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Research Article

Bridging climate refuges for climate change adaptation: A spatio-temporal connectivity network approach

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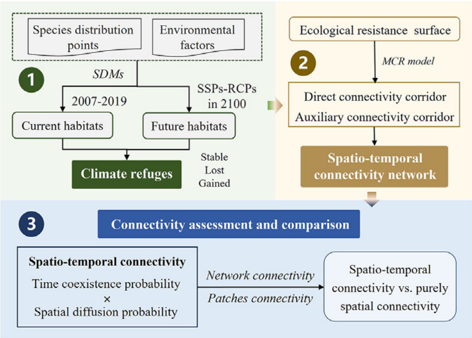
HIGHLIGHTS

- A spatio-temporal connectivity network approach is proposed to connect climate refuges.
- The importance of auxiliary connectivity corridors for Tibetan wild asses will gradually increase.
- The purely spatial perspective overestimates direct connectivity and underestimates auxiliary connectivity.
- This study highlighted the importance of spatio-temporal connectivity for species adapting to climate change.

GRAPHICAL ABSTRACT



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ABSTRACT

Enhancing the spatio-temporal connectivity of dynamic landscapes is crucial for species to adapt to climate change. However, the spatio-temporal connectivity network approach considering climate change and species movement is often overlooked. Taking Tibetan wild ass on the Qinghai-Xizang Plateau as an example, we simulated species distribution under current (2019) and future scenarios (2100), constructed spatio-temporal connectivity networks, and assessed the spatio-temporal connectivity. The results show that under the current, SSP2–4.5 and SSP3–7.0 scenarios, suitable habitats for the Tibetan wild ass account for 21.11 %, 21.34 %, and 20.95 % of the total area, respectively, with increased fragmentation projected by 2100. 78.35 % of the habitats which are predicted to be suitable under current conditions will remain suitable in the future, which can be regarded as stable climate refuges. With the increase in future emission intensity, the percentage of auxiliary connectivity corridors increases from 27.65 % to 33.57 %. This indicates that more patches will function as temporary refuges and the auxiliary connectivity corridors will gradually weaken the dominance of direct connectivity corridors. Under different SSP-RCP scenarios, the internal spatio-temporal connectivity is always higher than direct connectivity and auxiliary connectivity, accounting for 42 %–43 %. Compared with the spatio-temporal perspective, the purely spatial perspective overestimates network connectivity by about 28 % considering all current and future patches, and underestimates network connectivity by 16 %–21 % when only considering all current or future patches. In this study, a new approach of spatio-temporal connectivity network is proposed to bridge climate refuges, which contributes to the long-term effectiveness of conservation networks for species' adaptation to climate change.

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1. Introduction

Climate change will exacerbate habitat shrinkage and fragmentation, thereby reducing biomass and altering nutrient cycling, impairing biodiversity and critical ecosystem functions (Fu et al., 2022; Keeley et al., 2018; Haddad et al., 2015). In addition, climate change shifts species' suitable habitats and drives species movement to track suitable climatic conditions (Garcia et al., 2014; McGuire et al., 2016). Over time, some habitat patches may appear or disappear intermittently in dynamic landscapes, resulting in habitat patches only coexisting at certain periods (Zeigler and Fagan, 2014). Thus, species persistence is highly dependent on the spatial patterns of future habitats and the dispersal ability of species to track their climatic niches in space and time (Schloss et al., 2012; Wu et al., 2023). Enhancing landscape connectivity is recognized as a global imperative to help reverse biodiversity decline, as well as an important conservation measure to ensure the long-term persistence of populations and communities (Correa Ayram et al., 2016; Riordan-Short et al., 2023; Xu et al., 2024a). However, landscape connectivity changes over time following land cover change and climate change. Exploring spatio-temporal connectivity becomes pivotal in order to obtain a better understanding of the ecological patterns and processes within dynamic landscapes, especially for biodiversity conservation, but it is often overlooked (Uroy et al., 2021). It is also acknowledged that the enhancement of spatio-temporal connectivity can be achieved through ecological connectivity networks for climate change adaptation (Goicolea and Mateo-Sánchez, 2022).

The future suitable habitats and species movement pathways in dynamic landscapes may differ from the present. Spatio-temporal connectivity provides a more unbiased and realistic perspective of habitat connectivity assessment than purely spatial connectivity (Huang et al., 2020). Network theory (Saura and Pascual-Hortal, 2007; Urban and Keitt, 2001) and circuit theory (Brennan et al., 2022; McRae et al., 2008; Xu et al., 2024b), are the most widely used approaches for evaluating landscape connectivity. Early approaches for quantifying spatio-temporal connectivity mainly considered the spatial dispersion of organisms in order to quantify the temporal variability in spatial connectivity (Tulbure et al., 2014; Urban and Keitt, 2001; Uroy et al., 2021). Subsequently, Martensen et al. (2017) proposed a spatio-temporal connectivity model considering both spatial and temporal dispersal. They concluded that the extensively used purely spatial connectivity of a given snapshot time may underestimate the spatio-temporal connectivity of dynamic landscapes, thereby overestimating the risk of population isolation and associated extinction. Huang et al. (2020) demonstrated that this conclusion was correct in the context of climate change. However, the importance of species movement corridors in conservation planning is still overlooked. Moreover, so far few studies focused on ecological connectivity networks that simultaneously consider both climate change and species movement pathways. Efforts to incorporate future climate change scenarios into connectivity to identify critical habitats and movement pathways to increase connectivity remain significant but unresolved challenges (Littlefield et al., 2017; Xu et al., 2024a).

A spatio-temporal connectivity network is essentially a fused multilayer ecological network with nodes connected through spatio-temporal links (Pilosof et al., 2017). As a key spatial landscape configuration, the ecological network permits species movement among suitable habitat patches through corridors, thus being crucial for biodiversity conservation (Peng et al., 2018a, 2018b; Tarabon et al., 2020). Identifying and protecting critical habitats and movement corridors is key to address biodiversity and climate crises (Ding et al., 2023; Keeley et al., 2018; Peng et al., 2024). In the context of global climate change, stable habitats are also important climate refuges, because these areas provide shelter for species by reducing the negative impacts of climate change on them (Stralberg et al., 2020). However, some habitats exist only for a certain period and are referred to as temporary climate refuges, serving as stepping stones for species to migrate as a consequence of shifting suitable climatic conditions (Saura et al., 2014). Moreover, when the habitat patches where a certain species occur become unsuitable, individuals have to move towards other patches that have become suitable. Species movement corridors are often extracted using the minimum cumulative resistance model based on the resistance surface (Jiang et al., 2022; Peng et al., 2018a). Spatio-temporal connectivity networks, jointly considering spatial connectivity and temporal coexistence probabilities in dynamic landscapes, can provide scientifically effective strategies for species tracking and adapting to climate change (Martensen et al., 2017).

The Qinghai-Xizang Plateau is a global biodiversity conservation hotspot and sensitive to global climate change and human activities (Zhang et al., 2021). Tibetan wild ass (*Equus kiang*) is an endemic species of the Qinghai-Xizang Plateau, which has been listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora. Tibetan wild asses' suitable habitats will likely change with fragmentation due to climate change and human disturbance (Shi et al., 2023). Focusing on two points in time (i.e., 2019 and 2100), spatial-temporal connectivity was modeled considering two of the future scenarios delivered by the Intergovernmental Panel on Climate Change (IPCC) for climate change simulations. These scenarios are derived from the integration of Shared Socioeconomic Pathways (SSPs) and Representative Concentration Pathways (RCPs), which focus on the socioeconomic development and greenhouse gasses emission trajectories, respectively. Specifically, SSP2–4.5 (intermediate pathway, the scenario closest to its historical trend) and SSP3–7.0 (regional rivalry pathway, selected as a comparison) were considered in this study (Baisero et al., 2020; Carvalho et al., 2022). The scientific questions are: (1) how to construct a spatio-temporal network considering climate change and species movement? and (2) in dynamic landscapes, compared to spatio-temporal connectivity, will purely spatial connectivity underestimate or overestimate network connectivity? To answer these questions, we identified the current and future suitable habitats for Tibetan wild asses using species distribution models (SDMs). Subsequently, a spatio-temporal connectivity network was constructed by identifying climate refuges and connectivity corridors. Lastly, we assessed the spatio-temporal connectivity and compared it with purely spatial connectivity.

2. Materials and methods

2.1. Study area and data sources

The Qinghai-Xizang Plateau (26°00′N–39°47′N, 73°19′E–104°47′E) is the highest plateau in the world and is known as the third pole (Fig. 1). It accounts for approximately 25 % of China's total area, and is mainly characterized by the alpine climate. The vegetation types on the Qinghai-Xizang Plateau are mainly alpine meadows, grasslands, and forests. This region represents most of the distribution range of 28 ungulate wild animals such as Tibetan wild ass, Tibetan antelope (*Pantholops hodgsonii*), and wild yaks (*Bos mutus*), accounting for 42 % of Chinese ungulate species (Shi et al., 2023). Currently, the Qinghai-Xizang Plateau is under the combined impact of climate change and human activities, resulting in more sensitive ecosystems, further habitat loss or fragmentation, and increasingly severe biodiversity conservation challenges (Fan et al., 2021; Hua et al., 2022; Shi et al., 2023). In this study, we focused on Tibetan wild ass, which is a nationally first-class protected animal and endemic to the Qinghai-Xizang Plateau. Tibetan wild ass mainly feeds on grass. It is a good runner, which can migrate across climatic regions to adapt to seasonal climatic changes. China has established several nature reserves to protect Tibetan wild ass, including Qiangtang, Altun Mountain, Hoh Xil, Sanjiangyuan, and other nature reserves.

The data used in the study were as follows: (1) 305 Tibetan wild ass occurrence vector points from 2007 to 2019, derived from existing studies (Shi et al., 2023). This data include field observations along the G317 national highway in August 2019, as well as online observation records gathered from the Global Biodiversity Information Database

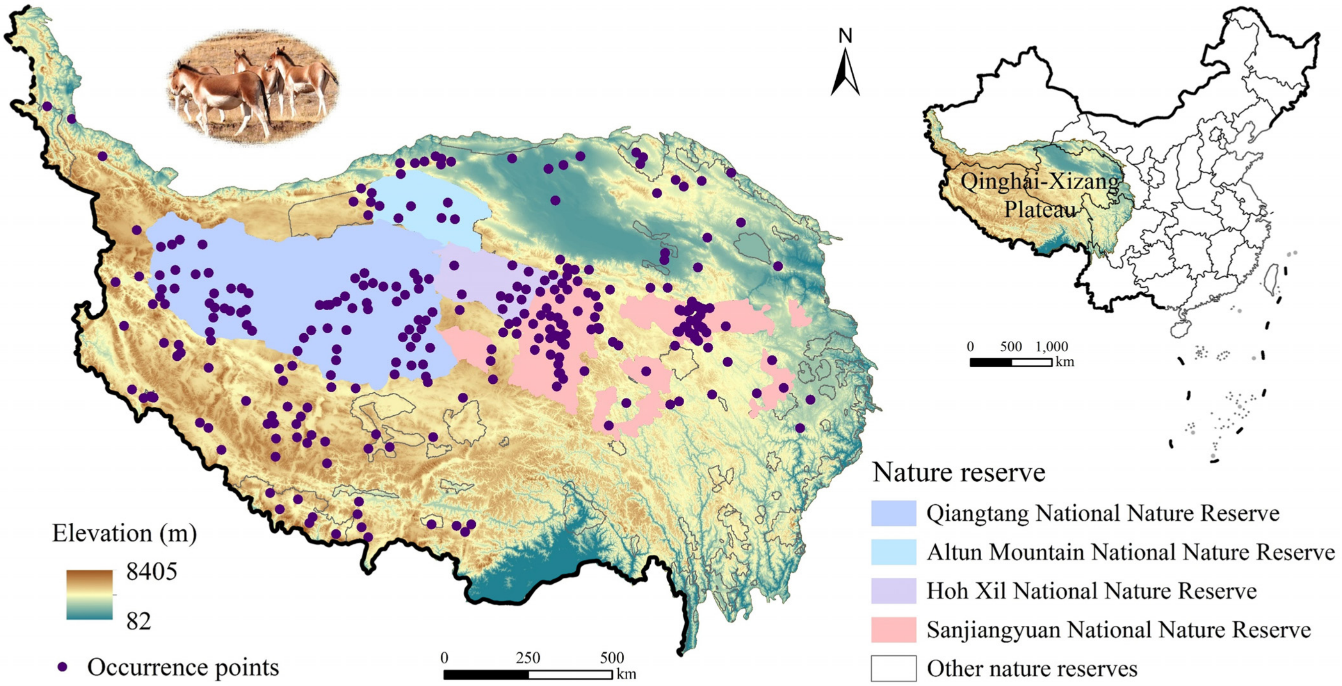

Fig. 1. Geographical location of the study area and occurrence points of Tibetan wild asses.

(www.gbif.org), the National Tibetan Plateau Science Data Center (http://data.tpdc.ac.cn/zh-hans/), and the China Nature Reserve Specimen Resource Sharing Platform (http://www.papc.cn/html/folder/1–1.htm); (2) The SSPs scenario land use simulation dataset for 2100, from the National Earth System Science Data Center (http://www.geodata.cn/data/), with a spatial resolution of 1 km; (3) 2007–2019 land use dataset, derived from the MCD12Q1 product of the MODIS satellite imagery project (https://modis.gsfc.nasa.gov/), with a spatial resolution of 500 m; (4) 2007–2019 monthly temperature and precipitation data from the National Earth System Science Data Center (http://www.geodata.cn/data/) with a spatial resolution of 1 km for synthesizing 15 bioclimatic variables; (5) 2081–2100 bioclimatic data from the WorldClim database (https://www.worldclim.org/data/index.html), with a spatial resolution of 30 s; (6) Digital elevation model from the Resource and Environmental Science and Data Center (https://www.resdc.cn/), with a spatial resolution of 1 km; (7) Normalized Difference Vegetation Index (NDVI) data during 2007–2019 from the Resource and Environmental Science and Data Center (https://www.resdc.cn/) with a spatial resolution of 1 km; and (8) 2007–2018 human footprint data from existing studies (Mu et al., 2022). The resampling method of nearest neighbor and bilinear interpolation was used to make maps of all selected variables at the same spatial resolution, i.e., 1 km.

2.2. Identification of suitable habitat based on SDMs

In this study we selected three commonly used SDM algorithms with high model discrimination performance: maximum entropy model (implemented using Maxent software, https://biodiversityinformatics.amnh.org/open_source/maxent), artificial neural network (calculated using MATLAB R2018a software), and random forest (calculated using MATLAB R2018a software). The three chosen algorithms utilize the principles of machine learning in order to estimate the relationships between species' observed distribution and environmental factors. The parameters for the three algorithms were set considering software manuals and relevant studies (Mi et al., 2023; Ohashi et al., 2019), which were summarized in Table 1. The codes used to fit and evaluate the SDMs were uploaded on GitHub, and are freely available at https://github.com/DongmeiXuGeo/spatiotemporal-connectivity. To reduce the uncertainty related to the single algorithm and obtain reliable predictions of suitable habitats for Tibetan wild asses, we fitted each algorithm 10 times, chose the best iteration for each algorithm, and then averaged their predictions using equal weights. The model fitting procedure was as follows: firstly, the original species occurrence points were thinned by collapsing multiple occurrence records falling within the same 1 km-wide pixel to a single record, in order to lower spatial autocorrelation; subsequently, collinear environmental factors were detected by looking at the Pearson correlation coefficient (setting the absolute value of the threshold to 0.8). The ones with a low contribution to habitat suitability within preliminary model fitting iterations were discarded.

Table 1
Explored parameters of the three SDM algorithms used to estimate habitat suitability for Tibetan wild ass.

SDMs	Critical parameters setting
Maxent model	Replicated run type: bootstrap; random seed: yes; random test percentage: 20 %; replicates: 10; regularization multiplier: 1
Artificial neural network	Training algorithm: gradient descent with momentum; training times: 5000; learning rate: 0.02; training goal: 0.1; momentum factor: 0.7
Random forest	The optimal number of leaves: 20; the number of decision trees: 500

For the Maxent model, all thinned occurrences were inputted as samples. For artificial neural networks and random forests, a number of background points equal to the number of thinned occurrences were generated, with each background point being at least 5 km away from the occurrence points. The obtained data were then randomly divided into a training group (80 %) and a test group (20 %). The receiver operating characteristic (ROC) curve method was used to verify the accuracy of the model (Swets, 1988). An area under the curve (AUC) of ROC greater than 0.8 indicates that the overall model discrimination performance is generally good (Swets, 1988). In this study, the lowest value of habitat suitability of all species points was selected as the binariza-

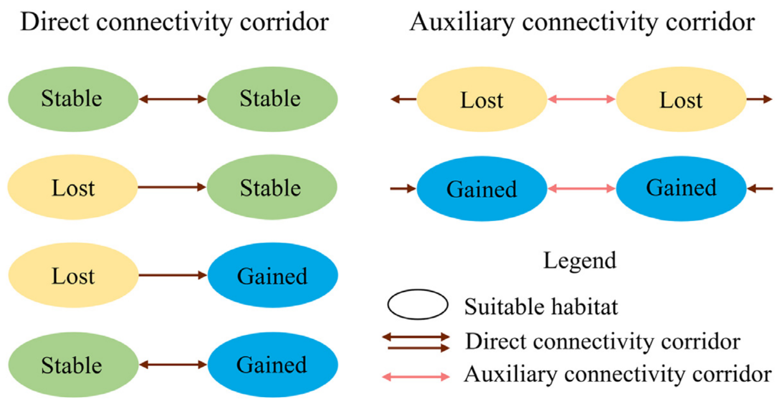

Fig. 2. Schematic diagram of direct and auxiliary connectivity corridors.

tion threshold distinguishing between suitable and unsuitable habitat patches for Tibetan wild asses. Successively, the areas with habitat suitability higher than the threshold of 0.613 were extracted, and the resulting suitable patches with an extent lower than 100 km^2 were discarded. Stable habitat patches (i.e., those being classified as suitable under both current and future conditions) represent climatic refuges for the species as they show relatively stable climatic conditions. Differently, patches being gained (i.e., currently unsuitable but suitable under future scenarios) or lost (i.e., suitable nowadays but unsuitable in the future) represent temporary climate refuges.

2.3. Construction of spatio-temporal connectivity network

Connectivity corridors can protect biodiversity by connecting fragmented habitats (Ding et al., 2023; Hawn et al., 2018; Xu et al., 2024b), and the determination of ecological resistance value is a very important step for delineating such corridors. The ecological resistance surface reflects the degree of horizontal obstruction of species movement and associated ecological processes in heterogeneous landscapes (Brennan et al., 2022), which is usually constructed using the land cover type assignment method (Dong et al., 2021; Fan et al., 2022). Land cover is an important characterization of human activities and food sources for Tibetan wild asses (Li et al., 2023; Zhang et al. 2017). Referring to related studies (Liu et al., 2024; Peng et al., 2018a; Zhang et al., 2017) and the behavior and dispersal of Tibetan wild asses, we set the resistance values as follows: grassland 1, forest land 10, cultivated land 30, waterbody 50, wetland 100, unused land 200, and construction land 500. The spatio-temporal ecological resistance surface was defined as the average of the moments before and after the future environmental change, meaning it represents the average resistance of both the current and future static resistance surfaces.

The minimum cumulative resistance (MCR) model is one of the most widely used methods for extracting connectivity corridors (Knaapen et al., 1992). This method defines connectivity corridors as the landscape 'channels' showing the lowest resistance considering target species during a hypothetical migration between the source and the target habitat patches (Harrison, 1992; Jiang et al., 2022). The formula used in this method is given in Eq. (1). Since the landscape is dynamic, two patches connected by a corridor may not completely coexist in time. As shown in Fig. 2, when the source patch is a stable or lost patch and the target patch is stable or gained, the species can move between patches directly through the corridor. So this corridor is called a direct connectivity corridor. When the source and target patches are both lost or gained, the species cannot rely solely on the corridor connecting them to complete the migration from the current habitat to the future habitat. So this corridor is called an auxiliary connectivity corridor.

$$\mathrm{MCR} = f \min \sum_{j=n}^{i=m} D_{ij} \times R_i \tag{1}$$

where f is the positive correlation function between MCR and ecological process, D_{ij} denotes the movement distance from adjacent source grid j to target grid i, R_i is the ecological resistance value of grid i, and Σ represents the cumulative cost of traversing all pathways between any adjacent two habitat patches. The Linkage Mapper tool of ArcGIS 10.5 was applied to extract corridors. The maximum corridor length was set to 100 km.

2.4. Spatio-temporal connectivity assessment

R-Studio software was applied to drive and improve the command-line version of landscape connectivity computing software Conefor (http://www.conefor.org/files/usuarios/conefor_directed.zip) to calculate the dynamic connectivity of ecological networks. The spatio-temporal connectivity code was developed by Martensen et al. (2017). Probability of connectivity (PC) was obtained by summing the internal connectivity index ($\mathrm{PC}_{\mathrm{intra}}$), direct connectivity index ($\mathrm{PC}_{\mathrm{direct}}$), and auxiliary connectivity index ($\mathrm{PC}_{\mathrm{step}}$) (Bodin and Saura, 2010; Huang et al., 2020; Saura and Rubio, 2010). The internal connectivity is the connectivity provided by the patches themselves, the direct connectivity is the connectivity provided by direct connectivity corridors, and the auxiliary connectivity is the connectivity provided by auxiliary connectivity corridors, whose formulas are shown in Eqs. (2)–(5).

The dynamic dispersal probability is obtained by multiplying the spatial probability by the temporal probability, which takes into account not only the ability of the species to disperse in space but also the probability of the coexistence of habitat patches in time (Goicolea and Mateo-Sánchez, 2022). The temporal coexistence probability was set as follows. The probability of the existence of a corridor starting from a gained patch or ending at a lost patch is related to the coexistence time of the source and destination patches during this period. Therefore, the likelihood of corridor connectivity at the beginning or end of a stable patch is 1. The likelihood of corridor connectivity from a lost patch towards a gained one is between 0 and 1, depending on how long the source and destination patches coexist during this period. Referring to related studies (Goicolea and Mateo-Sánchez, 2022; Huang et al., 2020; Martensen et al., 2017), the coexistence probability of lost patches and gained patches is set to 0.5 (40 years of coexistence) in this case. The connectivity importance of each habitat patch is characterized by dPC, the formula is shown in Eq. (6).

$$\mathrm{PC} = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i a_j p_{ij}^{*}}{A_{\mathrm{L}}^{2}} \tag{2}$$

$$\mathrm{PC}_{\mathrm{intra}} = \frac{\sum_{i=1}^{n} a_i^{2}}{A_{\mathrm{L}}^{2}} \tag{3}$$

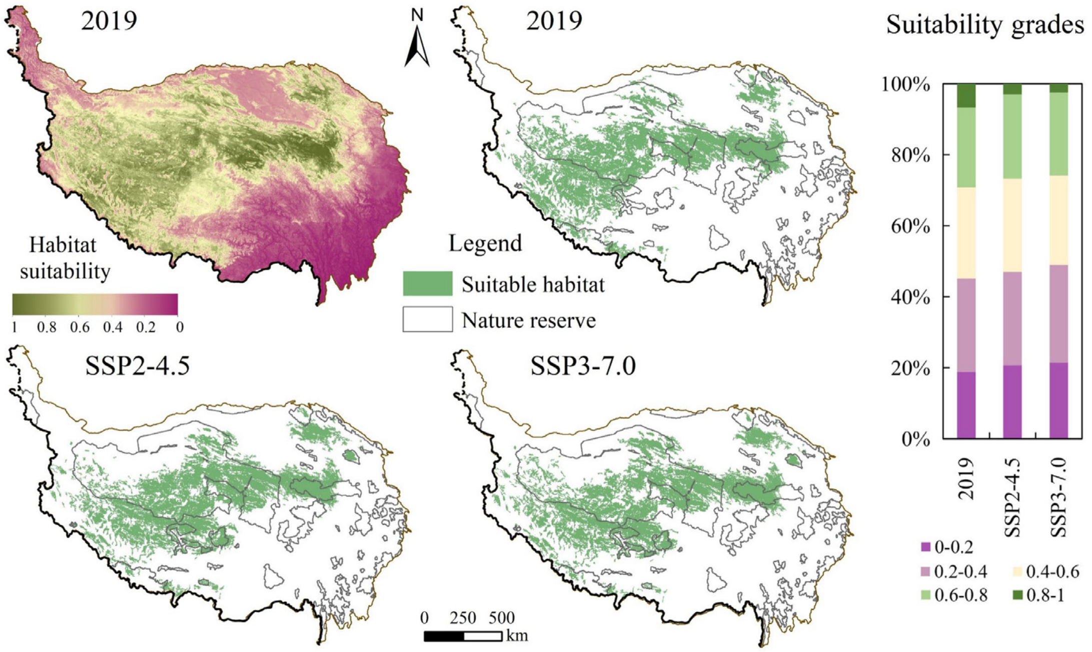

Fig. 3. Spatial distribution of current and future suitable habitats (SSP2–4.5 and SSP3–7.0 scenarios in 2100) for Tibetan wild asses, as well as the area percentage distribution of the five different grades of suitability for each scenario. Suitable habitats in the left figures are the areas with habitat suitability higher than 0.613 (most light green and all dark green in the right figure), which is the lowest value of habitat suitability of all species points.

$$\mathrm{PC}_{\mathrm{direct}} = \frac{\sum_{i=1}^{n}\sum_{j=1,i\neq j}^{n} a_i a_j p_{ij}}{A_{\mathrm{L}}^2} \tag{4}$$

$$\mathrm{PC}_{\mathrm{step}} = \frac{\sum_{i=1}^{n}\sum_{j=1,i\neq j}^{n} a_i a_j \left(p_{ij}^{*} - p_{ij}\right)}{A_{\mathrm{L}}^2} \tag{5}$$

$$\mathrm{dPC}_i = 100 \times \frac{\mathrm{PC} - \mathrm{PC}_{i-\mathrm{remove}}}{\mathrm{PC}} \tag{6}$$

where PC is the probability of connectivity of the overall ecological network; i and j represent the habitat patches; n is the total number of habitat patches; a_i and a_j represent the area of patch i and patch j, respectively; p_{ij} is the direct dynamic dispersal probability of patches (considering the spatial pattern and the coexistence probability in time of habitat patches, the length of the connectivity corridors, and the dispersal ability of species; without using any temporary climate refuges), calculated by R-Studio software to drive and improve Conefor software algorithm; $p_{ij}{}^{*}$ is the maximum dynamic dispersal probability of patches (accounting for both stable and temporary climate refuges); A_{L} represents the total area of the habitat patches; dPC_i is the connectivity importance index of patch i; and $\mathrm{PC}_{i\text{-remove}}$ is the probability of connectivity of the ecological network composed of remaining patches after removing patch i.

3. Results

3.1. Current and future suitable habitat for Tibetan wild asses

In addition to 302 species occurrence points, 10 environmental variables are obtained, i.e., human footprint, land use type, NDVI, distance to water source (calculated by land use data), elevation, slope, annual temperature range, average temperature of the hottest season, precipitation of the wettest month, and precipitation of the driest month. The overall discrimination performance of the SDMs is generally good, with an average AUC of 0.81. The suitable habitats for Tibetan wild asses under the current, SSP2–4.5 and SSP3–7.0 scenarios are mainly distributed in the central and western parts of the Qinghai-Xizang Plateau (Fig. 3). Encompassing 123, 144, and 126 patches, they account for 21.11 %, 21.34 %, and 20.95 % of the total area of the Qinghai-Xizang Plateau, respectively. The areas with high habitat suitability values (0.8–1) are predicted to have different degrees of loss under different future scenarios, with the loss of 96,733 km^2 (SSP2–4.5) and 110,977 km^2 (SSP3–7.0), respectively. Currently, 53.83 % of suitable habitats are distributed in the nature reserves, with the largest share in the Qiangtang National Nature Reserve (153,368 km^2), followed by the Sanjiangyuan National Nature Reserve (68,786 km^2), and the Hoh Xil National Nature Reserve (30,347 km^2). Under future scenarios, the proportion of suitable habitats in the nature reserves will decrease to 52.61 % (SSP2–4.5) and 52.64 % (SSP3–7.0), respectively. This indicates that the current delineation of the nature reserves cannot fully adapt to future climate change and that dynamic biodiversity conservation measures have to be formulated.

3.2. Climate refuges and spatio-temporal connectivity networks

The spatio-temporal connectivity networks are mainly concentrated on the western and central parts of the Qinghai-Xizang Plateau (Fig. 4). The Qinghai-Xizang Plateau shows varying degrees of warming and wetting trends under different future scenarios. Under the SSP2–4.5 and SSP3–7.0 scenarios, the stable climate refuges accounted for 78.79 % and 77.91 % (average 78.35 %) of the habitats in 2019, respectively. Differently, the lost temporary climate refuges accounted for 21.21 % and 22.09 %, the gained temporary climate refuges accounted for 22.33 % and 21.32 % of the habitats in 2019, respectively. The results indicate that with the intensification of future climate change, the extent of stable climate refuges tend to decrease. Those stable patches are mainly located in the center of suitable habitats (the northern Qinghai-Xizang Plateau and the southern Kunlun Mountains). The temporary lost climate refuges were predicted to increase from SSP 2–4.5 to SSP3–7.0 scenarios. This means that Tibetan wild asses will increasingly need to move from lost suitable patches to stable or gained suitable patches through corridors. As future emissions intensify from SSP2–4.5 to SSP3–7.0, the number of direct connectivity corridors decreased from 403 to

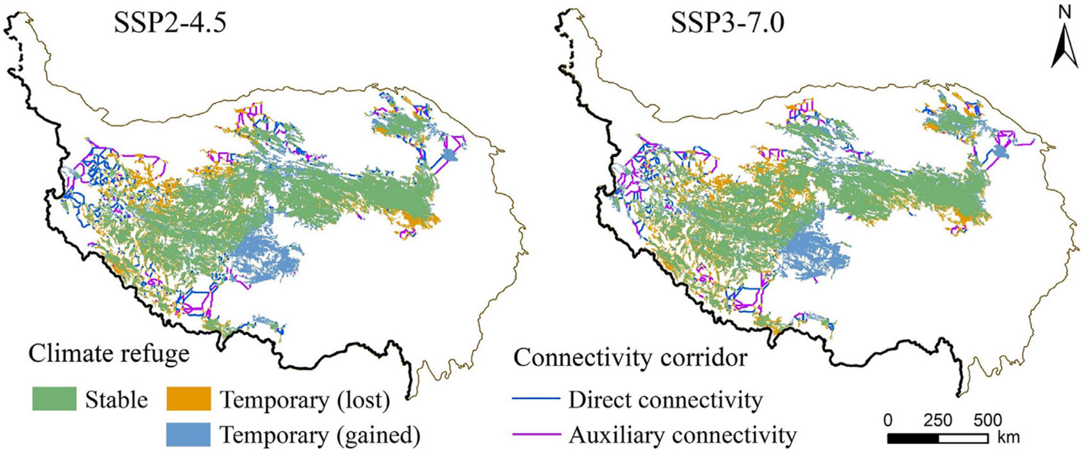

Fig. 4. Spatial distribution of climate refuges and connectivity corridors in SSP2–4.5 and SSP3–7.0 scenarios. Auxiliary connectivity corridors (purple line) were from lost to lost refuges and from gained to gained refuges during global climate change.

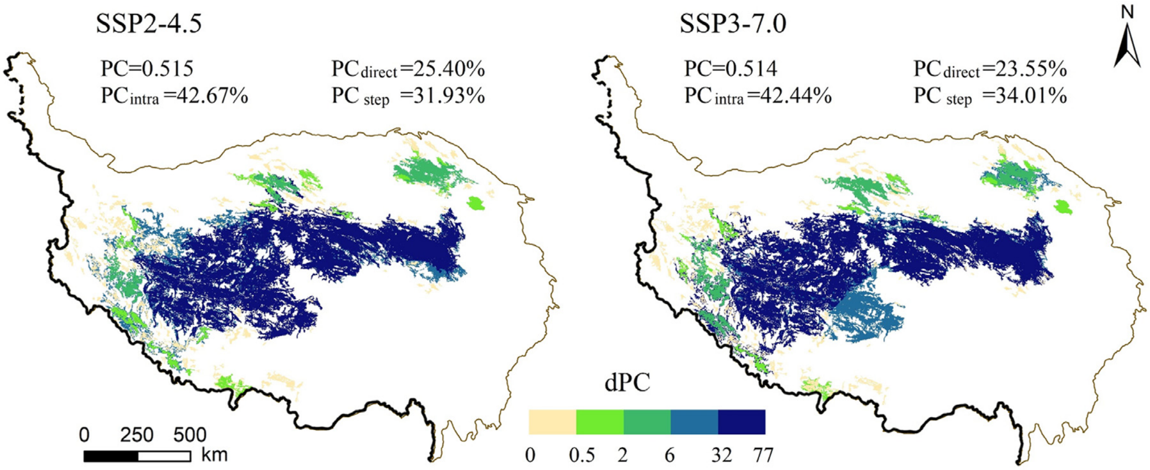

Fig. 5. Importance of spatio-temporal connectivity of habitat patches under future SSP-RCP scenarios. PC: probability of connectivity; PC_{intra}: internal connectivity index; PC_{direct}: direct connectivity index; PC_{step}: auxiliary connectivity index; and dPC: connectivity importance of each habitat patch.

372, with the average length increasing from 10.95 km to 11.29 km. Differently, the number of auxiliary connectivity corridors will increase from 154 to 188, with the average length increasing from 23.64 km to 24.15 km. The number proportion of auxiliary connectivity corridors will increase from 27.65 % to 33.57 % when moving from SSP2–4.5 to SSP3–7.0. This means that the auxiliary corridors will become more important for the dispersal of Tibetan wild asses under more severe warming conditions.

3.3. Spatio-temporal connectivity under different SSP-RCP scenarios

Under different SSP-RCP scenarios, the overall dynamic connectivity of the ecological connectivity network of Tibetan wild asses on the Qinghai-Xizang Plateau shows an intermediate PC value of about 0.51 (Fig. 5). Among the different connectivity types, internal connectivity provides the highest percent contribution as it accounts for 42 %–43 %, followed by auxiliary connectivity, accounting for 31 %–35 %, whereas direct connectivity shows the lowest contribution, accounting for 23 %–26 %. This indicates that the patches themselves are playing a key role in connectivity, but still contribute less than half to the overall connectivity. The other contributions to spatio-temporal connectivity are provided by the corridors. Although the total number of auxiliary connectivity corridors is lower than that of direct connectivity corridors, the contribution of the former to the overall connectivity is 25 %–45 % higher than that of the latter. Moreover, the importance of auxiliary connectivity will increase with intensifying climate warming. The spatial distribution of habitat connectivity importance measured in terms of dPC shows that the connectivity importance of the largest climate refuge is about 77 % (Fig. 5). Stable habitat patches cover more than 60 % of the total area of suitable habitat, showing a relative contribution to overall connectivity higher than 70 % under both the future climate change scenarios. The main reason is that stable climate refuges, which will persist in the future, are mainly distributed in the central region. Hence, they will be effectively connected with all suitable patches in the peripheral regions within the migration distance of the species, providing more possible pathways for the migration of Tibetan wild asses.

3.4. Comparison of spatio-temporal and purely spatial connectivity

The percent difference between purely spatial connectivity and spatio-temporal connectivity shows that the traditional connectivity quantification approach has the disadvantages of underestimation and overestimation (Table 2). The purely spatial connectivity overestimates network connectivity by about 28 % when considering all current and future patches compared to spatio-temporal connectivity. Moreover, the purely spatial connectivity considering only all current or future patches underestimates network connectivity by 16 %–21 %, and for more than 70 % of habitats, their connectivity importance will be underestimated.

Table 2
Percent difference between purely spatial connectivity and spatio-temporal connectivity under the two considered future scenarios.

SSP-RCP scenarios	Year	PC (%)	PC_{intra} (%)	PC_{direct} (%)	PC_{step} (%)
SSP2–4.5	2019∪2100	27.97	−38.82	33.98	−3.70
	2019	−16.36	8.14	9.14	−24.75
	2100	−20.38	11.80	15.58	−48.30
SSP3–7.0	2019∪2100	28.03	−38.94	35.19	−2.70
	2019	−19.77	11.83	20.31	−52.42
	2100	−17.64	8.73	4.80	−18.24

Note: The values in Table 2 were purely spatial connectivity minus spatio-temporal connectivity, then divided by spatio-temporal connectivity. So positive value indicates that connectivity from purely spatial perspective overestimates actual network connectivity, and vice versa indicates an underestimation. PC: probability of connectivity; PC_{intra}: internal connectivity index; PC_{direct}: direct connectivity index; and PC_{step}: auxiliary connectivity index.

As for internal connectivity (PC_{intra}), purely spatial connectivity computed considering all the current and future patches underestimates it by nearly 39 %, compared to the spatio-temporal approach. Differently, only considering all current or future patches overestimates network connectivity by 8 %–12 %. Differently, purely spatial connectivity is consistently higher than its spatio-temporal counterpart when considering direct connectivity (PC_{direct}) (overestimating by 4 %–36 %), and lower when considering auxiliary connectivity (PC_{step}) (understimating by 2 %–53 %). This indicates that the traditional purely spatial perspective overestimates direct connectivity and underestimates auxiliary connectivity.

4. Discussion

4.1. Understanding the difference between spatio-temporal and purely spatial connectivity

Our findings indicated that the actual connectivity for Tibetan wild asses within the Qinghai-Xizang Plateau, estimated considering both the spatial and temporal landscape dynamics, is generally higher than that estimated using static time snapshots. Thus, the extinction risk for this species will be lower than previously estimated based on purely spatial connectivity. This study revalidates and confirms the findings of Martensen et al. (2017), Huang et al. (2020), and Zhao et al. (2021), focusing on different bird and mammal species, respectively. In our study, the traditional purely spatial perspective overestimates direct connectivity and underestimates auxiliary connectivity. This suggests that temporary climate refuges are of higher importance in dynamic landscapes and need to receive key attentions because they can sustain rare but critical dispersal events (Saura et al., 2014).

The comparative study of purely spatial connectivity and spatio-temporal connectivity contributes to the development of network theory, as well as to landscape planning and management. Furthermore, spatio-temporal connectivity takes into account landscape dynamics and helps to develop species adaptation measures to climate change. Thus, spatio-temporal connectivity is more realistic than purely spatial connectivity (Huang et al., 2020; Uroy et al., 2021). However, the evaluation approaches and tools of purely spatial connectivity are relatively mature, while spatio-temporal connectivity is still in its infancy (Bishop-Taylor et al., 2018; Uroy et al., 2021). There are differences in conservation priorities of habitat patches from the perspective of spatio-temporal and purely spatial connectivity. Moreover, the importance of habitats also varies in different future scenarios (Fig. 5). Therefore, spatio-temporal connectivity should be incorporated into conservation priority ranking for the management of important biodiversity areas (Zhao et al., 2021). The spatio-temporal connectivity modeling framework can be applied to other regions, ecosystems, and species with certain abilities of movement, but the movement resistance value needs to be adjusted based on the target species and the social-ecological context of research area. Nonetheless, this approach may be less applicable to species with smaller dispersal distances, as they may mainly benefit from intra-patch connectivity (Zhao et al., 2021).

4.2. Importance of spatio-temporal connectivity networks under climate change context

The partial losses of species' range are generally lower inside nature reserves than outside (Mi et al., 2023). However, nature reserves suffer from location biases, with important biodiversity areas often remaining unprotected (Xu et al., 2017; Xu et al., 2024a). Based on predictions from the three implemented SDMs, 53.83 % of present suitable habitats are located within nature reserves, but the percentage consistently decrease under the considered future climate change scenarios. Nearly half of Tibetan wild ass habitats have not been formally protected. Climate change requires organisms to adapt by phenotypic plasticity or move to track environmental changes in space and time, although the places with rapid rates of climate change may also be rich in biodiversity (Burrows et al., 2011). Additionally, biodiversity greatly contributes to ecosystem functioning and sustainability (Zhang et al., 2023). Therefore, our findings highlight that biodiversity conservation targets need to take climate change into account (Arneth et al., 2020). Many studies on the impacts of climate and land use change on species distributions emphasized the need to incorporate climate refuges and movement corridors in dynamic landscapes into conservation planning (Bellard et al., 2012; Stralberg et al., 2020; Hua et al., 2022). Contemporary conservation planning often prioritizes historical conditions rather than proactively anticipating and conserving future species distributions (Adam et al., 2022).

Spatio-temporally connected landscape patches can provide refuges for species to adapt to climate change. However, climate-driven species' range shifts are not directly considered in most connectivity plans to address climate change's impact on biodiversity (Littlefield et al., 2019). Spatio-temporal connectivity is a key factor in delaying extinction under the status quo of habitat reduction and fragmentation. It can help to mitigate species extinction debt, which refers to the delay of decades or even centuries that exists between ecosystems perturbation and the resulting extinction of species living in the impacted regions (Kuussaari et al., 2009; Semper-Pascual et al., 2018). The construction of spatio-temporal connectivity networks compensates to some extent the damage caused by human activities to ecosystems, granting more time for ecological compensation. Therefore, climate refuges and species movement corridors will be increasingly important in enhancing climate resilience for species persistence and should be considered in connectivity planning and management (Keeley et al., 2018; Xu et al., 2024a). However, it should be noted that the relative importance of spatio-temporal connectivity depends on the intensity of climate change and the response of species to climate change (Huang et al., 2020).

4.3. Limitations and future prospects

This study also has some shortcomings. Firstly, we considered a fixed suitability threshold for future scenarios when discriminating between suitable and unsuitable patches. Yet, the species may adaptively respond to changing environmental conditions, so that suitability thresholds could be different under distinct climate change scenarios. Secondly, the sensitivity of our SDMs' projections to different parameter settings, and related consequences on connectivity modeling, should be tested (Merow et al., 2013; Valavi et al., 2021). Furthermore, incorporating additional resistance factors relevant to the dispersal patterns of Tibetan wild asses, such as fencing and grazing activities (Sun et al., 2021; Zhu et al., 2023), may improve our estimation accuracy of spatio-temporal connectivity. Consequently, the selection and setting of ecological resistance factors need to be further validated for sensitivity. Under this context, GPS tracking data need to be developed in the future to more accurately model the relationship between species movement and spatio-temporal resistance patterns (Brennan et al., 2022). Lastly, we assumed that lost patches and gained patches could coexist half of the time, but the time span is long and the uncertainty is relatively large. In the future, data with finer temporal resolution should be taken to better determine the time of coexistence between patches as this will further improve the overall accuracy as regards the connectivity analyses.

5. Conclusions

In this study, we incorporated movement corridors and future climate change scenarios into spatio-temporal connectivity models. Moreover, we clarified the difference between purely spatial connectivity and spatio-temporal connectivity. We found that over three-quarters of habitats predicted to be suitable under current conditions will remain suitable in the future, functioning as stabilizing climate refuges for Tibetan wild asses. The lost temporary climate refuges account for over 20%. Under different SSP-RCP scenarios, a notable proportion of suitable habitats located within the current nature reserves are predicted to be lost, indicating that the current delineation of nature reserves cannot fully adapt to future climate change. The percentage of auxiliary connectivity corridors increases from 27.65 % to 33.57 % with the intensification of global warming. Auxiliary connectivity corridors will gradually weaken the dominance of direct connectivity corridors as the climate warms, which provide more pathways for Tibetan wild asses to migrate and track temporal changes in the spatial arrangement of suitable patches. Compared with the spatio-temporal perspective, the purely spatial perspective overestimates network connectivity by about 28 % when considering all current and future patches, and underestimates network connectivity by 16 %–21 % when only considering all current or future patches. The purely spatial perspective also overestimates direct connectivity and underestimates auxiliary connectivity. Therefore, the risk of species extinction may be less severe than previously assessed based on purely spatial connectivity. Our spatio-temporal connectivity modeling framework applies to most regions and species with a certain movement ability, but movement resistance needs to be adjusted. Through proposing a new approach of spatio-temporal connectivity network to identify important climate refuges and movement pathways, this study highlighted the importance of spatio-temporal connectivity for species adapting to climate change in dynamic landscapes.

Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Dongmei Xu: Writing – original draft, Visualization, Software, Methodology, Conceptualization. **Jian Peng:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Menglin Liu:** Writing – original draft, Visualization, Software, Methodology, Conceptualization. **Hong Jiang:** Writing – review & editing, Methodology, Conceptualization. **Hui Tang:** Writing – review & editing, Methodology, Conceptualization. **Jianquan Dong:** Writing – review & editing, Methodology. **Jeroen Meersmans:** Writing – review & editing.

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