



Consequence of habitat specificity: a rising risk of habitat loss for endemic and sub-endemic woody species under climate change in the Hyrcanian ecoregion

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Received: 4 November 2023 / Accepted: 17 March 2024 / Published online: 20 April 2024
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Abstract

Endemic species are more impacted by climate change than other taxa. However, assessing the vulnerability of endemics to these changes in some regions, such as the Hyrcanian forest, is limited, despite its importance for biodiversity and ecosystem function. To address the question of expected habitat shifts under climate change across the Hyrcanian ecoregion, we built an ensemble of species distribution models (SDM) under two emission scenarios (RCP 4.5 and RCP 8.5) for 15 endemic woody taxa. To identify the potential priority conservation areas, we also applied a spatial prioritization approach. Overall, our results suggest that the impacts of climate change are more severe on the eastern parts of the region (Golestan) and the Talysh Mountains (north-western Hyrcanian ecoregion) with over 85% and 34% loss of suitable habitats over the next 80 years. The central part of the Alborz Mountains (Mazandaran) and some areas in the Talysh Mountains could be potential climatic refugia under the future conditions for endemic taxa. The most prominent changes are expected for *Ruscus hyrcanus*, *Gleditsia capsica*, *Acer velutinum*, *Frangula grandifolia*, and *Buxus hyrcana*. The worrying predicted loss of suitable habitats for most studied taxa would dramatically affect the stability and resilience of forests, threatening thus biodiversity of the Hyrcanian ecoregion. We present the first estimation of the potential risks involved and provide useful support for regional climate-adaptation strategy, indicating potential conservation priority areas for maintaining and preserving its resources. Notably, only 13.4% of areas designated for conservation and management under climate change will be located within the current Hyrcanian protected areas, yet the majority of these areas are classified as low priority.

Keywords Climatic refugia · Habitat suitability · Endemic species · Maxent · Spatial prioritization · Zonation

Introduction

Climate change is affecting biodiversity globally but is of special concern in areas that are disproportionately rich in biological diversity and uniqueness yet most highly

anthropogenically threatened—the hotspots of biodiversity (Bellard et al. 2012; Trew and Maclean 2021). In these areas, endemic species are consistently more adversely impacted than other taxa, owing to their narrow ranges, and persistence in regions of climatic stability over evolutionary time scales (Manes et al. 2021). At

Communicated by Wolfgang Cramer

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the species level, the most common response to climate change is range shifts. However, endemic species, especially trees, may not be able to track suitable conditions or adapt fast enough to keep up with the unprecedented speed of environmental changes. This is related to a specific set of life-history traits, mainly longevity, specific habitat preference, low dispersal ability, and genetic diversity (Lavergne et al. 2004). Therefore, the protection of those unique species that represent the evolutionary heritage of regions should be a conservation priority for ensuring their long-term sustainability in a changing environment. Consequently, predicting species-level effects of climatic changes requires unravelling the factors affecting their current distribution and mapping future changes in habitat suitability (Ashcroft 2010; Barrows et al. 2020; Keppel et al. 2015).

Currently, correlative species distribution modelling (SDM) provides the most accessible approach to predicting climate-related species extinction risk. This involves assessing spatially explicit changes in habitat suitability and identifying climatic refugia (Draper et al. 2019; Gavin et al. 2014; Guisan et al. 2013; Zurell et al. 2023). However, there are many limitations and uncertainties due to conceptual and methodological challenges inherent to SDM predictions, which must be considered and properly addressed, particularly in the context of risk assessments, conservation planning, and management (Davies et al. 2023; Draper et al. 2019; Zurell et al. 2023). A major challenge in predicting the response of species to climate change is to move beyond traditional SDM models that assume static environmental tolerance of species over time and neglect critical biological mechanisms, disregarding demographic processes, adaptive potential, and ecologically relevant factors such as dispersal ability and biotic interactions (Zurell et al. 2023). An additional important source of uncertainty in future projections referred to climate model uncertainty and validation of prediction accuracy. However, in the absence of more appropriate methods, careful application of SDM projections should be a part of vulnerability assessment, supporting decision-making but only when following good practice and when openly communicating the limitations and uncertainty (Davies et al. 2023; Zurell et al. 2023).

The UNESCO Natural World Heritage Hyrcanian Forest, which is a part of the Caucasus biodiversity hotspot, is one of the biologically richest yet the most highly anthropogenically threatened areas (Akhani et al. 2010; Tohidifar et al. 2016). The region is perceived as one of the unique relict ecosystems, which holds exceptional biodiversity and endemism (Ghorbanalizadeh and Akhani 2021), a sanctuary of the Neogene thermophilous relicts (Nakhutsrishvili et al. 2015), and a glacial refugia for the temperate broad-leaved trees (Sagheb-Talebi et al. 2014). However, the region still struggles with the high human pressure of agriculture,

afforestation, illegal and unsustainable logging, plant collecting, and poor management (Goushehgir et al. 2022; Joorabian Shooshtari et al. 2017; Müller et al. 2017; Panahi et al. 2021; Scharnweber et al. 2007). Consequently, lowland and sub-montane species, such as *Albizia julibrissin*, *Gleditsia caspica*, and *Populus caspica* are currently reduced to the small patches (Sagheb-Talebi et al. 2014). Moreover, according to recent projections for the ecoregion, an alarming reduction in suitable areas for major tree species, including endemic taxa, is expected in the next decades (Ahmadi et al. 2020; Alavi et al. 2019; Alipour and Walas 2023; Joorabian Shooshtari et al. 2017; Mahmoodi et al. 2023; Naqinezhad et al. 2022; Song et al. 2021; Taleshi et al. 2019). Among the Hyrcanian endemic trees, a strong reduction of the climatically suitable areas was projected for *Acer velutinum* (Taleshi et al. 2019), *Gleditsia caspica* (Taleshi et al. 2019; Yousefzadeh et al. 2022), *Parrotia persica* (Taleshi et al. 2019), *Populus caspica* (Alipour et al. 2023), and *Buxus hyrcana* (Alipour and Walas 2023). However, a comprehensive study of climate risk assessment for the Hyrcanian endemic and sub-endemic woody species in the ecoregion is still lacking. Most of these projections rely on a single species; however, predicting ecosystem vulnerability to climatic changes requires moving beyond that approach. Therefore, identifying priority conservation areas based on multiple species-specific responses and climate refugia appears as a promising approach for the conservation of species and thus communities. The expected range loss of the species would affect their long-term sustainability in a changing environment, leading to a pronounced biodiversity loss in the region. In this context, the recognition of factors that govern climate-driven distributional patterns and range shifts of endemic species is needed to assess the vulnerability to future climate threats in the Hyrcanian ecoregion, a unique relict ecosystem preserving the evolutionary heritage (Draper et al. 2019; Guisan et al. 2013; Keenan 2015).

We used the SDM approach to estimate risk projections of the potential impact of climate change on the distributional patterns of endemic and sub-endemic trees and shrubs across the Hyrcanian forests. Our study addressed the following specific questions (1) How are these endemics and sub-endemic species currently distributed, and what drivers influence their range under current and future environmental conditions?, (2) What distributional changes can be expected because of climate change?, and finally (3) Are there areas with stable conditions—i.e., potential in situ refugia from climate change? Finally, we aimed to identify regional conservation priority areas and climatic refugia to assess the Hyrcanian ecosystem's vulnerability to future climate. Obtaining reliable information on species distribution dynamics is now urgently required to support future actions aiming at effective conservation and management (Keenan 2015) which we discuss in the present study.

Material and methods

Study area and plant species

The study area encompasses the Hyrcanian ecoregion that extends along the southern coast of the Caspian Sea from the Talysh Mts. (southeastern Azerbaijan) in the west, passing through three Iranian Provinces (Gilan, Mazandaran, and Golestan), and ends in Golestan National Park (GNP) in the east (Fig. 1A). The area covers about 65,000 km² of the lowlands, montane forests and wetlands, north slopes of the Alborz, and north-eastern slopes of Talysh Mts. (Akhani et al. 2010; Naqinezhad et al. 2015) and encompasses a variety of different forest types (Gholizadeh et al. 2020). In terms of the vegetation, the Hyrcanian ecoregion was included in the Irano-Turanian floristic region (Manafzadeh et al. 2014), but due to the presence of many Euro-Siberian plants, which attain their southern limits of distribution there, it is treated as a part of the Euxino-Hyrcanian province within Euro-Siberian

floristic region (Akhani et al. 2010; Browicz 1989; Sagheb-Talebi et al. 2014). In this area, the vegetation is composed mostly of broadleaved deciduous lowland forests, deciduous mountain forests, and mixed deciduous and evergreen mountain forests near the upper treeline (Akhani et al. 2010). Differences in forest composition and structure reflect the gradients in climatic and edaphic conditions (Naqinezhad et al. 2015; Zohary 1973). The mean annual precipitation decreases from more than 1000 mm in the west to ca. 600 mm in the eastern part of Golestan, whereas average temperature rises in this direction from ca. 16 °C to ca. 17.5 °C (Fig. 1B).

Our target taxa consist of 15 endemic and sub-endemic trees and shrubs (Table 1 Online Resource 2) for the Hyrcanian forest (Akhani et al. 2010; Browicz 1982). For the analyses, the studied taxa were categorized into altitudinal vegetation belts following the classifications of Akhani et al. (2010) and Jafari et al. (2015), which encompass lowland, and montane zones. Two taxa included in the study have not fully resolved taxonomic status and are distinguished

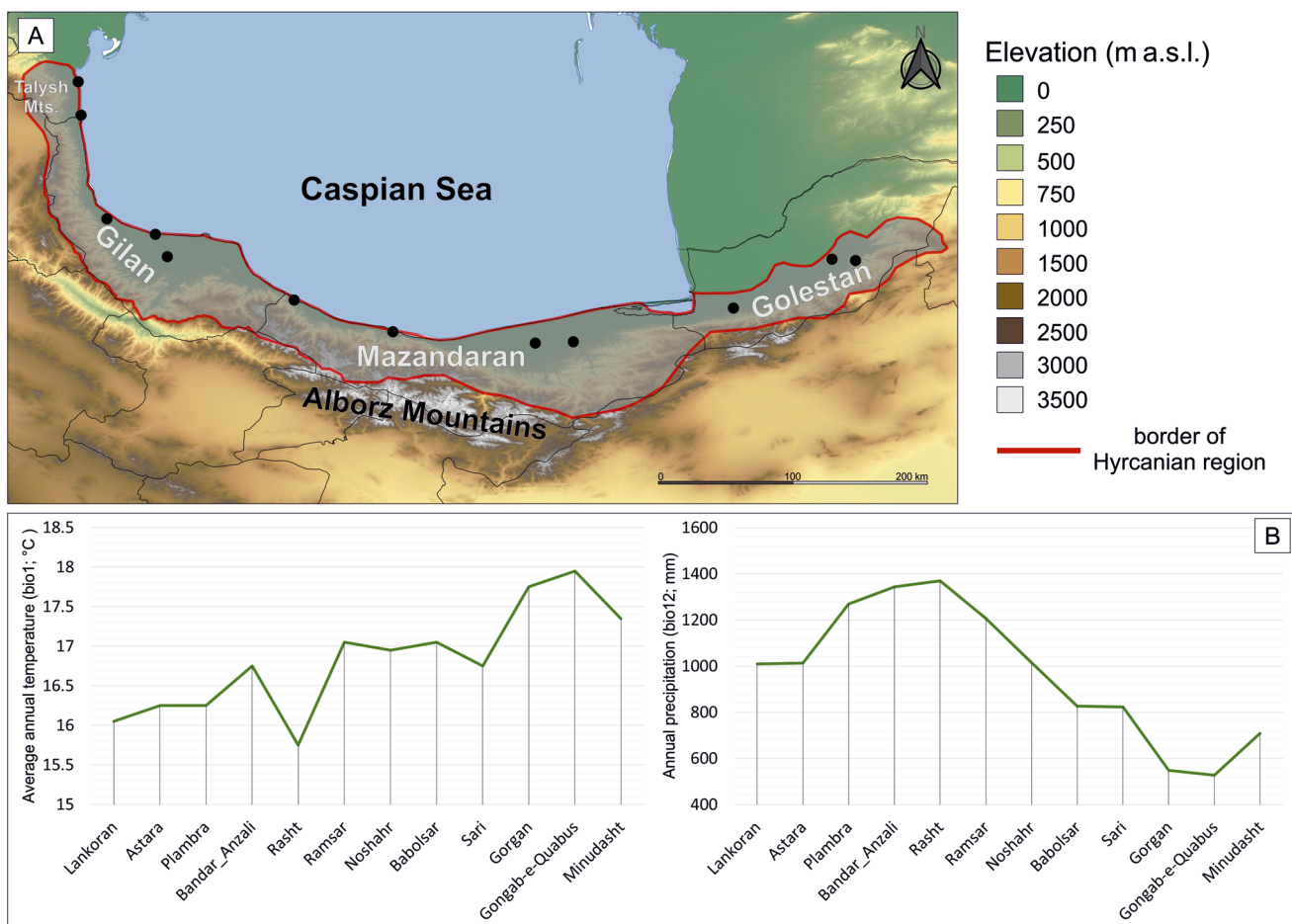


Fig. 1 Characterisation of the study area (A) border of the Hyrcanian ecoregion adopted from Akhani et al. (2010) and Nakhutsrishvili et al. (2015); (B) climatic data download from CHELSA showing

the average annual temperature (bio1) and the annual precipitation (bio12). Map generated with QGIS

only locally as subspecies: i.e., *Buxus hyrcana* Pojark. [= *Buxus sempervirens* L. subsp. *hyrcana* (Pojark.) Takht.], and *Populus caspica* Bornm., which was treated as a synonym of *Populus alba* L. (POWO 2023). However, the genetic divergence between *P. alba* and *Populus caspica* (Alipour et al. 2021; Yousefzadeh et al. 2019) suggests the separate taxonomic status of the latter. The high level of genetic differentiation between populations of *Buxus hyrcana* [= *Buxus sempervirens* subsp. *hyrcana* (Pojark.) Takht., Bot. Zhurn.] (Esmailnezhad et al. 2020) and their biochemical differentiation (Karimi et al. 2019) indicate the possible separate taxonomic status. We also included *Albizia julibrissin*, which occurs in the Japanese islands and, after disjunction, grows in western Asia, quite exclusively in the Hyrcanian ecoregion (Browicz 1982).

Species occurrence data acquisition

Presence-only occurrence data of the taxa were obtained from literature (Table 2 Online Resource 2), herbaria, Global Biodiversity Information Facility (GBIF), and the Hyrcanian Forest Vegetation Database (HFVD) (Gholizadeh et al. 2019). Initially, our dataset hosted more than 4000 georeferenced points. However, to reduce spatial bias and to remove records outside the natural range of the species (urban and rural areas) and incorrect records (plain steppes, alpine grasslands, glaciers, gardens, etc.), we first performed manual data handling using QUANTUM GIS 3.16.4 “Hanover” (QGIS.org, 2022). Subsequently, to remove duplicate records and to avoid model over-fitting, we filtered the data using a spatial thinning procedure following the recommendation of Phillips et al. (2022), considering only one occurrence point per grid cell (1 × 1 km). Thus, the final dataset used in the SDMs procedure consisted of 3354 unique records (Table 1 Online Resource 2).

Environmental variables

Thirty-two variable environmental predictors, including climatic, topographic, and edaphic variables, were utilized for modelling of the potential distribution of studied taxa under current conditions. However, to construct the SDM models under future projections, only climatic and topographic variables were kept. Specifically, topographic variables (elevation, slope, and aspect) were derived from the GMTED2010 (Danielson and Gesch 2011) (Table 3 Online Resource 2), while bioclimatic variables (bio1–19) were obtained from CHELSA 1.2 (Karger et al. 2017). We also included the Emberger’s pluviothermic quotient (embergerQ), Thornthwaite aridity index (aridityIndexThornthwaite), compensated thermicity index (thermInd), annual potential evapotranspiration (annualPET), the sum of monthly mean temperatures greater than 0 °C (growingDegDays0) and 5 °C (growingDegDays5),

relative wetness to aridity index (climaticMoistureIndex), and monthly variability in potential evapotranspiration (PETseasonality) that were downloaded from ENVIREM (Title and Bemmels 2018). Additionally, soil-related data such as soil type, soil pH, and soil carbon content were retrieved from SoilGrid (Hengl et al. 2017). All variables were processed into 30 arc-second rasters (~ 1 km) in QGIS. For building the SDM models, we decided to not assess the collinearity of all quantitative variables on a species-by-species basis, following the recommendation by Feng et al. (2019). Quantifying the effects of collinearity reveals that excluding highly correlated predictor variables does not significantly affect model performance due to the robustness of Maxent to redundant variables and collinearity (Feng et al. 2019).

Species niche modelling and spatial prioritization of climatic refugia

To investigate future range shifts in the spatial distribution of the Hyrcanian endemic and sub-endemic species, we used the correlative SDMs approach based on the maximum entropy predictive algorithms. The Maxent 3.4.4. (Phillips et al. 2022) was applied to build models, and the procedure of modelling follows those described by Salvà-Catarineu et al. (2021). Briefly, to construct the models, we used a set of bioclimatic variables at a resolution of 30 arc-sec (~ 1 km) derived for the reference period 1981–2010, representing current conditions and, for future projections, indicating mean values for the reference period 2071–2100. For investigating possible shifts in habitat suitability under future climate scenarios, we applied the Coupled Model Intercomparison Project Phase 5 (CMIP5) under two Representative Concentration Pathways—RCP 4.5 and RCP 8.5 scenarios, depicting the greenhouse gas concentration by the end of the twenty-first century (Collins et al. 2013). The RCPs were chosen because they represent the extremes of likely future greenhouse gas emissions and thus are representative of the range of possible future climates depending on future social and economic development. Due to the complex physiography of the study region, we did not exclude any of the topographic and soil variables from the models.

Maxent was run with 100 replicates using bootstrap resampling; the maximum number of iterations and the convergence threshold were set at 10^4 and 10^{-5} , respectively. The logistic output of the model prediction for suitability and a random test partition was used for each run. For model validation, the “random seed” option was applied, and the occurrence data were randomly partitioned into training (80%) and test (20%) data.

For each species, we estimated the relative contribution of each variable to the selected Maxent model based on permutation importance (Merow et al. 2013). Classification performance was estimated for each model by calculating the area under the curve (AUC) of the receiver operating characteristic (ROC) plot (Mas et al. 2013; Wang et al. 2007). To

define the ecological groups of the taxa, we conducted the component analysis (PCA) on the set of environmental variables that had the greatest impact on the distribution of the species using the *prcomp* R function (R Core Team 2022).

Finally, to gain a more comprehensive view of the threat posed by climate change to the Hyrcanian endemic and sub-endemic taxa, we calculated the proportional change in overall habitat suitability based on the output SDM maps according to the respective climatic scenarios at species and regional levels. We applied a baseline threshold of 25% of habitat suitability to calculate the three classes of areas: loss (currently suitable habitat that will not remain suitable in the future), gain (currently unsuitable habitat that will become suitable in the future), or stable (habitat suitable in both current and future conditions) of suitability areas. To evaluate habitat quality, we categorized habitat into three suitability criteria as follows: 75–100% for high suitability, 50–75% for medium suitability, and 25–50% for low suitability. To quantify species' vulnerability to future climate change, we used two metrics: (i) relative change in the total area of suitable habitat and for areas with > 50% habitat suitability and (ii) percentage loss of current suitable habitat. The relative change in range size measured as the difference in area between the current and future conditions was calculated for all species and at the regional level for both RCP scenarios. Lastly, we estimated the change in species richness between current and future periods. To calculate this metric, we first converted the individual species distributions into binary maps, where locations with a probability of occurrence < 0.7 were set to zero, and those ≥ 0.7 were set to 1. The results of SDMs across the landscape were visualized using QGIS. For each species, the mean altitudinal range shift was calculated in SAGA-GIS 8.0.1 (Conrad et al. 2015), and the area of distribution (in km²) was determined in QGIS using the *Sarea* function.

To identify climatic refugia and prioritize conservation areas under climate change, we applied a spatial priority ranking algorithm implemented in *Zonation 5* (Moilanen et al. 2022). The software integrates data on the biodiversity features (e.g., species diversity, ecosystem, habitats) and threats (e.g., land use, climate change, habitat loss) to produce spatial priority rank maps over the entire landscape based on principles of complementarity to support conservation planning in general. Priority maps showing all grid cells of the landscape with the highest complements of species were generated by iteratively ranking grid cells from high to low conservation values, removing the cells with the smallest marginal loss of conservation value. In the prioritization process, we included the predicted habitat suitability layers for all target species under current and future climatic conditions, including both RCP4.5 and RCP8.5 scenarios, assessed by the Maxent simulations. We assigned rankings to species based on IUCN threat categories, taking into account also the future habitat loss. For

the calculations, the core-area zonation (CAZ) approach was employed to determine the high-priority areas. This complementarity-based prioritization algorithm assigns conservation values by maximizing regional diversity and its complementarity. Essentially, CAZ emphasizes the selection of areas of high-quality habitats for the rarest or high-weighted species, and the prioritization aims to retain core areas for all species. To ensure that climatic refugia would be identified outside the urbanized and agricultural landscape, we excluded spatial surfaces of land use (cities and cropland) as a conditions mask layer. Moreover, the land cover classes (barren lands, lakes, grasslands, forests, and shrublands) were used as condition layers. These raster layers were derived from the global land cover change maps of the European Environment Agency (EEA 2023). We included in the analyses the already existing protected areas (PA), sourced by the Protected Planet: World Database on Protected Areas (UNEP-WCMC and IUCN 2023). As conservation planning due to resource limitations rarely allows all potential habitats' protection, the threshold used to select the highest priority areas was set to 20% of land as climatic stabilization areas based on the recommendation proposed by the Global Deal for Nature (Dinerstein et al. 2019). To determine each species' climatic niche's representation within its associated PA climate space, we calculated the proportion of its bivariate density grid covered by the PA density grid in QGIS.

Results

Current distributional patterns

The predictive accuracies of all models under current conditions were relatively high (AUC > 0.961), indicating the high reliability of the predictions (Table 1). The predictions properly described the current range for most of the taxa; however, potential distribution appeared slightly broader than their geographic range in the Hyrcanian ecoregion (Fig. 1 and Fig. 2 Online Resource 1). Some of them exceeded their potential niches by areas with at least 25–50% habitat suitability outside the main center of distribution (Fig. 1 Online Resource 1). Similarly, the potential niches of sub-endemic species, *Euonymus velutinus*, *Lonicera floribunda*, and *Quercus castaneifolia*, were much broader than the realized ones (Fig. 1 Online Resource 1).

The climatic factors were more important in determining taxa distribution than topography and soil (Table S3). At the regional level, the most limiting factors were the precipitation of the driest month (bio14), the precipitation of the coldest quarter (bio19), and temperature seasonality (bio4). Specifically, the precipitation of the driest month (bio14) had a relatively highest contribution, ranging from 18% to 33% in all tested taxa, except for lowland species. For *Albizia*

Table 1 Predictive performance of the species distribution models (SDMs) evidenced by the area under the curve (AUC) values and altitude changes for the Hyrcanian endemic and sub-endemic species at future climatic scenarios (RCP; ca. 2071–2100); (“–” decreasing of elevation)

Species	AUC			Average altitude (m a.s.l.)			Altitude changes (m)	
	Current	RCP 4.5	RCP 8.5	Current	RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5
<i>Acer velutinum</i>	0.972	0.971	0.972	728	761	923	33	195
<i>Albizia julibrissin</i>	0.993	0.993	0.992	339	468	414	129	75
<i>Alnus subcordata</i>	0.982	0.979	0.980	705	683	641	–22	–63
<i>Buxus sempervirens</i>	0.988	0.988	0.988	531	887	804	356	274
<i>Euonymus velutinus</i>	0.990	0.988	0.987	1042	1095	1054	53	12
<i>Frangula grandifolia</i>	0.993	0.992	0.992	812	1086	759	274	–53
<i>Gleditsia caspica</i>	0.987	0.986	0.986	404	497	306	93	–98
<i>Hedera pastuchovii</i>	0.985	0.982	0.982	641	551	554	–90	–87
<i>Ilex spinigera</i>	0.984	0.983	0.983	945	917	684	–27	–260
<i>Lonicera floribunda</i>	0.979	0.976	0.976	1243	1247	1450	5	207
<i>Parrotia persica</i>	0.977	0.977	0.976	409	713	786	304	376
<i>Populus caspica</i>	0.986	0.985	0.985	352	443	610	92	258
<i>Pyrus boissieriana</i>	0.991	0.989	0.989	1045	1419	1354	374	308
<i>Quercus castaneifolia</i>	0.961	0.960	0.961	775	832	772	56	–3
<i>Ruscus hyrcanus</i>	0.984	0.982	0.982	572	513	719	–59	147

julibrissin and *Gleditsia caspica*, the potential niches were determined mostly by the temperature seasonality (bio4), reaching nearly 27% of contribution in the simulations, and the precipitation of the coldest quarter (bio17; 17% and 28%, respectively), while for *Parrotia persica*, only bio17 was more significant with a contribution of ca. 34%. In most of the montane taxa except for *Hedera pastuchovii* and *Ruscus hyrcanus* and in lowland *Populus caspica*, the precipitation of the coldest quarter (bio19) was defined also as the most important variable limiting the distributional patterns. The sum of monthly mean temperatures greater than 0 °C had relatively moderate effects on the distributional patterns with a contribution of > 10% in *Acer velutinum*, *Populus persica*, and *Ruscus hyrcanus* (Table 3 Online Resource 2).

The synthetic Emberger’s pluviothermic quotient, evapotranspiration (annualPET), and drought indicators (aridity index “aridityIndex” and relative wetness to aridity “climaticMoistureIndex”) had a negligible contribution in all models. Within these predictors, only the evapotranspiration had a noticeable impact on the current potential *Lonicera floribunda* range (9.2%). The topographic factors, such as elevation and aspect, had a very low contribution; only slope inclination influenced the occurrence of *Euonymus velutinus* at a contribution of 6%. Similarly, only soil type was a limiting factor in *Euonymus velutinus*, *Hedera pastuchovii*, and *Lonicera floribunda* with a moderate contribution of > 5% (Table 4 Online Resource 2).

PCA revealed ecological divergence among studied taxa (Fig. 2C), displaying distinct groups that partly corresponded to the altitudinal vegetation belts. According to the two first axes, explaining most of the variance (89.9% in total), the lowland taxa were separated from the remaining

taxa and occupied areas associated with higher precipitation and the sum of monthly mean temperatures greater than 0 °C (growingDegDays0) and 5 °C (growingDegDays5). The lowland species are at the same time the most thermophilic, occupying areas with an average annual temperature of 14.6 °C and the highest annual precipitation above 983 mm (Table 4 Online Resource 2). For the montane group, precipitation predictors (bio12, bio19, bio17, and bio14) and slope had the highest positive effect (Fig. 3A) while for the most outstanding taxa, *Euonymus velutinus* and *Lonicera floribunda* temperature seasonality (bio4) and temperature annual range (bio7). The montane species have the average values of bioclimatic variables bio1 about 2.2 °C and bio12 about 30 mm lower than found in the lowlands. The two outstanding species, *Euonymus velutinus* and *Lonicera floribunda*, grew in the relatively harsher climate conditions, where average bio1 and bio12 had the lowest values (Table 3 Online Resource 2).

Patterns of habitat suitability change

The AUC scores were high, ranging from 0.960 to 0.993, indicating good fitness of the models under future conditions (Table 1). The contribution of precipitation- and temperature-derived variables varied largely depending on the ecological preferences of the studied species. For the majority of montane and lowland/montane species, future distribution patterns under both climatic scenarios were mainly driven by the precipitation of the driest month (bio14) and the precipitation of the coldest quarter (bio19). Additionally, the mean temperatures of the driest quarter (bio9), the annual range of temperature (bio7), and temperature seasonality (bio4) also

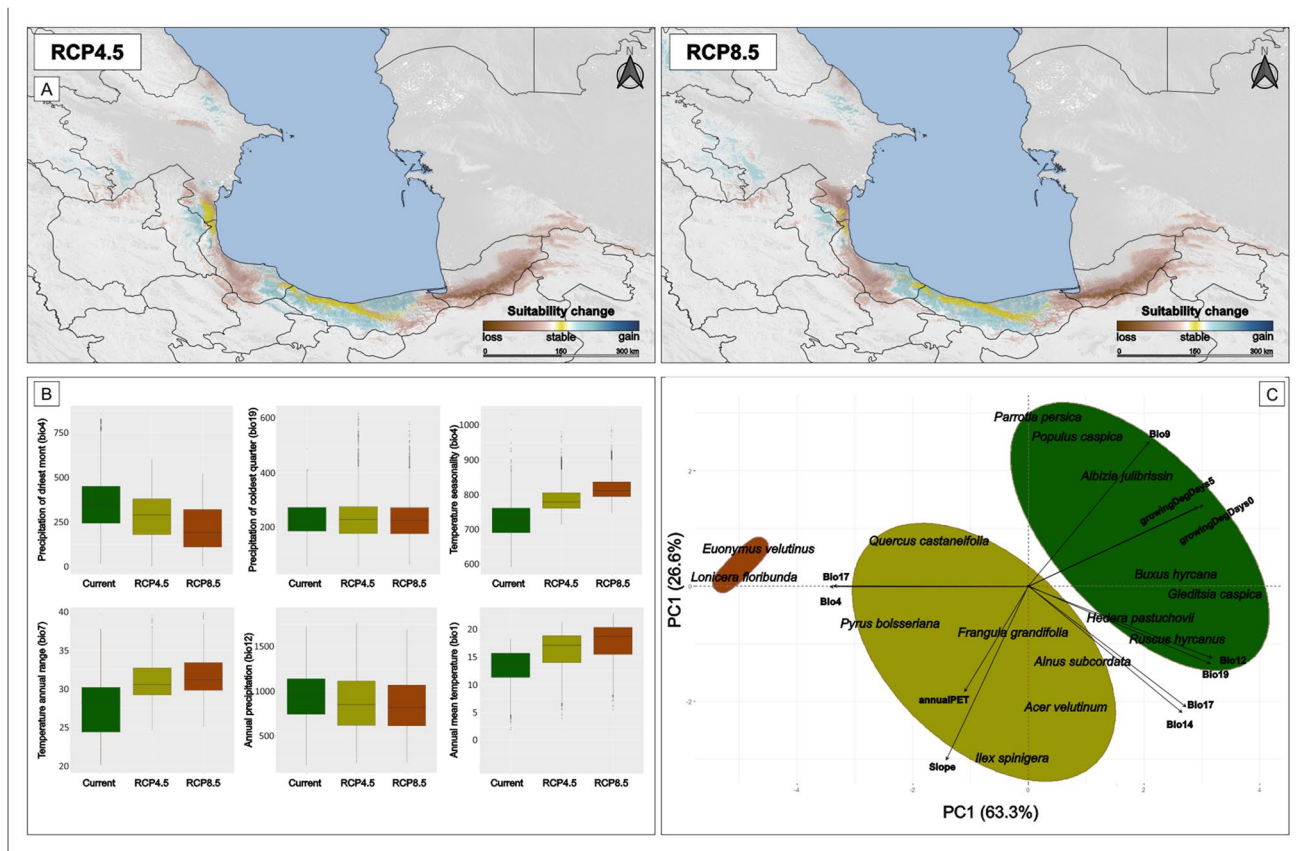


Fig. 2 Average changes in the suitable area for the Hyrcanian ecoregion for the year 2100 based on the SDM output maps using 25% presence thresholds in three categories: gain, stable, and loss (A, upper maps). Bar charts presenting variation in bioclimatic variables in the region for the current (ca. 1981–2010) and future projections (RCP4.5 and RCP8.5; 2100) (B; right panel), and principal compo-

nent analysis (PCA, C) showing the climatic preference of studied taxa based on the five bioclimatic variables that had the greatest impact on the distributional patterns in the region. Results of SDM projections and richness maps across the landscape were visualized using QGIS (QGIS.org, 2022)

showed noticeable contributions in these species. The temperature seasonality (bio4) emerged as the most important factor for lowland species, except for *Parrotia persica* and *Populus caspica*, for which the precipitation of the driest quarter (bio17) and bio14, respectively, was more significant (Table 5 and 6 Online Resource 2). Similarly, bio14 had a substantial contribution (above 20%) to the projected distribution of *Buxus hyrcana*, *Hedera pastuchovii*, and *Ruscus hyrcanus*. Topographic factors and soil type were less important in determining the geographic distribution of the studied species under both climatic scenarios (Table 5 and 6 Online Resource 2).

At the population level, concerning the species' overall potential distribution (i.e., total areas); the suitable habitats were projected to decrease for most of the studied taxa under both climatic scenarios (Table 2, Fig. 2 Online Resource 1). Specifically, under RCP4.5, the areas with high suitability ($\geq 75\%$) for *Frangula grandifolia* and *Gleditsia caspica* will be nearly lost. While the optimal conditions ($\geq 75\%$) for *Alnus subcordata*,

Buxus sempervirens, *Euonymus velutinus*, *Lonicera floribunda*, *Parrotia persica*, *Pyrus boissieriana*, and *Ruscus hyrcanus* will still be available, a notable reduction in those areas is projected compared with the current period. The exceptions, however, are *Acer velutinum*, *Albizia julibrissin*, *Hedera pastuchovii*, *Ilex spinigera*, *Populus caspica*, and *Quercus castaneifolia* for which the area with high suitability ($\geq 75\%$) is expected to increase.

The projected overall habitat loss is expected to be more extensive under RCP8.5 for most lowland and montane species, except for xerophytic *Euonymus velutinus*, *Lonicera floribunda*, and also hygrophilous *Populus caspica* (Fig. 2 Online Resource 1). The most substantial decrease in the overall distribution was projected for *Ruscus hyrcanus* and *Gleditsia caspica*, reaching 88% and 68%, respectively, with a complete loss of the currently highly suitable areas ($> 75\%$) (Table 2; Fig. 2D Online Resource 1). Similarly, notable range changes were modelled for *Acer velutinum*, *Buxus hyrcana*, and *Frangula grandifolia* (Fig. 2B Online Resource 1), for which areas with suitability $\geq 75\%$ are

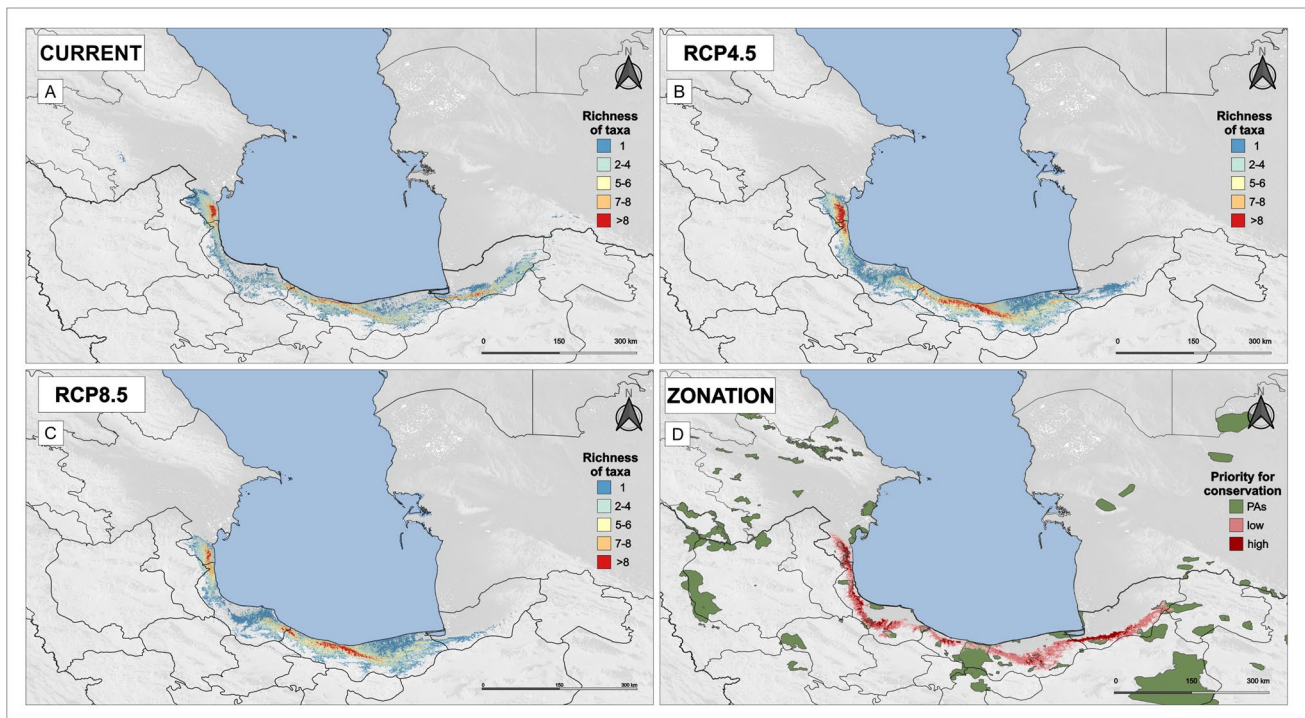


Fig. 3 Current species richness (A) and richness change maps of endemic and sub-endemic Hyrcanian taxa under the future climatic scenarios (B RCP4.5 and C RCP8.5) generated based on the SDMs results for 2100. Zonation priority rank maps (D) across the Hyrcan-

ian ecoregion (red areas) and current protected areas (PAs), sourced by the Protected Planet: World Database on Protected Areas (UNEP-WCMC and IUCN 2023) (green areas)

expected to decrease, representing just 24%, 23%, and 13% of the current highly suitable habitats. Areas with high suitability ($\geq 75\%$) might be lost particularly in the eastern parts of the ecoregion (Golestan), and only limited areas, mostly in the western part of Gilan, Talysh Mts., and Mazandaran, would be climatically stable in the future for the taxa. Contraction of the potential range with habitat suitability $\geq 75\%$ was also projected for *Alnus subcordata* (48%; Fig. 2A Online Resource 1) and *Quercus castaneifolia* (53%; Fig. 2D Online Resource 1) by 2070. A considerable increase in distribution considered with at least 75% habitat suitability was predicted for *Euonymus velutinus* (in total +6082 km²; Fig. 2A Online Resource 1), *Populus caspica* (+23,191 km²; Fig. 2C Online Resource 1), and *Ilex spinigera* (+5,490 km²; Fig. 2C Online Resource 1) compared to the current period (Table 2). However, for *Parrotia persica*, the areas with high suitability ($\geq 75\%$) might be lost under RCP4.5 but gain in RCP8.5 (Fig. 2B Online Resource 1), reaching an increase of 509 km², respectively (Table 2). Similarly, the overall distribution of *Lonicera floribunda* was predicted to gain by 33% under RCP8.5 while not vastly changing in the case of RCP 4.5 reaching almost 17% (Fig. 2C Online Resource 1).

The models incorporating the RCP 4.5 scenario demonstrated noticeable elevation shifts for most of the studied species, except for *Lonicera floribunda* (Table 1). The highest

upward distribution shifts (Table 1) were predicted for lowland species, such as *Buxus hyrcana* (average +356 m), *Parrotia persica* (average +304 m), and *Albizia julibrissin* (average +129 m), and montane, *Pyrus boissieriana* (average +374 m) and *Frangula grandifolia* (average +274 m). Conversely, the highest downward shifts were expected for lowland/sub-montane species, including *Hedera pastuchovii* (average -90 m) and *Ruscus hyrcanus* (average -59 m). Regarding the altitudinal distribution changes under the most pessimistic scenario (RCP8.5), elevation shifts to the higher altitude were expected for *Parrotia persica* (average +376 m), *Pyrus boissieriana* (average +308 m), *Buxus sempervirens* (average +217 m), *Populus caspica* (+258 m), *Lonicera floribunda* (+207 m), *Alnus velutinum* (+195 m), and *Ruscus hyrcanus* (+147 m). In contrast to the RCP4.5 scenario, downward shifts were expected for *Frangula grandifolia* and *Gleditsia caspica*, while *Quercus castaneifolia* altitudinal range is projected to be similar to its current distribution (Table 1). Notably, the most substantial downward range was predicted for *Ilex spinigera*, reaching 260 m compared to the current period (Table 1).

At the regional level, the most prominent changes are the distributional contractions projected in the western (Gilan) and eastern (Golestan) parts of the region in both climatic scenarios (Fig. 2A). According to RCP4.5, the central part

Table 2 Potential geographical range areas (km²) estimated using different threshold values of habitat suitability (HS) and range size changes for the Hyrcanian endemic and sub-endemic species at current (1960–1990) and future climatic scenarios (RCP; ca. 2071–2100), SDMs conducted across the range; (“-” decreasing of suitable habitats)

Species	Current				RCP 4.5			
	High (75–100%)	Medium (50–75%)	Low (25–50%)	Total	High (75–100%)	Medium (50–75%)	Low (25–50%)	Total
<i>Acer velutinum</i>	6649	25,868	21,181	53,698	9524	19,586	15,962	45,072
<i>Albizia julibrissin</i>	2070	7198	13,869	23,137	8133	8788	9617	26,538
<i>Alnus subcordata</i>	7078	19,923	24,145	51,145	4083	16,815	18,771	39,670
<i>Buxus sempervirens</i>	3597	12,448	18,322	34,366	1875	4132	9032	15 039
<i>Euonymus velutinus</i>	5907	11,453	35,271	52,631	4588	9483	26,007	40 078
<i>Frangula grandifolia</i>	5575	12,820	19,377	37,772	85	1907	9,351	11,344
<i>Gleditsia caspica</i>	2578	12,688	11,206	26,472	60	3053	11,472	14,585
<i>Hedera pastuchovii</i>	5141	15,148	21,726	42,014	6979	12,593	14,018	33,590
<i>Ilex spinigera</i>	4773	17,324	21,960	44,056	6562	14,653	19,446	40,660
<i>Lonicera floribunda</i>	11,081	18,940	45,362	75,383	4857	17,129	40,238	62,224
<i>Parrotia persica</i>	2709	16,492	21,031	40,232	2391	10,414	16,664	29,469
<i>Populus caspica</i>	3547	17,432	18,500	39,479	15,430	11,918	12,678	40,026
<i>Pyrus boissieriana</i>	4668	19,195	37,431	61,294	1884	11,706	33,064	46,653
<i>Quercus castaneifolia</i>	4768	21,911	36,838	63,516	6424	22,231	17,113	45,768
<i>Ruscus hyrcanus</i>	4075	14,511	17,636	36,222	2858	10,863	13,073	26,795

Species	RCP 8.5				Species range changes							
	High (75–100%)	Medium (50–75%)	Low (25–50%)	Total	RCP 4.5		RCP 8.5					
					Total	%	HS > 50%	%	Total	%	HS > 50%	%
<i>Acer velutinum</i>	1567	13,537	21,132	36,237	-8626	-16	-3407	-10	-17,461	-33	-17,412	-54
<i>Albizia julibrissin</i>	2558	8187	9713	20,459	3401	15	7652	83	-2678	-12	1477	16
<i>Alnus subcordata</i>	3676	14,006	15,207	32,889	-11,475	-22	-6102	-23	-18,256	-36	-9319	-35
<i>Buxus sempervirens</i>	826	2495	7740	11,061	-19,327	-56	-10,038	-63	-23,305	-68	-12,723	-79
<i>Euonymus velutinus</i>	11,989	19,546	33,305	64,841	-12,553	-24	-3289	-19	12,210	23	14,175	82
<i>Frangula grandifolia</i>	733	4707	14,099	19,539	-26,428	-70	-16,402	-89	-18,233	-48	-12,955	-70
<i>Gleditsia caspica</i>	6	1632	10,196	11,834	-11,887	-45	-12,153	-80	-14,638	-55	-13,628	-89
<i>Hedera pastuchovii</i>	4471	11,310	12,412	28, 193	-8424	-20	-717	-4	-13,821	-33	-4507	-22
<i>Ilex spinigera</i>	10,263	10,898	13,037	34,198	-3397	-8	-883	-4	-9,858	-22	-936	-4
<i>Lonicera floribunda</i>	10,519	22,420	67, 101	100,040	-13,159	-17	-8035	-27	24,657	33	2918	10
<i>Parrotia persica</i>	3218	10,447	15,156	28,821	-10,763	-27	-6395	-33	-11,411	-28	-5536	-29
<i>Populus caspica</i>	26,738	6793	8297	41,828	547	1	6369	30	2349	6	12,552	60
<i>Pyrus boissieriana</i>	2868	10,057	29,730	42,655	-14,640	-24	-10,274	-43	-18,638	-30	-10,938	-46
<i>Quercus castaneifolia</i>	2218	20,451	17,737	40,406	-17,748	-28	1977	7	-23,110	-36	-4009	-15
<i>Ruscus hyrcanus</i>	0	122	4327	4449	-9428	-26	-4865	-26	-31,774	-88	-18,464	-99

the southern Azerbaijan are densely settled and extensively used for agriculture, housing, tourism, and recreation (Bayramli 2019). Therefore, the decline of the Hyrcanian forest can be attributed mainly to anthropogenic disturbance impacts and human-induced fires. As a result, the natural habitats of species found in lowland and sub-montane vegetation belts, such as *Albizia julibrissin*, *Gleditsia caspica*, and *Populus caspica*, have become fragmented. These species now exist in small patches of forest that are scattered among fields and

settlements, as well as narrow strips along riverbanks in the Hyrcanian ecoregion.

Considering the species-specific altitudinal ranges, our results are consistent with existing data. However, it is worth noting that the highest recorded occurrences of these species appeared frequently somewhat higher than previously reported (Browicz 1989, 1982; Rechinger 2005) (Table 1). These discrepancies, apart from the georeferenced methods, could result from an upward shift caused by ongoing climate warming, a

pattern already observed for many plant species in the region (Joorabian Shoostari et al. 2017; Naqinezhad et al. 2022; Taleshi et al. 2019). Indeed, our SDMs suggest that the climatically suitable habitat for most of the Hyrcanian endemic and sub-endemic species will be displaced to higher altitudes, except for *Hedera pastuchovii*, *Ilex spinigera*, and *Alnus subcordata* under both climatic scenarios. We show that climate warming has resulted in a significant upward shift in species optimum elevation averaging 22.9 m per decade, as generally predicted for mountain forest plants (Lenoir et al. 2008). However, for lowland species, *Buxus hyrcana*, *Populus caspica*, and *Parrotia persica*, and montane species, *Pyrus boissieriana*, the highest altitudinal redistribution of the suitable habitats, reaching on average 32–47 m per decade over the next 80 years. The predicted habitat gain is primarily expected at mid- and upper elevations (800–2800 m a.s.l.). Nevertheless, given that trees are slow-migrating species and thus can experience time lags in range expansion in response to rapid climate change, the theoretical habitats projected at higher altitudes may not be accessible for studied species, leading to an even greater shrinkage of their distribution. At the same time, other factors such as competition of dominated temperature tree species such as *Fagus orientalis* for which climate-induced potential range shift has also been reported in the region (Khalatbari Limaki et al. 2021) could have prevented the range-filling for Hyrcanian endemic and sub-endemic species. Climate-driven range shifts of studied species can be mostly explained by expected temperature increases in the mountainous areas of the Hyrcanian ecoregion. According to the climate projection, the mean temperature is expected to rise by at least 2.0–3.5 °C by the end of this century compared with the current condition, posing a risk of intensification soil drought, forcing effect on potential evapotranspiration (Bergh et al. 2003), and in consequence reducing potential available suitable habitats.

Climate-change refugia in the Hyrcanian ecoregion: vulnerability assessment

By employing the species distribution modelling on multiple endemic and sub-endemic woody taxa across the Hyrcanian landscape, we were able to provide large-scale forecasts of biodiversity change over the next 80 years. Based on the assessment of species' vulnerability to future climate threats, our study allowed us to identify potential climate refugia in the Hyrcanian ecoregion, which, in the frame of climate adaptation actions, should be an integral part of conservation and management efforts for species and communities (Barrows et al. 2020; Keppel et al. 2015).

In general, a region disproportionately rich in biological diversity and endemism acts as long-term refugia, potentially serving as climatically suitable refugia in the future (Harrison and Noss 2017). However, because contemporary climate change has a different trajectory, past performance as

refugia does not necessarily guarantee that these areas will offer suitable habitats in the future (Barrows et al. 2020; Keppel et al. 2015; Sandel et al. 2011). The palaeoenvironmental and palynology data concurrently point to the Hyrcanian ecoregion as a long-time glacial refugial area (Connor and Kvavadze 2009; Leroy and Arpe 2007), acting as a sanctuary for the Neogene flora. Currently, the region is relatively buffered from contemporary climate change that enables the persistence of the unique relict ecosystems with high species richness and endemism. Nevertheless, our projections suggest that the climatically suitable habitats for endemic and sub-endemic woody taxa in the Hyrcanian forests are expected to contract by 2100, with a mean projected loss of up to 45%, as generally predicted for other major temperate forest trees in the ecoregion (Dering et al. 2021; Naqinezhad et al. 2022; Sękiewicz et al. 2022; Taleshi et al. 2019). Notably, according to our SDMs, a range shift to the western part of the region is predicted for most species. Specifically, we found that a considerable loss of suitable habitats for endemic woody taxa would be expected in the eastern parts of the region (Golestan) and in the Talysh Mountains (northwestern Hyrcania) with over 85% and 34%, where the highest species richness is currently observed (Fig. 3A). Although most of the mountainous areas of Gilan are likely to be lost with habitat shifts eastward were predicted in this subregion. The eastern Hyrcanian ecoregion is currently quite different in terms of climatic regimes, with the highest mean temperature and lowest precipitations (Fig. 1B), and the mean annual temperature would be more adversely impacted in the region in the coming decades with increases of even 4 °C. Consequently, these changes may put the local stands beyond the species' ecological optimum. At the same time, in Gilan, higher precipitation is expected compared to the remaining part of the region which leads to probable range expansion of species occurring in alluvial and lowland sites, such *Populus caspica* and *Alnus glutinosa*. Importantly, the mountainous areas located in the central part of the Alborz Mountains in the Mazandaran and some areas in the Talysh Mountains seem to offer suitable habitats continuously under the future conditions for studied taxa. According to the species richness map, the greatest species richness is expected in these areas in the future. Generally, long-term refugia might be either the most resistant or the most susceptible to future climate change (Gavin et al. 2014; Keppel et al. 2015). Given the limited palaeobotanical study from the Hyrcanian ecoregion, it is difficult to draw detailed conclusions about the location of glacial refugia in the region, and we cannot conclusively verify this assumption. Although our modelling represents the first approximation of potential areas that may serve as future climatic refugia for the Hyrcanian endemics and sub-endemic species, the SDMs are only a part of the comprehensive approaches applied to identify these areas (Gavin et al. 2014; Keppel et al. 2015). Additional data, including

genetics and palynological, are required for quantifying the spatial and temporal dimensions of refugia in the ecoregion.

At the species level, our SDMs showed that the effect of climate change on the extent and distribution of suitable conditions varied across studied taxa. We found that species occurring mostly in lowlands are more likely to be at higher risk from climate-driven habitat loss than montane species. Consequently, this group of species is potentially the most sensitive to future climate change. Of these, the most prominent changes are expected for evergreen *Ruscus hyrcanus* and deciduous *Gleditsia caspica*. Under the RCP8.5, the climatically stable areas (habitat suitability $\geq 75\%$) for the species practically disappear, and thus, the species may be at high risk of extinction. Similarly, the range of *Acer velutinum*, *Frangula grandifolia*, and *Buxus hyrcana* could be severely impacted, for which over 70% of highly suitable areas (habitat suitability $\geq 75\%$) would be lost under the most pessimistic scenario at the end of this century.

Conservation prioritization and study limitations

As demonstrated recently by Ludovicy et al. (2022), the existing protected areas in the Iranian Plateau cover only 50% of climatically stable habitats for endemic and sub-endemic plants under current conditions. However, this coverage is projected to decrease significantly to 15–25% in the future. This finding was also previously reported by Noroozi et al. (2019), who indicated that regional centers of plant endemism are inadequately represented by PAs. We found a similar pattern, showing that only 13% of suitable habitats (> 50% of habitat suitability) for endemic and sub-endemic woody species are currently covered by the Hyrcanian protected areas. Although this coverage may slightly increase to 18–20% in the future, it seems to be still insufficient to protect the broadest spectrum of the valuable habitat in the region, especially assuming the expected risk of habitat loss in the next 80 years. Furthermore, conservation prioritization analyses indicate that only 13.4% of areas designated for conservation and management under climate change will be located within the regional PAs, yet the majority of these areas are classified as low priority.

In the most pessimistic scenario, we predicted over 44% reduction in the overall distribution of endemic and sub-endemic Hyrcanian woody taxa. Accordingly, special attention should be paid to areas located in the Golestan and to some extent in Gilan, where species are the most exposed to climate change. Concurrently, our spatial prioritization analysis identifies these regions as potential areas for in situ conservation that should be considered in an expansion of the existing Hyrcanian PAs network. Considering that the adaptation potential of trees largely depends on the existing genetic variability, maintaining the broadest species' climatic niches and thus genetic diversity is crucial. Therefore,

of Mazandaran and limited areas in the western part of Gilan and Talysh Mountains (southeastern Azerbaijan) are likely to remain stable climatic refugia in the future. However, under the most pessimistic scenario (Fig. 2A), the expected change in the distribution of climatically suitable areas in the Talysh Mountains shows a slight reduction. The major gain of suitable habitats is expected to occur in the lowland and mountain ranges of Mazandaran under both climatic scenarios.

According to the richness map (Fig. 3A–C), species diversity will also be high in the main climatic refugia projected for the Hyrcanian endemic in the Mazandaran and Talysh Mountains, where ≥ 8 taxa may occur in the future (Fig. 3B, C). However, the Zonation analysis indicated that the high-priority areas for conservation and management under climate change for studied species will be inadequately represented by the existing protected areas (PAs) in the ecoregion (Fig. 3D), covering only 13.4%. Furthermore, up to 87% of the climatically suitable habitats for endemic and sub-endemic trees will be located beyond the regional PAs network, notably in the Golestan and eastern parts of Mazandaran. This coverage may slightly increase to 18–20% in the future. Interestingly, the projected future climatically suitable habitats for most studied species, except for *Ruscus hyrcanus*, will lie outside of the currently designated PAs, which have already offered limited protection to these species' populations, covering a small percentage of these areas, ranging from 16% (*Gleditsia caspica*) to 44% (*Euonymus velutinus*) (Table 7 Online Resource 2).

Discussion

Current distributional patterns of the Hyrcanian endemic and sub-endemic woody taxa

Our modelling indicates that the current potential distribution of the Hyrcanian woody endemic and sub-endemic appeared broader than their entire geographic range in the Hyrcanian ecoregion (Fig. 1 Online Resource 1). Given the strong human impact in the ecoregion (Gu et al. 2022; Ramezani et al. 2013; Sagheb-Talebi et al. 2014), the mismatches between realized and potential niches are not surprising but expected. This observed pattern is particularly noticeable for species that occur in lowland and sub-montane belts where considerable uncontrolled deforestation, habitat loss, and fragmentation have been noted. Vast forest areas in the lowlands were in great part, destroyed and converted into agricultural lands, and have become densely populated over the last centuries (Aghsaei et al. 2020; Gholizadeh et al. 2020; Gu et al. 2022). The Gilan, Mazandaran, and Golestan regions which are the main centers of the Hyrcanian forest are one of the most densely populated regions ("Iran Population Density Map," 1993). Similarly, the foothills of the Talysh Mountains in

the most promising strategies should consider the prioritization of climatically suitable areas for effective planning PAs. Based on our findings, Golestan, being part of the Alborz area of endemism (Noroozi et al. 2019), should receive the highest priority for conservation efforts due to significant predicted habitat loss, which is currently minimally represented by existing PAs (Fig. 3D). Therefore, we suggest, expanding the Jahannama PA, situated in the eastern parts of the Alborz Mountains, and considering the establishment of a new protected area in this region to encompass a broader spectrum of currently threatened areas, as predicted by our analysis. Additionally, considering that the main protected area, Alborz-e-Markazy (Central Alborz) in the Mazandaran, includes mainly areas with low conservation priority, it would be conceivable to consider expanding existing PAs in the eastern part of the region (such as Abshar-e-Shirgah, Khiboos, Anjilsee, and Asas) to form a more extensive protected complex. Similarly, the expansion of the Beles Kuh protected area, which also exhibits the highest species richness in the western part, should also be considered.

We are aware of SDM limitations and uncertainties (Keenan 2015), and thus, our results of SDMs should be considered only to be a first indication of possible risks of species maladaptation to future climates of the ecoregion. Firstly, due to the apparent disparity between the realized and potential niches of the species, we cannot exclude the possibility that the species would be able to cope with new environmental conditions without the need for adaptation. This is because the currently realized niche may not fully represent its ecological potential due to the strong human impact in the region. To address this, it would be necessary to consider historical data regarding the species' occurrence, which poses a challenge. Secondly, a further challenge in species range predictions is the choice of algorithms and climatic predictors, which strongly affect the accuracy of SDMs and are key to ensuring the reproducibility of the methods and thus provide a source of projections uncertainty (Konowalik and Nosol 2021; Zurell et al. 2023). Thus, the observed discrepancies between our estimation and the previous SDM projections reported by Alipour and Walas (2023), Alipour et al. (2023), and Taleshi et al. (2019) are due to the use of different methodological approaches. One of the major constraints relates to using climate rasters that may fail to capture the effects of topography on microclimate (Gavin et al. 2014; Karger et al. 2017). To account for this, contrary to previous projections (Alipour et al. 2023; Taleshi et al. 2019), we used climatic data from CHELSA that has higher accuracy in mountain-specific conditions than WorldClim (Karger et al. 2017). Additionally, in contrast to Taleshi et al. (2019), our predictions were less pessimistic for *Acer velutinum*, *Alnus subcordata*, and *Parrotia persica*, suggesting a lesser decline in habitat suitability under RCP8.5. Here,

to minimize the bias of algorithms affecting the final model, we employed maximum entropy (MaxEnt) which shows high predictive accuracy and yielded comparable results compared to the generalized linear model (GLM) utilized in this previous study (Taleshi et al. 2019), which over-predicts for non-sampled areas and shows lower specificity (Ahmadi et al. 2023; Konowalik and Nosol 2021). Notably, unlike prior studies, we omitted a procedure for reducing variable collinearity based on the recommendation that excluding highly correlated variables does not significantly impact model performance (Feng et al. 2019). Additionally, using different species occurrence datasets and coverage contributes as a source of obtaining diverse distributional patterns (Konowalik and Nosol 2021). Finally, our SDM estimations refer only to environmental-led predictions, overlooking the complexity of the evolutionary responses of species to environmental change, including adaptive potential, as well as other limiting non-climatic factors and threats (such as competition, dispersal ability, and ongoing human impact) in the region. However, given that SDM has increasingly been incorporated into the IUCN assessment and conservation prioritization (Cassini 2011; Doxa et al. 2022; Gilbert et al. 2012; Lehtomäki et al. 2019; Marvi Mohadjer and Fegghi 2020), our results may support scientific-based strategies oriented to mitigate the potential impact of climate change in the region. This study represents the initial approximation of potential risks involved under a future climate for the Hyrcanian woody endemics and sub-endemics and identifies regions that potentially match new climate conditions. Of these, only *Gleditsia caspica* and *Populus caspica* are listed on the IUCN Red List as endangered, while *Quercus castaneifolia* is listed as near threatened (IUCN 2023). At the same time, only *Buxus hyrcana* (EN), *Populus caspica* (EN), *Parrotia persica* (LR), and *Frangula grandifolia* (LR) are protected at the national level, classified as endangered (EN) and lower risk (LR) (Jalili and Jamzad 1999). The projected loss of suitable areas for these already declining species due to previously extensive degradation and fragmentation should be of particular concern, especially with insufficient protection. Our SDMs also indicate a rising risk for species not currently protected, suggesting that their conservation status should be evaluated, especially given that future suitable areas for those taxa will largely be found outside of existing PAs. This applies mostly to *Ruscus hyrcanus* for which the Hyrcanian ecoregion is predicted to be completely unsuitable in the future. Considering our pessimistic projections and the overuse of the species as a traditional herbal medicinal product (Ghorbani et al. 2020), there is a high risk of extirpation of the species' resources in the future.

In light of the projected habitat loss in the ecoregion, the genetic resources of the species may be greatly impoverished, affecting their adaptive potential, and thus resilience of the Hyrcanian forest. According to an available genetic

investigation, both *Gleditsia caspica* (Schnabel and Krutovskii 2004) and *Populus caspica* (Alipour et al. 2021) display low genetic diversity and signs of bottlenecks, possessing a threat of adverse demo-genetic processes. Climate change is driving the spread of pests and diseases and in some cases worsening existing problems. This applies to boxwood in the Hyrcanian ecoregion, for which the forecasted climate changes may markedly affect the species range across the landscape. Most present-day *Buxus hyrcana* populations are seriously threatened and devastated by the spread of boxwood blight and box-tree moth (Alipour and Walas 2023; Nacambo et al. 2014). Although the genetic diversity in the species currently remains relatively high (Esmaeil-nezhad et al. 2020; Salehi Shanjani et al. 2018), there is a justified concern for the loss of variability, especially if genetic drift becomes a dominant evolutionary force and is accompanied by an observed reduction in population size which are likely to get worse under future climate change. Another possible consequence of the climate-driven range shifts might be increasing sympatry among closely related species, potentially triggering hybridization. This could be a potential threat to *Gleditsia caspica* that hybridizes with introduced *Gleditsia triacanthos* L. which may lead to exposure to genetic erosion (Schnabel and Krutovskii 2004).

Conclusion

With climate change and our projections, efficient conservation planning should focus on incorporating integrative and proactive conservation approaches to maintaining and preserving the resources of the Hyrcanian endemic and sub-endemic woody species. However, applying management solutions in the frame of climate adaptation actions is generally a major challenge for future forest management. Given that efforts to conserve and manage species/biodiversity should focus on identifying climate change refugia (Barrows et al. 2020; Keppel et al. 2015), this study enriches our understanding of the general pattern of vulnerability to future climate threats in the Hyrcanian ecoregion, pointing Gilan and Golestan region to be prioritized for conservation management based on projected habitat decline across taxa. Certainly, given that the projected suitable habitats for the studied species are inadequately represented by regional protected areas, future conservation efforts should prioritize the evaluation and extension of this network, which currently covers only 15% of the entire Hyrcanian ecoregion. This expansion should focus on areas identified as long-term climatic refugia and those with high priority for conservation to protect a wide spectrum of biodiversity in the region under climate change. Secondly, climate change associated with ongoing human-induced habitat loss may further increase extinction risk for

the species already facing threats in the region. Therefore, the regional conservation and restoration program through in situ and ex situ management, accounting for the recognition of genetic variability and long-term monitoring of demographic and genetic threats, is urgently needed to preserve the existing resources. Moreover, to support our predictions, the incorporation of adaptive genetic variation in climate vulnerability assessments could provide more accurate forecasts of the species' potential response to future climate change. This approach is a recently integrative part of the climate change adaptation assessments of forest trees and provides the scientific basis for developing management solutions oriented towards climate change adaptation, such as assisted gene flow or assisted migration strategies (Rellstab 2021).

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1007/s10113-024-02222-7>.

Acknowledgements This work was supported by the Institute of Dendrology, Polish Academy of Sciences, under the statutory activity.

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