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Climatic, human-induced and biodiversity factors differently shape the suitable areas of *Bidens pilosa*

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Abstract

Bidens pilosa, a globally invasive Asteraceae plant, threatens both natural and agro-ecological habitats. Species distribution models (SDMs) are a valuable tool for predicting invasion potential, often exclusively based on climate variables. Here, we aimed to predict the current and future global distribution of *B. pilosa* by integrating climatic, human-induced and biodiversity factors, all of which are critical for accurate projections. Our more comprehensive results showed that climate conditions were the main driver of *B. pilosa*'s current distribution, with an expanded suitable area compared to previous studies, especially in eastern China and the Sichuan Basin. Incorporating human-induced factors significantly reduced predicted suitable areas, reflecting the species' association with disturbed environments shaped by human activities. Biodiversity factors further refined habitat suitability, as areas with high phylogenetic richness were identified as potential hotspots for invasion due to competitive or facilitative interactions. Future predictions, based on solely available climate data, suggested a high risk of habitat expansions in Asia, Europe and North America. Niche dynamic analyses revealed that introduced populations occupied a distinct environmental niche space compared to native populations, due to adapting to altered climatic and anthropogenic conditions. This ecological niche divergence is likely driving the increased invasion risk in the introduced range. Our study underscores the complex interactions between climate conditions, biodiversity and human activity in shaping the spread of *B. pilosa*. SDMs integrating climatic, biotic variables and human-influenced factors, together with updated occurrence data improve predictions of invasion spread and help guide targeted management.

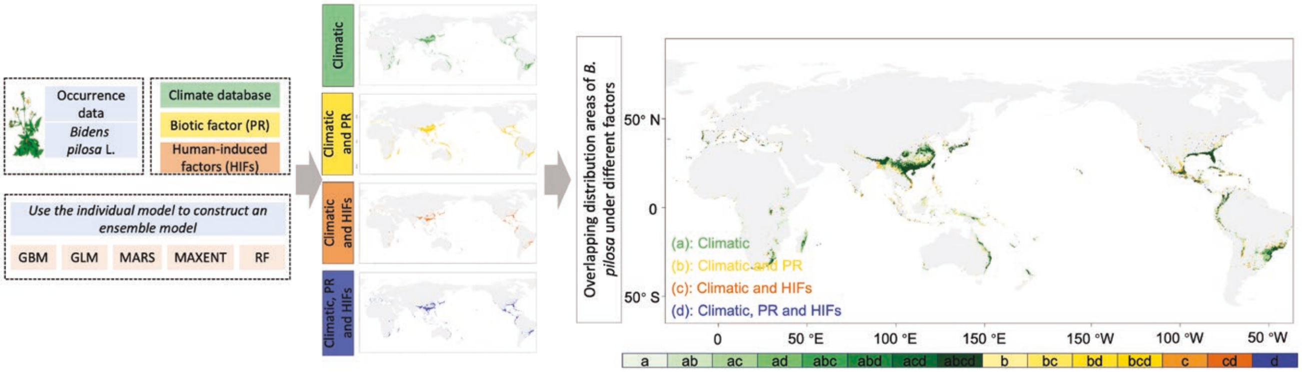
Keywords: biological invasions, climate change, environmental factors, potential geographical distribution, habitat suitability, niche overlap

气候、人为干扰和生物多样性对入侵植物三叶鬼针草适生区的差异化影响

摘要：三叶鬼针草(*Bidens pilosa* L.)作为全球性的菊科入侵植物，严重威胁自然生态系统及农业生产。尽管物种分布模型(SDMs)被广泛用于入侵潜力评估，但大多数研究仅聚焦于气候变量，忽视了人类活动与生物互作的协同效应。本研究通过整合气候、人类活动及生物多样性因素，解析三叶鬼针草当前全球分布格局的驱动因子，并预测其未来扩张的潜在热点地区。研究结果表明，气候因子是三叶鬼针草当前分布格局的主导因子，其潜在适生区较以往研究显著扩大，尤其在中国东部和四川盆地。人为干扰因素显著限制了其适生区范围，表明该物种对人类活动塑造的干扰环境具有适应性。生物多样性因素同样影响其适生区分布，植物系统发育多样性较高的区域因竞争或促进效应可能成为潜在入侵热点。未来气候情景预测显示，亚洲、欧洲及北美洲的适生区扩张风险显著提高。生态位分析显示，引入地种群因适应气候与人为环境变化，与原生种群发生显著生态位分化，这种分化可能驱动其入侵进程。本研究揭示了气候、人为干扰与生物因素对三叶鬼针草扩散的协同影响，表明整合多类型因素的SDMs有助于提升入侵物种扩散预测的准确性，为制定针对性防控策略提供科学依据。

关键词：生物入侵，气候变化，环境因素，潜在地理分布，生境适宜性，生态位重叠

Graphical Abstract



INTRODUCTION

Global climate change and invasive alien plant species (IAPs) are two growing global threats exerting unprecedented pressure on ecosystems and natural environments (Bellard *et al.* 2017; Early *et al.* 2016; O'Bryan *et al.* 2022; O'Neil *et al.* 2023; Pyšek *et al.* 2020). Comprehensive studies have shown that IAPs are a major driver of biodiversity loss (Bongaarts 2019; Roy *et al.* 2023). Besides reducing natural biodiversity, IAPs pose a significant threat to agriculture, infrastructure and human health (Jones 2019; Marchioro and Krechemer 2021; Paini *et al.* 2016). The intricate interplay between climate change and invasive species is accelerating the spread of IAPs (Christina *et al.* 2020; Xian *et al.* 2023). Human-mediated global trade has broken down geographical and environmental barriers, leading to a worrying increase in the invasion of IAPs (Laginhas and Bradley 2022; Seebens *et al.* 2015). These processes are expected to alter the distribution range of IAPs across the globe. Focusing on the IAP's responses to future climate changes is vital not just for anticipating the future geographical distribution of these species but also for crafting scientifically based prevention and management strategies (Osland and Feher 2020; Sun *et al.* 2017; Tu *et al.* 2021).

Species distribution models (SDMs) are increasingly used to forecast the potential geographical distributions of IAPs by linking environmental conditions with species occurrence data, and often integrating eco-physiological information under climate change (Fang *et al.* 2021; Gong *et al.* 2020). Currently, ample studies combine a range of predictors related to climate (e.g. temperature and precipitation) and other abiotic interactions (altitude, latitude and topography)

(Karger *et al.* 2017). However, despite the recognition of human-induced impacts on species distributions, the incorporation of human predictors in SDMs remains significantly underutilized. For example, the Human Influence Index (HII) provides a quantitative measure of anthropogenic activities, including urbanization, infrastructure and land-use changes, which are critical for accurately predicting species distributions under current scenarios (Sanderson *et al.* 2002). A systematic review of SDM articles revealed that surprisingly few studies incorporate human predictors, even though their critical role in accurately modelling species distributions under current and future scenarios (Frans and Liu 2024). In addition to climate and human-induced factors (HIFs), biotic interactions, such as those captured by species richness, significantly influence species distributions and the composition of species assemblages across regional, continental and global scales (Wisz *et al.* 2013). One critical biotic predictor is plant phylogenetic richness (PR), which measures the evolutionary diversity of plant communities in a given area. Unlike species richness, PR integrates phylogenetic relationships, providing insights into ecological and evolutionary dynamics that influence ecosystem resilience and the success of invasive species (Cai *et al.* 2023; Lawrence and Fraser 2020). By incorporating both HII and PR, our study advances a more comprehensive understanding to disentangle the synergistic effects of human activities and biotic interactions on the distribution of IAPs, addressing critical gaps in traditional SDM approaches.

Analysing the ecological niche dynamic of species involves understanding how their environmental requirements shift over time and space. The conceptual framework introduced by Guisan *et al.* (2014) integrates key concepts such as centroid shift, overlap, unfilling and expansion to analyse these dynamics. This framework has become fundamental in the study of ecological niche changes, especially in the context of IAPs. Methods such as principal component analysis (PCA) of environmental variables (PCA-env) are widely used to examine these dynamics. For instance, Christina *et al.* (2020) applied these approaches to investigate the ecological niche dynamics of the invasive shrub *Ulex europaeus* at both global and regional scales, revealing significant niche expansion in several regions, including a 49% increase in Australia, 111% in Northern Europe, 202% in North-West America and 283% in South America. Conversely, no niche shift was observed in New Zealand, despite its similar climatic conditions to the shrub's native habitat in Western Europe. To facilitate such analyses, tools like the *ecospat* R package with its environmental PCA scheme offer a coherent workflow for examining these ecological niche dynamics (Broennimann *et al.* 2012; Di Cola *et al.* 2017).

Bidens pilosa L., an annual weed of the Asteraceae family (Knope *et al.* 2013; Li *et al.* 2022), is native to tropical and central America, and has spread and become a pervasive invader throughout tropical, subtropical and temperate regions since 19th century (Ballard 1986; Lu *et al.* 2014). It occurs as various polyploid varieties (2n = 24, 36, 48, 72), producing up to 6000 seeds per year and its seeds can easily be dispersed attached to animals, birds, human clothes or by wind and water. It thrives along roadsides and can be dominant in plant communities of cultivated fields, plantations and ruderal areas (Khatri *et al.* 2022; Osaki *et al.* 2022). This species is known to exert allelopathic effects on a wide range of crops, resulting in a decline in biodiversity, soil fertility and crop productivity (Cheng *et al.* 2022; Xue *et al.* 2022). Research on *B. pilosa* has mainly focussed on its biological properties, invasive traits and allelopathy (Chauhan *et al.* 2019; Xian *et al.* 2023). Its wide range of suitable habitats and the limited information on its current distribution and environmental variables influencing its spread prompted us to review the present and future potential distribution of *B. pilosa* for China and worldwide in view of developing timely preventative and management strategies. This plant has recently especially expanded its range in central and southern China (Flora of China Editorial Committee 2018; Lu *et al.* 2014). A previous study, based on 338 occurrences and using the Maxent model, showed the potential suitable habitat areas of this species in China to be mainly in the southern regions, including Guangdong, Guangxi, Hainan and Taiwan (Yue *et al.* 2016). In contrast, our field surveys reveal that numerous locations in central and northern China are also heavily invaded by this species. This discrepancy highlights the dynamic nature of invasive species distributions and underscores the need for continuous monitoring and updates to the models predicting their spread.

Thus, this study aims to: (i) predict the potential geographical distribution of *B. pilosa*, and identify key environmental variables affecting its spread, (ii) understand the relative importance of human-induced and biodiversity factors in shaping the range of potential suitable habitats and (iii) explore and compare the ecological niche dynamics of *B. pilosa* in native and invasive ranges under future climate change scenarios. To achieve these objectives, we employ a combination of SDMs and PCA to dissect the climatic niche of *B. pilosa* for both the native and the introduced range.

MATERIALS AND METHODS

Species occurrence data

Occurrence records of *B. pilosa* were collated from online databases and literature sources. Specifically, we gathered 20 435 records from the Global Biodiversity Information Facility (https://www.gbif.org/), 34 547 from iNaturalist (https://www.inaturalist.org/), 417 from the Chinese Virtual Herbarium (https://www.cvh.ac.cn/), 363 from the National Specimen Information Infrastructure (http://www.nsii.org.cn/) and 1231 from the Plant Photo Bank of China (https://ppbc.iplant.cn/) database. In addition to the online database, we also obtained data from literature in the China National Knowledge Infrastructure (https://www.cnki.net/) and Web of Science, culminating in 147 worldwide distributional data sets, and ultimately yielding 57 270 unique occurrence data points of *B. pilosa*. After confirming the geographic information at the county level based on the location descriptions, we removed duplicate distribution records and a few records lacking detailed coordinate information. This process resulted in a final data set of 53 901 points for *B. pilosa*. In addition, occurrence records were filtered and cleaned by removing spatially invalid or suspect records that could lead to miscalculation of species' climatic niches using the *CoordinateCleaner* package in R (Zizka *et al.* 2019), finally resulting 50 583 points (Fig. 1).

Environmental variables

Climatic variables from the WolrdClim Database at 5 arc min (~10 km close to the equator) spatial resolution (https://worldclim.org, accessed December 2022) (Fick and Hijmans 2017) were downloaded to derive a set of meaningful predictors for this study. In a preliminary analysis, we modelled the species distribution (see Species Distribution Modelling) with 19 variables of WolrdClim climatic factors and growing degree days (GDD > 8 °C for *B. pilosa* following the baselines of sunflower; Pruess 1983) to select the most important variables for *B. pilosa* under various climatic scenarios. Based on the response curves of the models (i.e. showing how the predictions changed along each climatic variable), we eliminated variables that showed no variability in the response. We eventually chose seven climatic variables and GDD for both current and four future climate scenarios (Supplementary Table S1). Using the Community Climate System Model 4.0, future climate data for the 2040–2060 under four representative concentration pathways (i.e. RCP2.6, RCP4.5, RCP6.0 and RCP8.5) were obtained. As a biotic factor, we considered the global plant PR (Cai *et al.* 2023). PR represents the amount of unique phylogenetic history present in an assemblage, reflecting the evolutionary diversity and historical patterns of diversification within that assemblage

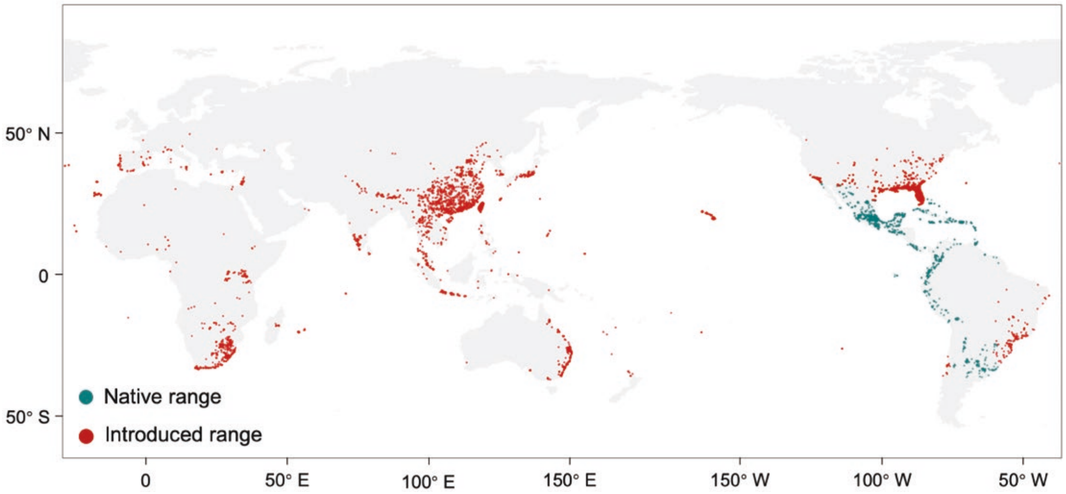


Figure 1: Worldwide occurrence records of *Bidens pilosa*. The dark cyan dots represent the native range of *B. pilosa*, while the dark red dots represent its introduced range.

(Tucker *et al.* 2017). Data on PR was downloaded from the Global Plant Diversity (https://gift.uni-goettingen.de/shiny/predictions/). For HIFs, we used the Global Roads Inventory Project type 4 density (Grip4) and the HII, which is a measure that quantifies the extent of human impact on the environment. It is typically derived from several factors, such as population density, land use, infrastructure development and access to natural resources. The HII is often used in ecological and environmental studies to assess how human activities influence natural habitats and biodiversity. The Grip4 was downloaded from the GLOBIO (https://www.globio.info/download-grip-dataset). HII values range from 0 to 64, with 0 representing no human influence and 64 representing maximum human influence, based on all 8 measures of human influence (Sanderson *et al.* 2002). The data were downloaded from the NASA Socioeconomic Data and Applications Center (http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-influence-index-geographic). All 11 variables are elaborated in Supplementary Table S1.

Species distribution modelling

We utilized an ensemble approach using the *biomod2* package of R (Thuiller *et al.* 2023) to model the current and future (according to four climate change scenarios) potential geographical distributions of *B. pilosa* based on their global occurrence data and above variables. Such an approach combines different modelling techniques to adjust for the inherent uncertainty of these models and was suggested to find the optimal solution from an ensemble of predictions (Wu and Levinson 2021; Zhang *et al.* 2019). We used five different algorithms, including generalized boosting models (GBM), generalized linear models (GLM), multivariate adaptive regression splines (MARS), maximum entropy (MaxEnt) and random forest (RF) (Zhao *et al.* 2021). For each modelling process, 80% of the distribution records were randomly selected for training and the remaining 20% were used for testing. As only occurrences were available, 100 000 pseudo-absences were randomly generated to fill the absence component of the models (Barbet-Massin *et al.* 2012; Graham *et al.* 2004). The model's performance was evaluated using the receiver-operating characteristic (ROC) curve and the true skill statistic (TSS) (Allouche *et al.* 2006; Peterson *et al.* 2008), and the area under the ROC curve (AUC) was applied, which ranges from 0 to 1. TSS considers the missing average error and is unaffected by the size of the verification data set. Generally, the higher the values of these two indicators, the higher the accuracy of the model results. We eliminated duplicated presences within a raster pixel. To guarantee the robustness and accuracy of the predictions and to obtain uncertainty estimates, the entire training-calibration process was repeated 100 times (20 iterations for each model), using a different set of calibrated presences and absences within each iteration (Broennimann and Guisan 2008). In order to convert the probability of presence into presence and absence, the suitability of the species distribution was then binary-transformed using thresholds maximizing the ratio of the number of corrected predicted presences to number of false absences.

Assessing the ecological niche dynamics

Based on the Global Naturalized Alien Flora and Centre for Agriculture and Bioscience International database, we classified the native and introduced range for *B. pilosa*, comprising 8851 points and 41 732 points, respectively (Fig. 1). To link species distribution data with environmental variables, we used the *ecospat.sample.envar* function in R, which enabled us to sample environmental variable data corresponding to the species' occurrence points. As a result, we obtained 390 data sets for the native range and 4129 data sets for the introduced range, which were used for the analysis of the ecological niche dynamics. Niche overlap between the *B. pilosa*'s native range and its introduced range was estimated using ordination techniques in the *ecospat* package of R (Broennimann *et al.* 2023; Di Cola *et al.* 2017). Initially, niches were quantified along the first two axes of a PCA-env based on a correlation matrix of the same eight climatic variables used for the SDMs of *B. pilosa* (Supplementary Table S1). Subsequent steps involved testing for niche equivalency and similarity. Niche equivalency tests determine whether the observed overlap between the two entities differs significantly from what would be expected by randomly reallocating their occurrences. Niche similarity tests address whether the overlap between observed niches in the two ranges is higher than the overlap between the observed niche in one range and a niche selected at random from the other range. These tests were performed in both directions (Native range ↔ Introduced range) and repeated 100 times for robustness.

Niche dynamics were studied by assessing niche equivalency and similarity through randomization tests, as described by Broennimann *et al.* (2012). In

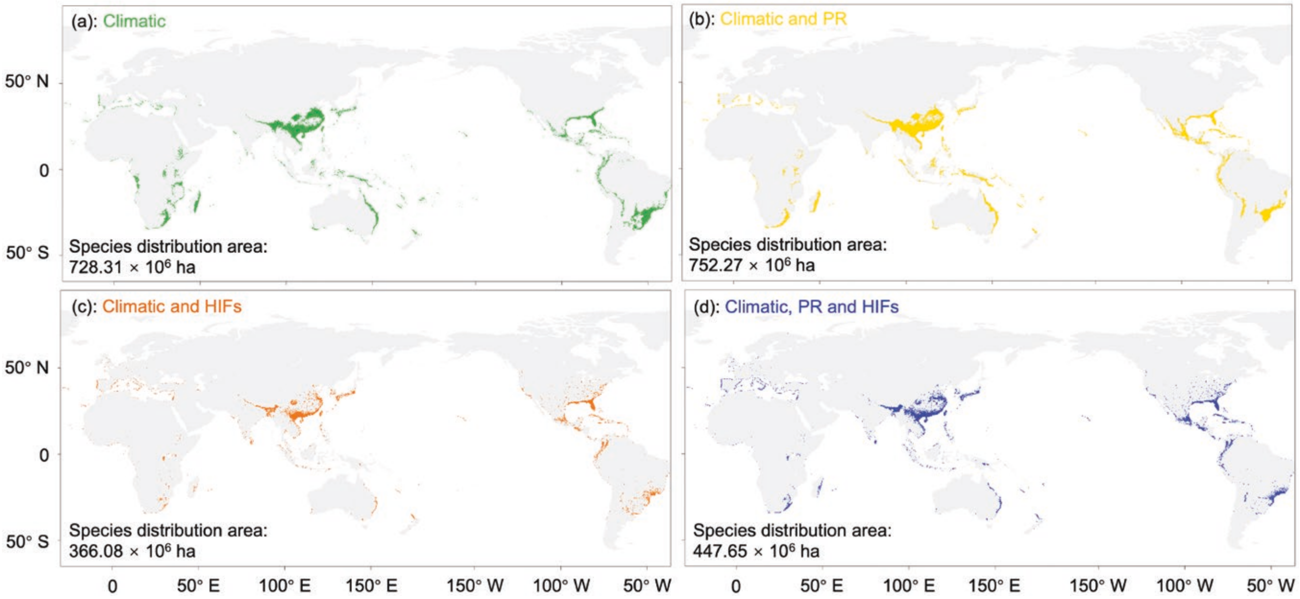


Figure 2: Predicted global geographical distribution of *Bidens pilosa* under current climatic scenarios. The climatic suitability indicates the optimal threshold of the percentage of models predicting *B. pilosa*, depicting the climatic suitability of *B. pilosa* based on (a) climatic conditions only; (b) climatic conditions and plant PR; (c) climatic conditions and HIFs (i.e. HII and road density); (d) climatic conditions, PR and HIFs.

addition, we calculated metrics of niche expansion, stability and unfilling. Niche expansion was calculated as the proportion of species' occurrence densities in the introduced distribution located in climates other than the native distribution. Niche stability is the proportion of occurrence densities that overlap with the native distribution's climate conditions. Niche unfilling refers to the proportion of occurrence densities in the native distribution found in climates outside the non-native distribution (Broennimann *et al.* 2012; Di Cola *et al.* 2017).

Our model procedures are based on the ODMAP (Overview, Data, Model, Assessment and Prediction) protocol, as proposed by Zurell *et al.* (2020) (see Supplementary Material). All analyses were performed using R statistical software, version 4.1.3.

RESULTS

Model accuracy/performance evaluation

Our models demonstrate robust predictive capabilities, with AUC values ranging from 0.82 to 0.99 across the five model types (Supplementary Fig. S3). These high AUC scores indicate that our models produce helpful and reliable data for an analysis of the climate suitability of *B. pilosa* through modelling of the species distributions, as our predicted distributions using ensemble models closely resemble the ones that have been observed (AUC = 0.5 indicates that model performance is equal to that of a random prediction, while AUC = 0.8 means that in places where a species is present, in 80 of cases the predicted values will be higher than where the species has not been recorded; Wisz *et al.* 2008).

Worldwide geographical distributions of suitable areas for *B. pilosa*

The predicted suitable habitats of *B. pilosa* are mainly found in subtropical and partial tropical regions reflecting the species' adaptation and the potential for further spread under changing climatic conditions. The latitudes are mostly between 20° and 35° in both northern and southern hemispheres, including the southern coast of the USA, southern China, Vietnam and India in the northern hemisphere, and the south-eastern coast of Brazil, southern Africa (including Madagascar) and the eastern coast of Oceania in the southern hemisphere. The total suitable area of *B. pilosa* accounts for 1.35%, 1.39%, 0.67% and 0.83% of the global area under current climatic conditions, for the climatic factor only, for climatic and PR conditions, for climatic and HIFs, and for climatic, PR and HIFs conditions, respectively (Fig. 2a–d).

Impact of the assessed factors on the potential distribution of *B. pilosa*

The impact of the various factors on the current potential distribution areas of *B. pilosa* varies widely. When considering only climatic factors, our model predicts a broad suitable range for *B. pilosa* under the current climate scenario, encompassing regions such as southern China, southern coast of the USA, Vietnam and India in the northern hemisphere, as well as the southeastern coast of Brazil, southern Africa (including Madagascar) and the eastern coast of Oceania in the southern hemisphere (Fig. 2a). Adding projections under climate and PR conditions shows only a small increase in total suitable distribution area (Fig. 2a and b). However, when non-climatic factors, particularly humans-induced influences are included, the average area of suitable habitats (based on 10 km^2 grid cells) significantly decreased. This reduction is most notable in China, South America and the eastern of Australia, while slight increases in the suitable areas are observed in parts of North America (Fig. 2c and d). Specifically, the predicted suitable distribution areas are 728.31×10^6 ha, 752.27×10^6 ha, 366.08×10^6 ha and 447.65×10^6 ha, under current climatic conditions, climate, and PR conditions, climate, HIFs conditions and climate, PR and HIFs conditions, respectively. Compared to scenarios that consider only climatic factors, the overlapping of potential geographical distribution areas for *B. pilosa* predicted by climate and PR, climate and HIFs, and climate, PR and HIFs are 77.5%, 43.3% and 35.9%, respectively (Fig. 3).

Future potential worldwide geographical distributions of *B. pilosa*

The future suitable global geographical distributions of *B. pilosa* are predicted based on RCP2.6, RCP4.5, RCP6.0 and RCP8.5 in 2040–2060, respectively (Fig. 4). The future suitable habitat area is predicted to increase with the severity of the most likely baseline scenario estimated by the IPCC (Thomson *et al.* 2011), being the largest under RCP4.5 (872.72×10^6 ha), followed by RCP2.6 (846.66×10^6 ha), RCP6.0 (686.53×10^6 ha) and RCP8.5 (614.76×10^6 ha) (Fig. 4).

Regionally, significant habitat expansion is projected in parts of Asia, especially in Japan, South Korea and eastern China, as well as across southeast Asia. In Europe, suitable habitats are expected to increase in countries like France, Germany and the UK. North America also shows notable growth in suitable areas, particularly in the eastern and midwestern USA. In South America, Brazil and Colombia also display increased habitat suitability. In the southern hemisphere, expansion is more limited, with Australia and South Africa mostly seeing changes in coastal and subtropical areas.

Comparison between the climatic niche in its native and introduced ranges

The first two principal components (PCs) contributed 66.47 % of the total variance in the occurrence

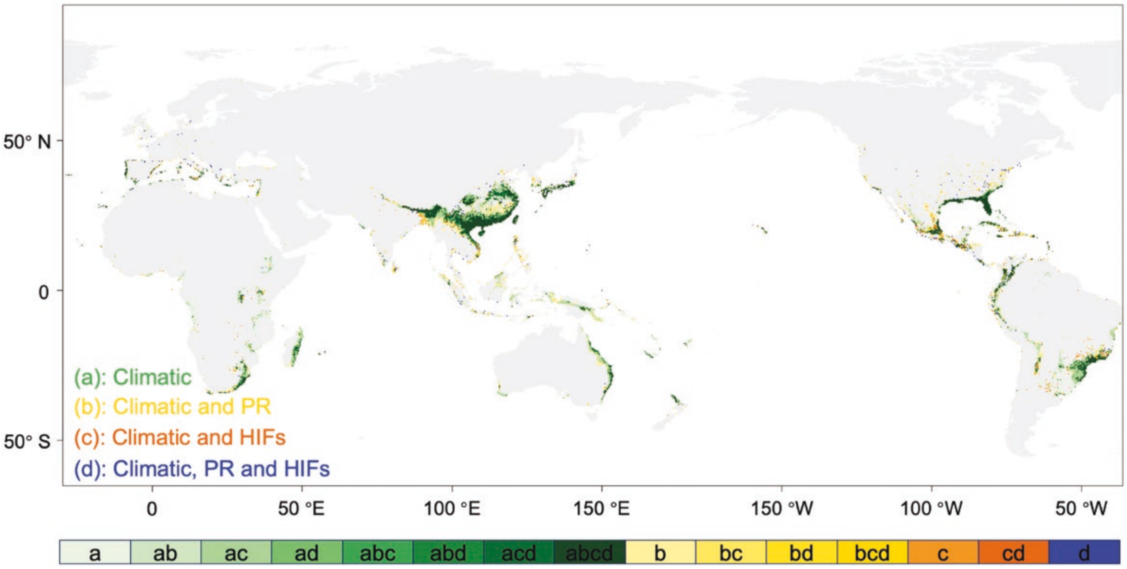


Figure 3: Overlapping geographical distribution areas of *Bidens pilosa* predicted by different factors under current climatic scenarios. The climatic suitability indicates the optimal threshold of the percentage of model predictions for each factor: (a) represents factors with climatic variable (green series); (b) represents factors with climatic and PR (yellow series); (c) represents factors with climatic and HIFs (orange series); (d) represents factors with climate, PR and HIFs (blue). The colour gradients illustrate the overlapping areas between these predictive factors. This visual representation displays how different factors contribute to the geographical distribution of *B. pilosa*.

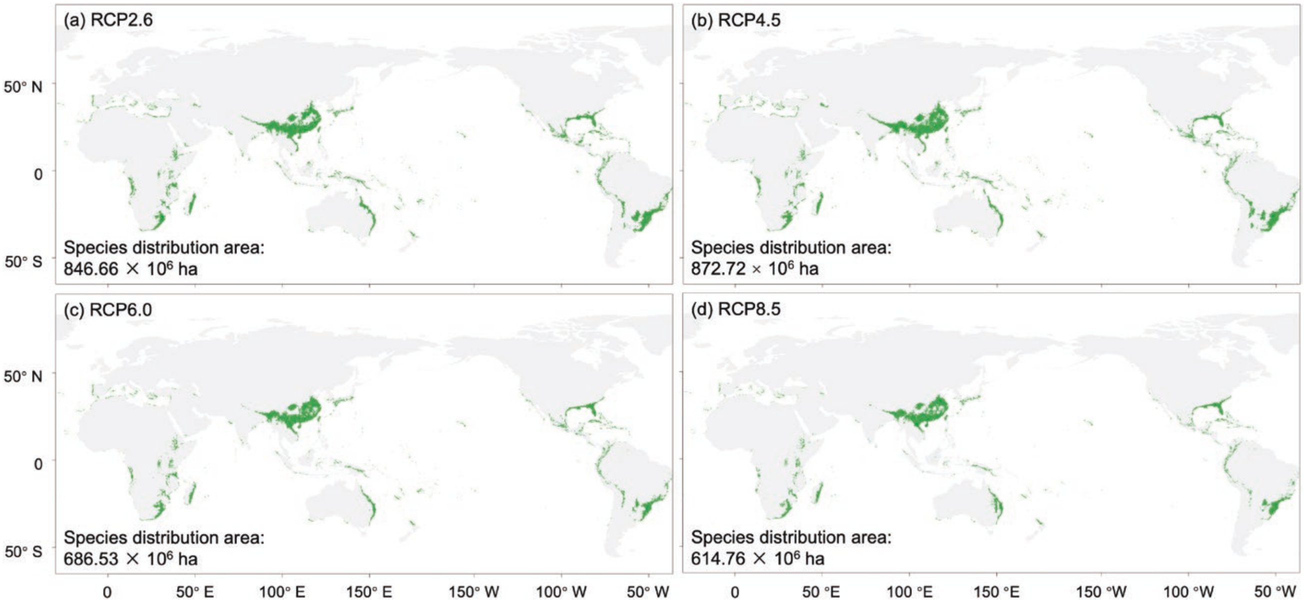


Figure 4: Potential global geographical distribution of *Bidens pilosa* in the 2050s using ensemble model. The climatic suitability indicates the optimal threshold of the percentage of models predicting *B. pilosa* under solely future climate scenarios, including (a) RCP2.6, (b) RCP4.5, (c) RCP6.0 and (d) RCP8.5 (see Materials and Methods for details).

data (PC1 = 45.65%, PC2 = 20.82%; Fig. 5). When comparing the niche dynamics between the native and introduced populations of *B. pilosa*, we observed a notable difference in their environmental space (Fig. 5a *vs*. Fig. 5b). Specifically, introduced populations exhibited a shift in niche occupation, likely due to variations in key environmental factors, such as annual and seasonal temperature, precipitation, GDD, HII and relative humidity (Fig. 5c). These shifts suggest that the species has expanded its niche in the introduced range, adapting to a different set of climatic and anthropogenic conditions compared to its native range. Our niche overlap analysis yielded an overlap of 18.1% (Schoener's $D = 0.181$), indicating limited overlap between the native and introduced niches (Fig. 5d). The null hypothesis of niche equivalence was not rejected ($P = 1$; Fig. 5d), suggesting no significant statistical difference in niche occupation between the two populations, meaning they may occupy similar environmental spaces. However, the niche similarity test (both directions) indicated (marginally) significant differences between the native and introduced ranges, with *P*-values of 0.029 and 0.095 for the native-to-introduced and introduced-to-native directions, respectively (Fig. 5e and f). This suggests that, although some overlap exists, each population has adapted to (marginally) distinct environmental conditions, demonstrating the species' ecological flexibility and potential for successful invasion under varying conditions.

DISCUSSION

The invasive plant *B. pilosa* poses a significant threat to biodiversity and agriculture in its invaded areas, making the prediction of its current and future distribution of considerable ecological and economic importance. In this study, we integrated multiple models and various environmental factors to comprehensively predict the current and future suitable habitats of *B. pilosa*. By this, our research provides a foundation for exploring the dynamics of exotic invasive plants under present and future climate conditions. Furthermore, evaluating the niche dynamics of invasive *B. pilosa* provides valuable insights into its ecological strategies. Such understanding is paramount for deriving effective management and control strategies aimed at mitigating its impact on native and agricultural ecosystems.

Models and prediction of distributions

To avoid over- or under-fitting in SDMs, various techniques such as increasing potential explanatory data, combining multiple models and regularization methods have been suggested (Fang *et al.* 2021; Xian *et al.* 2023). For this, we used ensemble models that combine predictions of several SDMs and included GBM, GLM, MARS, MaxEnt and RF, which allowed us to harness the strengths of each method, offering a nuanced understanding of the potential distribution

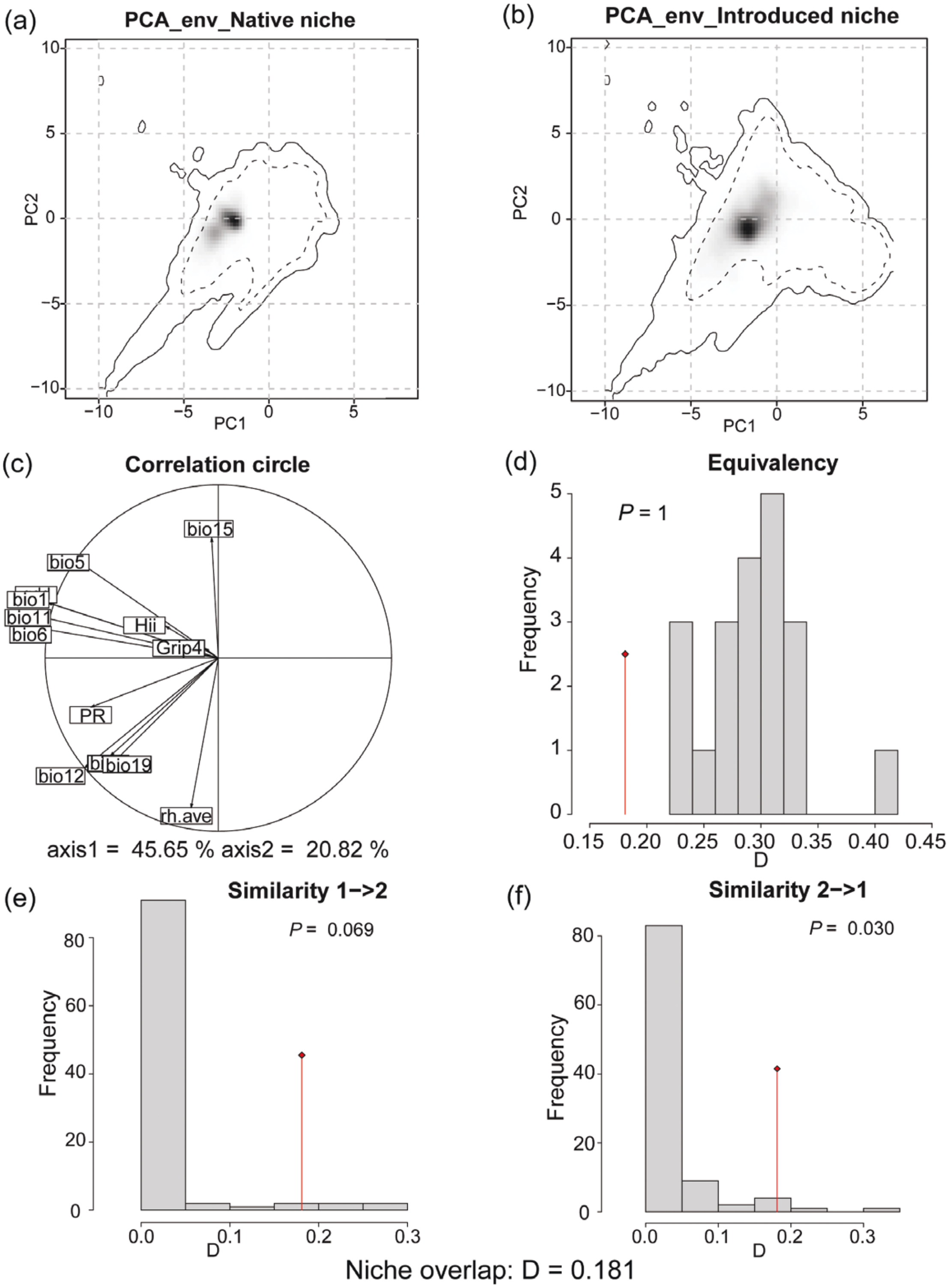


Figure 5: Niche of *Bidens pilosa* in climatic space using PCA-env. Panels (a) and (b) represent the niche of the species along the two first axes of the PCA for the native and the introduced range, respectively. Grey shading shows the density of the occurrences of the species by the cell. The solid contour lines illustrate 100% of the available environment, and dashed lines indicate the 50% of the most common background environment. The contribution of the climatic variables of the two axes of the PCA and the percentage of inertia explained by the two axes is given in (c). Histograms (d–f) show the observed niche overlap (d) between the two ranges (bars and a diamond) and simulated niche overlaps (grey bars) on which tests of niche equivalency (d), niche similarity of introduced range to native range (e) and niche similarity of native to introduced range (f) are calculated from 100 iterations, with the significance level of the tests.

patterns of the invasive *B. pilosa* under current and future climate (Aalto and Luoto 2014). Notably, it is important to integrate both climatic and non-climatic factors, i.e. a biotic (PR) and human-induced (HII and Grip4) factors, as these additional non-climatic factors have been shown to predict more accurately and realistically potential geographical distributions (Xian *et al.* 2023).

Compared to previous studies, the suitable area in southern and northern Africa is smaller, whereas we found more suitable areas in provinces in eastern China and the Sichuan Basin, slightly increasing the suitable latitudinal range (Yue *et al.* 2016). Our prediction also includes the previous occurrences of *B. pilosa* in Guam and the Hawaiian Islands. Island countries in the western Pacific, eastern Pacific, southeast Asia and Caribbean have small suitable areas for *B. pilosa*, but the exact area was not possible to locate accurately at a grid of 10 km × 10 km.

Key environmental factors affecting the distributions of *B. pilosa*

Climate is one of the main factors determining the occurrences of plants, as temperature and precipitation are key factors for their establishment, growth and reproduction. Our results from the PCA using multiple environmental factors illustrate an obvious niche expansion and a small niche shift towards lower overall temperature and higher precipitation in the wettest quarter in the introduced range (Fig. 5a and b). This reveals that *B. pilosa* can adapt to a more humid and cooler environment in the introduced regions, which might facilitate its spread into new areas.

Low-temperature stress is known to limit the latitudinal distribution pattern of invasive species, mainly due to physiological disorder caused by cold stress (0–15 °C) and injury by freezing stress (<0 °C) (Luo *et al.* 2020; Yue *et al.* 2021). The result of our niche dynamic analysis indicates a cold acclimation strategy of *B. pilosa* to the overall decrease of the highest and lowest temperature in the introduced area. Exposure to cold non-freezing temperatures can improve frost tolerance, a phenomenon known as cold acclimatization, which is a crucial mechanism for plants to endure extended periods of freezing (Sierra-Almeida *et al.* 2009). Furthermore, frequent and large temperature fluctuations due to global climate change (Hassan *et al.* 2021; Piao *et al.* 2019) may enhance this cold acclimation process, promoting the resilience of *B. pilosa* to increasingly variable environments.

The adaptation of *B. pilosa* to increased precipitation in the wettest quarter remains complex. The ability of *B. pilosa* to withstand drought-rewetting cycles may provide a competitive advantage over native species. In regions with irregular precipitation patterns, as in the Sichuan Basin, such adaptability can enable *B. pilosa* to occupy niches that are less accessible to other plants. Moreover, IAPs may be able to adapt resource allocations to increase root biomass, enhancing water update during dry periods and may also allowing them to conquer drought-rewetting conditions and thus adapt to increased precipitation in the rainy season than co-occurring native plants (Zhang *et al.* 2023). Similarly, opportunities for *B. pilosa* to establish and spread may arise in other regions with irregular or variable precipitation patterns, such as in the Mediterranean climates of California and southern Australia, the semi-arid regions of southwestern USA and South Africa, and tropical savannas in Central Africa and northern Australia. The ability of *B. pilosa* to adapt to these diverse environments underscores its potential for invasion and ecological impact across various regions.

Effect of biotic and human influence factors on potential geographical distribution

Most traditional SDMs solely rely on climatic variables to predict species distributions. While these models provide valuable insights into the potential habitats of species, they often overlook other crucial determinants of species ranges, most notably biotic interactions (Leach *et al.* 2016) and human influences (Xian *et al.* 2023). This limitation can lead to incomplete or less accurate predictions of species distributions. Our study incorporates plant PR and HIFs into the SDM, thus addressing these further key aspects that are often omitted in conventional models.

By including PR, which represents the evolutionary history and functional trait diversity within plant communities, we observed an expansion in the predicted potential geographical distribution of *B. pilosa*. This finding suggests that PR captures biotic interactions and community-level ecological processes that are not represented by climatic variables alone. For example, phylogenetically diverse communities may offer niche opportunities or facilitative interactions, such as mutualism or reduced competition (Flynn *et al.* 2011; Kraft *et al.* 2015). These interactions can create microhabitats or buffer environmental stress, thereby expanding the potential range for certain species (Cadotte *et al.* 2012).

Moreover, Pearson and Dawson (2003) proposed that while climate factors are influential at broader spatial extents, biotic interactions, including those reflected by PR, typically shape species distributions at local scales. This perspective highlights the limitations of relying solely on climatic conditions in SDMs. By incorporating PR, our SDMs capture these critical local-scale biotic interactions, revealing additional suitable areas for species that might not be identified through climate-based models alone.

Similarly, our study also highlights the significant impact of anthropogenic influences on species distribution (Xian *et al.* 2023). HIFs, such as habitat alteration and land-use changes can profoundly affect the availability of suitable habitats and the competitive dynamics between species (Frans and Liu 2024). Our study showed a reduction of the suitable areas for *B. pilosa* when HIFs were added to the model, compared with climatic factors alone, while the overall latitudinal range of the species showed only minor differences between the two models. The HII is a measure of direct human influence on terrestrial ecosystems, based on population density, built-up areas, roads, railroads, navigable rivers, coastlines, land use/land cover and night-time lights. *Bidens pilosa* is a common weed of gardens, parks, pastures, roadsides, disturbed sites and waste areas near villages. It also invades waterways, riverbanks, wetlands and forest margins (Flora of China Editorial Committee 2018; Sankaran and Suresh 2013) and grows as a weed in cultivated lands, pastures, and in crops such as cereals, pulses and cotton (Galinato *et al.* 1999; Holm *et al.* 1977; Karki *et al.* 2023; Más and Lugo-Torres 2013). These are all highly human-disturbed habitats, while the species apparently is much less common in native communities and areas with low anthropogenic disturbance. Thus, as *B. pilosa* is mainly present in human-influenced environments, the weighting of HII in the model compared to the other factors will be high, and the overall predictions of the model will be low for places not influenced by humans. This leads to more restricted potential areas that are suitable for *B. pilosa* than when only considering climate factors. This finding is in line with Baer and Gray (2022) who also found reduced predicted areas in the invaded range when HII is considered in SDMs, as IAP in general have high HII scores.

Accuracy for predicting the range of IAPs has been found to be higher when climatic variables have been combined with biotic factors and anthropogenic factors. For instance, Xian *et al.* (2023) reported that joint climatic variables and the HII better explained the species' potential distribution patterns than when analysed by one factor only. Similarly, Yang *et al.* (2023) also emphasized that models incorporating not only climatic variables but also factors such as human footprint and population density are crucial for accurately shaping species distribution patterns. Thus, such a combined approach allows for a more comprehensive understanding of the factors influencing IAP distributions and improves prediction accuracy by accounting for the complex interactions between environmental conditions and biotic and human impact relationships.

Potential geographical distribution shifts of *B. pilosa* under climate change

Expected changes in suitable habitats for *B. pilosa* under various future climate scenarios reflect the broader understanding of how climate change can facilitate the expansion and contraction of invasive species. Our results show an increase in the suitable habitats of *B. pilosa* under moderate climate scenarios (RCP2.6 and RCP4.5). The suitable habitat area for *B. pilosa* slightly increases compared to the current potential habitat, consistent with findings by Thapa *et al.* (2018) in the Western Himalaya. However, under higher emission scenarios (RCP6.0 and RCP8.5), the suitable habitat area decreases, suggesting that extreme climate conditions might limit the expansion potential of *B. pilosa*, likely due to environmental constraints at higher temperatures or reduced habitat suitability at higher altitudes. This pattern partially aligns with observations by Lamsal *et al.* (2018) on the reduced suitable habitats of invasive species at higher elevations under climate change. Our result, therefore, highlight that while climate change can create new opportunities for expansion, it can also impose new limitations under extreme scenarios, supporting a more nuanced understanding of climate-driven distribution shifts for *B. pilosa* (Fig. 4). It is important to note that our future distribution projections are based solely on projected changes in climate variables due to the unavailability of future data sets for biodiversity and HIFs (Araújo *et al.* 2019; Frans and Liu 2024). If such data sets become available in the future, research integrating projected changes in such factors would provide a more comprehensive understanding of species distributions under global change. Nevertheless, our work advances a nuanced understanding of how climate and biotic interactions jointly mediate invasive species distributions, urging the integration of multi-dimensional drivers in ecological forecasting.

Ecological niche dynamics of *B. pilosa*

Our ecological niche analyses provide evidence of *B. pilosa*'s niche heterogeneity between the native and introduced areas, indicating an expansion of the ecological niche in the introduced areas (Fig. 5) (Chapman *et al.* 2017). Previous studies have shown that invasive alien species often exhibit larger climatic niche breadths in the invasive ranges than in the native ranges (Broennimann *et al.* 2007; Wan *et al.* 2017). This pattern aligns with the 'niche shift' hypothesis, which suggests that invasive species may occupy different or broader niches in new environments, potentially due to reduced biotic constraints or novel selective pressures (Guisan *et al.* 2014). Such shifts complicate predictions of species distributions, as models built solely on native range data may not fully capture the potential spread in introduced areas (Petitpierre *et al.* 2012).

Consistent with Liu *et al.* (2022), our findings underscore the necessity of considering niche dynamics when applying SDMs to predict the spread of invasive species. Liu *et al.* (2022) highlight that niche shifts with niche expansion, as we observed in *B. pilosa*, could hinder the spatial transferability of SDMs, potentially reducing the predictive accuracy of SDMs, when based on native range data alone. This limitation has been widely acknowledged in the SDM literature when failure to account for niche shifts in invasive species can lead to underestimations of invasive risk (Early and Sax 2014; Peterson 2003).

For *B. pilosa*, this finding is crucial, as niche dynamics combined with the observed niche expansion in introduced ranges and dissimilarity between ranges suggest a high risk of global invasion and spread. The species not only maintains its core ecological preferences across regions but also exhibits exceptional adaptability, allowing it to establish and thrive under new environmental conditions. This adaptability has been observed in other invasive species and is attributed to factors such as phenotypic plasticity and rapid evolutionary changes (Richards *et al.* 2006; Sakai *et al.* 2001). Consequently, the resilience and adaptability of *B. pilosa* have significant implications for its management and control. While *B. pilosa*'s consistent ecological requirements across diverse geographies suggest that certain management practices could be universally applicable, the species' niche expansion underscores the need for tailored, region-specific adaptations. This confirms recommendations by Bradley *et al.* (2010) and Gallagher *et al.* (2010) to integrate both general and localized strategies to achieve effective management.

CONCLUSIONS

In conclusion, our study advances the understanding of *B. pilosa*'s potential distribution and ecological niche dynamics in the face of climate change and human influence. By integrating a range of modelling approaches and various abiotic and biotic environmental factors, we offer insights that allow identifying future areas under invasion risk and thus developing effective and targeted prevention and/or early detection-rapid response strategies to limit the spread of this invasive species. As climate change continues to reshape ecological landscapes, studies like ours will become increasingly important in guiding ecological management and policy decisions.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Figure S1: Predictions of global geographical distribution of *Bidens pilosa*, under present climatic scenarios.

Figure S2. Predicted potential global geographical distribution of *Bidens pilosa* in the 2050s using an ensemble model.

Figure S3: Evaluation indices of individual predictive models.

Figure S4: Response curves for all variables, i.e. climatic variable (a), climatic and biotic factor (b), climate and HIFs (c), and climate, biotic factor, and HIFs (d) and grouped by algorithm mean over all used models (red) and estimated committee averaging across predictions (blue).

Table S1: List of eight predictors for climatic variables, a biotic factor, and HIFs.

Table S2: Regional distribution table corresponding to the native and introduced range of *Bidens pilosa*.

Authors' Contributions

Zhikun Ren (Conceptualization, Data curation, Visualization, Writing—original draft, Writing—review & editing), Yuqi Ai (Writing—original draft), Müller-Schärer Heinz (Conceptualization, Writing—review & editing), Junqi Liu (Data curation, Investigation), Xinrou Yuan (Data curation, Investigation), Xinyi Tang (Data curation, Investigation), Jintao Liu (Data curation, Investigation), Wei Huang (Conceptualization, Methodology, Writing—review & editing), and Yan

Sun (Conceptualization, Methodology, Supervision, Writing—review & editing)

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