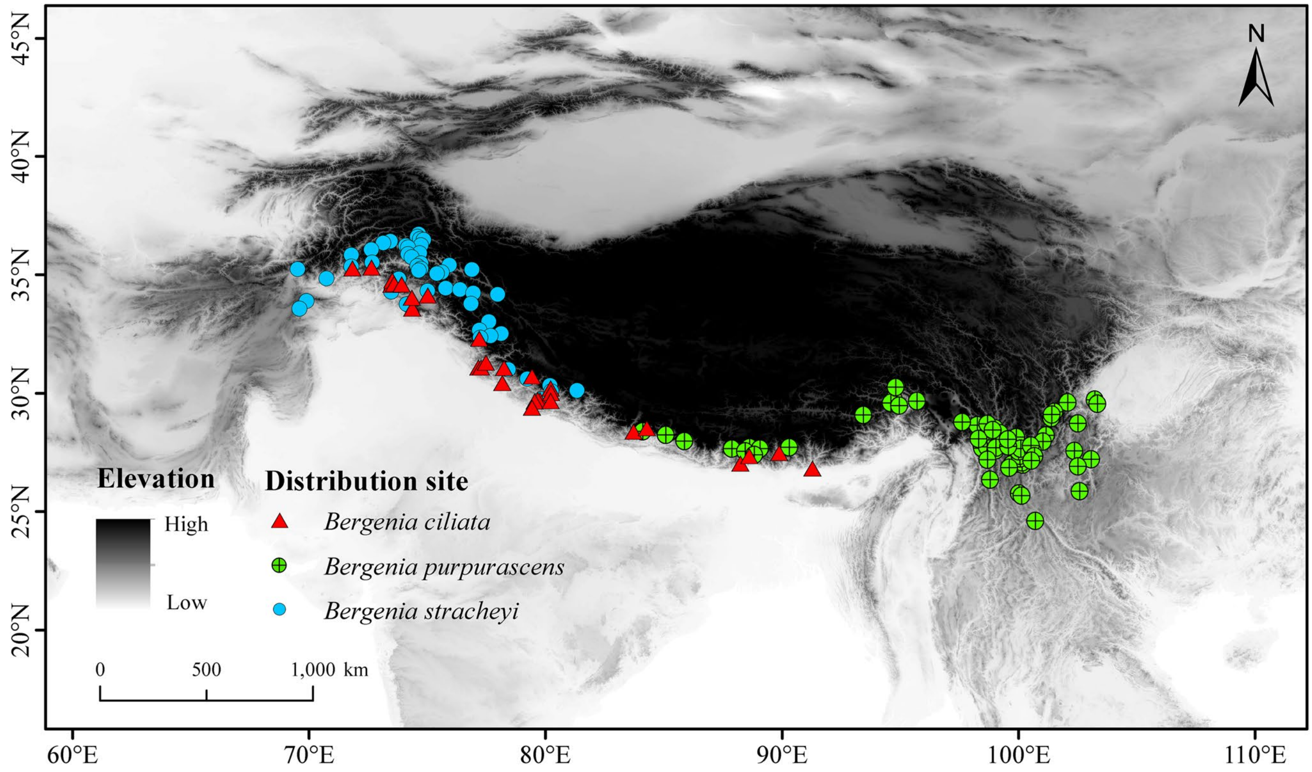

Fig. 1 Occurrences of *Bergenia stracheyi*, *B. ciliata*, and *B. purpurascens* in the Hengduan Mountains Region and the Himalaya

Ecological niche modeling is widely used to predict the potential habitat area of species under current and future climate scenarios, providing valuable information for biodiversity conservation and management. Biologists have paid significant attention to the impact of climate change on the distribution of mountain plants. For instance, Engler et al. (2011) assessed the effects of future climate change on 2632 plant species across all major European mountain ranges. They showed that species at higher elevations will lose more habitat. Similarly, Liang et al. (2018) modeled the potential distributions of 151 plant species in the HDM. They showed a general trend of species shifting towards higher elevations and latitudes, with plants at high elevations expanding their range size. In another study, Shrestha et al. (2022) modeled the distribution change of 29 medicinal and aromatic plants in the Nepal Himalaya. They concluded that future climate change could reduce climatically suitable areas for two-thirds of the studied species.

In this study, we applied the MaxEnt model to predict the potential distribution of *B. stracheyi*, *B. ciliata*, and *B. purpurascens* under current and future climate change scenarios. Specifically, the objectives are as follows: (1) to identify the critical environmental factors limiting the potential distribution of *B. stracheyi*, *B. ciliata*, and *B. purpurascens*; (2) to assess the effects of future climate change on the geographic range changes of these three *Bergenia* species; and (3) to investigate the validity of the "nowhere to go" hypothesis. This study will provide valuable insights for conserving and managing these three medicinal plant species and enhance our understanding of the vulnerability of alpine plants across varying elevations and geographical ranges in the Himalaya and HDM under climate change.

2 Materials and methods

2.1 Species distribution data

We obtained species occurrence records for all species of *Bergenia* from various sources, including the Chinese Virtual Herbarium (http://www.cvh.ac.cn/), Global Biodiversity Information Facility (https://www.gbif.org/), National Specimen Information Infrastructure (http://www.nsii.org.cn), published literature, and our own field collections, yielding a total of 2165 original distribution records for the three target species (*B. stracheyi*—259, *B. ciliata*—232, and *B. purpurascens*—1674). Records were removed from the dataset when (1) they were duplicates, (2) had no spatial coordinates or specific locations, (3) showed obvious identification errors, or (4) an unreliable distribution (Qiu et al. 2023). To mitigate the effects of spatial autocorrelation and potential overfitting, we retained only one occurrence record within a 5-km radius. Our final dataset for species distribution modeling included 48 occurrence records for *B. stracheyi*, 29 records for *B. ciliata*, and 70 records for *B. purpurascens* (Fig. 1).

2.2 Environmental data

We downloaded current (1970–2000) and future (2090, average of 2081–2100) bioclimatic variables (Table S1) at a 2.5 arc-min spatial resolution from the WorldClim database v2.1 (https://www.worldclim.org/). The future climate scenarios used in the study were derived from CMIP6, as presented in the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC6). We selected the Global Circulation Model BCC-CSM2-MR (Wu et al. 2019; Ren et al. 2021), with a focus on the period of 2081–2100 in the SSP1-2.6, SSP2-4.5, and SSP5-8.5 scenarios. Furthermore, we downloaded the elevation layer from the Geospatial Information Authority of Japan (https://globalmaps.github.io/el.html). Then, we extracted slope and aspect from the elevation layer using ArcGIS 10.6. To ensure operability of the model, all the layers were cut and standardized to the same resolution (2.5 arc-min) using a mask suited to the species distribution zone (60° E-110° E, 18° N-45° N) with the same coordinate system (WGS 1984).

2.3 Correlation analysis and screening of environmental variables

To avoid distortion of MaxEnt model estimation caused by multicollinearity among the bioclimatic variables, we performed a Pearson correlation test for the 19 bioclimatic variables (Fig. S2). We selected one bioclimatic variable with a higher percent contribution among any pair of variables with Pearson's r greater than 0.8 (Yang et al. 2013, 2020). Following this procedure, we selected ten environmental variables for modeling the distribution of *B. purpurascens*. These variables included mean diurnal range (Bio2), isothermality (Bio3), temperature annual range (Bio7), mean temperature of coldest quarter (Bio11), precipitation seasonality (Bio15), precipitation of driest quarter (Bio17), precipitation of warmest quarter (Bio18), elevation, slope, and aspect. For modeling the distributions of *B. ciliata*, we also used ten environmental variables. These variables comprised the annual mean temperature (Bio1), Bio2, temperature seasonality (Bio4), mean temperature of the wettest quarter (Bio8), precipitation of driest month (Bio14), Bio17, Bio18, elevation, slope, and aspect. Similarly, we used ten environmental variables for modeling the distributions of *B. stracheyi*. These variables included Bio2, Bio3, Bio8, mean temperature of driest quarter (Bio9), Bio14, Bio15, Bio18, elevation, slope, and aspect.

2.4 Model development and evaluation

The filtered occurrence records and environmental variables were imported into samples and environmental layers, respectively, in MaxEnt version 3.4.1. The relative importance of predictor variables was assessed using the jackknife method. We randomly selected 25% of the data for testing and 75% for training. A total of 10 runs were conducted to build the model (Dad and Rashid 2022).

To determine the suitable and unsuitable regions for the species, we followed the methodology described in Qiu et al. (2023). We reclassified the MaxEnt output file using the 10-percentile training presence logistic threshold value (TH) (Radosavljevic and Anderson. 2014; Hughes et al. 2017). We combined the average value of TH output by MaxEnt with the classification criteria of IPCC to classify the potential habit into three categories: unsuitable area (< threshold), suitable area (threshold to 0.66), and highly suitable area (> 0.66). Similar methods for classifying suitable habitats have been applied in previous studies (Duan and Zhou 2012; Shi et al. 2021).

To assess changes in the extent of suitable habitat under different emission scenarios in the future compared to the present, we calculated the contraction, expansion, and unchanged areas using the "distribution changes between binary SDMs" tools from the SDM toolbox v2.4. The "centroid changes clines" tool from the SDM toolbox was used to predict the centroid of the distribution area of each species and the moving direction and amplitude of suitable areas under different climate scenarios in the future (Brown 2014).

The accuracy of the predictive model was evaluated using the area under the receiver operating characteristic (ROC) curve (AUC) (Lobo et al. 2008). The AUC value ranges from 0 to 1, which is categorized as excellent (0.9–1), good (0.8–0.9), fair (0.7–0.8), poor (0.6–0.7), and failing (0.5–0.6) (Swets 1988; Elith et al. 2006). Percent contribution and jackknife test were used to evaluate the importance of environmental variables contributing to the observed species distribution (Phillips et al. 2009).

We used the centroid's longitude and latitude to represent the species' average longitude and latitude. The average elevation of the highly suitable area of the species was used to describe the average elevation of the suitable area of this species. First, we used the "extract by attributes" tool to extract the highly suitable area layer from the result layer after suitable area classification and converted this into a surface. We then use the "mask extraction" tool to extract the elevation of the highly suitable area and

Table 1 AUC mean value of the simulated distribution of *Bergenia stracheyi*, *B. ciliata*, and *B. purpurascens* under current and three climate change scenarios in 2090

Species	Current	2090		
		SSP1-2.6	SSP2-4.5	SSP5-8.5
Bergenia purpurascens	0.9862	0.9866	0.9865	0.9861
Bergenia ciliata	0.9927	0.9924	0.9925	0.9922
Bergenia stracheyi	0.9749	0.9746	0.9766	0.9761

calculated for each the average elevation of the highly suitable area.

3 Results

3.1 Main environmental variables determine species distribution

The AUC values for all models in this study were greater than 0.97, indicating excellent model performance (Table 1). For *B. stracheyi*, precipitation seasonality (Bio15), elevation, slope, and mean diurnal range (Bio2) were the main environmental variables determining its geographical distribution (Fig. 2, Table S2). When used in isolation, the environmental variable that best explained the distribution of the species was precipitation seasonality (Bio15) (Fig. S3).

For *B. ciliata*, precipitation of the driest quarter (Bio17) was the most important environmental variable determining its geographical distribution, with elevation ranking as the second important environmental variable (Fig. 2, Table S3). Precipitation of the driest quarter (Bio17) was the environmental variable with the highest gain when used in isolation (Fig. S3).

For *B. purpurascens*, precipitation of the warmest quarter (Bio18), elevation, and temperature annual range (Bio7) were the main environmental variables influencing its distribution (Fig. 2, Table S4). Temperature annual range (Bio7) was the environmental variable with the highest gain when used in isolation (Fig. S3).

The relationship between a species' existence probability and environmental factors can be assessed using the environmental response curve drawn by MaxEnt. When the existence probability is greater than 0.5, the corresponding environmental factors are suitable for

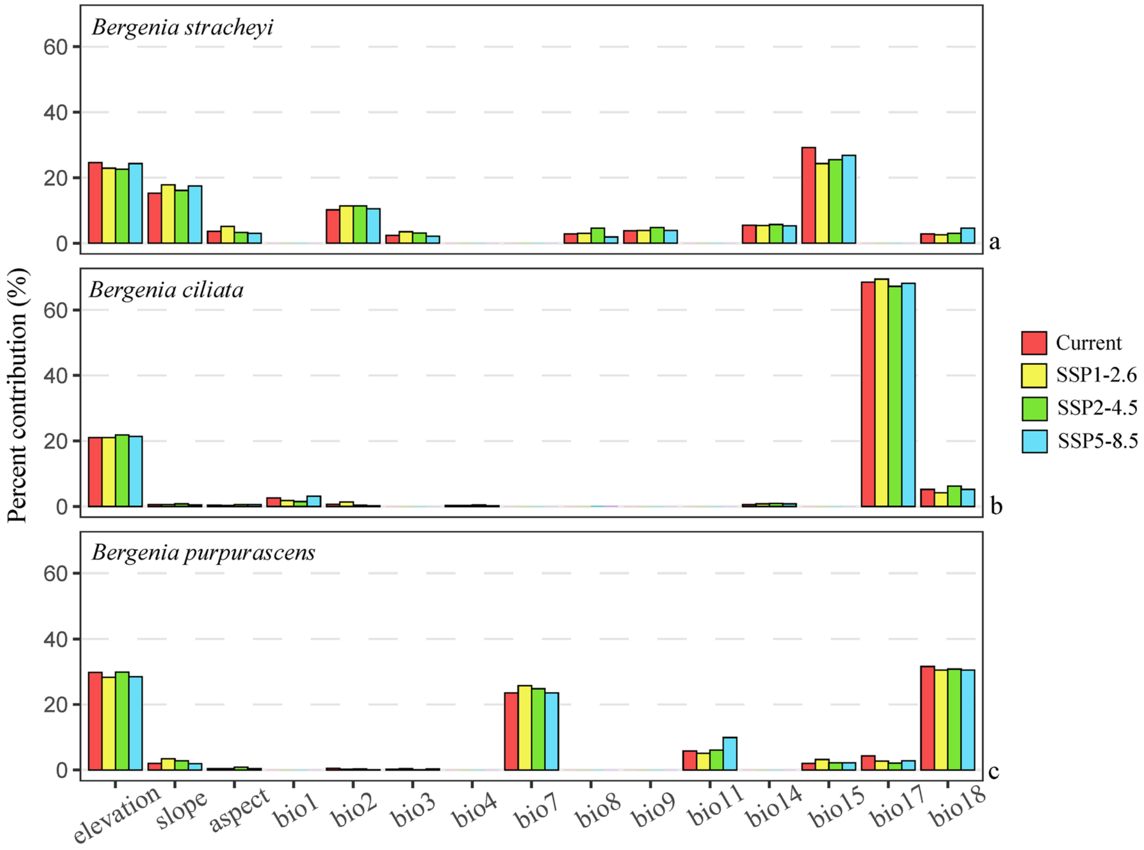

Fig. 2 Percent contribution of environmental variables to explaining the distributions of *Bergenia stracheyi* (**a**), *B. ciliata* (**b**), and *B. purpurascens* (**c**) under current climate and three future climate change scenarios

plant growth (Yan et al. 2021). The suitable ranges of the main environmental variables for the three *Bergenia* species are as follows: for *B. stracheyi*, suitable habitat has a precipitation seasonality that ranges from 37.19 to 57.37, elevation that varies between 2794.74 and 4546.81 m, a slope between 4.13 and 16.85°, and a mean diurnal temperature range between 9.72 and 11.70 °C (Fig. S4). The most important variables affecting the occurrence of *B. ciliata* are precipitation of the driest quarter (Bio17) (90.48–213.4 mm) and elevation (1710.44–3326.40 m) (Fig. S4). The main environmental variables affecting the occurrence of *B. purpurascens* are precipitation of the warmest quarter (Bio18) (340.87–512.36 mm), elevation (2324.51–4380.13 m), and annual temperature range (23.33–26.81 °C) (Fig. S4).

3.2 Projected suitable areas under current climate scenario

The projected suitable areas under current climate conditions for the investigated *Bergenia* species are congruent with their existing physical distributions. The current

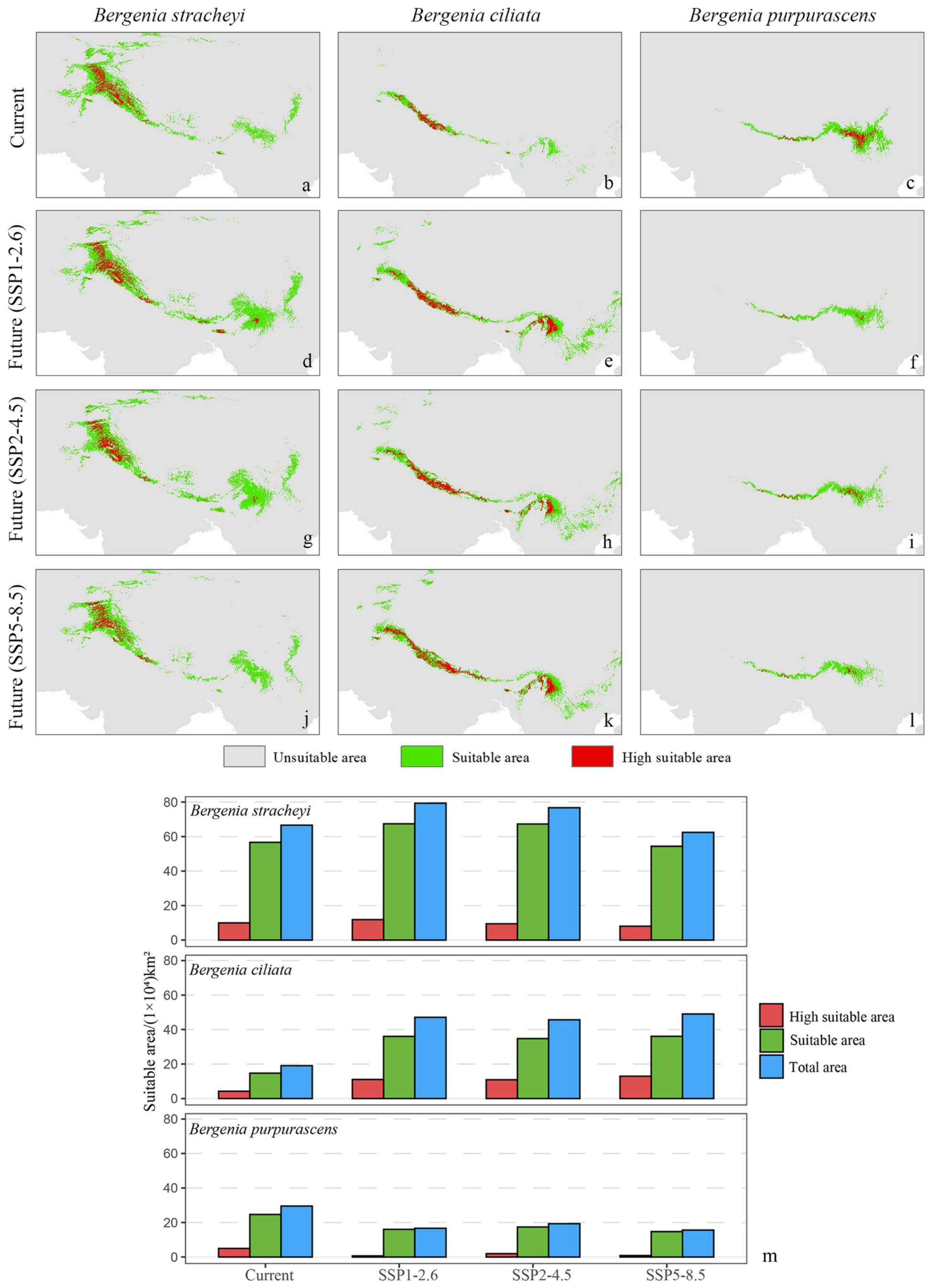

Fig. 3 Potential suitable distribution areas of *B. stracheyi*, *B. ciliata*, and *B. purpurascens* under the current climate (**a**–**c**) and three future climate change scenarios, SSP1-2.6 (**d**–**f**), SSP2-4.5 (**g**–**i**), and SSP5-8.5 (**j**–**l**), and future suitable area changes (**m**)

highly and total suitable areas for *B. stracheyi* comprise 9.97×10^4 km^2 and 66.63×10^4 km^2, respectively, and are mainly located in the western Himalaya (Fig. 3a, m). The current highly and total suitable areas for *B. ciliata* comprise 4.27×10^4 km^2 and 19.01×10^4 km^2, respectively, and are mainly distributed in the Himalaya (Fig. 3b, m). The current highly and total suitable areas for *B. purpurascens* comprise 4.93×10^4 km^2 and 29.55×10^4 km^2, respectively, most of which is distributed in the HDM and a narrow part of the Himalaya (Fig. 3c, m).

3.3 Range changes of Bergenia species under future climate change

By 2090, the suitable habitat area of *B. stracheyi* is projected to expand with 25.54×10^4 km^2 (21.93%) and 26.91×10^4 km^2 (17.36%), under the scenarios of SSP1-2.6 and SSP2-4.5, respectively. However, under the pessimistic SSP5-8.5 scenario, its suitable area is expected to shrink with 19.79×10^4 km^2 (5.26%) (Fig. 4). For *B. ciliata*, its suitable area is predicted to expand with 30.52×10^4 km^2 (150.36%), 29.18×10^4 km^2 (142.42%), and 32.38×10^4 km^2 (157.14%) under the scenarios of SSP1-2.6, SSP2-4.5, and SSP5-8.5 in 2090, respectively. In contrary, the suitable area of *B. purpurascens* is predicted to shrink with 15.29×10^4 km^2 (43.60%), 13.70×10^4 km^2 (34.88%), and 18.22×10^4 km^2 (47.24%) under the scenarios of SSP1-2.6, SSP2-4.5, and SSP5-8.5 in 2090, respectively.

In terms of distribution range shift, the Himalayan *Bergenia* species *B. stracheyi* and *B. ciliata* are projected to shift their ranges southeastward by 2090, while the HDM species *B. purpurascens* will shift its distribution northwestward direction. Specifically, under the scenarios of SSP1-2.6, SSP2-4.5, and SSP5-8.5, the centroid of the suitable area of *B. stracheyi* is expected to shift 528.88 km, 535.49 km, and 313.68 km to the southeast in 2090, respectively (Fig. 5). Under the scenarios of SSP1-2.6 and SSP2-4.5, the centroid of the suitable area of *B. ciliata* will shift 539.71 and 482.83 km to the southeast, respectively. However, under the pessimistic scenario (SSP5-8.5), the centroid will shift 290.12 km to the east (Fig. 5). Under the scenarios of SSP1-2.6, SSP2-4.5, and SSP5-8.5, the centroid of the suitable area of *B. purpurascens* is expected to shift 95.56 km, 168.72 km, and 266.56 km to the northwest, respectively (Fig. 5).

By 2090, the three *Bergenia* species are projected to shift their ranges to higher elevations, although the Himalayan species *B. stracheyi* and *B. ciliata* will shift their ranges to lower elevations under the optimistic SSP1-2.6 scenario. Specifically, *B. stracheyi* is expected to shift 155.99 m to lower elevations under the SSP1-2.6 scenario, while shifting 79.59 and 299.38 m to higher elevations under the SSP2-4.5 and SSP5-8.5 scenarios, respectively (Fig. 6). Similarly, *B. ciliata* is expected to shift 52.89 m to lower elevations under the SSP1-2.6 scenario, while shifting 78.17 and 379.65 m to higher elevations under the SSP2-4.5 and SSP5-8.5 scenarios, respectively (Fig. 6). Surprisingly, *B. purpurascens* is expected to shift 404.88 m, 625.51 m, and 979.05 m to higher elevations under the SSP1-2.6, SSP2-4.5, and SSP5-8.5 scenarios, respectively (Fig. 6).

4 Discussion

4.1 Determinant environmental variables on species distributions

Our study showed that precipitation and elevation play significant roles in determining the geographical distribution of *B. stracheyi*, *B. ciliata*, and *B. purpurascens*. Specifically, for *B. stracheyi*, precipitation seasonality (Bio15), elevation, and slope were identified as the most influential environmental variables. Similarly, for *B. ciliata*, the distribution was strongly influenced by precipitation of the driest quarter (Bio17) and elevation, consistent with findings by Kaliyathan et al. (2016) in the Mussoorie range of Lesser Himalaya. In the case of *B. purpurascens*, the most important environmental variables were precipitation of the warmest quarter (Bio18), elevation, and temperature annual range (Bio7). These findings align with our long-term field investigations, showing that *B. purpurascens* usually grows on slopes within *Rhododendron* understories. Furthermore, we observed a significant decline in population size and the number of flowering individuals during years characterized by intense droughts in spring and summer. The importance of precipitation in determining the distribution of other alpine plants in the Tibetan Plateau has been documented before. For instance, Naudiyal et al. (2021) showed that precipitation in the wettest month was the most important environmental variable determining habitat suitability of *Abies*, *Picea*, and *Juniperus* in the east of the HDM. Additionally, Hu et al. (2019) showed that the distribution of six typical *Kobresia* species in the Tibetan Plateau was strongly affected by annual precipitation and the precipitation in the wettest and driest quarters of the year. All these results highlight the critical role of precipitation in shaping the distribution of *Bergenia* species and other high-elevation plants in the Tibetan Plateau. Consistent with our results, Kunwar et al. (2023) recently reported that elevation represents a major environmental variable in determining the geographical distribution of medicinal plant species in the Nepal Himalaya, including *B. ciliata*. However, the distribution range of some other plants in this region was also influenced by temperature. For instance, You et al. (2018) reported that temperature-related variables were the most important bioclimatic variables associated with the distribution of *Rhodiola* species on the Tibetan Plateau.

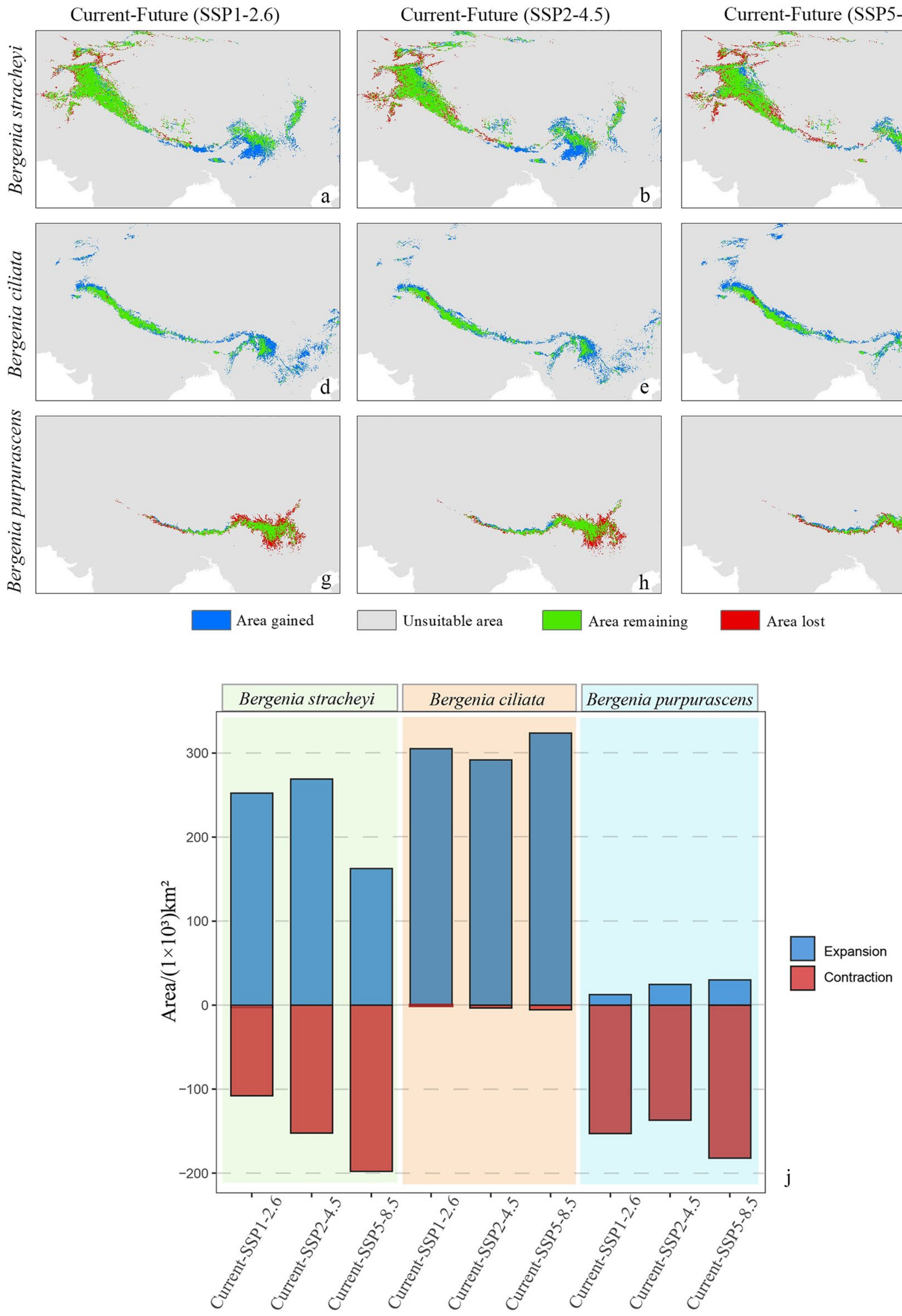

Fig. 4 Changes of suitable habitat area of *Bergenia stracheyi*, *B. ciliata*, and *B. purpurascens* under three future climate scenarios. (**a**–**i**) The red area represents potential range contraction, the blue area represents potential range expansion, and the green area represents the overlap of current and future projected ranges. In the bar plots, red indicates area contraction, and blue indicates area expansion (**j**)

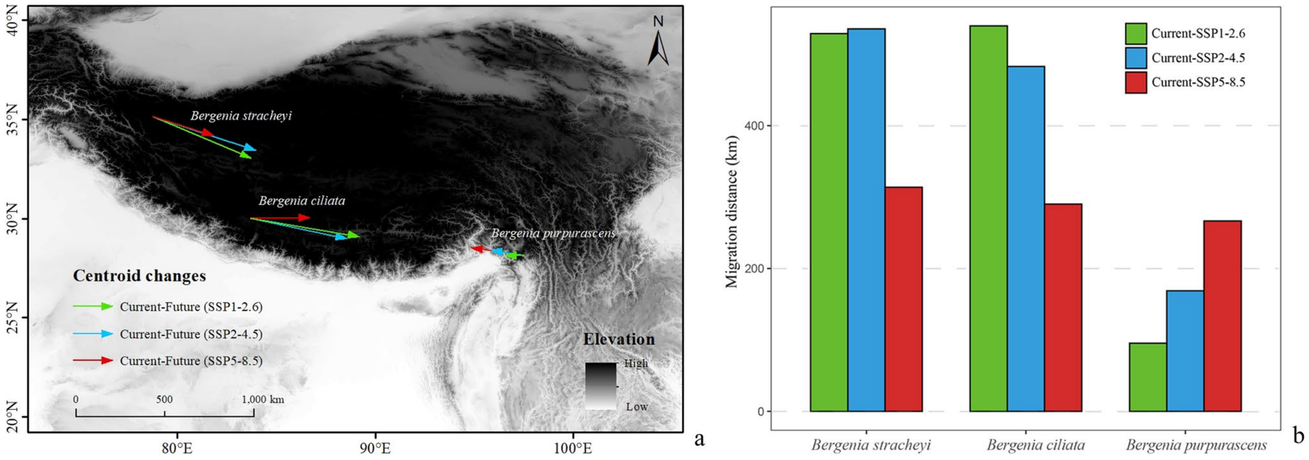

Fig. 5 Centroid migration routes and distances of *Bergenia stracheyi*, *B. ciliata*, and *B. purpurascens* between now and 2090 under three potential climate change scenarios

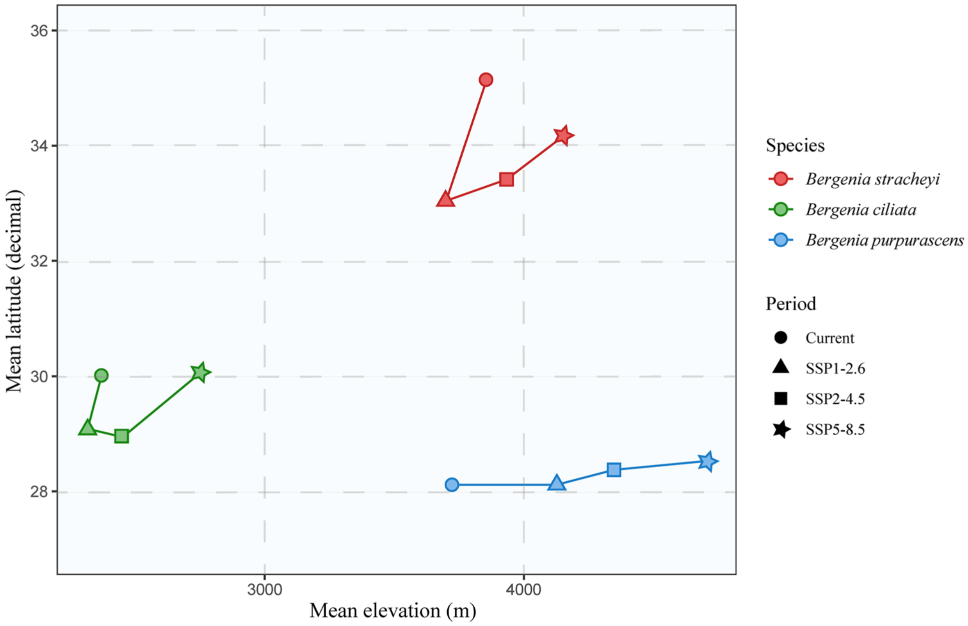

Fig. 6 Changes in altitude and latitude of *Bergenia stracheyi*, *B. ciliata*, and *B. purpurascens* between now and 2090 under three potential climatic scenarios

4.2 Species distribution range shift and potential causes

Previous studies (Parmesan and Yohe 2003; Lenoir et al. 2008; Chen et al. 2011a, b; Rumpf et al. 2018) have documented the upslope shift of plant species in the European Alps in response to climate warming. Recent research has suggested that such a trend will also occur among montane plants in the HDM (Liang et al. 2018). A similar result has been reported by He et al. (2019a, b) for *Cyananthus*, *Primula*, and *Meconopsis* from the Tibetan Plateau. Interestingly, our results show that the Himalayan *Bergenia* species, *B. stracheyi* and *B. ciliata*, are predicted to experience a different range shift compared to the HDM congeneric species, *B. purpurascens*, under future climate change. By 2090, the Himalayan species are expected to shift their ranges southeastward, while the HDM species will shift its range northwestward. However, all three *Bergenia* species are projected to shift their ranges to higher elevations in response to temperature increases under moderate SSP2-4.5 and pessimistic SSP5-8.5 scenarios. Under the optimistic SSP1-2.6 scenario, however, the two Himalayan species are expected to shift their ranges to lower elevations, which may indicate a response to water availability instead of temperature changes. A similar finding was observed by Crimmins et al. (2011), who compared historical and current distributions of plant species in California. Additionally, Zu et al. (2021) recently investigated the historical and current occurrence records of 83 plant species in Gongga Mountain, the highest mountain in the HDM, and they demonstrated that 19 species (22.9%) showed a significant downslope shift.

4.3 Vulnerability of Bergenia species to climate change

Our study revealed that the east Himalaya-HDM alpine species *B. purpurascens* is particularly vulnerable to climate change. By 2090, its suitable habitat area is projected to shift upwards with 404.88–979.05 m, resulting in a loss of approximately 34.88–47.24% of suitable habitat area. Suitable habitats in the southeast marginal chains of the HDM, with relatively lower summit heights, are especially at risk of disappearing due to climate warming. In contrast, the Himalayan mid-elevation species *B. ciliata* is expected to benefit from climate warming, with its suitable area anticipated to expand with 142.42–157.14%. The Himalayan alpine species *B. stracheyi* is also predicted to be a winner under optimistic and moderate climate change scenarios, although the range expansion magnitude is only moderate (17.36–21.93%). However, under the pessimistic climate scenario, its suitable area is projected to shrink by 5.26%.

Geographical range size is generally positively correlated with niche breadth (Slatyer et al. 2013), and narrowly distributed species tend to be more sensitive to climate change than widespread species (Yu et al. 2019; Wang et al. 2022a). Surprisingly, our study showed that the most widely distributed species, *B. purpurascens*, is more vulnerable to climate change than its two congeners. Similar results were also found in our recent study, which indicated that narrowly distributed terrestrial orchid species are not more sensitive to climate change than their widespread congeners (Qiu et al. 2023). In contrast, our findings in *Bergenia* differ from Liang et al. (2018), who observed that the distribution range of low- and mid-altitude plants in the HDM would decrease, while that of subalpine and alpine plants would increase under future climate change. Our results support the notion that alpine plants at higher elevations face greater vulnerability to climate warming compared to their congeners at lower elevations, thus corroborating the “nowhere to go” hypothesis.

The complex and diverse habitats that characterize the HDM have created the ideal conditions for plant diversification and at the same time provided refugia that allowed plants to withstand climate fluctuations (Sun et al. 2017; Xing and Ree 2017). Our results indicate that under future climate change, most of the southeast lower-elevational habitats of *B. purpurascens* are at risk of being lost. However, suitable habitats for *B. purpurascens* in the western HDM and east Himalaya are relatively more resilient to climate change, and the species may gain some new habitats in the east Himalaya. Similarly, *B. stracheyi* and *B. ciliata* are projected to gain new habitats in the HDM due to the complex topography of the western HDM, which might serve as refugia for *B. stracheyi*, *B. ciliata*, and *B. purpurascens* under future climate change. Our findings are also in line with a recent study that showed that the HDM will act as a refuge for *Rhodiola* species (Wang et al. 2021).

4.4 Limitations and conservation implications

Our study assumes that species distributions were primarily determined by climate and topography, and that species can colonize all areas with suitable climate conditions and topography. However, other abiotic factors like land use and edaphic features, as well as biotic factors including evolutionary history, species dispersal ability, and biological interactions, may also constrain the distribution range of species. In addition, populations of *Bergenia* species have long been suffering from overexploitation for medicinal purposes (Tiwari et al. 2015). Therefore, the realized distributions of these three species may be overestimated when considering climate and topography alone. Future studies should conduct additional surveys across the species distribution range and incorporate more comprehensive abiotic and biotic factors to more accurately estimate the distribution of these species.

Most of the core distribution of the Himalayan species, *B. stracheyi* and *B. ciliata*, will remain unaffected by climate change. In addition, the western HDM region provides potential new habitats for these two species to colonize. Therefore, in situ conservation is the most effective approach to protect these two species. In contrast, *B. purpurascens* is particularly sensitive to climate change, and its distribution range is expected to shift dramatically upwards, resulting in the loss of large proportions of its currently suitable area under climate warming. As most of the habitats in the southeast marginal chains of the HDM with lower elevations will be lost, these populations should be ex situ conserved to prevent local extinction. The complex topography at the higher elevation ranges of the HDM may provide refugia for *B. purpurascens* under future climate change. Therefore, populations in the core area of the HDM should be prioritized for in situ protection. Based on our survey and communications with the residents in the core area of the HDM, the populations of *B. purpurascens* in this area are severely threatened by human activities, including excavation for rhizomes used in medicine and deforestation of old-growth *Rhododendron* forests, where the species typically grows. Most *B. purpurascens* populations below 4000-m asl are currently nearly extirpated, with only fragmented populations remaining above 4000-m asl. Artificial propagation and cultivation of *Bergenia* species for medicinal purposes, as well as the protection of *Rhododendron* forests in alpine and subalpine zones where *Bergenia* species grow, will help preserve populations in the future.

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Data availability The data sets analyzed in this study are available in the Global Biodiversity Information Facility (GBIF: https://www.gbif.org/), Chinse Virtual Herbarium (https://www.cvh.ac.cn/), and National Specimen Information Infrastructure (http://www.nsii.org.cn). GBIF.org (29 September 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.zyz67s. GBIF.org (29 September 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.v6tesc. GBIF.org (29 September 2023) GBIF Occurrence Download https://doi.org/10.15468/dl.gy54uz.

Declarations

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