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Wild Apples Are Not That Wild: Conservation Status and Potential Threats of *Malus sieversii* in the Mountains of Central Asia Biodiversity Hotspot

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Abstract: As one of the global biodiversity hotspots, the mountains of Central Asia are home to a large number of wild fruit species. Although the hotspots are constantly being seriously affected by climate and land-use changes, effective assessments of the impacts of these changes for the dominant species of wild fruit forests, wild apple (*Malus sieversii*), have been limited. We compiled 8344 occurrence records for wild apple across its whole distribution ranges from field surveys and herbarium and literature records. After data thinning to reduce sampling bias, we used ensemble niche models to project current and future suitable habitats, examined the importance of environmental factors, and assessed whether current national protected areas (PAs) are effective in protecting the suitable habitats. We found that the distribution of wild apple is currently fragmented. Under future scenarios, it would shift 118–227 km towards high latitudes and ~200 m towards high elevations, losing nearly 27–56% of suitable habitats in the south, and gaining some habitats in the north. The increased temperature and expansion of cropland contributed to these shifts. Nevertheless, about 13% of the suitable habitats are covered by existing PAs and less than 25% of suitable habitats will be protected in the future. The cold spots for protecting intact wild fruit forests are located in Xinjiang, China and Kyrgyzstan. Overall, we provide a detailed evaluation of the impacts of climate and land-use changes on current and future distributions of wild apple in Central Asia. Considering that this species faces a greater risk of habitat loss in the south of Central Asia, we advocate developing effective in situ conservation strategies with long-term monitoring that will provide deep insights into the fate of wild fruit forests.

Keywords: crop wild relatives; ecological niche model; protected area; range shift; useful plant species; wild fruit forest

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1. Introduction

Crop wild relatives (CWRs) are important socio-economic resources [1] that provide unique ecosystem functions and services in their native habitats and represent key sources of genetic material [2,3]. Human-induced climate change represents a particular challenge for CWRs [4,5] through increasing ambient temperatures, altered hydrological cycles and more frequent extreme weather events [6]. Globally, Vincent et al. [5] reported that 726 of 1261 CWRs will lose 50% or more of their current habitats due to climate change in the

2070s. At regional scales, the negative impacts of climate change in the distributions of CWRs were also documented in China [7], Europe [8], and North America [9]. Nevertheless, the role of land-use changes in reshaping the distributions of CWRs is largely neglected, although dramatic changes in land-use are increasingly impacting natural and semi-natural habitats of CWRs [10,11]. Meanwhile, a large geographic bias exists in these studies, with many studies in Europe and North America and a few in Central Asia, Africa, and South America, although these regions hold a high richness of CWRs [9,12,13]. In addition, compared to agriculture-related CWRs (e.g., maize, wheat, and rice), the effects of habitat suitability and trends in climate change and land-use change on wild fruit tree species are less examined [14].

Wild fruit trees are an important component of CWRs [10,15,16]. Wild fruit trees are widely distributed in tropical and temperate climatic regions [9,10,17]. The climate changes and other environmental crises have triggered a dramatic loss in wild fruit trees' genetic diversity [10,16], while their conservation has yet to be addressed systematically. In situ conservation of wild fruit trees has been largely neglected. Among the world's protected areas, only a few were established for wild fruit trees [18]. Less than 22% of the average proportion of suitable habitats for wild fruit trees are protected currently [5]. Considering their importance, there are large knowledge gaps on how wild fruit trees and the forests will respond to climate and land-use changes in the future, especially in global biodiversity hotspots.

The mountains of Central Asia, one of 36 global biodiversity hotspots, cover about 86 million hectares in area and are one of the most important centers of origin and diversity for temperate wild fruit trees [19]. More than 90% of temperate-zone fruit species are found here, including wild apple (*Malus sieversii*), walnut (*Juglans regia*), and apricot (*Armeniaca vulgaris*) [20,21]. Wild apple and other wild fruit trees together form ancient forests, wild fruit forests, which have both biological and economic value for fruit production and play an important ecological role in Central Asia [22]. Meanwhile, with approximately 60 million people living here, biodiversity in this region is under serious threats and is especially sensitive and vulnerable to changes in climate and land-use [6,23]. The increases in air temperature in this region were projected to be the most pronounced in summer and winter, with the largest magnitudes of 5.0 °C and 5.4 °C, respectively, by the end of the century [6]. Moreover, the expanding cropland, deforestation, and other human activities are dramatically changing this region's ecosystems [24]. During the last decades, wild fruit trees have been diminished to half of their original habitats [10,21,22]. There are 44 wild fruit tree species that have been listed in the Red List of endangered trees of Central Asia, including wild apple [25]. Therefore, it is particularly important to assess the impacts of climate and land-use changes on wild fruit trees for regional agricultural production and food security in this biodiversity hotspot [26].

Wild apple is a dominant species of wild fruit forests in Central Asia and an ancient progenitor of the domesticated apple [27,28], which contains precious genetic resources and provides key ecosystem services [22]. In Central Asia, its distribution covers a large percentage of the total area of wild fruit forests, e.g., over 70% in the mountain leskhozes of Kazakhstan [29]. In wild fruit forest communities, wild apple trees usually dominate solely or co-dominate with 1–2 other wild fruit tree species [29]. For example, in one 4 ha sampling plot in Xinjiang, China, nearly 99% of 1715 tree individuals were wild apple trees, while others belonged to another seven species [30]. In 95 plots of wild fruit forests we surveyed in China, wild apple contributed ~50% of total biomass, with over 80% biomass for 49 plots (unpublished data). However, due to over 70% habitat loss in the last three decades, wild apple has been listed in the red list of IUCN [31] and in the 'Red Data Book of China, Kazakh and Kyrgyz' [10]. In this study, we aimed to gain a better understanding of habitat requirements of wild apple, predict future population dynamics under climate and land-use change scenarios, and evaluate whether existing national protected areas (PAs) have effectively protected this species. By combining detailed species distribution data of wild apple and climate and land-use data, we used ensemble niche models to predict the suitable habitats of wild apple across its entire range under current and future periods. Specifically, we addressed the following questions: (a) What is the current status of wild apple's native distributions? How will its range shift under future scenarios of climate change and land-use? (b) Which environmental factors have dramatic impacts in shaping spatial distributions of wild apple? (c) Are the current national PAs effective in protecting suitable habitats of wild apple in the current and future scenarios? Where are the hot and cold spots for maintaining intact wild fruit forests in this region?

2. Material and Methods

2.1. Study Area

The mountains of Central Asia, most of the Tarbagatai and Barlyk Mountains, and a small part of the Altai Mountains were selected as the current study area (37° N–51° N, 65° E–88° E; Figure 1). The study area stretches from Tajikistan in the south to Kazakhstan and Russia in the north, including a large area of seven countries: western Tajikistan, northeastern Afghanistan, Kyrgyzstan, eastern Kazakhstan and Uzbekistan, western Xinjiang in China, and a small part of Russia. This region is surrounded by desert on three sides, with elevations ranging from 200 m in the low-lying desert to more than 7000 m in the Tien Shan Mountains. Annual precipitation ranges from about 250–450 mm, and precipitation in the driest month is less than 20 mm [32]. The average temperature in January is −20 °C to −5 °C, and average July temperature reaches 18 °C to 29 °C [33]. The soils have relatively high nitrogen and organic content in the wild fruit forests [29].

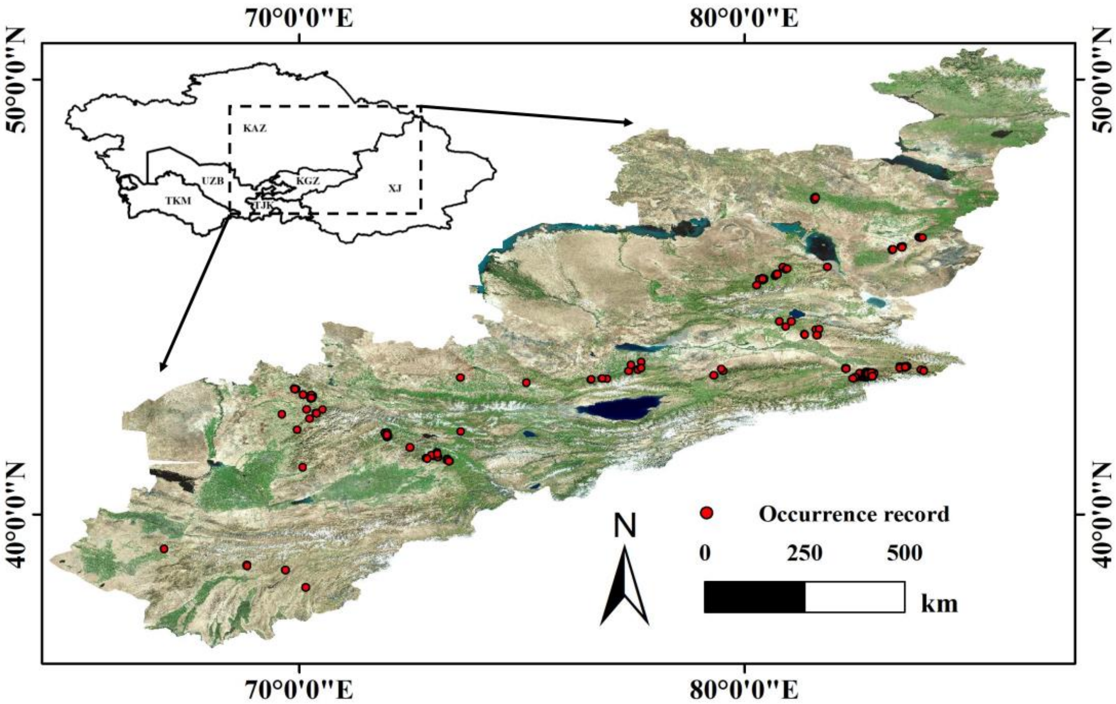

Figure 1. Location of the study area in Central Asia. XJ: Xinjiang, China, KAZ: Kazakhstan, KGZ: Kyrgyzstan, TJK: Tajikistan, UZB: Uzbekistan, TKM: Turkmenistan. Red points represent occurrence records for wild apple.

2.2. Data Source

2.2.1. Species Occurrence Records for Wild Apple

To obtain high-quality occurrence records for wild apple across its whole distribution range, we compiled data from field surveys, herbariums and the literature. The field surveys were conducted in all of the countries with wild apple distribution in Central Asia. Precisely, we had several exhaustive investigations of wild apple populations in Xinjiang, China from 2008 to 2021, including distribution range and abundance of wild apple across its whole elevational ranges in six counties. For herbarium data, we combined the records from Global Biodiversity Information Facility [34] and Chinese Virtual Herbarium [35]. Finally, we obtained 8344 occurrence records for wild apple. To reduce the potential effects of spatial sampling bias in these records, we deleted duplicate and pseudo-presence points (e.g., records of planted wild apple located in water or snowy mountains), removed records outside the distribution boundaries of wild apple, and then performed spatial thinning for retained records using the 'thin' function in R package 'spThin' [36]. The cleaned and thinned dataset contained 352 occurrences (Figure 1).

2.2.2. Current and Future Climate Data

The current and future climate was derived from the WorldClim database at a 2.5 arc-min resolution [37]. To reduce multicollinearity, we removed highly correlated variables using Pearson's correlation coefficients ($|r^2| > 0.7$) [38], considering that mean diurnal range (Bio 2) has no clear biological significance in explaining the distribution of wild apple [29]. Finally, we selected three climate variables: annual mean temperature (MAT), temperature seasonality (TEMP_season), and precipitation of driest month (PREC_dry). The future climate in the 2050s (2040–2060) and 2090s (2080–2100) was characterized by two different CMIP-6 scenarios from Shared Socio-economic Pathways (SSPs): SSP1-RCP2.6 (SSP126, the sustainability-oriented scenarios) and SSP5-RCP8.5 (SSP585, the unconstrained growth scenarios) [39].

2.2.3. Current and Future Land-Use Data

We used the Land-Use Harmonization (LUH2) dataset [40], which reports the proportional coverage of 12 land-use classes within each 15 arc-min grid cell of the globe in the current and future scenarios (SSP126 and SSP585). We reclassified 12 LUH classes into five major types, including forested land, non-forested land, grazed land, cropland and urban land [41]. Forested land includes forested primary land and potentially forested secondary land; non-forested land includes non-forested primary land and potentially non-forested secondary land (e.g., shrubland, national parks and wilderness recreational areas); grazed land includes managed pasture and rangeland; cropland includes C_3 annual crops, C_3 perennial crops, C_4 annual crops, C_4 perennial crops, and C_3 nitrogen-fixing crops. To derive a continuous surface matching the climate resolution, we downscaled the LUH2 surface to 2.5 arc-min using the 'bilinear' method of the 'resample' function in R package 'raster' [42].

2.2.4. Topographic and Edaphic Variables

Considering the large elevational range in this region, topographic and edaphic variables might be critical factors that control plants' distribution [29]. Thus, we selected elevation (ELEV) and soil pH (pH) in the models. Elevation was derived from the SRTM elevation data. Soil pH was obtained from the SoilGrids at a 250 m resolution [43]. Elevation and soil pH were assumed to remain constant in the projections for the 2050s and 2090s.

2.3. Species Distribution Models

As ensemble species distribution modeling (SDM) produces more robust predictions and allows quantifying uncertainties [44], we chose an ensemble niche model to model species distribution for wild apple. According to previous studies, random forests (RF), gradient boosting machines (GBM), and maximum entropy (MaxEnt) are often regarded as having strong predictive performance [45]; therefore, we selected these three algorithms for ensemble predictions. We generated ten sets of pseudo-absences by randomly selecting absence with the same number as presence records from the whole study area [46]. We evaluated the models by randomly dividing the original data set into two parts, one for calibrating models (80%) and the other for evaluating them (20%) by Kappa, means of the true skill statistic (TSS) and the area under the receiver operating characteristic curve (AUC) [47]. In order to avoid overfitting, we used internal cross-validation in model fitting [48,49]. Then, this process was repeated five times to ensure that the random partitioning did not influence the estimated predictive accuracy [50]. These models were then projected under the current and two future scenarios at a 2.5 arc-min resolution, using ensemble forecasting classified into binary presence–absence predictions of suitable habitat with the threshold that maximizes TSS [51]. All models and ensemble forecasts were calculated for a full dispersal (no dispersal constraints) scenario and performed within R package 'BIOMOD2' [50].

2.4. Data Analysis

To test the expansion or contraction of the distributional range of wild apple under different climate and land-use scenarios, we calculated the percentage of suitable habitat changes for wild apple in the current and future periods [52]. The latitudinal range shifts (north–south) were assessed using the centroids of the predicted present and future distributions [8]. Further, we calculated the elevational range shifts for potential range size along elevation at 200 m intervals and compared the variety of the range size between the current and two future scenarios in the same elevation zone.

To determine the importance of environmental variables for the current distribution of wild apple, we firstly created a pseudo-absence dataset for modeling instead of assuming that a non-presence equals a true absence [46,50]. Second, to reduce the potential effects of sampling effort bias of background points, we selected random presence and pseudo-absence points to model 100 times in R packages 'rfPermute' and 'A3' [53]. In addition, we used Monte Carlo tests to plot the density distribution of environment variables. We randomly selected presence and pseudo-absence points to model using the function 'enmtools.rf' and plot bivariate heat figures using the 'visualize.enm' function in R package 'ENMtools 1.0' [54].

To assess the effectiveness of PAs for conserving wild apple under climate and land-use changes, we calculated the range size and proportion of potentially suitable habitat within PAs for both current and future scenarios. We used the databases provided by the World Database on Protected Areas [55] and Resources and Environmental Science Data Center, Chinese Academy of Sciences to select 110 international or national terrestrial PAs in the study area (Table S1). These PAs cover a total of 232,891.31 km^2 (ca. 17% of the study area), and 45 of them were established to protect wild fruit forests as their major targets [10,55]. All analyses were performed in R software v4.2.0 [56].

3. Results

3.1. Range Shifts of Wild Apple

All SDMs showed high performance (mean Kappa, TSS and AUC values: >0.89; model sensitivity: >0.92; model specificity: >0.95). Currently, wild apple is fragmentally distributed (ca. 49,956 km^2), and more than 29% of the distributions are in Xinjiang of China, Kyrgyzstan and Kazakhstan, respectively, and less than 3% in Tajikistan and Uzbekistan (Figure 2a; Table S2).

In the 2050s, wild apple is expected to shift 118–167 km towards the north, gaining a small part of suitable habitats in the northern regions, while losing most current distribution areas in southern regions (Figures 2b,c and 3a,b). In particular, it is expected to completely lose its suitable habitats in Uzbekistan under SSP585 (Figure 3a,b; Table S3). Additionally, wild apple will shift towards higher elevations and gain suitable habitats in the mid-elevations (Figure 4).

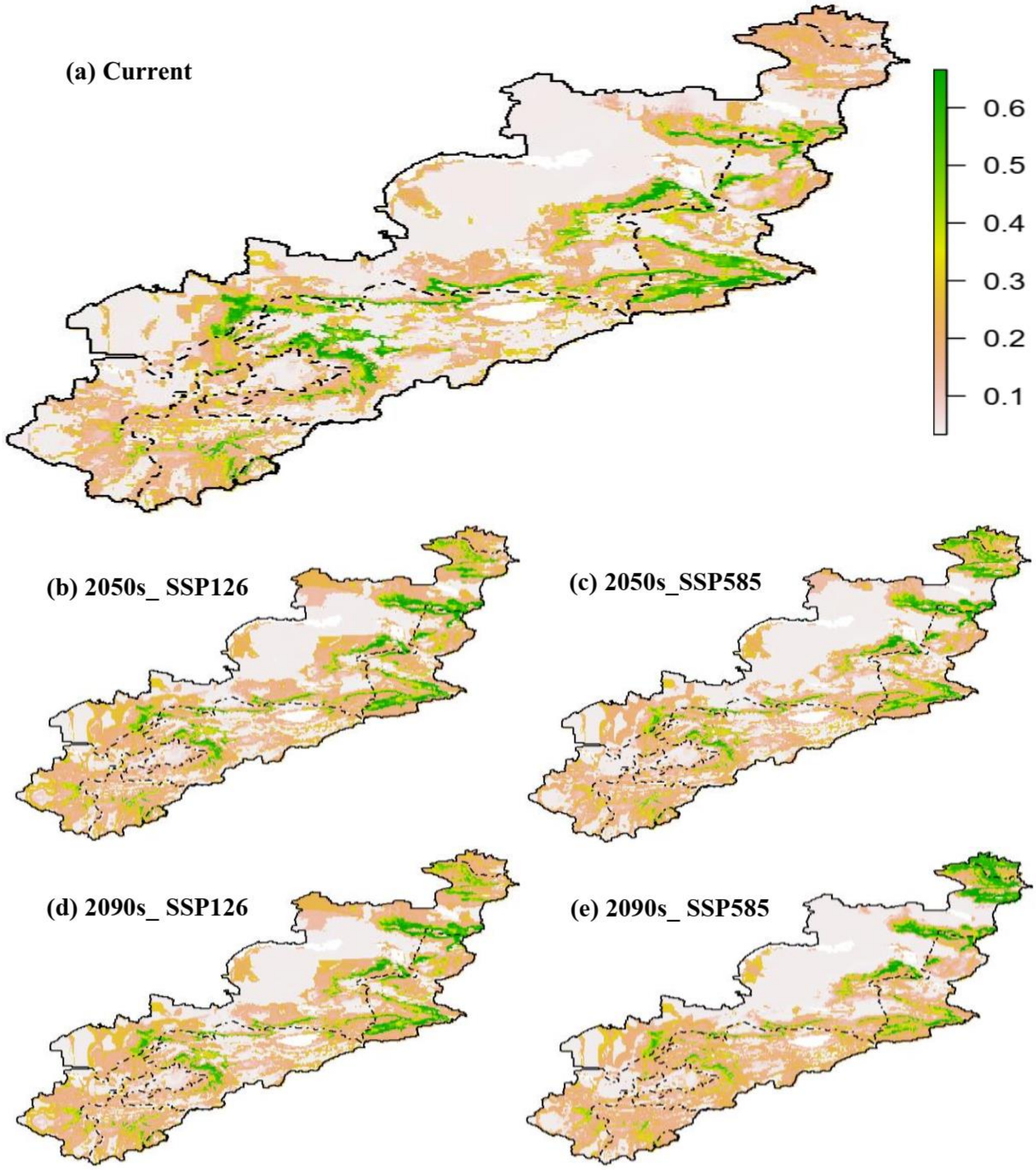

Figure 2. The distribution range of suitable habitat for wild apple in the current (**a**) and future scenarios (**b**–**e**). Green areas indicate highly suitable habitats, while gray regions indicate absence. The dashed lines show country boundaries in this region.

In the 2090s, wild apple would shift further towards the north and lose most of its suitable habitats in southern Uzbekistan and Tajikistan (Figures 2b,c and 3a,b). In particular, they will lose ca. 100% of suitable habitats in Uzbekistan and Tajikistan under SSP126 and SSP585 (Figure 3c,d; Table S3). Along elevations, wild apple will shift further towards higher elevations (ca. 200 m) under the SSP585, gain a large number of suitable habitats in the mid and high elevations, and lose part of its suitable habitat in lower elevations (<1000 m; Figure 4).

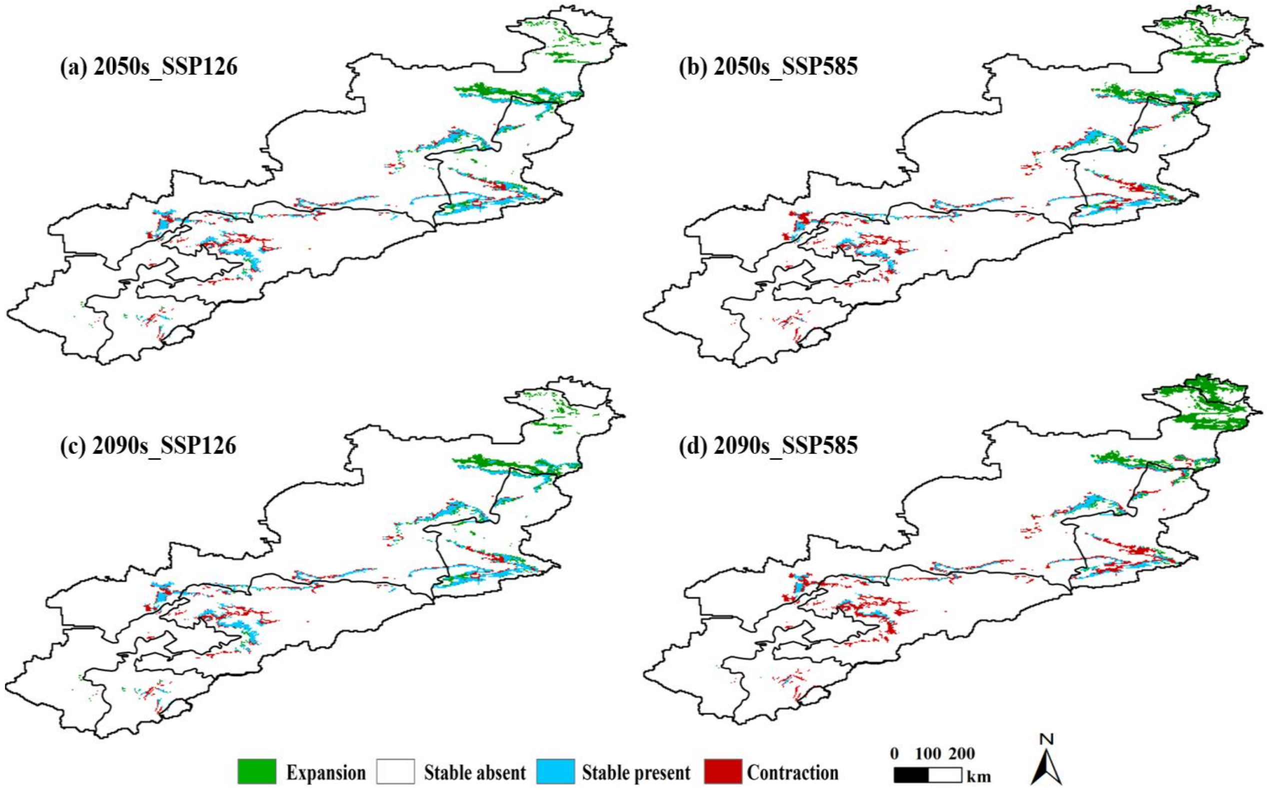

Figure 3. Changes in suitable habitat for wild apple in the 2050s (**a**,**b**) and 2090s (**c**,**d**). Red colors indicate the loss of suitable habitats, green indicates newly increased suitable habitats, and blue indicates stable habitats.

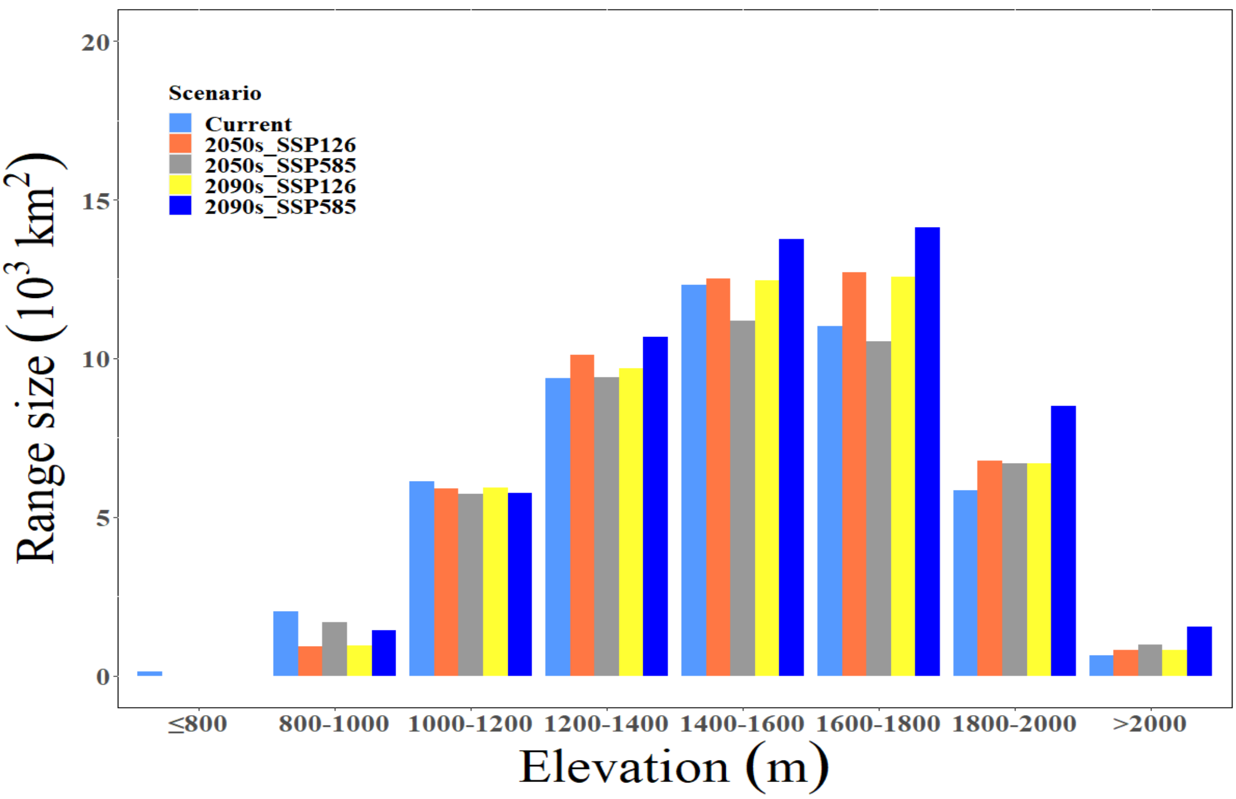

Figure 4. The changes in range size for wild apple along elevations under the current and future scenarios.

3.2. The Importance of Environmental Factors

Among the predictor variables of limiting species distribution (Figure 5), ELEV explained 15% of the spatial variations, followed by soil pH (10% of the variations) and MAT (9% of the variations). Among land-use variables, cropland and non-forested land explained about 7% of the variations. It is predicted that wild apple is mainly suitable to grow in the regions with MAT of 5–15 °C and soil pH between 6.5 and 7 (Figure 6a,b) in whole distribution ranges. In addition, wild apple can survive in regions with PREC_dry of <20 mm, but cannot survive in regions with high cropland expansion (Figure 6c,d).

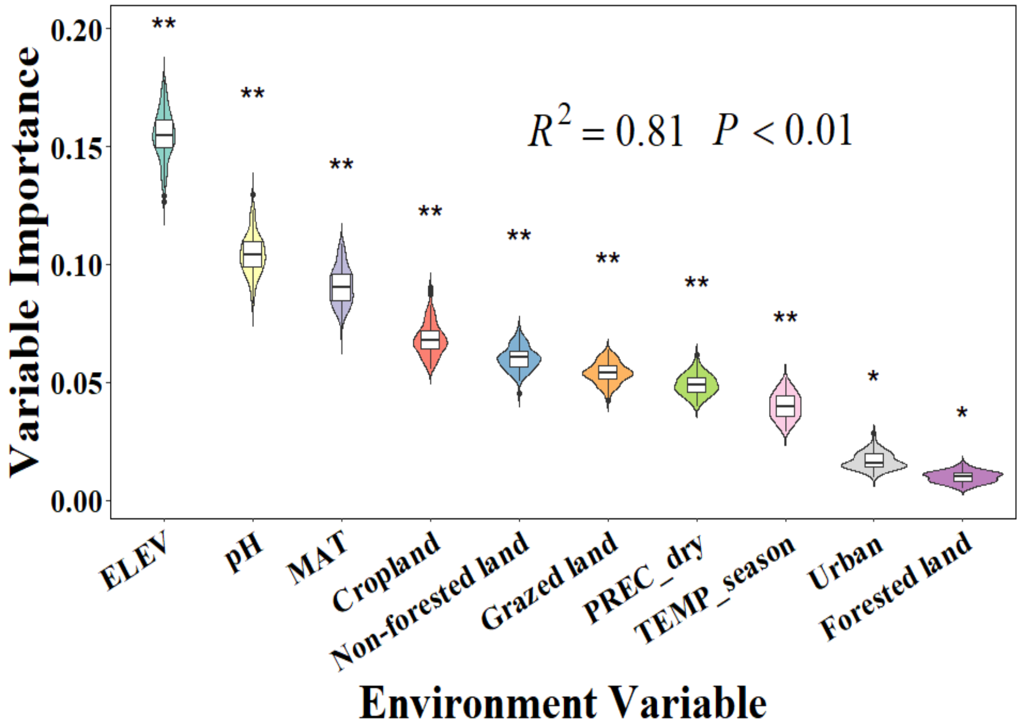

Figure 5. The relative importance of environmental predictors for the wild apple distributions. ELEV: the elevation; pH: soil pH; MAT: annual mean temperature, TEMP_season: temperature seasonality, PREC_dry: precipitation of driest month. *p* value significance codes: '**' $p < 0.01$, '*' $p < 0.05$.

3.3. The Effectiveness of Current Protected Areas

The current PA network only covers 13% of suitable habitats for wild apple, leaving the regions of Kyrgyzstan, Xinjiang of China, and Zhambyl of Kazakhstan under poor protection (Figure 7a; Table 1). In the future, wild apple will lose all suitable habitats in Zhambyl of Kazakhstan, Tajikistan and Uzbekistan, although there will be an increase in protected suitable habitats in other regions (Figure 7a; Table 1). Additionally, 80% of PAs for this species are located in the south of Central Asia, including South Kazakhstan, Kyrgyzstan, Tajikistan, and Uzbekistan (Table S1). In particular, sixteen of 34 international or national PAs for this species are located in Tajikistan. Notably, suitable habitats for wild apple will be fully protected in Uzbekistan under the SSP126 and SSP585 by the 2050s. In the 2090s, the suitable habitats that are protected will be less than 25% in Central Asia. Moreover, suitable habitats under protection still will be low in Xinjiang of China and Zhambyl of Kazakhstan under the two future scenarios (Figure 7; Table 1).

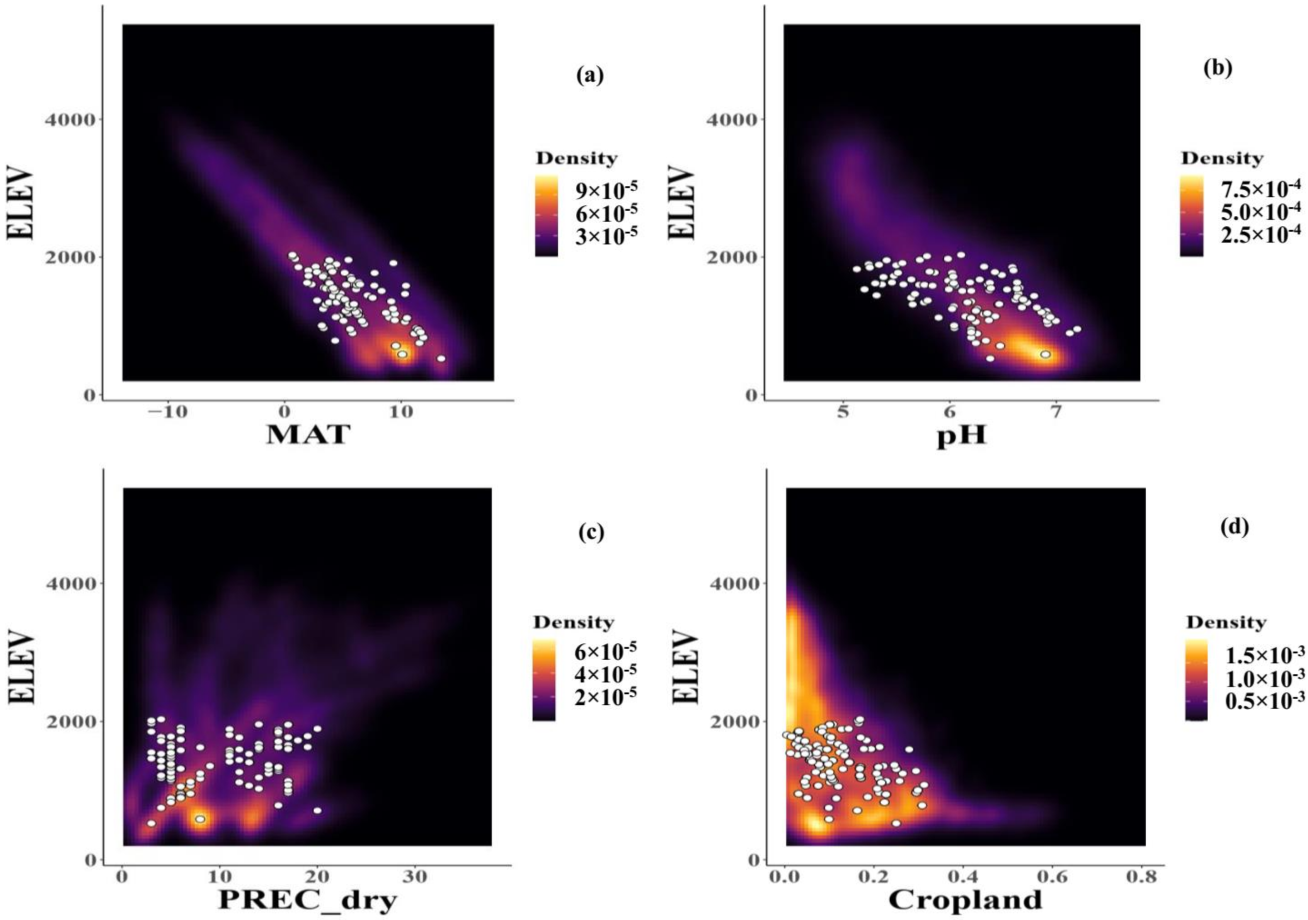

Figure 6. The density distributions of selected environmental predictors for the current occurrence records for wild apple. The white dots represent the occurrence records we used for the ENM. MAT: annual mean temperature; pH: soil pH; PREC_dry: precipitation of driest month.

Table 1. The range size and proportion of suitable habitats for wild apple within current protected areas under the current and future scenarios.

Country	Region	Range Size (km^2) and Proportion (%)				
		Current	2050s (SSP126)	2050s (SSP585)	2090s (SSP126)	2090s (SSP585)
China	Xinjiang	693 (4.93%)	966 (5.76%)	903(7.19%)	966(5.74%)	609(7.29%)
Kazakhstan	East Kazakhstan	588 (19.05%)	2961 (19%)	4536(21.82%)	2730(18.08%)	7497(26.27%)
	Almaty	3171 (36.39%)	3759 (48.77%)	3591(52.13%)	3780(50.42%)	3087(49.49%)
	Zhambyl	21 (0.74%)	0	0	0	0
	South Kazakhstan	903 (27.04%)	504 (33.33%)	315(46.88%)	483(31.08%)	294(36.84%)
Kyrgyzstan	/	483 (3.55%)	294 (4.86%)	168(4.37%)	294(4.88%)	105(8.47%)
Tajikistan	/	84 (7.27%)	63 (17.65%)	0	42(15.38%)	0
Uzbekistan	/	42 (25%)	21 (100%)	21(100%)	0	0
Total		5985 (12.75%)	9534 (17.27%)	9534(20.72%)	8295(16.96%)	11,592 (25.1%)

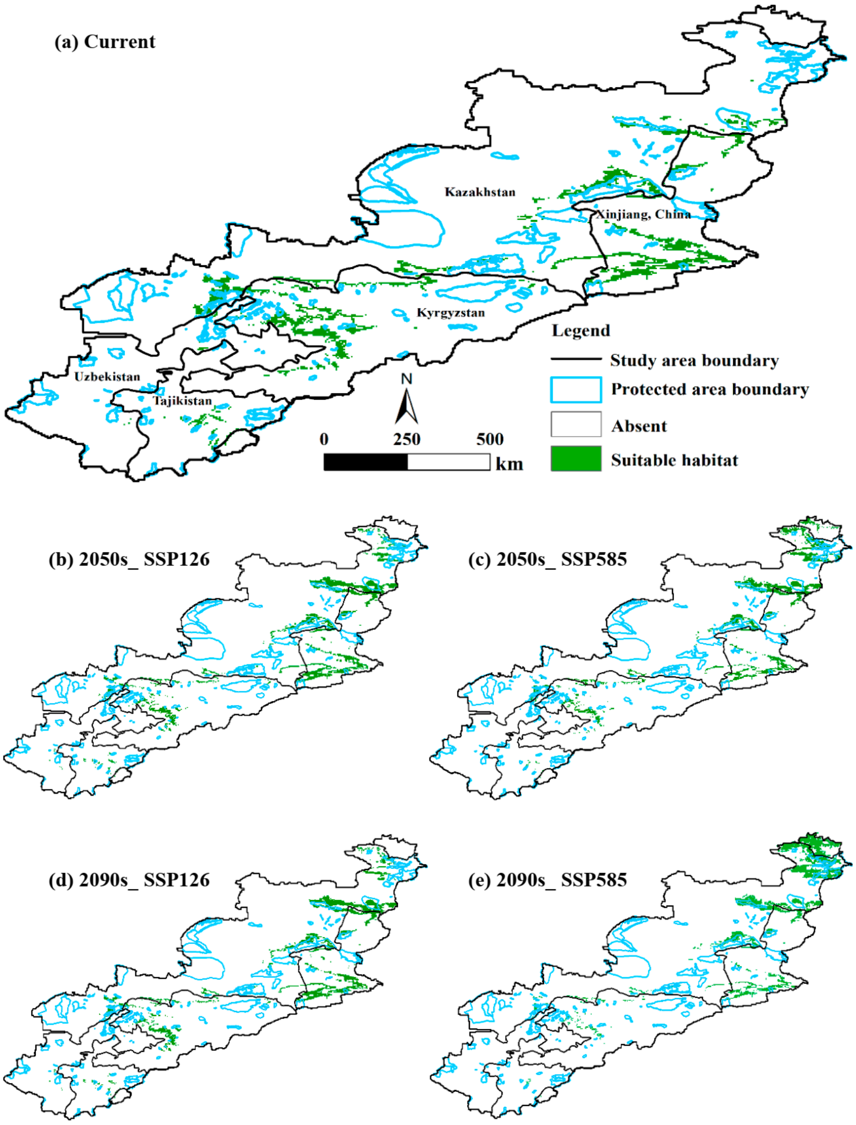

Figure 7. The wild apple suitable habitats within current protected areas under the current and future scenarios. Green areas indicate suitable habitats, while white regions indicate unsuitability.

4. Discussion

4.1. Dramatic Range Shifts of Wild Apple

As an ancient progenitor of the domesticated apple and the dominant species in wild fruit forests, wild apple in the mountains of Central Asia has extreme protection value. With hyper-dominant contributions to wild fruit forests in forest productivity and regional food and ecological security, the current and future distributions of wild apple populations strongly represent the conservation status of the forests [28,29]. In this study, our detailed analyses of the distribution range of wild apple in the scenarios of climate and land-use changes represent a significant step in developing effective conservation strategies. Currently, the distribution of this endangered species is scattered across the biodiversity hotspot regions. Due to dispersal limitations, the fragmented geographic distributions are highly vulnerable to environmental changes, such as long-term aridification [57] and cropland expansion [58]. A recent study in genetic structure of 15 wild apple populations reported that long-distance migrations and associated gene exchanges rarely occurred among fragmented populations [57]. Therefore, wild apple and other wild fruit species would be at greater risk of extinction in a rapidly changing climate in Central Asia.

Under future scenarios of climate and land-use changes, wild apple would have strong range contractions in the southern parts and low elevations by the 2050s and 2090s, and range expansions in the northern parts and higher elevations. Strong range contraction has mainly occurred in southern Kazakhstan, Tajikistan, Kyrgyzstan, and Uzbekistan. By the end of the century, the increase in air temperature would reach its largest magnitudes of 5–5.4 °C in Central Asia [6]. Such an increase in temperature would certainly stimulate the outbreak of insect pests [59] and exacerbate the range contraction of wild apple in the south of Central Asia. Additionally, the aridity index and potential evapotranspiration will increase significantly due to increased temperatures in Central Asia [60,61]. Furthermore, significant expansions of cropland and urban areas will lead to a contraction in the range of wild apple [62], especially in low elevations. These results indicate that wild apple will be in a dangerous state due to the increased temperature and the expansion of cropland and urban areas in the southern mountains of Central Asia.

As a consequence of range contractions and expansions in different regions, the center of wild apple distributions will need to move ~160 km northward and ~200 m higher in elevation to catch up with the speed of climate change by the 2050s. Due to the limited natural migration of wild apple [28,29], future distribution ranges should be considerably smaller than the current prediction. It is worth noting that the migrating abilities of crop wild relatives vary significantly in different species. For example, seven herbaceous CWRs in Europe were expected to shift in their distributional centroids 46–360 km northward by the 2070s [8]. Furthermore, climate change is expected to cause wild apple to shift toward higher latitudes and higher elevations. Successful migrations depend not only on the potential speed of migration of a species, but also on ecological connectivity of current habitats and the availability of healthy environments in potential destinations for the migration [3,4]. These findings suggest that, for CWRs with high economic and ecological value, species-specific distribution modeling and the assessment of conservation status are urgently needed for their effective conservation.

4.2. The Influence of Climate Change on Wild Apple and Wild Fruit Forests

Our ensemble model suggests a strong effect of future climate on potentially suitable habitats for this endangered species. Its geographic ranges are mainly limited by mean annual temperature, temperature seasonality, and precipitation of the driest month. Although vegetation dynamics in the Central Asian dryland are commonly believed to be dominated by total precipitation [63], our study showed that temperature change is a major factor shaping wild apple distributions. This finding is consistent with the dendroclimatological evidence of wild apple in non-degraded forests in Xinjiang of China [58] and southeast Kazakhstan [22]. Two possible mechanisms were used to explain the importance of temperature for this species. First, the spring phenology of wild apple has both chilling and heat requirements and is favored by the combined effects of the fall/winter cold and spring heat [64,65]. Second, during the growing seasons, the increasing temperature promotes tree growth by alleviating low-temperature stress and its effect on soil nutrient supply, promoting water and carbon absorption, and prolonging the growing seasons [29,66].

Although precipitation does not mainly limit the spatial ranges of wild apple, the precipitation in dry seasons determines where it could survive to some degree. The root systems of wild apple feature with extreme thickness, sufficient depth, and numerous horizontal branches that enable the species to survive in mean precipitation of less than 20 mm in dry seasons [22,29,32]. In addition, plant species distributions could be affected by the combination of temperature and precipitation, as extreme warming exacerbates water evaporation and further increases water stress in mountain ecosystems [63]. Considering this, further studies based on field observations and control experiments are needed to evaluate how wild apple and other wild fruit trees (e.g., *Juglans regia* and *Armeniaca vulgaris*) in the biodiversity hotspots are affected by the interactions of temperature and precipitation.

4.3. The Influence of Land-Use Changes on Wild Apple and Wild Fruit Forests

Habitat loss due to cropland expansion and urbanization could result in species population decreases and eventually cause local and regional extinction [11,67,68]. We revealed a significant negative correlation between wild apple and cropland coverage, indicating that wild apple could not survive in the regions with intensive cropland expansion even if the climatic niche is suitable. This species was classified as a vulnerable species due to over 70% of the habitat loss within the last 30 years in Kazakhstan [31]. One recent estimation showed that the rate of expansion of cropland will exceed more than 22%, and urban areas will expand more than 300% in this region [62]. These dramatic changes in the region would certainly affect the populations of wild apple and other wild fruit trees.

Land-use changes could indirectly affect species distributions by having uneven impacts at different elevations and adjusting soil physicochemical properties. In this study, we found that elevation and soil pH are the important environmental factors for limiting wild apple. Since intensive agricultural activities and urbanization in low elevations, rapid range reduction in these areas is happening and will continue due to land-use driven changes in the abiotic environment. Towards a mechanistic understanding of these processes, long-term monitoring of the changes in land use, climate, soil, and plant community composition and structure is urgently needed for the protection of rare and endangered species [69,70], especially in globally significant biodiversity hotspots.

4.4. Implications for the Protection of Wild Apple and Wild Fruit Forests

Protected areas are safeguarding biodiversity against direct human impacts [71]. Under climate and land-use changes, protected areas may facilitate species' range expansions as stepping stones that facilitate colonization at the leading edges of species distributions [72]. Our results showed that a proportion of wild apple's range size is less protected under current conditions. For example, the currently suitable habitats (more than 29%) for this species are mainly distributed in Xinjiang of China and Kyrgyzstan; however, the proportion of protected suitable habitats is less than 9%. Additionally, the distribution of protected areas is uneven, with 80% of protected areas distributed in the south of Central Asia, and nearly 50% in only one country (Tajikistan). These findings suggest that current protected areas are not guaranteed to provide suitable habitats for wild apple.

In future scenarios, our results show that wild apple will lose all suitable habitats in Zhambyl of Kazakhstan, Tajikistan and Uzbekistan. This suggests that habitat-based conservation strategies cannot compensate for climate-change-induced range loss [73]. Moreover, long-distance migrations and associated gene exchanges rarely occur among fragmented populations of wild apple [57], suggesting that conservation efforts for this species might fail in some regions. To effectively protect wild apple, a dynamic prioritization approach should be taken into consideration in the planning of future protected areas [74]. These strategies should guide in situ conservation practices with long-term ecosystem-level monitoring through the whole ranges of wild apple populations and wild fruit forests.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d14060489/s1, Table S1: The number, range size and proportion of current protected areas (PAs) for wild fruit forests and wild apples in the study area. Table S2: The range size and proportion of suitable habitats for wild apples in the current and future scenarios. Table S3: Proportional changes of suitable habitats for wild apples in the future scenarios.

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