



Original Article

Climate Change–Driven Shifts in Weed and Invasive Alien Plant Distributions in Iran: A Species Distribution Modelling Approach

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Abstract

Climate change is altering the environmental suitability of plant species, with responses varying based on traits and ecological niches. We used climate suitability modeling to assess the current and future distributions of 38 plant species, including weeds, invasive alien plants (IAP), and potential invasive alien plants (PIAP) across Iran, and to identify trait-based patterns of range shifts. Random Forest predicted climate suitability under current and future scenarios (2041–2070) for RCP 4.5 and RCP 8.5, averaged across five global climate models. Suitability changes were quantified by comparing future and current distributions. Projected shifts in climatic suitability reveal distinct responses among the studied species. Woody trees and shrubs like *Acacia saligna* Labill., *Ailanthus altissima* Mill Swingle, *Neltuma juliflora* Sw. Raf., and *Opuntia ficus-indica* L. are expanding in northern coastal and southeastern regions, while *Dalbergia sissoo* DC. is declining in the south. Aquatic and moisture-dependent taxa, such as *Pontederia crassipes* Mart. and *Azolla filiculoides* Lam., generally gain suitability under warming. Most cropland weeds and ruderal species, including *Amaranthus blitoides* S. Watson, *Ambrosia psilostachya* DC., and *Sinapis arvensis* L., show increased suitability, especially in northern Khorasan. Annual and perennial grasses predominantly expand, particularly *Echinochloa crus-galli* L. and *Sorghum halepense* L., while *Bromus tectorum* L. and *Secale cereal* L. decline locally. Climbing species show variable responses: *Araujia sericifera* Brot. contracts, *Merremia dissecta* Jacq. expands mainly under RCP 4.5, and *Cynanchum acutum* L. becomes more suitable. Cumulative gain-loss maps indicate coasts as hotspots of simultaneous expansion and decline driven by steep climatic and topographic gradients. Trait analyses reveal that annual, herbaceous, and C₃ species with high plasticity and dispersal ability dominate range expansions, while woody, aquatic, and CAM taxa have limited adaptive capacity under warming. Cluster analysis shows distinct patterns among weed species, IAP, and PIAP. These findings indicate that climate-driven changes in environmental suitability will reshape the composition and dominance structure of Iran's invasive and weedy flora, highlighting the importance of combining trait-based frameworks with species distribution modeling to anticipate future floristic shifts under global change.

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مقاله پژوهشی

مدلسازی اثر تغییر اقلیم بر پراکنش علف‌های هرز و گیاهان مهاجم در ایران

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چکیده

تغییرات اقلیمی در حال تغییر زیستگاه گونه‌های گیاهی است. در این میان اما، گونه‌های گیاهی ممکن است پاسخ‌های متفاوتی نشان دهند. در این پژوهش، با استفاده از مدل‌سازی تناسب اقلیمی، پراکنش کنونی و آینده ۳۸ گونه، شامل (۱) گونه‌های علف هرز، (۲) گیاهان مهاجم بیگانه و (۳) گونه‌های بیگانه دارای پتانسیل تهاجم در ایران بررسی و الگوهای تغییر در گستره زیستگاه در پاسخ به تغییر اقلیم پیش‌بینی شد. داده‌های حضور تأیید شده از پایگاه‌های جهانی GBIF و CABI و پایگاه‌های ملی SID.ir و Magiran.com گردآوری گردید. مدل Random Forest با استفاده از متغیرهای زیست‌اقلیمی از مجموعه داده ۷۲۱ CHLSA آموزش داده شد و عملکرد مدل با شاخص‌های AUC، TSS و OOB ارزیابی شد. پیش‌بینی‌های آینده (۲۰۴۱-۲۰۷۰) تحت سناریوهای ۴/۵ RCP و ۸/۵ RCP بر اساس میانگین پنج مدل گردش عمومی اقلیم تولید شد و تغییرات تناسب اقلیمی با مقایسه پراکنش‌های آینده و اکنون برآورد گردید. براساس نقشه‌های پیش‌بینی، زیستگاه مناسب برای درختان و درختچه‌های چوبی مانند *Acacia saligna*، *Ailanthus altissima*، *Neltuma juliflora* و *Opuntia ficus-indica* در مناطق ساحلی شمالی و جنوب شرقی گسترش می‌یابند، در حالی که *Dalbergia sissoo* در جنوب با کاهش در تناسب زیستگاه روبرو می‌شود. گونه‌های آبی مانند *Pontederia crassipes* و *Azolla filiculoides* به‌طور کلی تحت گرمایش جهانی افزایش نشان می‌دهند. اکثر گونه‌های علف‌های هرز مزارع از جمله *Amaranthus blitoides*، *Ambrosia psilostachya* و *Sinapis arvensis* گستره ی تناسب زیستگاه افزایش می‌یابد. دامنه زیستگاه برای گونه‌های *Echinochloa crus-galli* و *Sorghum halepense* افزایش و برای گونه‌های *Bromus tectorum* و *Secale cereale* کاهش می‌یابد. تحت سناریوی RCP 4.5 گونه‌های بالا رونده پاسخ‌های متغیری نشان می‌دهند. گونه *Araujia sericifera* کاهش می‌یابد، در حالیکه *Merremia dissecta* گسترش می‌یابد و *Cynanchum acutum* با افزایش سطح زیستگاه مناسب همراه خواهد بود. بر اساس نقشه‌های تجمعی گسترش-کاهش، بیشترین میزان افزایش پهنه زیستگاه و درعین حال کاهش زیستگاه، هم‌زمان در مناطق ساحلی شمالی متمرکز است. تحلیل ویژگی‌های گونه‌ای نیز حاکی از این است که بیشترین گسترش زیستگاه مربوط به گونه‌های یک‌ساله، علفی و دارای مسیر فتوسنتزی C₃ خواهد بود. در مقابل، گونه‌های چوبی، آبی و دارای مسیر فتوسنتز CAM ظرفیت سازگاری محدودی در برابر گرمایش و خشکی دارند. براساس نتایج تجزیه کلاستر، گونه‌های مورد بررسی در دسته‌های مجزا از گونه‌های بیگانه مهاجم یا با پتانسیل تهاجم و گونه‌های علف هرز طبقه‌بندی شدند که نشانگر پاسخ متفاوت این گونه‌ها به تغییرات اقلیمی می‌باشد. براساس پیس‌بینی‌های این مطالعه تغییرات اقلیمی، گستره ی زیستگاه، ساختار و ترکیب فلور گیاهان بیگانه و علف‌های هرز ایران را دستخوش تغییر خواهد کرد. این نتایج بر لزوم برنامه‌ریزی‌های پیشگیرانه در مورد محدود کردن گسترش گونه‌های مهاجم و علف‌های هرز تحت تأثیر تغییر اقلیم و درعین حال راهکارهای مرتبط با حفظ تنوع زیستی به‌ویژه در مناطق حساس تأکید دارد.

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حق انتشار این مستند، متعلق به نویسندگان است. ۱۴۰۴ ©. ناشر این مقاله، انجمن علوم علف‌های هرز ایران و موسسه تحقیقات گیاهپزشکی کشور است. این مقاله تحت گواهی زیر منتشر شده و هر نوع استفاده غیرتجاری از آن مشروط بر استناد صحیح به مقاله و با رعایت شرایط مندرج در آدرس زیر مجاز است.



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Introduction

Climate change is among the most pressing challenges of our time, with far-reaching consequences for biodiversity, ecosystem functioning, and agricultural sustainability worldwide (Rastgordani et al., 2023). These challenges are particularly evident in regions with high environmental variability, such as Iran (Veisi et al., 2014). Over recent decades, rising temperatures, more frequent droughts, and altered precipitation patterns have begun to reshape ecological processes and vegetation dynamics across the country (Torkaman Pary et al., 2024; Golmohammadi et al., 2018). Climatic pressures interact with land-use change, agricultural intensification, and the increasing movement of species beyond their native ranges, collectively driving substantial shifts in plant community composition and spatial distribution (Franklin et al., 2016; Savic et al., 2021; Poinas et al., 2025). Iran's complex geography and ecological heterogeneity make it particularly sensitive to these transformations. The country spans extensive arid and semi-arid zones, rugged mountain systems, vast rangelands, and the humid Hyrcanian forests along the Caspian Sea (Sarani et al., 2014). The Hyrcanian forests, recognized as a global biodiversity hotspot, harbor numerous endemic taxa (Ghorbanalizadeh & Akhani, 2022) yet remain highly vulnerable to even modest changes in temperature and moisture regimes (Hadinezhad et al., 2025). At the same time, Iran's extensive agricultural landscapes, dominated by cereal-based production systems, are increasingly exposed to these climatic stressors. Weed infestations already cause substantial yield losses, and many weed species are expected to respond more positively than crops to rising temperatures and increasing water scarcity (Miri, 2013).

Iran's location at the intersection of several biogeographic regions, combined with intensive trade and land-use transformations, heightens

the risk of alien plant introductions. Several alien plant species have also been recorded in Iran, including *A. altissima* (Mehrabian et al., 2021) and *A. psilostachya* (Tokasi et al., 2017), both of which are rapidly spreading within agricultural and semi-natural environments, threatening ecosystem stability and food security (Karyda & Roussos, 2025; Prasad et al., 2013). In natural systems such as the Hyrcanian forests and mountain rangelands, invasive plants like *A. sericifera* can disrupt community structure, alter ecological interactions, and accelerate biodiversity loss, often facilitated by disturbances and climate-induced niche openings (Oveisi et al., 2025).

For ecological relevance, we distinguish between three categories of plants (Sun et al., 2021): 1) weed species, which interfere with crop growth and reduce agricultural productivity; 2) invasive alien plant (IAP) species, which have been introduced beyond their native ranges and have disrupted habitats, causing significant ecological or economic impacts; and 3) potential invasive alien plants (PIAP), which are non-native but not yet causing major impacts, although they possess traits associated with invasiveness.

Species distribution models (SDMs) provide a robust framework for quantifying how environmental factors influence current and potential species distributions (Guisan & Thuiller, 2005). By linking species occurrences with climatic predictors, SDMs can be projected under future climate scenarios to estimate potential range expansions, contractions, or shifts (Bond et al., 2011; Zurell et al., 2023). Although SDMs have been widely applied to native and alien species worldwide, studies in Iran have largely focused on endemic or medicinal taxa, leaving invasive and weedy species comparatively underexplored. Yet these groups often possess traits, such as high reproductive capacity, rapid dispersal, and broad environmental tolerance that enable them

to capitalize on changing climatic conditions (Adhikari et al., 2019; Bradley et al., 2010).

To address this gap, we compiled occurrence data for 38 plant species, including weeds, IAP, and PIAP, representing diverse growth forms such as annual herbs, perennial grasses, shrubs, and trees, across a wide range of habitats in Iran. We deliberately selected these 38 widespread and problematic species, which include major crop-land weeds and established or potentially invasive plants, based on two criteria: (i) they are among the most significant threats currently facing the country, and (ii) they have sufficient, high-quality occurrence data to support reliable species distribution modeling. This dataset enables us to compare their climatic suitability, identify potential hotspots and areas of species overlap, and assess how the biological traits and habitat preferences of these species influence their responses to future climate change. Although climate-induced range shifts have already been observed in northern Iran and the Hyrcanian region (Taleshi et al., 2019), the potential trajectories of alien plants and weeds remain poorly understood, despite their significant implications for agriculture and biodiversity. As climate change intensifies disturbances and creates new ecological niches, invasive species may gain competitive advantages (Wolkovich & Cleland, 2014), accelerate floristic turnover, and destabilize native communities. Understanding how climate change will reshape the distribution of weeds and alien invasive plants is essential for anticipating risks to food security and ecosystem resilience (Syngkli & Rai, 2025). Given Iran's climatic variability, ecological richness, and exposure to species introductions, substantial shifts in plant composition and distribution are expected, with implications extending from crop management to the conservation of global biodiversity hotspots (Yousefi et al., 2025).

We hypothesize that under future climate scenarios (RCP 4.5 and RCP 8.5), many weed species, IAP, and PIAP will expand or shift their habitats across Iran. This expansion is expected to be most pronounced in northern regions and

higher elevations, particularly within the Hyrcanian forests (Limaki et al., 2021), while contraction will dominate in increasingly arid zones (Behzadi et al., 2025). We further hypothesize that fast-growing, disturbance-adapted annuals with broad climatic tolerance will exhibit the greatest potential for expansion, whereas species with narrow ecological niches or low drought tolerance are likely to decline. Accordingly, this study addresses three key questions: 1) Which of the 38 study species are most likely to expand or shift their ranges under future climate scenarios? 2) Which ecological and geographic zones will experience the highest changes in climate suitability? and 3) How do responses differ among weeds, IAP, and PIAP across growth forms, habitat types, life-history traits, and climatic tolerance, particularly regarding drought and salinity?

Methods

Climatic Suitability Modelling

Occurrence records for 38 plant species, including weeds, IAP, and PIAP were compiled from GBIF.org (2024), the CABI Invasive Species Compendium, and Iranian literature databases (SID.ir, Magiran.com) (see Table 1). To enhance the international datasets, Iranian publications in both English and Persian were systematically reviewed to extract additional records. These species represent a diverse array of growth forms, ranging from annual herbs and perennial grasses to shrubs and trees, and they inhabit various agricultural and natural habitats in Iran. All occurrence data underwent quality control: only georeferenced records with spatial uncertainty ≤ 100 m were retained, duplicates were removed, and spatial thinning was applied to ensure a maximum of one record per 1 km² grid cell, aligning with the resolution of environmental predictors.

Nineteen bioclimatic variables related to temperature and precipitation were obtained from the CHELSA v2.1 database (Karger et al., 2017), which provides climatic means from 1981 to 2010 at approximately 1 km resolution. To minimize multicollinearity, we calculated

pairwise Spearman's rank correlations among the predictors at occurrence locations. For pairs with high correlations ($|\rho| \geq 0.8$), we retained the variable deemed more ecologically relevant. Additionally, we conducted a Variance Inflation Factor (VIF) analysis, excluding any variables with VIF values of 10. The final set of predictors for each species, typically 6–10 variables, is provided in Table 1. Across species, the most frequently retained predictors were those associated with temperature and precipitation seasonality and extreme climatic conditions potential impacts of climate change on climate suitability were assessed using downscaled projections from CHELSA v2.1 (Karger et al., 2021), which provide high-resolution (~1 km) climate layers derived from multiple global climate models (GCMs) under RCP 4.5 and RCP 8.5 scenarios. Analyses focused on the mid-century period (2041–2070). Climate suitability for each species was modeled for each GCM–scenario combination using a Random Forest algorithm (Prasad et al., 2006; Elith & Leathwick, 2009) trained on current occurrence records and climatic predictors. To account for inter-model variability and reduce uncertainty, ensemble predictions were generated by averaging results across five GCMs per RCP scenario to explicitly account for inter-model uncertainty (Porfirio et al., 2014).

Random Forest models were implemented in R using the *randomForest* package. Hyperparameters were optimized through 5-fold cross-validation, exploring *mtry* values of {2,3,4,5} and *ntree* values of {100,200,500,1000}. The dataset was partitioned into 70% training and 30% testing subsets, and out-of-bag (OOB) error was recorded as an additional measure of model robustness. Model performance was evaluated using the Area Under the Receiver Operating Characteristic Curve (AUC), True Skill Statistic (TSS), and OOB Error. Final models, parameterized with optimal hyperparameters, were used to generate continuous climatic suitability maps for each species across Iran. Continuous suitability predictions were

converted into binary maps (suitable vs. unsuitable) using objective thresholding methods (Jiménez-Valverde & Lobo, 2007). Two thresholding criteria were compared: (i) Youden's J statistic, and (ii) a prevalence-based threshold that aligns predicted prevalence with observed occurrence frequency. For each species, the most conservative threshold was selected to minimize the risk of underestimating potential invasions. The final thresholds for all 38 species are reported in the Supplementary Material (Table 1).

Climatic Gain and Loss Analysis

To quantify changes in climatic suitability under future scenarios, we subtracted current suitability values from those predicted under RCP 4.5 and RCP 8.5. Positive differences were interpreted as gains, indicating areas where conditions become more favorable for the species, whereas negative differences were considered losses, indicating areas where suitability decreases. Gain and loss maps were overlaid across all species, and the number of species experiencing gains or losses per grid cell was calculated to generate cumulative maps of potential change. Two thresholds were applied to highlight the magnitude of change: 0.1 and 0.2, corresponding to 10% and 20% changes in climatic suitability, respectively.

Results

Model Performance

Species distribution models for the 38 alien plant species demonstrated high predictive performance. AUC values ranged from 0.901 to 0.992, TSS values from 0.78 to 0.96, and overall accuracy from 0.89 to 0.99. OOB error rates were low, ranging from 3% to 8%. The thresholds for converting continuous suitability into binary presence–absence predictions varied from 0.28 to 0.44. Precision, recall, and F1-scores were generally balanced across presence and absence classes, indicating reliable model predictions.

Climatic Suitability Under Current and Future Scenarios

Projected changes in climatic suitability (Figure 1) reveal heterogeneous spatial dynamics across the studied species, reflecting their differing life-history traits, ecological preferences, and stress tolerances.

Woody Trees and Shrubs

Woody invaders exhibit diverse and often divergent climate-driven trajectories. *Acacia saligna*, now primarily suitable along the Caspian coast with fragmented patches in the south and southwest, expands significantly under warming. The eastern Caspian coast becomes increasingly suitable, while southern and southeastern patches shift toward higher suitability classes. *Ailanthus altissima* currently demonstrates its core suitability in the Alborz foothills and northern provinces (Guilan, Mazandaran, Golestan), with a small patch in the central south. Under climate change, suitability spreads continuously along the northern coastal belt and extends northeast into Golestan, while fragmented pockets in the northwest and central south also intensify.

In contrast, *D. sissoo*, which is currently highly suitable across the southern belt, shows declining suitability under warming, particularly in southeastern coastal regions such as Sistan and Baluchestan, where highly suitable areas diminish to suitable. *Neltuma juliflora* (Prosopis), already highly suitable from Khuzestan to Sistan and Baluchestan, becomes even more dominant. Climate change renders Sistan and Baluchestan highly suitable and pushes suitability northward and inward to the central regions and northeastern Khorasan. *Opuntia ficus-indica*, currently suitable across the north and southwest, experiences southern

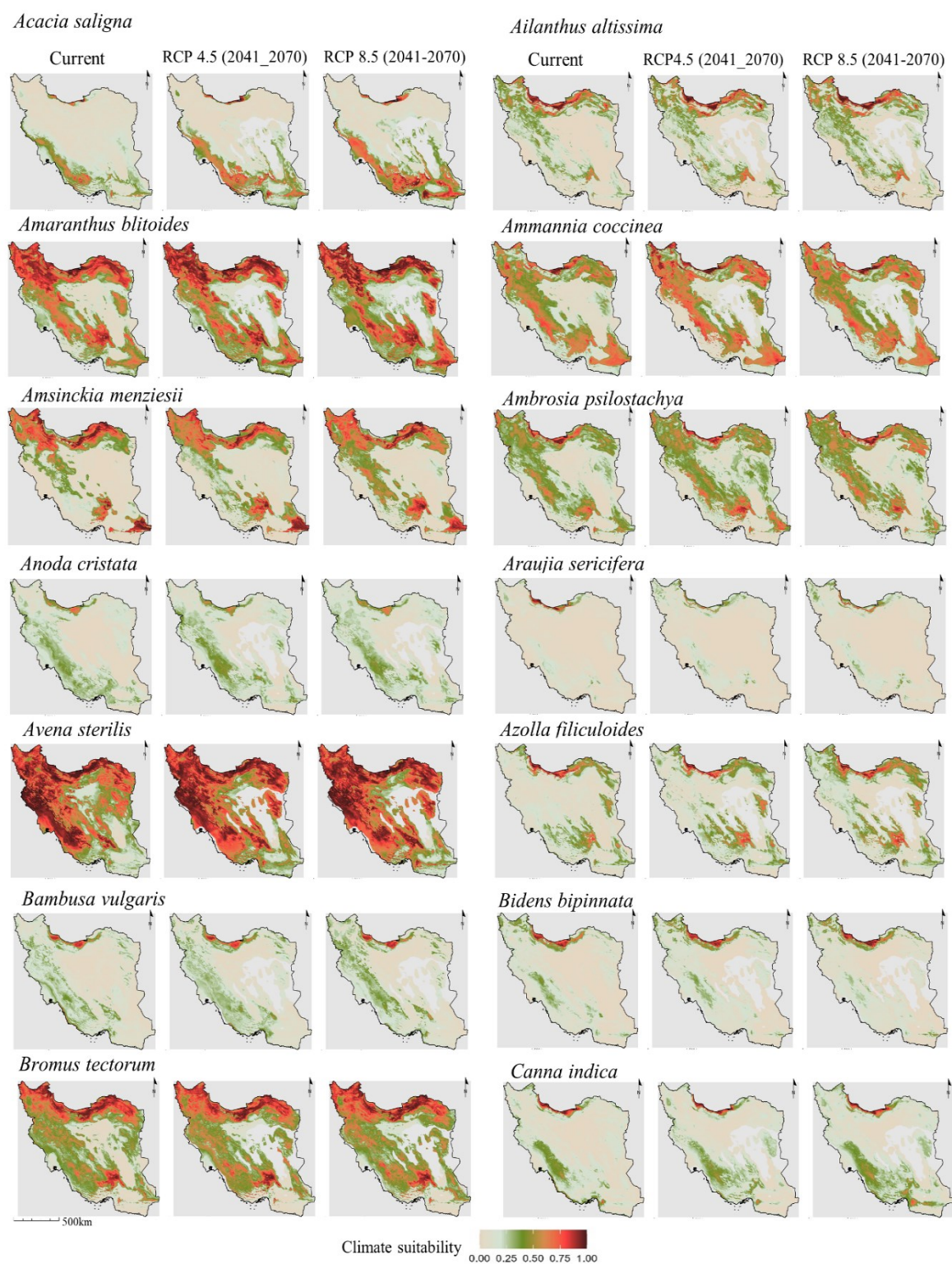
expansion into Kerman and Sistan and Baluchestan under climate change scenarios, broadening its ecological footprint.

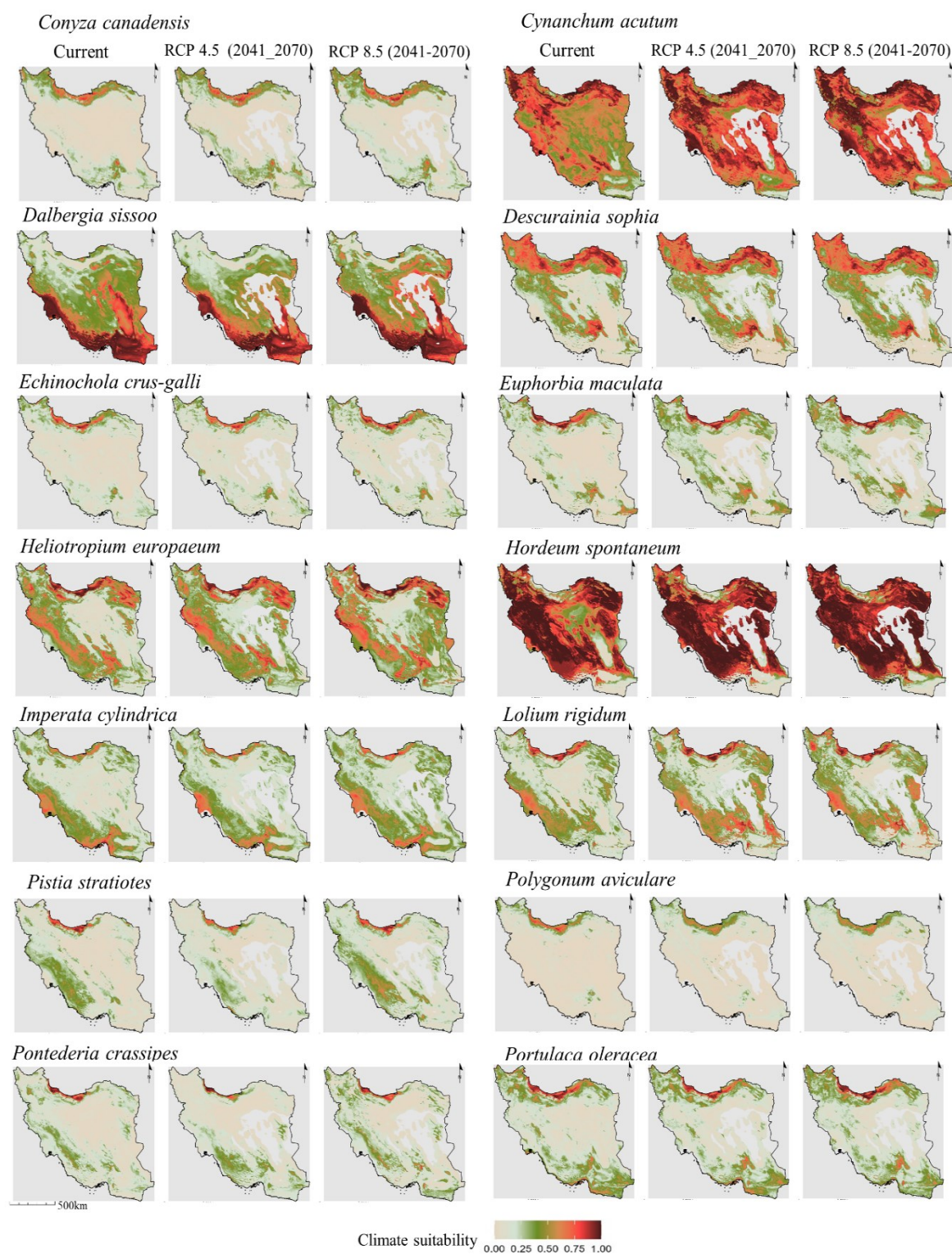
Aquatic and Moisture-Dependent Species

Aquatic and semi-aquatic taxa generally respond positively to warming, although some local declines are observed. *Azolla filiculoides*, which is now highly suitable across northern wetlands (Guilan, Mazandaran), is projected to expand into northeastern and northern Khorasan under future scenarios, despite localized losses in some northern areas. *Pistia stratiotes* L., currently highly suitable in northern Iran, is expected to gain new suitable areas in the southeast and show upward shifts toward high suitability. *Pontederia crassipes* is now highly suitable in northern provinces and is predicted to increase further under climate change, with marginal gains expected in the southeast. *Canna indica* L., a moisture-dependent species, is highly suitable along the northern coastal band with a scattered distribution elsewhere, and it is projected to form new suitable patches in the southern provinces as temperatures rise. Hydrological variables, along with climatic factors, are significant determinants of future spread.

Weeds of Croplands and Disturbed Habitats

Annual weeds and ruderal taxa exhibit strong geographic shifts, often tracking disturbance and warming. *Amaranthus blitoides*, already suitable from west to east across northern Iran and extending southeast through Khorasan and Sistan and Baluchestan, is expected to experience increased suitability and broader high-suitability patches due to warming.





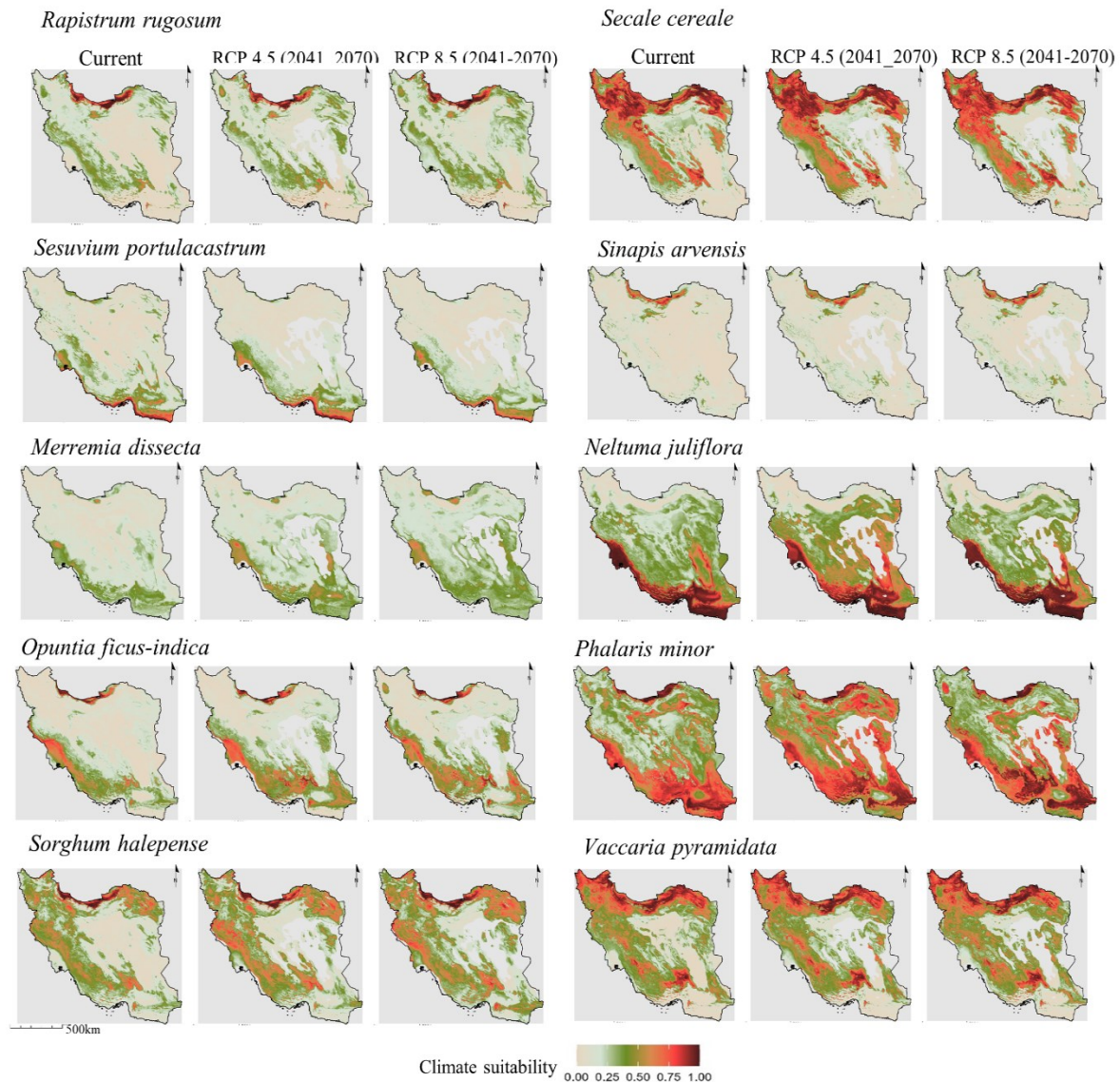


Figure 1. Climate suitability maps for 38 species under current conditions and future climate scenarios (RCP 4.5 and RCP 8.5). Species maps for *Acacia saligna*, *Ailanthus altissima*, *Ambrosia psilostachya*, *Ammannia coccinea*, *Amsinckia menziesii*, *Anoda cristata*, *Azolla filiculoides*, *Bambusa vulgaris*, *Canna indica*, *Cynanchum acutum*, *Dalbergia sissoo*, *Euphorbia maculata*, *Imperata cylindrica*, *Merremia dissecta*, *Prosopis juliflora* [formerly *Neituma juliflora*], *Opuntia ficus-indica*, *Paulownia fortunei*, *Pistia stratiotes*, *Pontederia crassipes*, and *Sesuvium portulacastrum* are adapted from Oveisi et al. (2026), *NeoBiota*, 107, 243–268. <https://doi.org/10.3897/neobiota.107.182605>.

Ambrosia psilostachya, highly suitable in Guilan and Mazandaran, with additional patches in the northwest, central south, and Zagros, is projected to expand significantly under RCP 8.5, particularly into northern Khorasan, mirroring the trends of *A. blitoides*. In contrast, *Anoda cristata* L., currently suitable mainly in Mazandaran, is expected to lose suitability under climate change. *Bidens bipinnata* L. shows increased suitability in the north, especially in Mazandaran, under warming. *Conyza Canadensis* L., highly

suitable in the north with scattered patches elsewhere, is projected to extend decisively into the northeast under RCP 8.5. *Descurainia sophia* L., suitable in the northwest and highly suitable across the north and northeast, is expected to increase in suitability in the central south while experiencing minor reductions in the northeast. *Euphorbia maculata* L. remains concentrated in northern Iran with small southern pockets. *Heliotropium europaeum* L., forming a band from Guilan through northern Khorasan and southward toward Lorestan and

south-central Iran, is projected to increase markedly in northern Khorasan under warming. *Portulaca oleracea* L., already highly suitable across the northern belt and parts of the south, is expected to expand particularly toward the northeast. *Rapistrum rugosum* L., currently suitable to highly suitable across the north with scattered southern patches, is predicted to increase to high suitability across an expanded range. *Sinapis arvensis*, now suitable to highly suitable in the north, is expected to expand both in area and intensity under climate change, including the emergence of new suitable patches in the south. However, *Polygonum aviculare* L. is projected to decline in suitability despite its currently broad northern distribution. *Vaccaria pyramidata*, which is suitable across the entire northern belt and through the west along the Zagros to Kerman, is expected to experience little overall change under climate change scenarios.

Annual and Perennial Grasses

Annual and perennial grasses exhibit complex but often expansionary responses to climate change. *Echinochloa crus-galli*, which is suitable across northern Iran and the Alborz foothills, shows increased suitability with warming. *Hordeum spontaneum* L., one of the grasses with the broadest range, remains suitable to highly suitable across most of Iran (except the extreme southeast), with only marginal increases projected. *Imperata cylindrical* L., currently suitable in the north, Khuzestan, and the southern provinces, shows a slight increase in suitability under climate change. *Lolium rigidum* L., highly suitable along the Caspian coast and suitable in Khuzestan, is expected to expand eastward from Khuzestan. *Phalaris minor* L., highly suitable in both northern and southern regions (from Khuzestan to Sistan and Baluchestan), is projected to further increase in suitability, with the southeast becoming highly suitable. *Sorghum halepense*, highly suitable in both northern Iran and a southern band, is expected to expand its area and intensity under both RCP 4.5 and 8.5 scenarios. *Bromus tectorum*, suitable across a broad northern band and in

central southern regions, shows mixed regional responses: suitability declines in some areas while it increases in others. *Secale cereale*, widely suitable from west to east across northern Iran and extending through the Zagros, shows declining suitability in northern Khorasan under RCP 8.5. For weeds, factors such as cropping systems and herbicide use should also be considered equally important determinants, in addition to climatic suitability.

Halophytes and Coastal Specialists

The dominant coastal halophyte *Sesuvium portulacastrum* L., currently suitable in Khuzestan and highly suitable in Bushehr, Hormozgan, and Sistan and Baluchestan, is projected to decline in suitability under future climate conditions, indicating sensitivity to anticipated warming and shifts in moisture availability.

Twining Vines and Climbing Weeds

Climbing species display contrasting future responses. *Araujia sericifera*, highly suitable in Guilan and Mazandaran and moderately suitable in Golestan, is expected to undergo a clear contraction under both climate scenarios. *Merremia dissecta*, suitable in Mazandaran and Khuzestan, is projected to expand under RCP 4.5 into Kerman and Sistan and Baluchestan; however, under RCP 8.5, suitability remains focused in Mazandaran and Khuzestan but at higher suitability levels. *Cynanchum acutum*, already suitable to highly suitable across most of Iran, is expected to experience even broader suitability under warming, with many areas shifting into higher-suitability categories.

Regional Gains and Losses

Cumulative projections of invasive species gain and loss across Iran (Figure 2) reveal strong spatial and threshold-dependent patterns. Under RCP 4.5 at the 0.1 threshold, the largest gains (20–25 species per cell) are concentrated in central-southern deserts (Dasht-e Kavir, +Dasht-e Lut), eastern Baluchestan, and the southern coastal strip (Hormozgan, Bushehr), with moderate gains (10–15 species) along the Zagros foothills (Fars, Kerman) and northeastern plains (Golestan, North Khorasan),

while northern Caspian forests and high Alborz show minimal expansion.

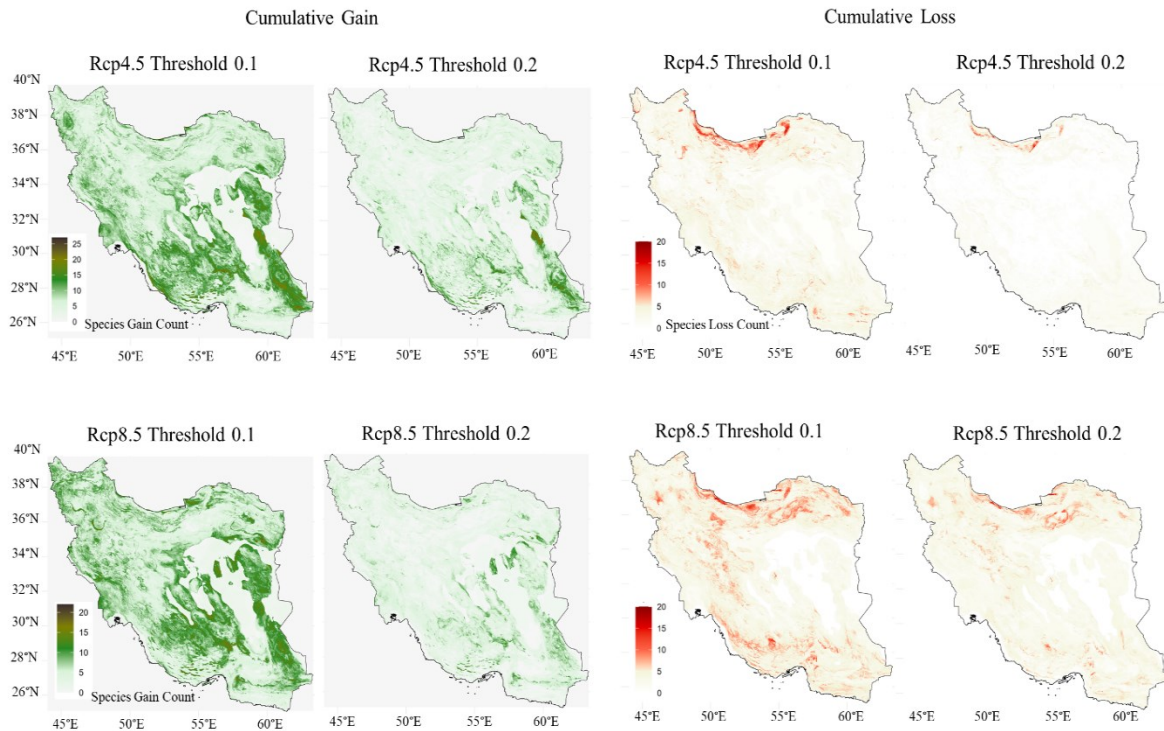


Figure 2. Habitat gain and loss maps under future climate scenarios (RCP 4.5 and RCP 8.5) using two thresholds (0.1 and 0.2) for changes in habitat suitability.

Increasing the threshold to 0.2 sharply restricts gains to ≤ 5 species in scattered southern and eastern patches, leaving over 95% of the country unchanged. Under RCP 8.5 at the 0.1 threshold, gains are far more extensive, with the southern half of Iran, central plateaus (Semnan, Isfahan, Yazd), and eastern Caspian lowlands (Golestan) exhibiting 20–25+ species per cell, and widespread interior arid zones showing moderate gains (10–20 species). At the 0.2 threshold, expansion remains substantial but more localized, with 10–15 species per cell in southeastern and south-central regions, and scattered ≤ 5 species in central and eastern interiors. Overall, southern and eastern arid zones, central deserts, and eastern Caspian lowlands emerge as consistent gain hotspots, while northern humid regions remain largely unaffected.

Loss patterns mirror climatic and geographic gradients. Under RCP 4.5 at the 0.1 threshold, highest losses (15–20 species per cell) occur

along the northern Caspian coast (Gilan, Mazandaran) and northwest highlands (East Azerbaijan, Ardabil), with moderate loss (5–10 species) in the western Zagros (Kermanshah, Kurdistan) and scattered northern Alborz foothills, whereas southern and central deserts experience minimal contraction. At the 0.2 threshold, detectable loss is nearly eliminated, appearing only as faint traces in extreme northwest and northeast regions. Under RCP 8.5 at the 0.1 threshold, loss intensifies and expands, with northern humid zones, western Zagros, and northeastern agricultural belts showing 15–20+ species per cell, and moderate losses (10–15 species) extending across northwest and north-central foothills. At the 0.2 threshold, loss decreases but remains notable in northwest and Caspian coastal areas, while central and southern Iran remain largely unaffected. Across scenarios, RCP 8.5 consistently exhibits greater intensity and

coverage of both gain and loss, with lower thresholds capturing early-stage range shifts.

Integrating these patterns, RCP 8.5 at the 0.1 threshold predicts a pronounced southward and eastward redistribution of invasive species richness, with arid southern biomes gaining 20–25+ species per cell, while northern humid regions lose 15–20+ species. Threshold effects highlight that low suitability (0.1) identifies early-stage colonization and contraction, whereas higher suitability (0.2) reflects established ranges with reduced detectable change, particularly under RCP 4.5. These dynamics indicate a climate-driven reassembly of Iran's flora, dominated by proliferation of arid-adapted invaders in warming interiors and contraction of species from northern refugia. From a management perspective, central-southern deserts, eastern borders, and southern coasts represent high-risk gain zones, while northern forests and northwest mountains are prone to species loss and potential native displacement. Overall, RCP 8.5 imposes substantially higher invasion pressure than RCP 4.5, particularly across arid interiors.

Trait- and Habitat-Based Responses

Trait-based analysis revealed distinct patterns between invasive and potential invasive alien species (IAS) and weed species in terms of area gain and loss (p -value < 0.02) (Figure 3). For IAS, growth form accounted for the largest

proportion of effect size in both gain and loss areas, followed by seasonality and photosynthetic pathway (p -value < 0.05), while life cycle contributed minimally. In contrast, for weed species, growth form and life cycle contributed comparably (p -value < 0.05) to area gain, whereas growth form remained dominant in area loss, followed by seasonality and photosynthesis. Overall, growth form emerged as the primary trait influencing both expansion and contraction dynamics across species categories.

Violin plots summarize projected gains and losses in climatically suitable area (km^2) across 38 species under RCP 4.5 and RCP 8.5 (2041–2070), categorized by six functional traits. Considering life cycle, perennials exhibited the largest gains, with a median of approximately $9 \times 10^5 \text{ km}^2$, whereas annuals experienced both substantial gains ($\sim 1 \times 10^6 \text{ km}^2$) and losses ($\sim 6 \times 10^5 \text{ km}^2$), reflecting high turnover rates. Annual/biennial species contributed minimally, with median gains of $\sim 6 \times 10^5 \text{ km}^2$ and negligible losses (Figure 4a). Regarding photosynthetic pathway, C_3 species dominated both expansion and contraction, with median gains of $\sim 9 \times 10^5 \text{ km}^2$ and losses of $\sim 5 \times 10^5 \text{ km}^2$. In contrast, C_4 taxa exhibited moderate gains ($\sim 4 \times 10^5 \text{ km}^2$) and minimal losses, while CAM and parasitic species showed negligible contributions to either gain or loss (Figure 4, b).

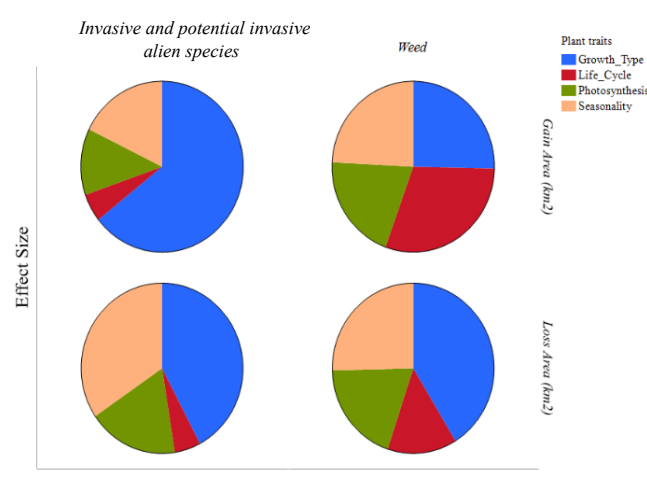


Figure 3. Comparison of habitat gains and losses between alien invasive plants and weed species under climate change, categorized by life cycle, growth type, seasonality, and photosynthetic pathway.

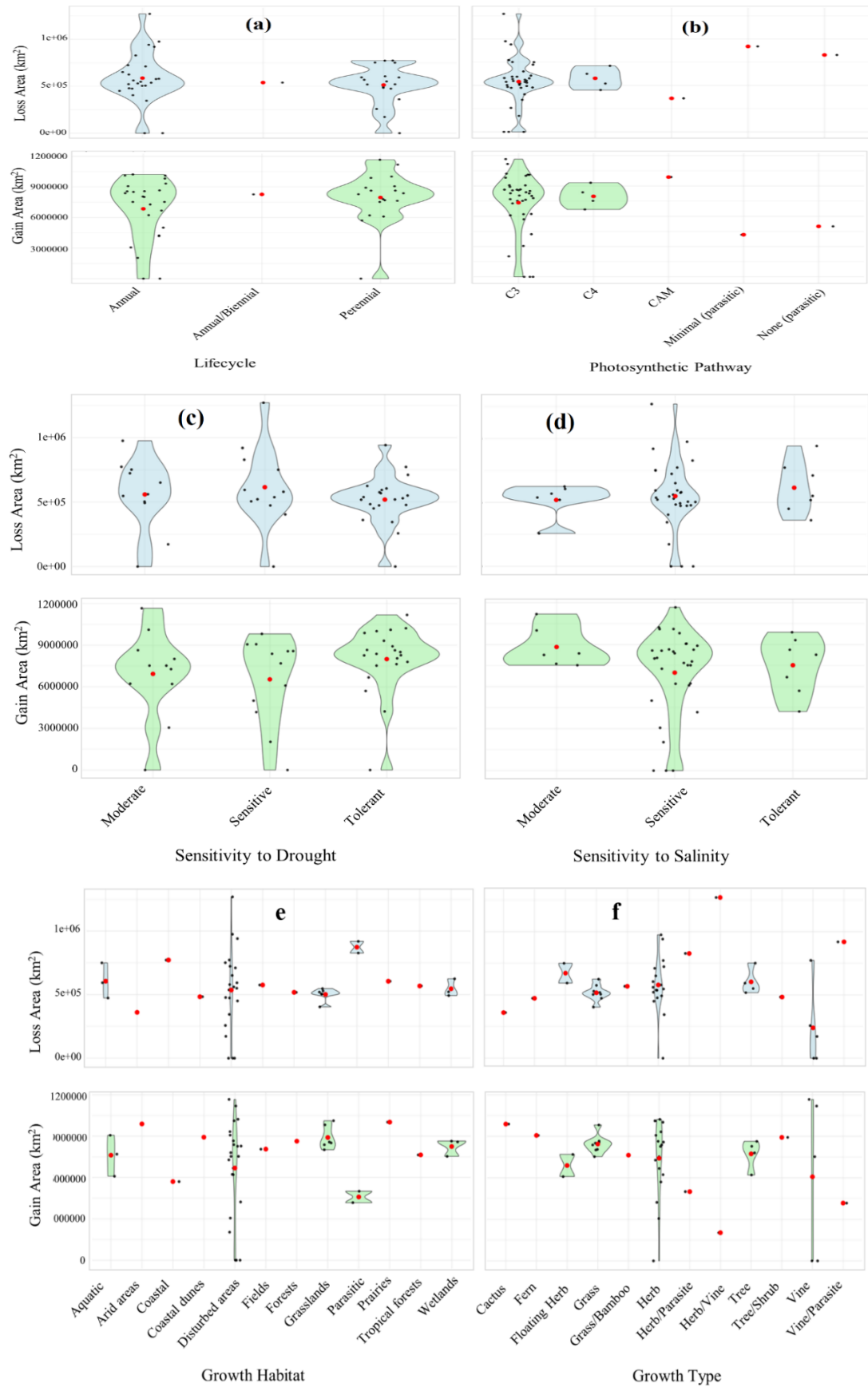


Figure 4. Comparison of species' habitat gain and loss according to life cycle (a), photosynthetic pathway (b), sensitivity to drought (c) and salinity (d), and habitat type (e), growth form (f).

Moderately sensitive taxa also showed considerable gains ($\sim 9 \times 10^5 \text{ km}^2$) but experienced moderate losses ($\sim 4 \times 10^5 \text{ km}^2$). By contrast, drought-sensitive species demonstrated limited gains ($\sim 5 \times 10^5 \text{ km}^2$) and disproportionately high losses ($\sim 7 \times 10^5 \text{ km}^2$), highlighting their vulnerability under projected aridification (Figure 4c; tolerance categories: tolerant = survive prolonged soil moisture deficit, moderate = intermediate response, sensitive = require reliable water availability). From the perspective of sensitivity to salinity, salinity-sensitive species exhibited both high gains ($\sim 8 \times 10^5 \text{ km}^2$) and losses ($\sim 6 \times 10^5 \text{ km}^2$), indicating strong responsiveness to changing climatic conditions.

Moderately sensitive taxa maintained more balanced dynamics ($\sim 6 \times 10^5 \text{ km}^2$ gain, $\sim 5 \times 10^5 \text{ km}^2$ loss), whereas tolerant species showed minimal expansion and contraction (Figure 4, d).

Considering habitat type, species adapted to arid and disturbed environments recorded the highest gains (median $> 1 \times 10^6 \text{ km}^2$) alongside moderate losses ($\sim 5\text{--}6 \times 10^5 \text{ km}^2$). In contrast, forest-associated taxa experienced substantial contractions, while aquatic and wetland species showed limited but localized expansions, reflecting targeted responses along freshwater and coastal systems (Figure 4, e).

Finally, in terms of growth form, herbs and grasses/bamboos were the principal contributors to projected area gains (medians $\sim 1\text{--}1.1 \times 10^6 \text{ km}^2$) and losses ($\sim 6\text{--}7 \times 10^5 \text{ km}^2$). Tree species exhibited variable outcomes, with some experiencing substantial gains and others considerable contractions.

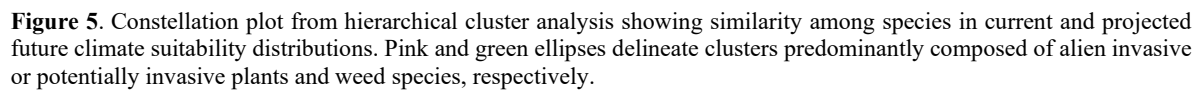
Cactus and floating herb species displayed restricted but notable expansions (Figure 4, f). Overall, these patterns indicate that perennial, drought-tolerant C_3 herbs and grasses associated with arid or disturbed habitats are the primary drivers of projected range expansions, whereas annual, drought- and salinity-sensitive

C_3 herbs and trees dominate contractions. Collectively, these results suggest a future shift in Iran toward arid-adapted, disturbance-tolerant, perennial herbaceous communities under continued warming and drying.

Hierarchical Clustering of Species

Hierarchical clustering (Figure 5) identified five distinct groups reflecting functional and life-history differences. Cluster 1, comprising herbaceous and grass species ($n \approx 10$), exhibited moderate variability and included species such as *B. tectorum*, *Avena sterilis* L., *H. europaeum*, *R. rugosum*. Cluster 2, consisting of annual herbaceous species (including forbs and aquatic herbs) ($n \approx 7$), was relatively compact, with representative species including *D. sophia*, *P. aviculare*, and *P. stratiotes*.

Cluster 3, representing woody species ($n \approx 8$), was tightly grouped and comprised species such as *A. saligna*, *D. sissoo*, and *O. ficus-indica*. Cluster 4 included parasitic and semi-parasitic plants ($n \approx 4$) along with *Galium aparine* L., which although not parasitic clustered with these species due to similar gain–loss patterns rather than shared trophic strategy. Representative species within this cluster included *Orobancha aegyptiaca* L. and *Cuscuta campestris* L. Finally, Cluster 5, the smallest group ($n = 2$), consisted of climbers and vines, represented by *Ipomoea purpurea* L. and *Pueraria montana* (Lour.) Merr. Cluster analysis revealed distinct grouping patterns between weed species and alien invasive or potentially invasive plants. Although some overlap occurred among a few species, the majority formed well-defined clusters corresponding to their respective categories. Large clusters predominantly composed of either weeds or IAP were clearly separated, and the grouping structure was supported by a high confidence level (approximately 0.9), indicating consistent differentiation between the two species groups.



Species distribution models for 38 alien plant species demonstrated high predictive performance, supporting the reliability of projections under future climate scenarios. The results collectively indicate that climate change will profoundly reorganize Iran's invasive flora, favor arid-adapted, drought-tolerant taxa while reducing the dominance of humid and montane-associated species. These outcomes align with global observations that warming and aridification selectively promote functional groups with high physiological plasticity and stress tolerance (Boyko et al., 2023; Baladrón et al., 2023).

psilostachya). These opposing trends reflect a climate-driven reassembly in which warm-dry ecosystems expand at the expense of cool-humid ones, mirroring global transitions in dryland biomes (Fischer et al., 2020; García Criado et al., 2023).

Physiological pathways and stress tolerance further explain observed patterns. Trait-based violin plots indicate that perennial, drought-tolerant C_3 species dominate projected expansions, while annual, drought- and salinity-sensitive C_3

species experience extensive contractions. C₄ taxa, though fewer, demonstrate moderate or stable gains, consistent with superior thermal and water-use efficiency under rising temperatures (Edwards & Still, 2008; Yamori et al., 2014). These patterns indicate that climate filtering favors long-lived, stress-tolerant perennials, reshaping communities toward persistent, ruderal assemblages adapted to aridity. Such physiological resilience underpins the strong expansion of species such as *S. halepense*, *cylindrica*, and *N. juliflora* under RCP 8.5. Environmental heterogeneity mediates these outcomes, producing marked regional contrasts. High-gain southern deserts and arid eastern plateaus coincide with low-loss zones, while northern forests and montane areas experience contractions. The sharp north–south climatic gradient in Iran generates mosaics of emerging niches, where annuals and ruderal grasses rapidly colonize disturbed or newly suitable areas, whereas woody perennials and aquatic taxa are constrained by physiological limits (Noroozi & Körner, 2018; Fazlollahi Mohammadi et al., 2022). Episodic climatic extremes, including heatwaves, droughts, and cold snaps, further exacerbate these patterns, creating overlapping gain–loss hotspots that highlight the dual role of environmental heterogeneity in promoting both invasion opportunities and extinction risks (Taleshi et al., 2019).

Hierarchical clustering revealed five distinct functional groups aligned with life-history strategies. Expansion-prone clusters comprised annual herbs and grasses (e.g., *A. blitoides*, *B. tectorum*), whereas contraction-prone clusters included woody perennials, aquatic, and parasitic taxa. These clusters reflect convergent adaptive strategies, confirming that traits related to growth form, lifespan, and photosynthetic efficiency can predict expansion potential and provide a trait-based framework for forecasting invasion risk under continued warming (Pazzaglia et al., 2021; García Criado et al., 2023). The observed decoupling of gains and losses across space further emphasizes that climate-driven responses are context-dependent and nonlinear, with trade-offs between growth strategies, physiological tolerances, and landscape-mediated opportunities (Yin et al., 2021). For parasitic weeds, future spread depends on the climatic suitability of both

the parasite and its host plants, as establishment and persistence are closely linked to host availability (Oveisi et al., 2010). Favorable climatic conditions for hosts may facilitate parasitic weed spread even where the parasite's own tolerance is limited; therefore, flora change predictions should account for the overlapping climatic niches of both species.

Mechanistically, our findings illustrate that species-specific functional traits, life-history strategies, and environmental tolerances collectively shape invasion dynamics. Annual and ruderal species exploit ephemeral habitats through short life cycles and prolific reproduction, rapidly colonizing emerging niches (Li et al., 2023; Silva et al., 2021). In contrast, woody perennials, long-lived trees, and hydrophilic taxa face constraints due to slower growth, longer generation times, and habitat specificity (Tian et al., 2023; Erlichman et al., 2024; Springate & Kover, 2014; Abell et al., 2008). Photosynthetic pathways modulate responses further, with C₃ taxa showing broad expansion due to flexible physiology, whereas C₄ and CAM species display moderate or context-dependent gains (Kumar et al., 2017; Edwards & Still, 2008; Yamori et al., 2014; Havrilla et al., 2023). Drought- and salinity-tolerant species show pronounced range shifts, whereas sensitive taxa are disproportionately lost, highlighting the selective pressures imposed by warming and aridification (Oveisi et al., 2025; Sohrabi et al., 2025).

Conclusion

Our findings indicate a substantial reorganization of Iran's flora of weeds, IAP, and PIAP under mid-century climate change. There is clear differentiation between weed species and IAP/PIAP, with limited overlap and distinct climatic response patterns. Together with trait-based assessments, these results point to a shift toward drought-tolerant, disturbance-adapted vegetation dominated by perennial C₃ herbs and C₄ grasses, while forest-associated and cold-adapted species decline. This transition toward arid, ruderal-dominated systems highlights emerging risks for biodiversity and ecosystem function, emphasizing the need for targeted management in southern, eastern, and coastal regions and protection of northern refugia.

Table 1. Life-history traits, functional characteristics, and projected climate-driven range changes for 38 alien invasive plant (IAP) and weed species in Iran, including lifecycle, habitat type and growth form, photosynthetic pathway, stress sensitivities, and predicted loss, gain, and net change under future climate scenarios (RCP 4.5 and RCP 8.5, 2041–2070). Net Change (%) = ((Gain – Loss) / Current suitable area) × 100 Net Change Proportion = (Gain – Loss) / Current suitable area.

Full Name	Weed/ IAP /PIAP	Lifecycle	Habitat type	Growth form	Photosynthetic Pathway	Sensitivity to Salinity	Sensitivity to Drought	Loss (km ²)	Gain (km ²)	Net Change (%)	Net Change SD	Mean Net Change Proportion	Functional Group	Expected Climate Response	Notes
<i>Acacia saligna</i>	IAP	Perennial	Disturbed areas	Tree/Shrub	C3	Sensitive	Tolerant	483,536	891,745	-37.1	76.5	19.7	Woody	Contraction-prone	Vulnerable to warming and coastal drying
<i>Ailanthus altissima</i>	IAP	Perennial	Disturbed areas	Tree	C3	Sensitive	Tolerant	593,310	779,600	-45.7	66.9	10.6	Woody	Contraction-prone	Rapid expansion limited by life span
<i>Amaranthus blitoides</i>	Weed	Annual	Disturbed areas	Herb	C4	Tolerant	Tolerant	450,424	931,720	-34.5	79.9	22.7	Annual	Expansion-prone	High reproductive output facilitates range gain
<i>Ambrosia psilostachya</i>	IAP	Perennial	Prairies	Herb	C3	Moderate	Tolerant	605,460	1,001,160	-46.7	85.9	19.6	Perennial Herb	Expansion-prone	Moderate sensitivity to climate stress
<i>Ammannia coccinea</i>	IAP	Annual	Wetlands	Herb	C3	Sensitive	Sensitive	521,625	857,585	-40.1	73.6	16.7	Annual	Expansion-prone	Wetland specialist; drought-sensitive
<i>Amsinckia menziesii</i>	PIAP	Annual	Grasslands	Herb	C3	Sensitive	Moderate	546,983	1,011,246	-42.1	86.7	22.3	Annual	Expansion-prone	Moderate drought tolerance enhances expansion
<i>Araujia sericifera</i>	IAP	Perennial	Disturbed areas	Vine	C3	Sensitive	Moderate	772,901	752,504	-59.9	64.5	2.3	Woody/Vine	Contraction-prone	Moderate expansion limited by long lifespan
<i>Avena sterilis</i>	Weed	Annual	Disturbed areas	Grass	C3	Sensitive	Tolerant	474,194	865,628	-36.3	74.2	18.9	Annual Grass	Expansion-prone	Widely distributed grass; high colonization potential
<i>Azolla filiculoides</i>	IAP/ Weed	Perennial	Aquatic	Fern	C3	Sensitive	Sensitive	473,662	905,931	-36.3	77.7	20.7	Aquatic	Contraction-prone	Water-limited expansion; sensitive to drought
<i>Bambusa vulgaris</i>	IAP	Perennial	Tropical forests	Grass/Bamboo	C3	Moderate	Tolerant	568,360	763,285	-43.8	65.5	10.8	Woody Grass/Bamboo	Contraction-prone	Tropical specialist; limited northern expansion
<i>Bidens bipinnata</i>	IAP/ Weed	Annual	Disturbed areas	Herb	C3	Sensitive	Moderate	723,231	622,435	-56.0	53.4	-1.3	Annual	Expansion-prone	Ruderal; small net gain
<i>Bromus tectorum</i>	Weed	Annual	Grasslands	Grass	C3	Sensitive	Tolerant	529,466	850,361	-40.7	72.9	16.1	Annual Grass	Expansion-prone	Widely distributed grass; drought-tolerant
<i>Canna indica</i>	IAP	Perennial	Wetlands	Herb	C3	Sensitive	Moderate	493,052	863,491	-37.8	74.1	18.1	Perennial Herb	Expansion-prone	Wetland specialist; moderate sensitivity

Full Name	Weed/ IAP /PIAP	Lifecycle	Habitat type	Growth form	Photosynthetic Pathway	Sensitivity to Salinity	Sensitivity to Drought	Loss (km ²)	Gain (km ²)	Net Change (%)	Net Change SD	Mean Net Change Proportion	Functional Group	Expected Climate Response	Notes
<i>Conyza canadensis</i>	Weed	Annual/Biennial	Disturbed areas	Herb	C3	Moderate	Tolerant	538,417	826,329	-41.4	70.9	14.7	Annual/Biennial	Expansion-prone	Ruderal; climate-resilient
<i>Cuscuta monogyna</i>	Weed	Annual	Parasitic	Vine/Parasite	Minimal	Sensitive	Sensitive	919,363	417,318	-71.4	35.8	-17.8	Parasitic	Contraction-prone	Highly sensitive to climate; limited expansion
<i>Cynanchum acutum</i>	IAP/ Weed	Perennial	Disturbed areas	Vine	C3	Moderate	Tolerant	257,614	1,118,039	-19.3	95.9	38.3	Woody/Vine	Expansion-prone	Strong potential for range expansion
<i>Dalbergia sissoo</i>	IAP	Perennial	Forests	Tree	C3	Tolerant	Tolerant	518,083	863,018	-39.8	74.0	17.1	Woody	Expansion-prone	Moderate vulnerability; forest specialist
<i>Descurainia sophia</i>	Weed	Annual	Disturbed areas	Herb	C3	Sensitive	Moderate	650,717	727,563	-50.3	62.4	6.1	Annual	Expansion-prone	Ruderal; moderate climate tolerance
<i>Euphorbia maculata</i>	IAP/ Weed	Annual	Disturbed areas	Herb	C3	Sensitive	Tolerant	344,788	1,022,024	-26.2	87.7	30.7	Annual	Expansion-prone	High reproductive potential; wide tolerance
<i>Galium aparine</i>	Weed	Annual	Disturbed areas	Herb/Vine	C3	Sensitive	Sensitive	1,269,598	203,338	-99.0	17.4	-40.8	Annual	Contraction-prone	Ruderal; high loss due to climate stress
<i>Heliotropium europaeum</i>	Weed	Annual	Disturbed areas	Herb	C3	Sensitive	Tolerant	477,461	1,010,844	-36.6	86.7	25.0	Annual	Expansion-prone	Ruderal; high colonization capacity
<i>Hordeum spontaneum</i>	Weed	Annual	Grasslands	Grass	C3	Sensitive	Moderate	503,550	800,956	-38.7	68.7	15.0	Annual Grass	Expansion-prone	Widely distributed grass; drought-tolerant
<i>Imperata cylindrica</i>	IAP/ Weed	Perennial	Grasslands	Grass	C4	Moderate	Tolerant	520,105	837,158	-40.0	71.8	15.9	Perennial Grass	Expansion-prone	Grassland specialist; moderate drought tolerance
<i>Ipomoea purpurea</i>	PIAP IAP	Annual	Disturbed areas	Vine	C3	Sensitive	Sensitive	0	0	0	0	0	Annual Vine	Stable	Not predicted to expand or contract
<i>Lolium rigidum</i>	Weed	Annual	Grasslands	Grass	C3	Sensitive	Sensitive	505,578	856,411	-38.8	73.4	17.3	Annual Grass	Expansion-prone	Widely distributed; moderate drought tolerance
<i>Merremia dissecta</i>	PIAP IAP	Perennial	Disturbed areas	Vine	C3	Sensitive	Moderate	172,273	1,165,983	-12.6	100.0	43.7	Woody/Vine	Expansion-prone	Rapid colonization potential; disturbed habitat specialist
<i>Neltuma juliflora</i>	IAP	Perennial	Disturbed areas	Tree	C3	Tolerant	Tolerant	550,448	827,635	-42.4	71.0	14.3	Woody	Expansion-prone	Moderate drought tolerance

Full Name	Weed/ IAP /PIAP	Lifecycle	Habitat type	Growth form	Photosynthetic Pathway	Sensitivity to Salinity	Sensitivity to Drought	Loss (km ²)	Gain (km ²)	Net Change (%)	Net Change SD	Mean Net Change Proportion	Functional Group	Expected Climate Response	Notes
<i>Opuntia ficus-indica</i>	IAP	Perennial	Arid areas	Cactus	CAM	Tolerant	Tolerant	360,754	988,093	-27.4	84.7	28.7	Succulent	Expansion-prone	Drought-tolerant cactus; benefits from warming
<i>Orobancha aegyptiaca</i>	Weed	Annual	Parasitic	Herb/Parasite	None	Sensitive	Sensitive	827,635	500,001	-64.2	42.9	-10.7	Parasitic	Contraction-prone	Parasitic; climate-sensitive
<i>Phalaris minor</i>	Weed	Annual	Grasslands	Grass	C3	Sensitive	Sensitive	404,101	981,633	-30.8	84.2	26.7	Annual Grass	Expansion-prone	Widely distributed grass; drought-tolerant
<i>Pistia stratiotes</i>	IAP	Perennial	Aquatic	Floating Herb	C3	Sensitive	Sensitive	594,129	768,869	-45.8	65.9	10.1	Aquatic	Contraction-prone	Floating aquatic; water-limited
<i>Polygonum aviculare</i>	Weed	Annual	Disturbed areas	Herb	C3	Sensitive	Moderate	560,777	752,602	-43.2	64.5	10.7	Annual	Expansion-prone	Ruderal; moderate tolerance
<i>Pontederia crassipes</i>	IAP	Perennial	Aquatic	Floating Herb	C3	Sensitive	Sensitive	750,062	608,749	-58.1	52.2	-2.9	Aquatic	Contraction-prone	Aquatic specialist; sensitive to warming
<i>Portulaca oleracea</i>	Weed	Annual	Disturbed areas	Herb	C4	Tolerant	Tolerant	710,808	667,485	-55.0	57.2	1.1	Annual	Expansion-prone	Ruderal; C4 physiology enhances drought tolerance
<i>Pueraria montana</i>	PIAP IAP	Perennial	Disturbed areas	Vine	C3	Sensitive	Moderate	0	0	0	0	0	Woody Vine	Stable	Not predicted to expand or contract
<i>Rapistrum rugosum</i>	Weed	Annual	Disturbed areas	Herb	C3	Sensitive	Sensitive	579,462	906,753	-44.6	77.8	16.6	Annual	Expansion-prone	Ruderal; high colonization potential
<i>Secale cereale</i>	Weed	Annual	Fields	Grass	C3	Sensitive	Tolerant	576,011	805,289	-44.4	69.1	12.3	Annual Grass	Expansion-prone	Widely cultivated; high colonization capacity
<i>Sesuvium portulacastrum</i>	IAP	Perennial	Coastal	Herb	C3	Tolerant	Tolerant	772,131	570,021	-59.8	48.9	-5.5	Coastal Herb	Contraction-prone	Coastal specialist; limited expansion

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