

1 **Strengthening protected areas for climate refugia on the Tibetan Plateau, China**

2 **Abstract**

3 Protected areas (PAs) are at the forefront of efforts to conserve and restore biodiversity.
4 However, there are risks that climate change can compromise the ecological benefits of PAs.
5 Therefore, targeting conservation and adaptation efforts necessitate a well-understand of the
6 relationship between PAs and climate refugia, defined as the regions that can buffer the impact of
7 climate change. Recent attempts to identify climate refugia were primarily based on terrain-
8 mediated features or climatic velocity, which ignore the ecosystem's internal processes. This work
9 identified climate refugia on the Tibetan Plateau (TP), an amplifier of drastic global climate
10 warming based on environmental diversity, phenology stability, and climatic velocity. It highlights
11 the capacity to cope with extreme weather events, synchronization with plant growth cycles, and
12 future climate adaptation, respectively. The results show that the distribution of climate refugia
13 using different environmental diversity indicators (e.g., vegetation and topography) vary slightly
14 but differs substantially from the priorities using phenology stability and climatic velocity. For
15 instance, the high distribution probability of climate refugia derived from environmental diversity
16 and climatic velocity is mainly concentrated at low (< 3000 m) or high elevations (> 6000 m), while
17 the one using phenology stability is mainly observed at 3000m – 3800m. The inconsistent
18 distribution of different types of climate refugia weakens the potential of functional
19 complementarity. The existing nature reserves, the primary type of PAs in China, have critical
20 conservation gaps in different types of climate refugia, indicating the urgency of incorporating
21 climate refugia into PAs conservation planning on TP. Our work could help inform local
22 conservation policies and improve the effectiveness of PAs.

23 **Keywords** Protected areas; Climate refugia; Nature reserves; Tibetan Plateau; Biodiversity;
24 Conservation planning

26 **1 Introduction**

27 Protected areas (PAs) are the mainstream and extensive solution for conserving and restoring
28 biodiversity by limiting human impacts ([Gonçalves-Souza et al., 2021](#)). However, many PAs are
29 experiencing rapid climate change ([Hoffmann et al., 2019](#); [Asamoah et al., 2021](#); [Dobrowski et al.,](#)
30 [2021](#)), which is a major threat to biodiversity and hampers PA's core objective ([Garcia et al., 2014](#);
31 [Pecl et al., 2017](#); [Hoffmann et al., 2019](#)). Climate refugia, defined as buffer regions for species
32 against exposure to changes in climatic conditions, are expected to mitigate the climate change
33 impact on biodiversity and reinforce the PAs' effectiveness ([Ashcroft, 2010](#); [Keppel et al., 2012](#);
34 [Meddens et al., 2018](#)). Consequently, identifying and safeguarding such climate refugia is
35 increasingly acknowledged as a critical component of biodiversity conservation ([Groves et al., 2012](#);

36 [Carrol et al., 2017](#)).

37 The importance of climate refugia has been widely demonstrated, although the approach by
38 which they are identified is diverse ([Ashcroft et al., 2012](#)). In general, environmental diversity and
39 climatic velocity are the two main criteria. For instance, areas of high environmental diversity (i.e.,
40 high spatial variability of some environmental variables, such as topography, and vegetation) can
41 be delineated as potential refugia because they provide various resources, habitats, and
42 microclimatic conditions ([Oliver et al., 2010](#); [Carrol et al., 2017](#)), enhancing the resilience to
43 external disturbance ([Malika et al., 2009](#)). Climatic velocity assesses the proximity and accessibility
44 of future suitable climate conditions for species ([Loaries, 2009](#)). Areas with reduced climatic
45 velocity can serve as refugia because species can track the changes in climate by moving short
46 distances ([Carrol et al., 2017](#)). Many cases have used these criteria for climate refugia identification,
47 particularly in North America (e.g., [Carroll et al., 2017](#); [Michalak et al., 2018](#); [Stralberg et al., 2020](#)).

48 Internal ecosystem processes have received scant consideration in identifying climate refugia
49 despite their potential significance ([Stralberg et al., 2020](#)). For instance, vegetation phenology
50 stability can reflect the synchronism between the plant growth cycle and animal behaviour, such as
51 foraging, hibernation, and reproduction ([Menzel et al., 2006](#); [Reed et al., 2013](#)). Climate refugia
52 identified using various approaches may form useful complementarities regarding climate
53 adaptation capacity and scale-dependent ([Carrol et al., 2017](#)). Furthermore, recent works suggested
54 that planners should consider a variety of alternative metrics to overcome the shortcomings of
55 individual approaches ([Gillson et al., 2013](#); [Garcia et al., 2014](#)). Therefore, to promote biologically
56 meaningful climate adaptation solutions, efforts need to be made to incorporate internal and external
57 ecological processes to improve climate refugia identification ([Brito-Morales et al., 2018](#)) and
58 understand the refugia distribution identified by multiple approaches ([Michalak et al., 2020](#)).

59 Incorporating climate refugia into PAs conservation planning can potentially increase PAs
60 conservation effectiveness ([Michalak et al., 2020](#)). Furthermore, protecting climate refugia sites will
61 help managers gain time to develop long-term adaptation strategies ([Morelli et al., 2016](#)). However,
62 comprehensive and comparative studies on PAs' coverage and evolution of climate refugia using
63 different approaches are still lacking.

64 An ideal area to explore these aspects is the Tibetan Plateau (TP) in China, which is located in
65 two crucial global biodiversity hotspots (the Mountains of Southwest China and the Himalayas)
66 ([Myers et al., 2000](#)). The region is highly sensitive to climate disturbance, and accelerated climate
67 change risks jeopardize biological conservation efforts ([Kuang & Jiao, 2016](#)). Over the past decades,
68 the Chinese government has gradually established several nature reserves (NRs, the primary type of
69 PAs), forming a dense PAs network to protect these sensitive ecosystems. However, there is a
70 growing concern about these PAs' conservation status and effectiveness ([Li et al., 2020](#); [Hua et al.,](#)

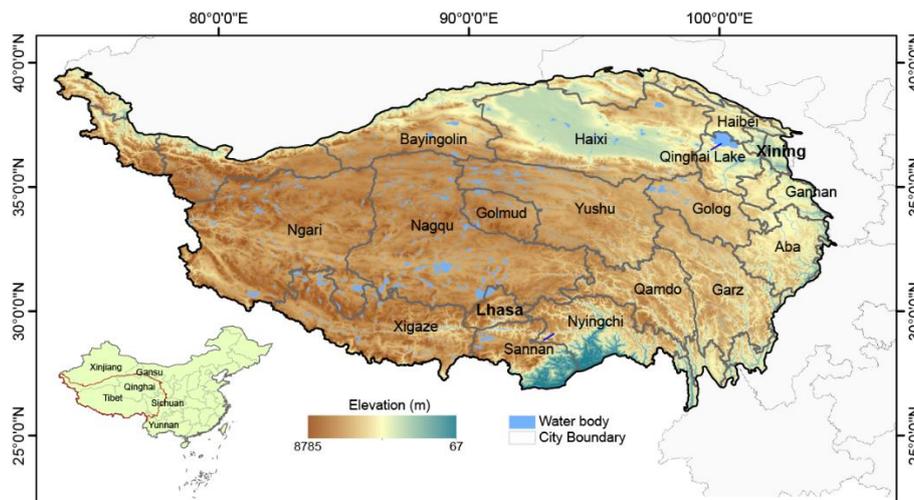
71 2022). As climate refugia on the TP are still poorly understood, their identification and distribution
72 within PAs can favour more effective conservation policies.

73 The aim of this study is multifold: (1) to map the climate refugia based on different approaches;
74 (2) to discuss the inconsistencies among various types of climate refugia; (3) to investigate the
75 elevation gradient characteristics of climate refugia distribution; and (4) to identify the relationship
76 between NRs and climate refugia.

77 2 Materials and Method

78 2.1 Study area

79 The TP includes Qinghai Province, Tibet Autonomous Region, and parts of four other
80 provinces of Gansu, Xinjiang, Yunnan, and Sichuan. It is also known as "The Roof of the World".
81 TP has an average elevation of over 4000 m above sea level. The annual precipitation spans from
82 1000 mm to 100 mm in the southeast, with annual temperatures ranging between 20 °C to − 5 °C
83 (Sun et al., 2020). A warming trend, faster than the global average, was observed in TP in the
84 previous decades (Kuang & Jiao, 2016). This can have negative impacts on habitats and valuable
85 species.



86
87 Figure 1. Study area location.
88

89 2.2 Data

90 To identify the climate refugia, we used enhanced vegetation index (EVI) derived from
91 MOD13Q1 (250 m-resolution and 16 day-frequency) and land surface temperature (LST) from
92 MOD11A2 (1 km-resolution and 8 day-frequency) from 2001 to 2020 (Tab. 1). We collected these
93 datasets from Google Earth Engine (Gorelick et al., 2017) and selected only high-quality images
94 according to the MODIS Quality Assurance flags. Also, we used a land cover dataset from
95 MCD12Q1 with 500 m resolution and a digital elevation model (DEM) from Shuttle Radar
96 Topography Mission with 90m resolution. We collected future climate data (annual mean
97 temperature and annual precipitation) from WorldClim database generated from 8 CMIP6 global

98 climate models (BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, IPSL-CM6A-LR,
 99 MIROC-ES2L, MIROC6, and MRI-ESM2-0). Our dataset consisted of 53 NRs, representing
 100 approximately 40% of the total area currently covered by terrestrial NRs in China (Fig. S1).

101

102

Table 1. Data types and sources

Variables	Sources	Units	Period	Resolution	Website
TP boundary	Global Change Research Data	-	-	-	
China's prefecture administrative boundary	Publishing and Repository	-	-	-	http://www.geodoi.ac.cn
NRs boundary	Resource and Environment Science and Data Center, Chinese Academy of Sciences	-	-	-	http://www.resdc.cn
DEM	SRTMDEM from Geospatial Data Cloud	m	-	90 m	http://www.gscloud.cn/
EVI	MOD13Q1	-	2001- 2020	250 m	https://lpdaac.usgs.gov/products/mod13q1v006
LST	MOD11A2	K	2001- 2020	1000 m	https://lpdaac.usgs.gov/products/mod11a2v006
Land cover	MCD12Q1	-	2010	500 m	https://lpdaac.usgs.gov/products/mcd12q1v006
Future climate	WorldClim database	°C/ mm	2040- 2060	2.5 minutes	https://worldclim.org/data/c mip6/cmip6climate.html

103

104 2.3 Assumptions of climate refugia

105 We assumed that regions with high environmental diversity, stable vegetation phenology, and
 106 reduced climatic velocity are suitable climate refugia for biodiversity. The reasons are the following.
 107 Environmental diversity metrics are a generalizable approach to identifying climate refugia. A
 108 heterogeneous environment (e.g., vegetation, topography, land cover) increases the resistance to
 109 climate change (Malika et al., 2009). Diverse ecosystems indicated the availability of a range of
 110 resources, as well as the existence of varied microclimatic conditions (Oliver et al., 2010). This is
 111 key to biodiversity and ecosystem stability through a variety of plant diversity and structure (Levin
 112 et al., 2007). Furthermore, high spatial variability of microclimates is key to the thermal shelter for
 113 different species within a small area (Keppel et al., 2012; Elsen et al., 2020, 2021). A global meta-
 114 analysis by Stein et al. (2014) found that species richness is associated closely with abiotic drivers
 115 such as topography, vegetation, land cover, and climate.

116 Many animals have periodic life behaviours that correspond with vegetation phenology. The
 117 high interannual vegetation phenology variability may negatively impact the availability of
 118 resources, with implications to animal survival needs (e.g., reproduction) (Menzel et al., 2006;
 119 Thackeray et al., 2010; Reed et al., 2013). Observational and experimental evidence showed that

120 phenological shifts reduce biodiversity and change regional species density (Plard et al., 2014; Wolf
121 et al., 2017), pointing to the importance of stable vegetation phenology for biological conservation.

122 Climatic velocity is a function considering both the spatial and temporal gradient in climate
123 variables in a particular location. It can be regarded as an initial rate at which species migrate to
124 preserve stable climate conditions (Loarie et al., 2009; Hamann et al., 2015). Since the climate is a
125 primary constraint to species distribution, they may be at risk of extinction when climate conditions
126 to which they are adapted change quickly or disappear (Williams et al., 2007; Loarie et al., 2009).
127 Therefore, it is possible to identify the potential exposure to climate shifts, which is key to measuring
128 the exposure of organisms to climate change (IPCC, 2014) or identifying climate refugia (Carrol et
129 al., 2017; Brito-Morales et al., 2018; Michalak et al., 2020).

130 **2.4 Calculation of climate refugia indicators**

131 **2.4.1 Environmental diversity**

132 We developed and compared five metrics of environmental diversity (elevation, landcover, EVI,
133 summer LST, and winter LST) following Carroll et al. (2017) and Silveira et al. (2021). For EVI
134 diversity, we constructed a composite image by generating the 90th percentiles of EVI from 2001
135 to 2020 with the selection of high-quality pixels using the Quality Assurance flags and vegetation
136 layers of MCD12Q1. Using this approach, we reduced high EVI values' disturbance and obtained
137 the EVI peak values (Farwell et al., 2020). The standard deviation (STD) of EVI composite images
138 was then calculated using a moving window with a size of 5×5 pixels. The size of moving windows
139 (5 pixels) is a compromise between animals' mobility in a short time and the data input amount for
140 STD calculations. The STD value was allotted to the moving windows' center pixel. With this, we
141 delineated the spatial diversity of EVI.

142 LST images were composited in summer and winter by using the median of all high-quality
143 images available in summer and winter from 2001 to 2020, derived from MOD11A2. Using median
144 rather than mean can minimize the effects of extreme high/low values and reduce cloud cover
145 impacts (Elesen et al., 2020). Overall, two LST composited images for summer and winter were
146 produced. Similarly, we calculated the STD within a moving window with a size of 5 pixels to
147 represent the LST spatial diversity.

148 Similarly, we used the STD within a moving window with a size of 5 pixels to assess the
149 elevation spatial diversity pattern. Land cover diversity was represented by Shannon's diversity
150 index assessed with FRAGSTATS v4.2. We also used the moving window with a size of 5 pixels to
151 match other calculations. The environmental diversity calculation just considered grasslands,
152 cropland, and forests, since other land cover types do not provide the necessary food resource or
153 have poor accessibility.

154 2.4.2 Phenology stability

155 We extracted the STD from 20 years (2001-2020) of vegetation phenology to describe the
156 phenology stability. The extraction of vegetation phenology was based on EVI images from
157 MOD13A1. First, we replaced the median of the uncontaminated EVI between November and
158 March of the next year for the snow-contaminated EVI values during the non-growing season. This
159 process was required to eliminate this snow-related influence during the non-growing season, in line
160 with previous works (Ganguly et al., 2010; Zhang et al., 2006). We used the Savitzky-Golay filter
161 to reconstruct the EVI series following Chen et al. (2004), and the grassland class of MCD12Q1
162 was used to determine the phenological calculation areas.

163 After data preprocessing, we used three widely accepted methods (Derivative method,
164 Threshold method, RC_{max} method) to calculate two-phenology metrics for each year, namely the
165 start date of the growing season (SOS) and the end date of the growing season (EOS) following
166 Cong et al. (2012), Shen et al. (2014) and Zhang et al. (2018). The average of these phenology
167 metrics was finally calculated as vegetation phenology. The average ensemble method can reduce
168 the error of using a single method (Cong et al., 2017), and is also widely applied in the current
169 phenological calculations, such as Shen et al. (2014), Cong et al. (2017), and Shen et al. (2022).

170 In the Derivative method (Fig. S2a), a rapid increase in EVI indicated active growth of
171 vegetation. Therefore, the SOS/EOS is characterized as the day on which NDVI increases/decreases
172 at the fastest rate in a year when the derivative of the EVI series [$f'(t)$] was the maximum/minimum
173 (Studer et al., 2007). In the Threshold method (Fig. S2b), we firstly used the formula (1) to convert
174 EVI series from each pixel to calculate EVI_{ratio} , and 50% was used as the threshold to determine the
175 SOS and EOS according to local observations (White et al., 1997; Yu et al., 2010).

$$176 \quad EVI_{ratio} = \frac{EVI_t - EVI_{min}}{EVI_{max} - EVI_{min}} \quad (1)$$

177 Where EVI_t is the EVI value at a given time t , and EVI_{min} , EVI_{max} is the annual maximum and
178 minimum EVI values at this pixel, respectively.

179 In the RC_{max} method (Fig. S2c), we firstly used the formula (2) to obtain the rate of change
180 (RC) of EVI. And the SOS/EOS was determined as the time when $EVI_{rc}(t)$ reached its maximum,
181 following Piao et al. (2006) and Cong et al., (2012).

$$182 \quad EVI_{rc}(t) = \frac{EVI_{t+1} - EVI_t}{EVI_t} \quad (2)$$

183 Where $EVI_{rc}(t)$ is the RC of EVI value at a given time t and EVI_t is the EVI value at a given
184 time t .

185 Finally, the average of SOS generated by three methods was determined as the ultimate SOS
186 (Fig. S2d). We chose SOS instead of EOS to calculate phenology stability, considering the
187 reproductive needs of animals highlighted in Silveira et al. (2021). We computed the STD of SOS

188 among 20 years (2001-2020) for each pixel to quantify phenology stability.

189

190 **2.4.3 Climatic velocity**

191 The calculation of future climatic velocity was derived from dividing the temporal gradient of
192 climate change (units: °C yr⁻¹ for temperature and mm yr⁻¹ for precipitation) by the spatial gradient
193 of climate variability (units: °C km⁻¹ or mm km⁻¹) and then obtaining the velocity variable (units:
194 km yr⁻¹), as shown in [formula \(3\)](#).

$$195 \quad V = \frac{\text{Temporal gradient}}{\text{Spatial gradient}} = \frac{^{\circ}\text{C} \times \text{year}^{-1}}{^{\circ}\text{C} \times \text{km}^{-1}} \text{ OR } \frac{\text{mm} \times \text{year}^{-1}}{\text{mm} \times \text{km}^{-1}} = \frac{\text{km}}{\text{year}} \quad (3)$$

196 Climate data from the WorldClim database for the current (1970-2000) and future (2041-2060)
197 were used as input for calculation. Two extreme future climate scenarios: SSP1-2.6, SSP5-8.5 were
198 considered. We used the average of the output from eight global climate models to describe the
199 future climate condition since it can overcome a single model analysis's error. Additionally, we
200 conducted a standard error estimate to map the uncertainty of future climate from 8 global climate
201 models for each pixel ([Fig. S3](#)). The velocity calculation just considered grasslands, cropland, and
202 forests, for other land cover types do not provide a necessary food resource or be poor accessibility.
203 More detailed calculations about the climatic velocity can be consulted in [Loarie et al. \(2009\)](#).

204 **2.5 Relationship among different climate refugia indicators**

205 Spearman rank correlation was used to analyze the relationships among the different climate
206 refugia indicators. We extracted the values of all refugia indicators based on about 5000 random
207 points for analysis. We used the tool 'Create Random Points' of ArcGIS 10.5 to generate the random
208 points, and the distance between random points is no less than 10 km. We hypothesized that regions
209 with high environmental diversity, stable vegetation phenology, and slow climatic velocity could be
210 climate refugia. Therefore, before the correlation analysis, the extracted values of phenology
211 stability indicators (STD of SOS) and climatic velocity of precipitation/temperature were multiplied
212 by -1 to guarantee a consistent interpretation of correlation coefficients. Statistical analysis was
213 applied with Statistical Package for Social Science (SPSS) version 22.

214 **2.6 Identification of priority climate refugia**

215 The climate refugia priority areas were delimited by considering areas where each indicator is
216 in the respective top 20%, referring to the determination of ecosystem services and biodiversity
217 hotspots in the previous studies ([Qiu et al., 2013](#); [Xu et al., 2017](#); [Li et al. 2020](#)). This follows the
218 assumption that regions with high environmental diversity, stable vegetation phenology, and
219 reduced climatic velocity are suitable climate refugia. Therefore, 20% of the areas with the highest
220 values were designated as priority areas for environmental diversity indicators, and 20% of regions
221 with the lowest values were determined for phenology stability indicators and climatic velocity
222 indicators. We also conducted a sensitivity analysis on other thresholds (15%, 25%, 30%) to identify

223 priority areas and explore the analysis's robustness.

224 To assess the climate refugia pattern along the elevation gradient, we calculated the distribution
225 probability of climate refugia in each 100 m interval. This is expressed as the pixels' proportion
226 identified as climate refugia within the elevation interval of 100 m. Locally weighted regression
227 (LWR) was used to fit the distribution probability.

228 **2.7 Analysis of coverage of NRs to climate refugia**

229 NRs' boundary was introduced to identify the conservation gaps between the NRs and climate
230 refugia identified by 8 indicators, using a spatial overlap analysis. If the climate refugia were
231 identified within the NRs relative to its total area (i.e., coverage of NRs to climate refugia) being
232 above the NRs proportion of the TP, the NRs had a good conservation status for climate refugia.
233 Otherwise, the existing NRs in the TP had poor conservation. We also analyzed the proportion of
234 climate refugia identified in NRs. NRs consist of three parts: 1) strictly-protected core zones, 2)
235 buffer zones with limited scientific observation, 3) and experimental zones. The proportion of
236 climate refugia in different components of the NRs was also analyzed.

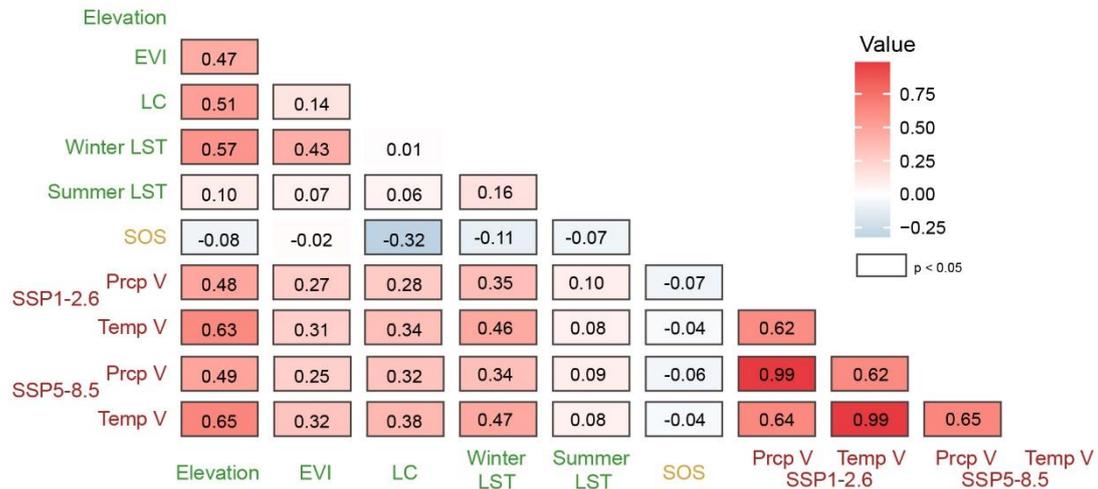
237 **3 Results**

238 **3.1 Inconsistency among the climate refugia indicators**

239 High-value regions of different refugia indicators showed different patterns (Fig. S4). In
240 general, high values of environmental diversity indicators were mainly distributed in the southeast
241 of TP (Fig. S4a-e). The land cover diversity with high value was mostly concentrated in the
242 southeastern areas with dense forests and shrubs (Fig. S4c). SOS's low-STD (i.e., stable phenology)
243 region was scattered over the vegetative land (Fig. S4f). The regions with low precipitation velocity
244 (Fig. S4g) were mainly distributed in the south of the TP, including Xigaze, Sannan, Nyingchi, and
245 the low temperature-velocity regions (Fig. S4h) were concentrated in the south and southeast of the
246 study area (e.g., Sannan, Nyingchi, Qamdo, Garz).

247 Spearman's rank correlation analysis shows that the climate refugia indicators have an
248 inconsistent pattern, especially phenology stability (Fig. 2). For example, summer LST diversity
249 showed a weak positive correlation with all other environmental diversity indicators and climatic
250 velocity. All correlation coefficients were all lower than 0.16. According to significantly negative
251 or low correlations, the differences between phenology stability (i.e., SOS) and diversity/climatic
252 velocity indicators were greater than any contrast among the diversity/climatic velocity indicators.
253 For example, there was a significant negative correlation between phenological stability indicator
254 (i.e., SOS) and land cover diversity with a correlation coefficient of -0.32 ($p < 0.05$), and a weak
255 negative correlation with other environmental diversity/ climatic velocity indicators. Elevation
256 diversity, winter LST diversity, and precipitation and temperature velocity formed a group of closely
257 correlated metrics, with all the correlation coefficients being greater than 0.34 ($p < 0.05$). Overall, an

258 inconsistency was observed among these climate refugia indicators, especially between the
 259 phenology stability indicator and the other two categories of indicators (i.e., environmental diversity
 260 and climatic velocity).
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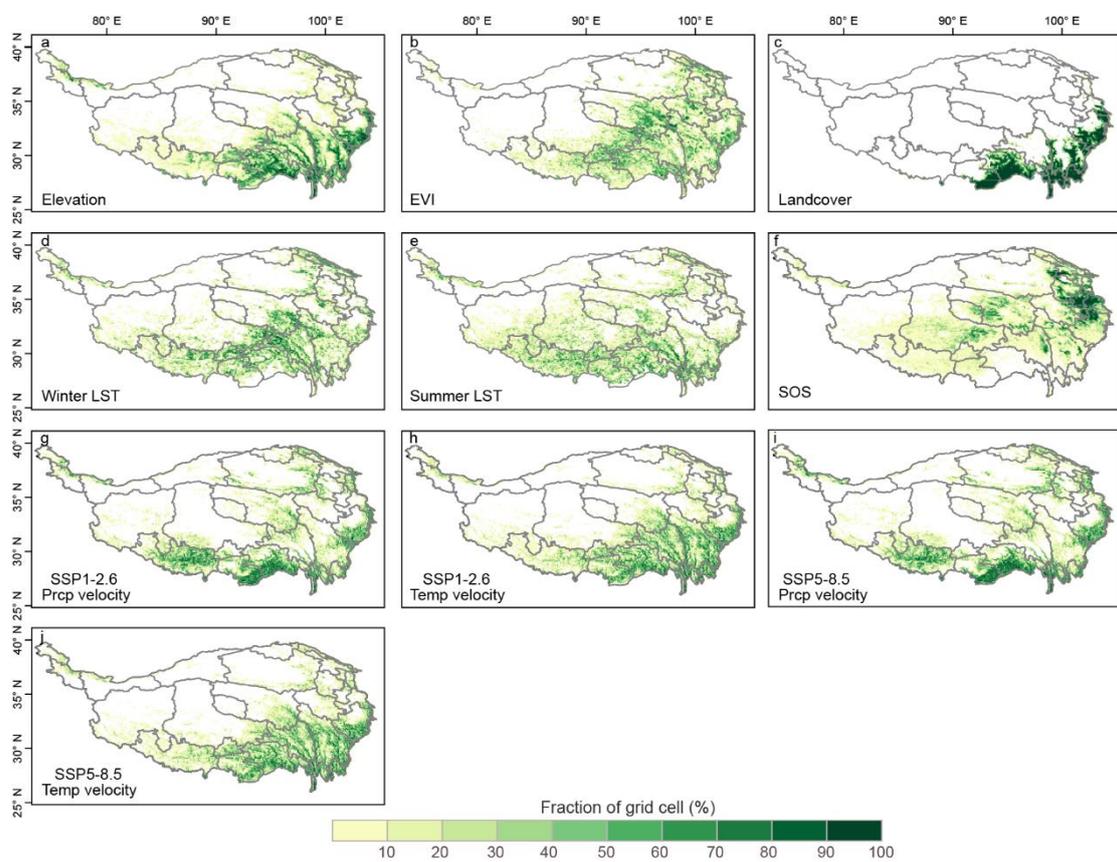
262
 263 Figure 2. Spearman correlation coefficient among climate refugia indicators. The colour shade
 264 represents the correlation coefficient. The thick border of the box is used to indicate the significance
 265 ($p < 0.05$). Green labels are environmental diversity indicators, the orange label is phenology
 266 stability indicator, and red labels are climatic velocity indicators. Land cover (LC), land surface
 267 temperature (LST), climatic velocity (V), precipitation (Prcp), temperature (“Temp”) and start of
 268 the growing season (SOS).
 269

270 3.2 Distribution of priority climate refugia

271 The priority areas for climate refugia are mainly concentrated in the eastern and southern parts
 272 of the TP (Fig. 3). There is a clear distinction between the northwest and southeast areas. In terms
 273 of elevation diversity, priority areas were mainly distributed in the southeast of TP (Fig. 3a). This
 274 pattern is consistent with other priority regions based on EVI (Fig. 3b), winter LST (Fig. 3d),
 275 summer LST (Fig. 3e), and temperature velocity (Fig. 3h, j). Regarding landcover diversity, priority
 276 areas are concentrated in the southeast of the study area (e.g., Sannan, Nyingchi, Garz, and Aba)
 277 (Fig. 3c). The priority regions based on SOS stability are mostly distributed in the eastern TP,
 278 including the surrounding regions around Qinghai Lake (Fig. 3f). There is a small distribution in the
 279 middle of the study area (e.g., Nagqu, Golmud, and Yushu), however different from the previous.
 280 Besides, the priority regions based on precipitation velocity are mainly distributed in Xigaze and
 281 have finite distribution in several southeastern cities such as Nyingchi, Qamdo, and Garz (Fig. 3g,
 282 i).

283 The results indicate that the distribution of climate refugia identified using different
 284 environmental diversity indicators vary slightly from each other, particularly in landcover diversity

285 (Fig. 3c), but differed substantially from the priorities using phenology stability (Fig. 3f) and
 286 climatic velocity (Fig. 3g-j). This confirmed the observed in Fig. 3. According to the sensitivity test,
 287 the different thresholds to determine the priority climate refugia (15%, 25%, 30%) showed a
 288 relatively similar pattern (Fig. S5-S7).
 289



290
 291 Figure 3. Distribution of priority climate refugia based on different indicators (%). The figures are
 292 aggregated to 0.1-degree resolution for improved visualization. The colour shade green represents
 293 the percentage of priority climate refugia. Grey lines represent the municipal administrative
 294 boundary. (a-e) showed the environmental diversity of elevation, EVI, landcover, winter LST and
 295 summer LST, (f) showed the phenology stability indicator, and (g-j) showed the future climate
 296 change velocity for precipitation and temperature for SSP1-2.6 and SSP5-8.5, respectively.
 297 Enhanced vegetation index (EVI), land surface temperature (LST), the start of the growing season
 298 (SOS), precipitation (Prcp), and temperature (Temp).

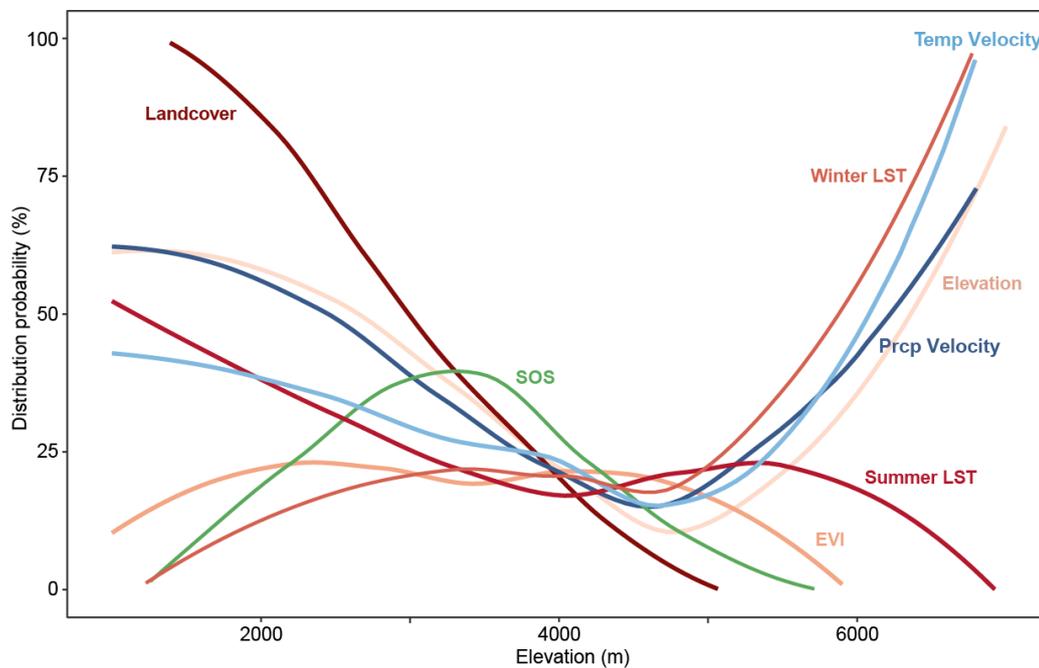
300 **3.3 Contrasting relationship of priority climate refugia to elevation**

301 Fig. 4 shows the distribution probability of different climate refugia indicators along the
 302 elevation gradient. Elevation diversity, two future climatic velocities (precipitation and temperature)
 303 indicators showed a similar trajectory, with a high probability at low elevation and high elevation,
 304 and low probability at medium elevation. The distribution probability increased gradually when the

305 elevation was above 4800 m, which matched the winter LST pattern. This suggested that, at least in
 306 the TP, the highest mountain area and low-elevation regions are most topographically diverse. The
 307 probability of SOS and EVI presented a symmetrical distribution along the axis of 3600 m. Land
 308 cover diversity has a very high probability of distribution below 2000 m but then decreases rapidly
 309 with the increasing elevation.

310 The high distribution probability of terrain-based/velocity-based indicators is concentrated in
 311 low (<3000 m) and high elevations (>6000 m). The probability derived from the phenology stability
 312 indicator (SOS) performed the best between 3000 m and 3800 m (Fig. 4). This inconsistency
 313 emphasized that different climate refugia indicators may differ in some elevation ranges (e.g., <2000
 314 m and > 4800 m).

315



316

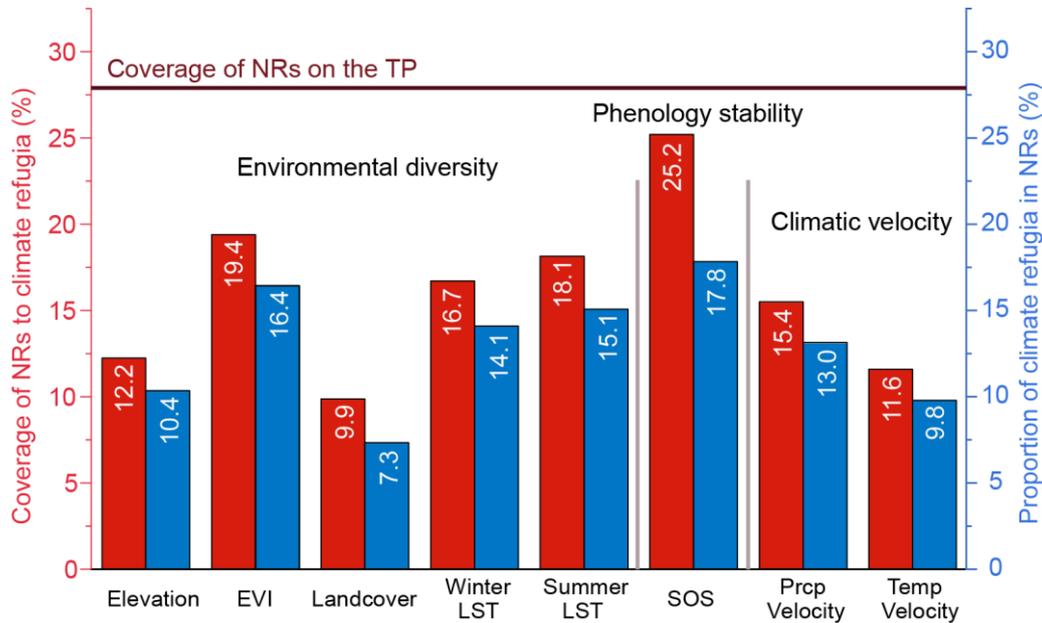
317 Figure 4. Climate refugia distribution probability in their relationship with elevation. Land surface
 318 temperature (LST), precipitation (Prcp), and temperature (Temp), start of the growing season (SOS),
 319 and enhanced vegetation index (EVI).

320 3.4 Relationship between NRs and priority climate refugia

321 TP's NR has a low coverage for the prior climate refugia based on different indicators (Fig. 5).

322 Compared to NRs' 27.3%, TP total land surface contributions to climate refugia are, on average 15.3%
 323 for environmental diversity, 16.1% for climatic velocity, and 25.2% for phenology stability. Among
 324 different environmental diversity indicators, the maximum coverage percentage was observed in
 325 EVI diversity (19.4%), and the minimum is 9.9% for landcover diversity. Regarding climatic
 326 velocity, current NRs covered 15.4% (15.5%) of priority regions with precipitation velocity and
 327 11.6% (11.8%) for temperature velocity under SSP5-8.5 (SSP1-2.6). Phenology stability showed a
 328 higher coverage (25.2%) than the previous.

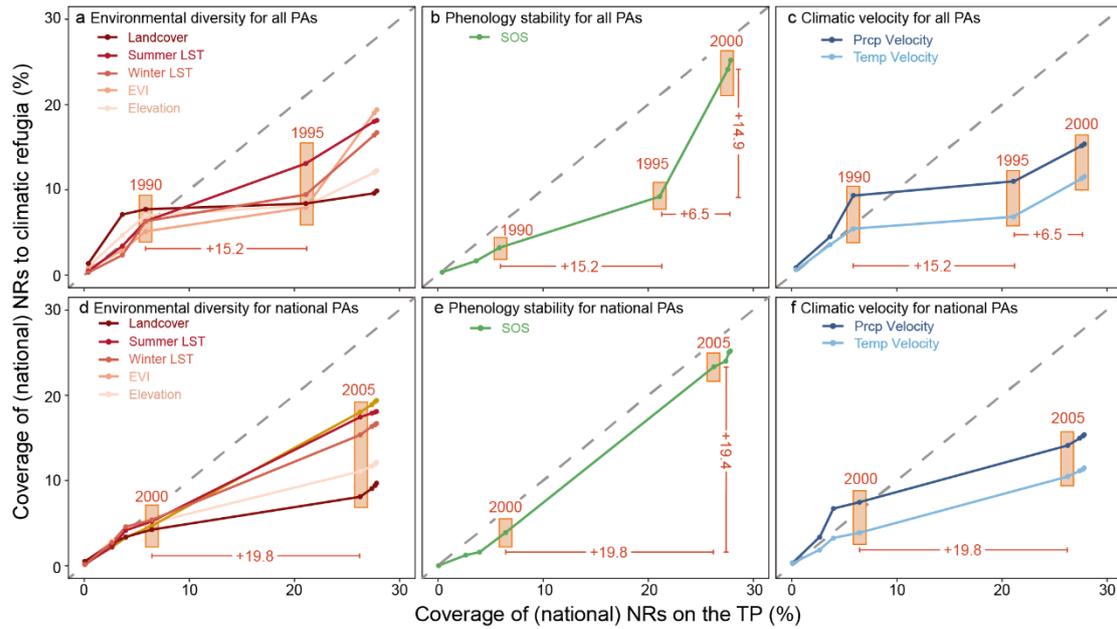
329 The above patterns still hold if considering the proportion of climate refugia in NRs. On
 330 average, 13.0% of the NRs can be considered climate refugia based on different indicators. The
 331 maximum proportion was observed in SOS stability (17.8%), and the minimum (7.3%) for
 332 landcover diversity. Even the core zones of NRs have a relatively low proportion of climate refugia
 333 (Fig. S8). These results highlighted that climate refugia within the NRs are also limited.
 334



335
 336 Figure 5. Coverage of NRs for climate refugia and proportion of climate refugia in NRs. The red
 337 bar means the coverage of NRs to climate refugia (%) and the blue bar means the proportion of
 338 climate refugia in NRs (%). The dark red line is the coverage rate of NRs on the TP, which is 27.3%.
 339 Only climatic velocity under SSP5-8.5 was showed because the situation in SSP1-2.6 is very similar
 340 to that in SSP5-8.5. Land surface temperature (LST), precipitation (Prp), temperature (Temp), start
 341 of the growing season (SOS), and enhanced vegetation index (EVI).
 342

343 The coverage of NRs on the TP experienced an increase of 15.2 percentage points between
 344 1990 and 1995. However, the coverage of NRs for climate refugia was not substantially increased
 345 correspondingly in all eight refugia indicators during this period (Fig. 6a-c). After 1995, the
 346 unbalanced growth between NRs and climate refugia improved. For instance, compared with the
 347 6.5 percentage point increase in the Rs coverage on the TP between 1995 and 2000, SOS coverage
 348 and EVI increased by 14.9, and 11.1 percentage points, respectively. This showed that with the
 349 expansion of NRs, the coverage of NRs to climate refugia also increased.

350 Although national-level NRs expanded rapidly from 2000 to 2005, the coverage for climate refugia
 351 did not attain the expansion rate of national-level NRs, except for SOS (Fig. 6d-f).
 352



353

354 Figure 6. The evolution process of NRs and their coverage for climate refugia. Two types of NRs
 355 were considered: (a-c) for all NRs and (d-e) for national NRs. The grey dotted line is the 1:1 line.
 356 The orange rectangle was used to label key time nodes, and the red font was used to label the growth
 357 rate of coverage (units: percentage points). Only climatic velocity under SSP5-8.5 was showed
 358 because the situation in SSP1-2.6 is very similar to that in SSP5-8.5. Land surface temperature
 359 (LST), precipitation (Prcp), and temperature (Temp), start of the growing season (SOS), and
 360 enhanced vegetation index (EVI).

361

362 4 Discussion

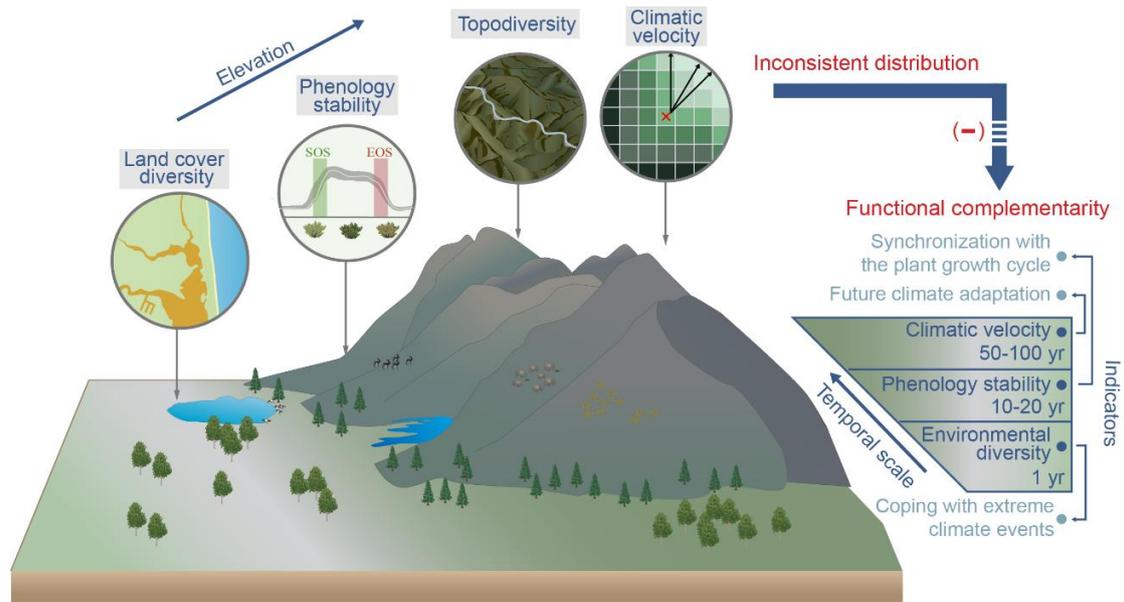
363 4.1 Inconsistent distribution limits functional complementarity of various climate refugia

364 The adaptation capacity of climate refugia, mapped by different indicators, is different (Fig. 7).
 365 For instance, climate refugia derived from environmental diversity are aimed at tackling extreme
 366 weather events (Keppel et al., 2012; Elsen et al., 2020, 2021; Silveira et al., 2021). Their distribution
 367 largely depends on the neighbourhood's topographic characteristics. Those derived from climatic
 368 velocity emphasized the adaptation to future climate change (Carroll et al., 2017) and were mainly
 369 controlled by large-scale topographic conditions. According to 20 years of phenological observation,
 370 phenology stability reflected the plants' growth cycles synchrony and animal life habits (Menzel et
 371 al., 2006; Thackeray et al., 2010; Reed et al., 2013). Therefore, the climate refugia in these three
 372 aspects complement each other in terms of temporal scale and climate adaptation capacity (Fig. 7).
 373 However, our analysis showed that climate refugia using different environmental diversity and
 374 climatic velocity indicators, differed from the priorities derived from phenology stability, according
 375 to distribution probability along an elevation gradient (Figs. 4 and 5). For instance, the former's
 376 highest probability of climate refugia being identified is mainly distributed in low or high elevations,

377 and the latter is mostly observed at 3000m – 3800m (Fig. 4, 7). This inconsistent distribution of
378 different types of climate refugia weakens this potential for functional complementarity,
379 highlighting the complexity of biological conservation on the TP.

380 Land cover and topography are key to potential climate refugia. For instance, priorities of
381 landcover diversity were observed in a combination of forest, shrub, and grassland at low elevations
382 such as the Sannan, Nyingchi, and Hengduan mountains. The distribution probability decreases
383 rapidly with elevation, as the land use type shifts to a single type, such as alpine meadows (Fig. 5).
384 Forest at low elevation has a limited warming effect in winter. However, a significant cooling effect
385 in summer (Li et al., 2015), resulted in a divergent distribution of winter and summer LST diversity.
386 Because complex terrain features have steep climatic gradients, they can facilitate local microscale
387 separation from regional climates, potentially mitigating regional climatic exposure (Ashcroft, 2010;
388 Dobrowski, 2011). For instance, when cold air moves from higher elevations and gathers in valley
389 bottoms, incised valleys squint towards temperature inversions, increasing the resistance to the
390 rising regional temperatures (Dobrowski, 2011). North-facing slopes can buffer the impact of
391 temperature change, for mean annual temperature differences of 6 °C between north- and south-
392 facing slopes of steep mountainous terrain (Gruber et al., 2004). Therefore, higher distribution
393 probability based on elevation diversity was mainly found at low (< 3000 m) and high elevations (>
394 6000 m), as shown in Fig. 4.

395 The high distribution probability of the two climatic velocity indicators was also concentrated
396 at elevations above 6000 m (Fig. 4). This is due to air temperature decreasing predictably with
397 elevation. The species at the bottom of a hill tend to move uphill to maintain their thermal conditions
398 as the climate warms. However, conversely, flat regions have more homogenous thermal conditions,
399 and the species need to move a considerable distance to locate a suitable thermal environment, which
400 would manifest as a high climatic velocity (Brito-Morales et al., 2018). The phenology stability
401 difference in low- and high-elevation regions may be related to precipitation change. Previous
402 research has indicated that water availability restricts plant growth in arid areas (Jeong et al., 2011;
403 Shen et al., 2011), and the large-scale atmospheric circulation systems can influence precipitation.
404 According to local stations observation, surface wind speed fluctuations were stronger in regions
405 with a higher elevation than in lower-elevation environments (Guo et al., 2016), and it possibly
406 leads to larger precipitation variations in higher-elevation, further disturbing the phenology stability.
407



408

409 Figure 7. Distribution mode of different types of climate refugia and their ability to buffer the
 410 climate change effects.

411 4.2 Conservation gaps in existing PAs for climate refugia

412 Conservation efforts in China started late, and the NRs are an emergency solution to avert
 413 biodiversity loss and ecosystem degradation (Huang et al., 2019). However, the quick creation of
 414 part NRs lacked systematic and coherent conservation planning, which is essential for maximizing
 415 protection targets' effectiveness and representativeness (Wu et al., 2011). The low coverage of PAs
 416 for climate refugia is a typical example (Fig. 5). The current distribution of NRs on the TP covered
 417 a limited proportion of climate refugia (9.9%-25.2%). The proportion of protected land that can
 418 buffer climate change impacts ranges from 7.3%-17.8% (Fig. 5). This shows that most of the
 419 protected land has a limited capacity to protect itself from extreme weather events or future climate
 420 change, even in the core zones of NRs (Fig. S8). It illustrated that the rapid establishment of PAs on
 421 the TP has not properly incorporated climate refugia into their planning.

422 The low coverage is primarily due to a spatial mismatch between NRs locations and climate
 423 refugia. NRs are mainly distributed in the northwest, but climate refugia are mostly distributed in
 424 the southeast. For instance, Chang Tang, Altun, and Hoh Xil, three large-size NRs located in the
 425 northwest, account for 54.4% of the entire reserve areas on the TP and 15.2% of the entire TP, but
 426 they cover only a limited number of the climate refugia (0% to 4.6%) based on different indicators.
 427 The NRs located in the southeast of the TP, although numerous, are small and fragmented, still
 428 hardly forming an effective coverage of climate refugia. Also, previous works reported that the
 429 quantity and spatial allocation of PAs on the TP are short regarding biodiversity conservation goals
 430 and ecosystem services supply (Xu et al., 2017; Zhang et al., 2018; Li et al., 2020). The notable
 431 conservation gaps mean that the current NRs cannot effectively protect these hotspots with crucial

432 ecological value. NRs are the strictest management type of PAs in China, and resource exploitation
433 inside NRs is severely limited. It implies that the establishment of inefficient NRs squeezes the
434 productive space of local people, which in turn affects their livelihood. Together with our results,
435 these analyses highlight the urgency to optimize PAs on the TP. And the low coverage of climate
436 refugia in NRs was also observed in North America, which highlights that climate refugia values
437 were not fully understood in current conservation planning (Michalak et al., 2018; Stralberg et al.,
438 2020).

439

440 **4.3 Limitations and uncertainty**

441 Some limitations and uncertainties should be further addressed in this study. First, the climatic
442 velocity approach, which is species-neutral, does not account for the climatic requirements of
443 individual species due to data availability. We assumed that areas with low climatic velocity are
444 appropriate refugia. However, likely, different species would respond differently to the same
445 disturbance. Therefore, future works need to consider these aspects, especially flagship species (e.g.,
446 Tibetan antelope and the giant panda). Second, our analysis is also affected by limitations stemming
447 from data resolution. For example, data with different resolutions were used, especially the
448 resolution of DEM (30 m) is quite different from others (500/1000m). Previous studies also
449 mentioned these limitations (e.g., Gomes et al., 2021). Another concern is the uncertainty of climate
450 models (e.g., Wootten et al., 2017). The climate refugia identification may inherit the uncertainties
451 of these models, even though the multi-model ensemble mean of 8 climate models is used to mitigate
452 this concern.

453 **4.4 Ecological and policy implications**

454 Most of the climate refugia sites were identified in TP southeastern area (Fig. 3). Our results
455 showed that the current NRs do not cover a large climate refugia potential area (Fig. 5). Therefore,
456 it is key to expand the NRs to territories with a high climate refugia potential. This will improve
457 PAs effectiveness. Our work identified these areas and recommended establishing NRs clusters in
458 these priority areas, such as Sannan, Nyingchi, Qamdo, and Garz. One approach is to merge multiple
459 small-size and fragmented NRs, which would solve the problem of insufficient habitat connectivity
460 and isolation. Furthermore, given the moderately high overlap between biodiversity, ecosystem
461 services, and climate refugia (Xu et al., 2017; Zhang et al., 2018; Li et al., 2020), expanding NRs in
462 these regions can help protect more sources with high ecological value. The results showed that the
463 high distribution probability of terrain-based/velocity-based indicators is concentrated in high
464 elevations (Fig. 4). This particular type of climate refugia will be a low-cost adaptation strategy for
465 low accessibility, low land use cost, and less potential for agricultural development and resources
466 exploitation (Joppa & Pfaff, 2009).

467 The applicability and efficiency of future conservation strategy also affected by the interactions
468 between climate change and extensive land use (Alagador et al., 2014; Maxwell et al., 2019). Indeed,
469 a sizable part of the climate refugia identified is predicted to be located southeast of the study area.
470 Better hydrothermal conditions and increased food demand are likely to accelerate agricultural
471 development in this region. The agricultural reclamation and forestry operations may further
472 negatively affect species to track the climate niche movement (Ordonez et al., 2014) and thus
473 increase extinction risks (Hansen et al., 2020; Pillay et al., 2022). Therefore, future climate
474 adaptation strategies should include specific types of agricultural land, such as cropland with high
475 nature value (Doxa et al., 2010, 2012), and focus on the agricultural areas connected to PA networks
476 (Kleijn et al., 2020).

477 Our work also supported the development of the first national park system in China. The
478 Chinese government is seeking to establish a national park system and the Third Pole National Park
479 Group in this region. If resources and funds permit, we suggest incorporating these prior climate
480 refugia in the conservation planning of the national parks system. Although our analysis identifies
481 areas that help species adapt to climate change as candidates for conservation planning, we do not
482 suggest that regions with a low proportion of climate refugia should be ignored. In such areas,
483 including Hoh Xil and Selinco NRs, continuous monitoring and proactive intervention (e.g.,
484 increasing habitat connectivity) may be appropriate conservation measures (Gillson et al., 2013;
485 Kong et al., 2021).

486 Several promising proposals are being planned for post-2020. For instance, the post-2020
487 Convention on Biological Diversity framework embraced the goal of "reducing threats". Therefore,
488 it is paramount to integrate climate adaptation considerations into PA's planning and management
489 (Tittensor et al., 2019). Furthermore, according to the UN declaration of "a Decade on Ecosystem
490 Restoration", 350 million hectares of degraded land are scheduled to be restored by 2030 (UN
491 Environment Agency, 2019). The Chinese government has further improved the compensation
492 mechanism for ecological protection. A nationwide pilot plan for comprehensive ecological
493 compensation has encompassed twenty-three counties in TP (National Development and Reform
494 Commission of China, 2019). These restoration efforts will favour species conservation, restoration
495 of natural communities, and enhance their climate resilience (Ordonez et al., 2014; Asamoah et al.,
496 2021). Furthermore, SDG13 (Climate Action), SDG 15 (Life on Land), and other related targets of
497 SDGs framework (e.g., 13.2, 15.5, and 15.9) also advocated for tangible actions to improve the
498 climate resilience, as well as the integration of these goals into conservation planning (UN, 2015).
499 Incorporating climate refugia into PAs planning can be a solution to promote these goals.

500

501

502 **5 Conclusion**

503 Given the challenges associated with conserving biodiversity in a changing climate,
504 conservation planning should consider climate refugia to mitigate the climate change effect on
505 species extinction. The identification methods that combine various physical and ecological
506 processes can provide more nuanced depictions of the usefulness of climate refugia. This study
507 compared several climate refugia based on diverse indicators and assessed how they are distributed
508 in NRs on the TP. The climate refugia identified by environmental diversity, climatic velocity, and
509 phenology stability indicators differed substantially, indicating the possible absence of functional
510 complementarity of climate adaptation. Furthermore, existing NRs have notable conservation gaps
511 for these refugia identified, particularly in the southeastern part of TP. It highlighted the urgency of
512 strengthening PAs for climate refugia on the TP. Our work provides a comprehensive understanding
513 of climate refugia, which can support better climate-driven conservation policies in the face of
514 global warming.

515

516 **References**

517 Ackerly, D.D., Loarie, S.R., Cornwell, W.K., Weiss, S.B., Hamilton, H., Branciforte, R., Kraft,
518 N.J.B., 2010. The geography of climate change: Implications for conservation biogeography. *Divers.*
519 *Distrib.* 16, 476–487.

520 Alagador, D., Cerdeira, J.O., Araújo, M.B., 2014. Shifting protected areas: Scheduling spatial
521 priorities under climate change. *J. Appl. Ecol.* 51, 703–713.

522 Asamoah, E.F., Beaumont, L., Maina, J., 2021. Climate and land-use changes reduce the
523 benefits of terrestrial protected areas. *Nat. Clim. Chang.* 11.

524 Ashcroft, M., 2010. Identifying refugia from climate change. *J. Biogeogr.* 37, 1407–1413.

525 Brito-Morales, I., Molinos, J., Schoeman, D., Burrows, M., Poloczanska, E., Brown, C., Ferrier,
526 S., Harwood, T., Klein, C., McDonald-Madden, E., Moore, P., Pandolfi, J., Watson, J., Wenger, A.,
527 Richardson, A., 2018. Climate Velocity Can Inform Conservation in a Warming World. *Trends Ecol.*
528 *Evol.* 33.

529 Carroll, C., Roberts, D., Michalak, J., Lawler, J., Nielsen, S., Stralberg, D., Hamann, A., McRae,
530 B., Wang, T., 2017. Scale-dependent complementarity of climatic velocity and environmental
531 diversity for identifying priority areas for conservation under climate change. *Glob. Chang. Biol.*
532 23.

533 Chen, J., Jönsson, P., Tamura, M., Gu, Z., Matsushita, B., Eklundh, L., 2004. A simple method
534 for reconstructing a high-quality NDVI time-series data set based on the Savitzky–Golay filter.
535 *Remote Sens. Environ.* 91 (3–4), 332–344.

536 Cong, N., Piao, S., Chen, A., Wang, X., Lin, X., Chen, S., Han, S., Zhou, G., Zhang, X., 2012.

537 Spring vegetation green-up date in China inferred from SPOT NDVI data: A multiple model analysis.
538 *Agric. For. Meteorol.* 165, 104–113.

539 Dobrowski, S., Littlefield, C., Lyons, D., Hollenberg, C., Carroll, C., Parks, S., Abatzoglou, J.,
540 Hegewisch, K., Gage, J., 2021. Protected-area targets could be undermined by climate change-
541 driven shifts in ecoregions and biomes. *Commun. Earth Environ.* 2, 198.

542 Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate.
543 *Glob Change Biol* 17: 1022–35.

544 Doxa, A., Bas, Y., Paracchini, M.-L., Pointereau, P., Terres, J.-M., Jiguet, F., 2010. Low-
545 intensity agriculture increases farmland bird abundances in France. *J. Appl. Ecol.* 47, 1348–1356.

546 Doxa, A., Paracchini, M.-L., Pointereau, P., Devictor, V., Jiguet, F., 2012. Preventing biotic
547 homogenization of farmland bird communities: The role of High Nature Value farmland. *Agric.*
548 *Ecosyst. Environ.* 148, 83–88.

549 Elsen, P.R., Farwell, L.S., Pidgeon, A.M., Radeloff, V.C., 2020. Landsat 8 TIRS-derived
550 relative temperature and thermal heterogeneity predict winter bird species richness patterns across
551 the conterminous United States. *Remote Sens. Environ.* 236

552 Elsen, P.R., Farwell, L.S., Pidgeon, A.M., Radeloff, V.C., 2021. Contrasting seasonal patterns
553 of relative temperature and thermal heterogeneity and their influence on breeding and winter bird
554 richness patterns across the conterminous United States. *Ecography* 1–13.

555 Farwell, L.S., Elsen, P.R., Razenkova, E., Pidgeon, A.M., Radeloff, V.C., 2020. Habitat
556 heterogeneity captured by 30-m resolution image texture predicts bird richness across the
557 conterminous USA. *Ecol. Appl.* 30 <https://doi.org/10.1002/eap.2157>.

558 Ganguly, S., Friedl, M.A., Tan, B., Zhang, X.Y., Verma, M., 2010. Land surface phenology
559 from MODIS: characterization of the collection 5 global land cover dynamics product. *Remote Sens.*
560 *Environ.* 114 (8), 1805–1816.

561 Garcia, R. A., Cabeza, M., Rahbek, C. & Araujo, M. B. 2014. Multiple dimensions of climate
562 change and their implications for biodiversity. *Science* 344, 1247579–1247579.

563 Gillson, L., Dawson, T. P., Jack, S., & McGeoch, M. A. 2013. Accommodating climate change
564 contingencies in conservation strategy. *Trends in Ecology & Evolution*, 28, 135–142.

565 Gomes, E., Inácio, M., Bogdzevič, K., Kalinauskas, M., Karnauskaitė, D., Pereira P., 2021.
566 Future scenarios impact on land use change and habitat quality in Lithuania. *Environ Res*
567 197:111101

568 Gonçalves-Souza, D., Vilela, B., Phalan, B., Dobrovolski, R., 2021. The role of protected areas
569 in maintaining natural vegetation in Brazil. *Sci. Adv.* 7.

570 Groves CR, Game ET, Anderson MG, et al. 2012. Incorporating climate change into systematic
571 conservation planning. *Biodivers Conserv* 21: 1651–71.

572 Gruber, S., Hoelzle, M., Haeberli, W., 2004. Rock-wall temperatures in the Alps: modelling
573 their topographic distribution and regional differences. *Permafrost Periglac* 15: 299–307.

574 Guo, X.Y., Wang, L., Tian, L.D., Li, X.P., 2016. Elevation-dependent reductions in wind speed
575 over and around the Tibetan Plateau. *Int. J. Climatol.* 36, doi: 10.1002/joc.4727.

576 Hamann, A., Roberts, D.R., Barber, Q.E., Carroll, C. Nielsen, S.E., 2015. velocity of climate
577 change algorithms for guiding conservation and management. *Glob. Change. Biol*, 21: 997-1004.

578 Hoffmann, S., Irl, S.D.H. & Beierkuhnlein, C., 2019. Predicted climate shifts within terrestrial
579 protected areas worldwide. *Nat. Commun.* 10, 4787. <https://doi.org/10.1038/s41467-019-12603-w>

580 Huang, Y., Fu, J., Wang, W., Li, J., 2019. Development of China's nature reserves over the past
581 60 years: An overview. *Land Use Policy* 80, 224–232.

582 IPCC., 2014. Climate change 2014: impacts, adaptation and vulnerability. In: Summary for
583 Policy Makers. Contribution of Working Group II to the Fifth Assessment Report of the
584 Intergovernmental Panel on Climate Change (eds. Field CB, Barros VR, Dokken DJ, Mach KJ,
585 Mastrandrea MD, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES,
586 Levy AN, MacCracken S, Mastrandrea PR, White LL), pp. 1–32. Cambridge University Press,
587 Cambridge, UK.

588 Jeong, S.J., Ho, C.-H., Brown, M., Kug, J.-S., Piao, S., 2010. Browning in desert boundaries
589 in Asia in recent decades. *J. Geophys. Res.* 116, D02103.

590 Joppa, L. N., & Pfaff, A., 2009. High and far: Biases in the location of protected areas. *PLoS*
591 *One*, 4(12), 1–6.

592 Koppel, G., Van Niel, K.P., Wardell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L., Schut,
593 A.G.T., Hopper, S.D., Franklin, S.E., 2012. Refugia: Identifying and understanding safe havens for
594 biodiversity under climate change. *Glob. Ecol. Biogeogr.* 21, 393–404.

595 Kleijn, D., Biesmeijer, K., Klaassen, R., Oerlemans, N., Raemakers, I., Scheper, J., Vet, L.,
596 2020. Integrating biodiversity conservation in wider landscape management: Necessity,
597 implementation and evaluation, in: *Advances in Ecological Research*. pp. 127–159.

598 Kong, L., Xu, W., Xiao, Y., Pimm, S., Shi, H., Ouyang, Z., 2021. Spatial models of giant pandas
599 under current and future conditions reveal extinction risks. *Nat. Ecol. Evol.* 5, 1–8.

600 Kuang, X., Jiao, J., 2016. Review on climate change on the Tibetan Plateau during the last half
601 century. *J. Geophys. Res. Atmos.* 121.

602 Lawler, J.J., Ackerly, D.D., Albano, C.M., Anderson, M.G., Dobrowski, S.Z., Gill, J.L., Heller,
603 N.E., Pressey, R.L., Sanderson, E.W., Weiss, S.B., 2015. The theory behind, and the challenges of,
604 conserving nature's stage in a time of rapid change. *Conserv. Biol.* 29, 618–629.
605 <https://doi.org/10.1111/cobi.12505>

606 Levin, N., Shmida, A., Levanoni, O., Tamari, H., Kark, S., 2007. Predicting mountain plant

607 richness and rarity from space using satellite-derived vegetation indices. *Divers. Distrib.* 13, 692–
608 703.

609 Li, S., Zhang, H., Zhou, X., Yu, H., Li, W., 2020. Enhancing protected areas for biodiversity
610 and ecosystem services in the Qinghai–Tibet Plateau. *Ecosyst. Serv.* 43, 101090.

611 Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B., Ackerly, D.D., 2009. The
612 velocity of climate change. *Nature*, 462, 1052–1055.

613 Malika, V.S., Lindsey, G., Katherine, J.W., 2009. How does spatial heterogeneity influence
614 resilience to climatic changes? *Ecological dynamics in southeast Madagascar. Ecol. Monogr.* 79,
615 557–574.

616 Maxwell, S., Reside, A., Trezise, J., McAlpine, C., Watson, J., 2019. Retention and restoration
617 priorities for climate adaptation in a multi-use landscape. *Glob. Ecol. Conserv.* 18, e00649.

618 Meddens, A.J.H., Kolden, C.A., Lutz, J.A., et al. 2018. Fire refugia: what are they, and why do
619 they matter for global change? *BioScience* 68: 944–54.

620 Menzel, A., Sparks, T.H., Estrella, N., Roy, D.B., 2006. Altered geographic and temporal
621 variability in phenology in response to climate change. *Glob. Ecol. Biogeogr.* 15, 498–504.

622 Michalak, J.L., Lawler, J.J., Roberts, D.R., Carroll, C., 2018. Distribution and protection of
623 climatic refugia in North America. *Conserv. Biol.* 32, 1414–1425.

624 Michalak, J.L., Stralberg, D., Cartwright, J.M., Lawler, J.J., 2020. Combining physical and
625 species-based approaches improves refugia identification. *Front. Ecol. Environ.* 18, 254–260.

626 Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T., et al.,
627 2016. Managing climate change refugia for climate adaptation. *PLoS One* 11, 1–17.

628 National Development and Reform Commission of China, 2019. Circular of the National
629 Development and Reform Commission on printing and distributing the Pilot Program for
630 Comprehensive Ecological Compensation.
631 https://www.ndrc.gov.cn/xxgk/zcfb/tz/201911/t20191120_1204116.html?code=&state=123

632 Oliver, T., Roy, D.B., Hill, J.K., Brereton, T., Thomas, C.D., 2010. Heterogeneous landscapes
633 promote population stability. *Ecol. Lett.* 13, 473–484.

634 Ordonez, A., Martinuzzi, S., Radeloff, V.C. & Williams, J.W., 2014. Combined speeds of
635 climate and land-use change of the conterminous US until 2050. *Nat. Clim. Change* 4, 811–816.

636 Pecl, G., Araújo, M., Bell, J., Blanchard, J., Bonebrake, T., Chen, I.-C., Clark, T., Colwell, R.,
637 Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R., Griffiths, R., Hobday, A.,
638 Janion, C., Jarzyna, M., Jennings, S., Williams, S., 2017. Biodiversity redistribution under climate
639 change: Impacts on ecosystems and human well-being. *Science*, 355.

640 Piao, S., Fang, J.Y., Zhou, L.M., Ciais, P., Zhu, B., 2006. Variations in satellite-
641 derived phenology in China's temperate vegetation. *Global Change Biol.* 12 (4), 672–685.

642 Plard, F., Gaillard, J.M., Coulson, T., Hewison, A.J.M., Delorme, D., Warnant, C., Bonenfant,
643 C., 2014. Mismatch Between Birth Date and Vegetation Phenology Slows the Demography of Roe
644 Deer. *PLoS Biol.* 12, 1–8.

645 Reed, T.E., Grotan, V., Jenouvrier, S., Saether, B., Visser, M.E., 2013. Population growth in a
646 wild bird is buffered against phenological mismatch. *Science* 340, 488–491.

647 Shen, M., Tang, Y., Chen, J., Zhu, X., Zheng, Y., 2011. Influences of temperature and
648 precipitation before the growing season on spring phenology in grasslands of the central and eastern
649 Qinghai-Tibetan Plateau. *Agric. For. Meteorol.* 151, 1711-1722.

650 Shen, M., Zhang, G., Cong, N., Wang, S., Kong, W., Piao, S., 2014. Increasing altitudinal
651 gradient of spring vegetation phenology during the last decade on the Qinghai-Tibetan Plateau.
652 *Agric. For. Meteorol.* 189–190, 71–80.

653 Silveira, E.M.O., Radeloff, V.C., Martinuzzi, S., Martínez Pastur, G.J., Rivera, L.O., Politi, N.,
654 Lizarraga, L., Farwell, L.S., Elsen, P.R., Pidgeon, A.M., 2021. Spatio-temporal remotely sensed
655 indices identify hotspots of biodiversity conservation concern. *Remote Sens. Environ.* 258, 112368.

656 Stein, A., Gerstner, K., & Kreft, H., 2014. Environmental heterogeneity as a universal driver
657 of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17, 866–880.

658 Stralberg, D., Arseneault, D., Baltzer, J.L., Barber, Q.E., Bayne, E.M., Boulanger, Y., Brown,
659 C.D., Cooke, H.A., Devito, K., Edwards, J., Estevo, C.A., Flynn, N., Frelich, L.E., Hogg, E.H.,
660 Johnston, M., Logan, T., Matsuoka, S.M., Moore, P., Morelli, T.L., Morissette, J.L., Nelson, E.A.,
661 Nenzén, H., Nielsen, S.E., Parisien, M.A., Pedlar, J.H., Price, D.T., Schmiegelow, F.K.A., Slattery,
662 S.M., Sonnentag, O., Thompson, D.K., Whitman, E., 2020. Climate-change refugia in boreal North
663 America: what, where, and for how long? *Front. Ecol. Environ.* 18, 261–270.

664 Stralberg, D., Carroll, C., Nielsen, S.E., 2020. Toward a climate-informed North American
665 protected areas network: Incorporating climate-change refugia and corridors in conservation
666 planning. *Conserv. Lett.* 13, 1–10.

667 Studer, S., Stockli, R., Appenzeller, C., Vidale, P.L., 2007. A comparative study of satellite and
668 ground-based phenology. *Int. J. Biometeorol.* 51 (5),405–414.

669 Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R., Botham, M.S.,
670 Brereton, T.M., Bright, P.W., Carvalho, L., Clutton-Brock, T., Dawson, A., Edwards, M., Elliott,
671 J.M., Harrington, R., Johns, D., Jones, I.D., Jones, J.T., Leech, D.I., Roy, D.B., Scott, W.A., Smith,
672 M., Smithers, R.J., Winfield, I. J., Wanless, S., 2010. Trophic level asynchrony in rates of
673 phenological change for marine, freshwater and terrestrial environments. *Glob. Chang. Biol.* 16,
674 3304–3313.

675 Tittensor, D., Beger, M., Boerder, K., Boyce, D., Cavanagh, R., Cosandey-Godin, A., Ortuno
676 Crespo, G., Dunn, D., Ghiffary, W., Grant, S., Hannah, L., Halpin, P., Harfoot, M., Heaslip, S.,

677 Jeffery, N., Kingston, N., Lotze, H., MCGowan, J., Mcleod, E., Worm, B., 2019. Integrating climate
678 adaptation and biodiversity conservation in the global ocean. *Sci. Adv.* 5, eaay9969.

679 UN, 2015. Transforming our world: the 2030 Agenda for Sustainable development (United
680 Nations, 2015).

681 United Nations Environment Agency. Resolution 73/284: United Nations Decade on
682 Ecosystem Restoration (2021–2030). <https://undocs.org/A/RES/73/284> (2019)

683 White, M.A., Thornton, P.E., Running, S.W., 1997. A continental phenology model for
684 monitoring vegetation responses to interannual climatic variability. *Global Biogeochem. Cycles* 11
685 (2), 217–234.

686 Williams, J., Jackson, S., 2007. Novel climates, no-analog communities, and ecological
687 surprises. *Front. Ecol. Environ.* 5, 475–482.

688 Wolf, A.A., Zavaleta, E.S., Selmants, P.C., 2017. Flowering phenology shifts in response to
689 biodiversity loss. *Proc. Natl. Acad. Sci. U. S. A.* 114, 3463–3468.

690 Wotten, A., Terando, A., Reich, B.J., Boyles, R.P., Semazzi, F., 2017. Characterizing sources
691 of uncertainty from global climate models and downscaling techniques. *J. Appl. Meteorol. Climatol.*
692 56:3245–3262

693 Xu, W., Xiao, Yi, Zhang, J., Yang, W., Zhang, L., Hull, V., Wang, Z., Zheng, H., Liu, J., Polasky,
694 S., Jiang, L., Xiao, Yang, Shi, X., Rao, E., Lu, F., Wang, X., Daily, G.C., Ouyang, Z., 2017.
695 Strengthening protected areas for biodiversity and ecosystem services in China. *Proc. Natl. Acad.*
696 *Sci. U. S. A.* 114, 1601–1606.

697 Yu, H.Y., Luedeling, E., Xu, J.C., 2010. Winter and spring warming result in delayed spring
698 phenology on the Tibetan Plateau. *Proc. Natl. Acad. Sci. U.S.A.* 107 (51), 22151–22156.

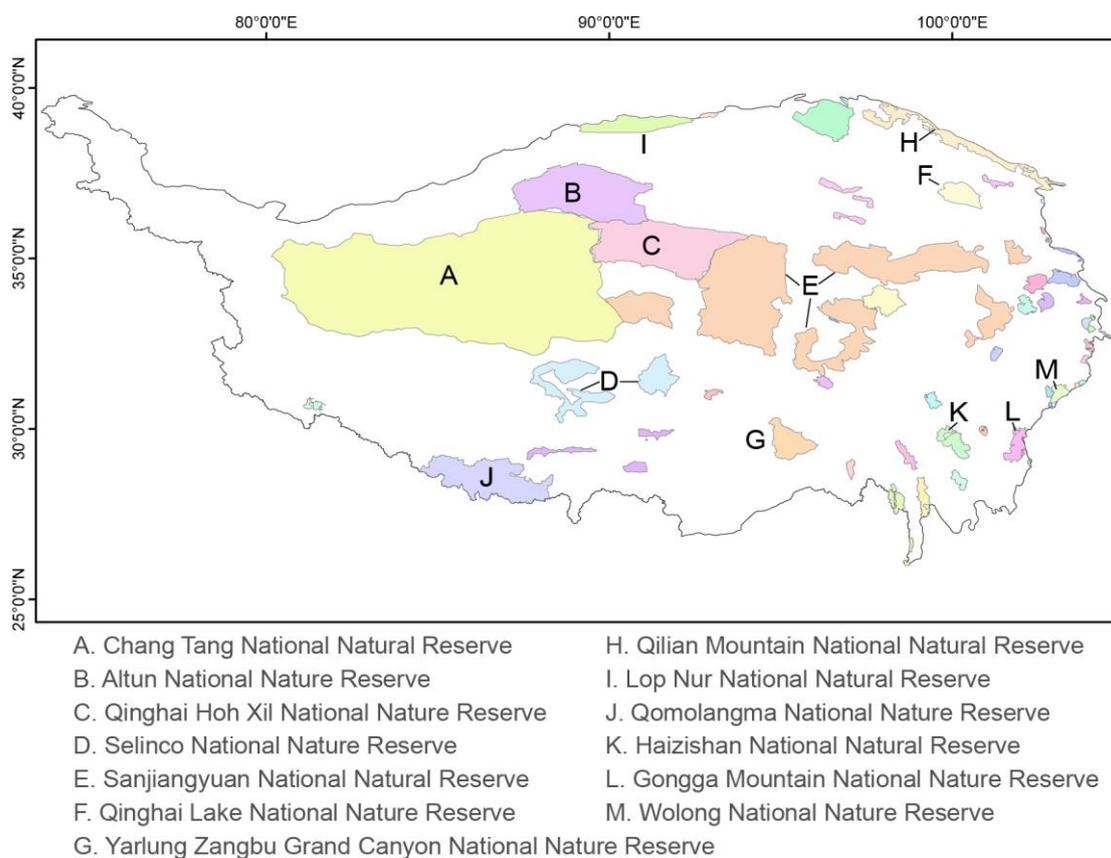
699 Zhang, J., Xu, W., Kong, L., Hull, V., Xiao, Yi, Xiao, Yang, Ouyang, Z., 2018. Strengthening
700 protected areas for giant panda habitat and ecosystem services. *Biol. Conserv.* 227, 1–8.

701 Zhang, Q., Kong, D., Shi, P., Singh, V.P., Sun, P., 2018. Vegetation phenology on the Qinghai-
702 Tibetan Plateau and its response to climate change (1982–2013). *Agric. For. Meteorol.* 248, 408–
703 417.

704 Zhang, X., Friedl, M., Schaaf, C., 2006. Global vegetation phenology from Moderate
705 Resolution Imaging Spectroradiometer (MODIS): Evaluation of global patterns and comparison
706 with in situ measurements. *J. Geophys. Res.* 111.

707 Pillay, R., Venter, M., Aragon-Osejo, J., González-del-Piiego, P., Hansen, A. J., Watson, J.
708 E. M., & Venter, O., 2022. Tropical forests are home to over half of the world’s vertebrate
709 species. *Frontiers in Ecology and the Environment*, 20(1), 10–15.

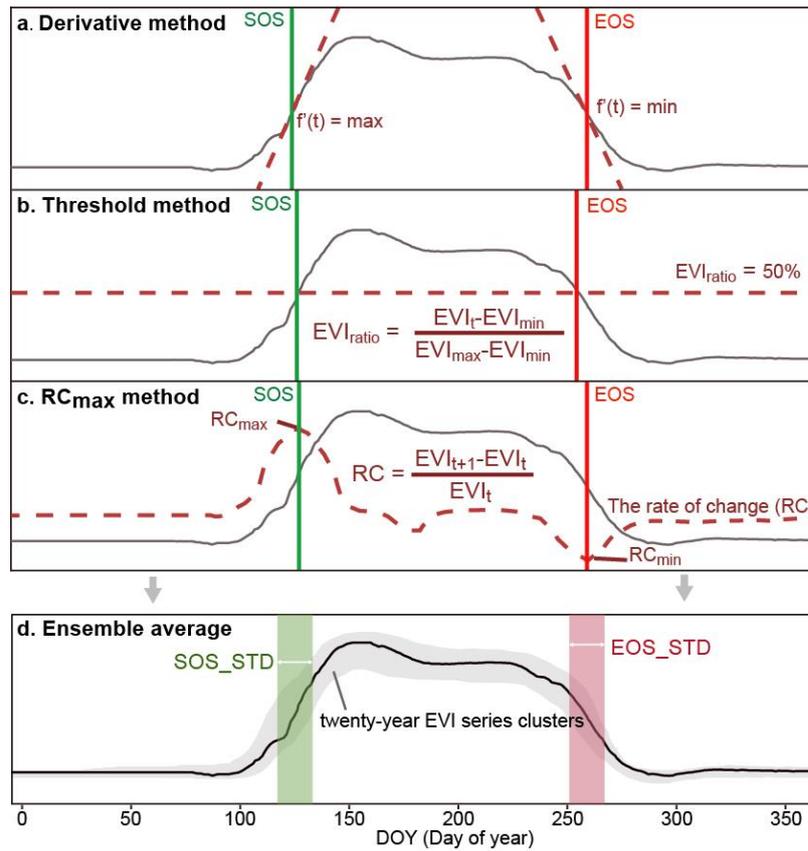
710 Hansen, A., Burns, P., Ervin, J., Goetz, S., Hansen, M., Venter, O., Watson, J., Jantz, P.,
711 Virnig, A., Barnett, K., Pillay, R., Atkinson, S., Supples, C., Rodriguez-Buritica, S., &
712 Armenteras, D., 2020. A policy-driven framework for conserving the best of Earth’s remaining
713 moist tropical forests. *Nature Ecology & Evolution*, 4, 1–8.



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716 Figure S1. Distribution and name of PAs on the Tibetan Plateau. We only marked the
717 names of major national nature reserves.

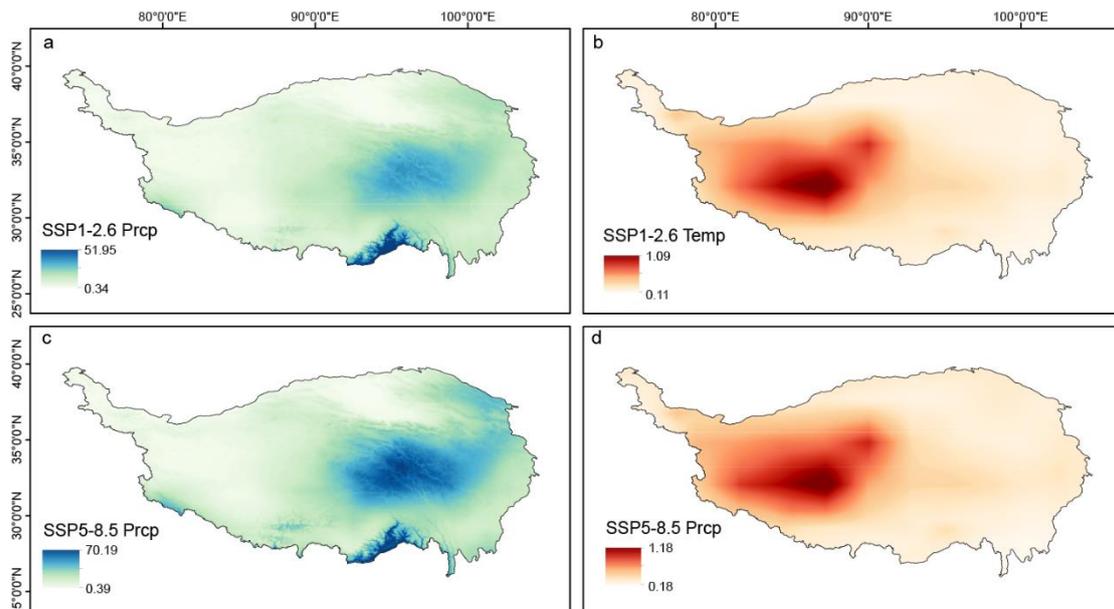
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720 Figure S2. Schematic diagram of phenology calculation. (a-c) indicates the Derivative method,
 721 Threshold method, and RC_{max} method, respectively. Start date of the growing season (SOS) and the
 722 end date of the growing season (EOS). Please see [Section 2.4.2](#) for the detailed phenology
 723 calculation process.

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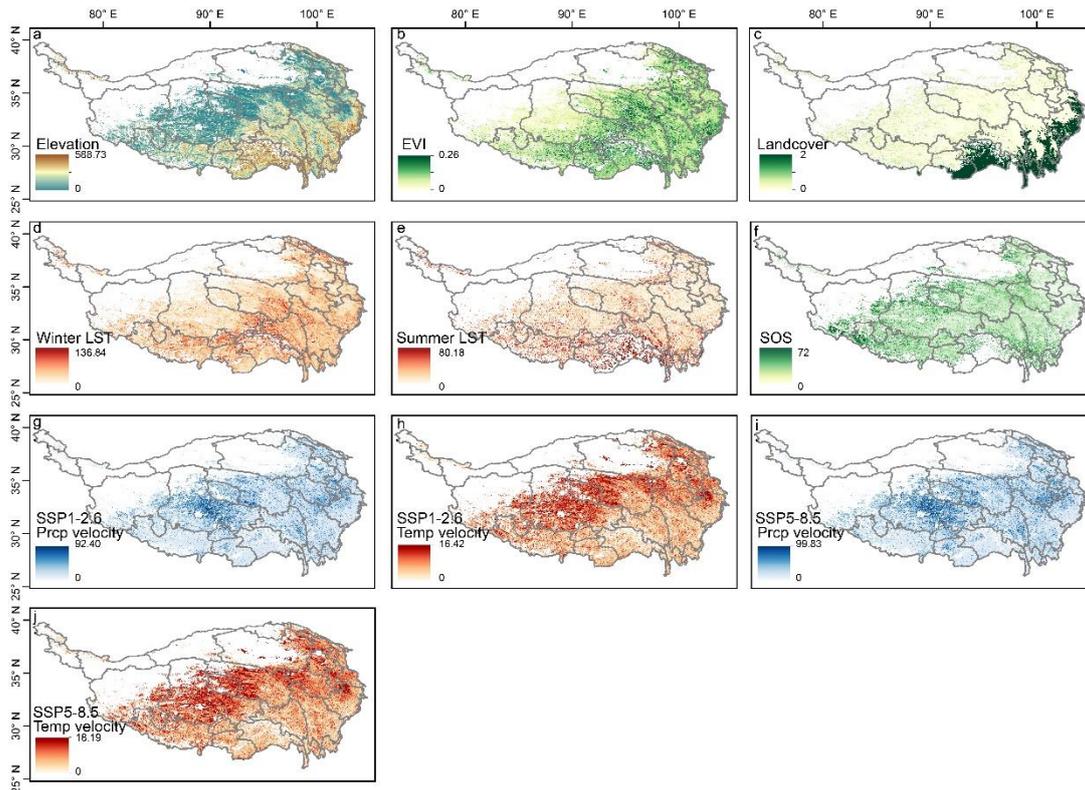
726 Figure S3. Standard error of future climate under 8 global climate models. “Prp” means
 727 precipitation, and “Temp” means temperature.

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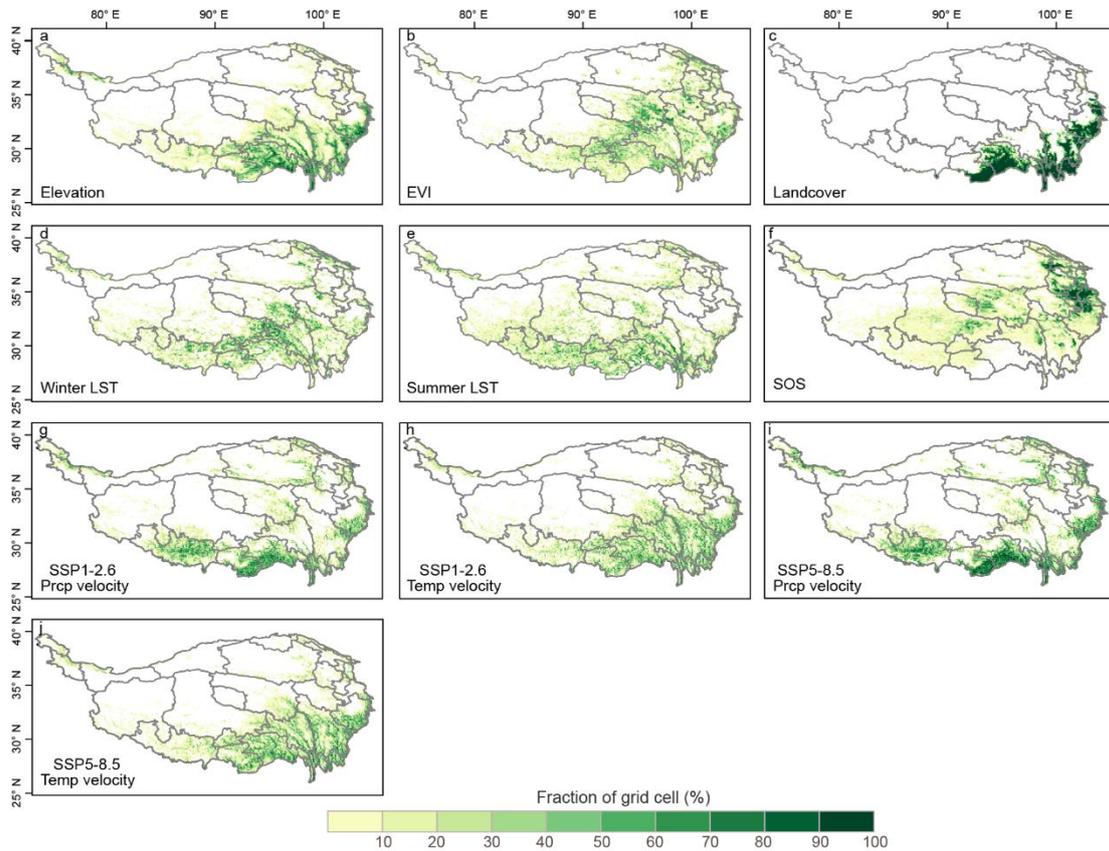


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733 Figure S4. The distribution of climate refugia indicators. “EVI” means enhanced vegetation index,
 734 Land surface temperature (LST), precipitation (Prcp), and temperature (Temp), start of the growing
 735 season (SOS), and enhanced vegetation index (EVI).

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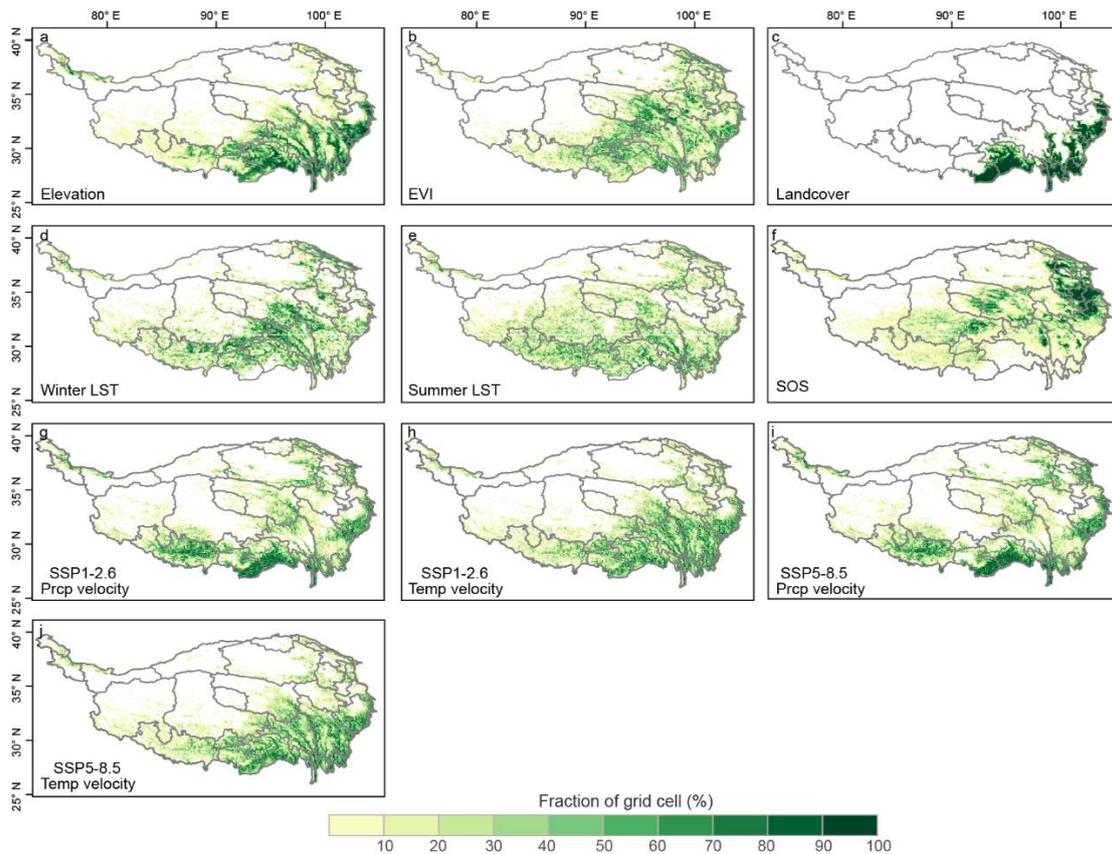
739 Figure S5. Distribution of priority climate refugia based on different indicators (%) according to **the**
 740 **threshold of 15%**. This figure is part of the sensitivity test with a threshold of 25% ([Section 2.5](#)).

741 The figures are aggregated to 0.1 degree resolution for improved visualization. (a-e) showed the
 742 environmental diversity of elevation, EVI, landcover, winter LST and summer LST, (f) showed the
 743 phenology stability indicator, and (g-j) showed the future climate change velocity for precipitation
 744 and temperature for SSP1-2.6 and SSP5-8.5, respectively. The color shade of green represents the
 745 percentage of priority climate refugia. Land surface temperature (LST), precipitation (Prpc), and
 746 temperature (Temp), start of the growing season (SOS), and enhanced vegetation index (EVI).

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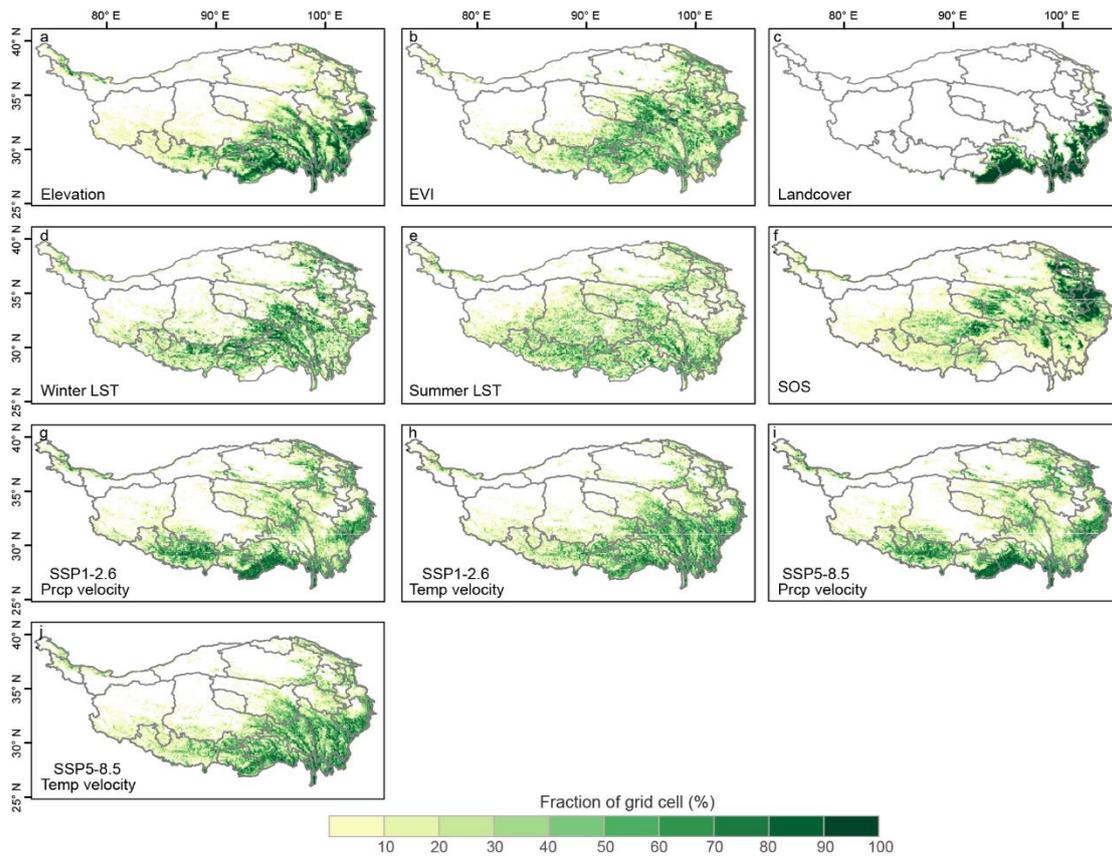
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751 Figure S6. Distribution of priority climate refugia based on different indicators (%) according to **the**
 752 **threshold of 25%**. This figure is part of the sensitivity test with a threshold of 25% (Section 2.5).

753 The figures are aggregated to 0.1 degree resolution for improved visualization. (a-e) showed the
 754 environmental diversity of elevation, EVI, landcover, winter LST and summer LST, (f) showed the
 755 phenology stability indicator, and (g-j) showed the future climate change velocity for precipitation
 756 and temperature for SSP1-2.6 and SSP5-8.5, respectively. The color shade of green represents the
 757 percentage of priority climate refugia. Land surface temperature (LST), precipitation (Prpc), and
 758 temperature (Temp), start of the growing season (SOS), and enhanced vegetation index (EVI).

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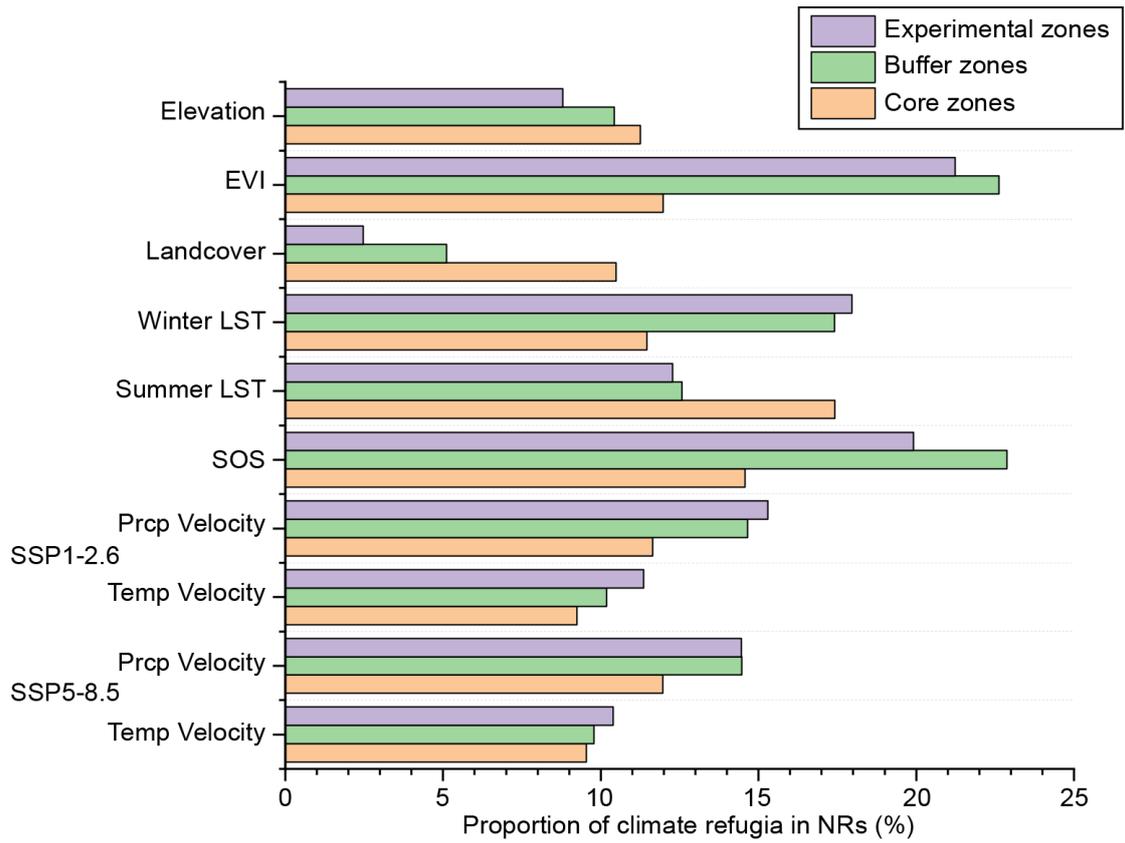
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762 Figure S7. Distribution of priority climate refugia based on different indicators (%) according to **the**
 763 **threshold of 30%**. This figure is part of the sensitivity test with a threshold of 30% (Section 2.5).

764 The figures are aggregated to 0.1 degree resolution for improved visualization. (a-e) showed the
 765 environmental diversity of elevation, EVI, landcover, winter LST and summer LST, (f) showed the
 766 phenology stability indicator, and (g-j) showed the future climate change velocity for precipitation
 767 and temperature for SSP1-2.6 and SSP5-8.5, respectively. The color shade of green represents the
 768 percentage of priority climate refugia. Land surface temperature (LST), precipitation (Prpc), and
 769 temperature (Temp), start of the growing season (SOS), and enhanced vegetation index (EVI).

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772

773 Figure S8. Proportion of climate refugia in different part of NRs: 1) experimental zones, 2) buffer
 774 zones, and 3) core zones. Land surface temperature (LST), precipitation (Prcp), and temperature
 775 (Temp), and enhanced vegetation index (EVI).

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