Article
The Adaptive Capacity of Alien and Rare Species in China
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Abstract: Alien and rare plants tend to adapt to contrasting biotic and abiotic conditions. However, the adaptability assessments of alien and rare plants using biological and habitat characteristics in stressful and disturbed environments are limited. We collected and demonstrated the biological and habitat characteristics and assessed the adaptive capacity of alien and rare plants in China using the analytic hierarchy process. Biological characteristics, such as dispersal strategy, sexual and asexual reproduction modes, life form, and habitat characteristics (e.g., habitat type and distribution spatial extent), are important indicators of the adaptability of alien and rare plants to stressful and disturbed environments. Alien plants have a higher adaptive capacity to disturbed environments than rare plants, while rare plants have a higher adaptive capacity to stressful environments than alien plants. Stressful and disturbed environments constrain the adaptive capacity of alien and rare plants, respectively. However, the constraint on alien plants from stressful environments is weaker than that on rare plants from disturbed environments. Understanding the adaptive capacity of alien and rare plants will help researchers and policymakers develop strategies for preventing the invasion of alien plants as well as protecting rare and endangered plants.

Keywords: analytic hierarchy process; dispersal strategy; distribution spatial extent; life form; habitat type; reproductive mode; stressful environments; disturbed environments

1. Introduction
Alien plants have received great attention because of the possible threats they pose to the biodiversity, structure, function, and stability of ecosystems, as well as to society and the economy [1–3]. Alien plants may dominate an area after introduction, naturalization, and spread [4]. Rare plants are at risk of extinction, if they, for example, have a restricted range, occur only in one or few specific habitats, or maintain small populations. [5]. Habitat changes resulting from natural and anthropogenic disturbances pose high pressure on rare plants [6–8]. Alien and rare plants tend to occupy very different environments and exhibit different functional traits [9,10]. Therefore, the contrasting characteristics of the alien and rare plants can help to reveal adaptive mechanisms of invasiveness or extinction in new environments. Previous studies have defined adaptive capacity as the capacity or potential of a system, organism, or community to adapt to new climate conditions and other changing abiotic factors [11–14]. Considering this definition, we defined the adaptive capacity of alien and rare plants as their tolerance to possible disturbed and stressful environments based on their biological and habitat characteristics.
Dispersal strategy (e.g., autochory, anemochory, hydrochory, zoochory, and anthropochory), reproductive mode (e.g., seed, ramet, rhizome, and budding), and life forms (e.g., annual herbs, biennial herbs, perennial herbs, vines, shrubs, and trees), as well as other closely related factors, are important biological indicators for assessing adaptive capacity. Firstly, dispersal strategies are important for the diaspores of alien and rare plants to use natural and anthropogenic dispersal agents arriving in a new environment [15–19]. Some diaspores with special structures have multiple reproduction modes for successful dispersal [20]. Generally, a diaspore that has multiple modes might have advantages to extend the dispersal distance and adapt to new environments [21]. Secondly, the sexual and asexual reproduction mode of plants is a result of long-term response to the environment [22]. Sexual reproduction can increase offspring diversity, while asexual reproduction is highly efficient in terms of the energy and time requirements [23,24]. Multiple modes of sexual and asexual reproduction present trade-offs between the two reproduction modes under different environmental conditions [24]. Finally, life form (or growth form) that is a characteristic of plants’ adaptation to ecological conditions [25] is key for estimating adaptability to a new environment [26].

Habitat type and distribution scale are important habitat characteristics for assessing adaptive capacity [27,28]. Differences in the habitat type exploited by plants reflect differences in species’ traits [29]. Plants thriving in different habitats may have the capacity to tolerate high disturbance and stress [27]. The plant distribution spatial extent might be a result of the adaptive capacity to different biotic and abiotic conditions. For example, plants distributed in large areas, such as Acacia nilotica [28], might have a higher adaptive capacity than those distributed in small areas, such as Manihot walkerae [8].

Adaptive capacity of plants often involves response or tolerance to disturbed and stressful environments. Disturbances resulting from natural disasters (e.g., earthquakes, volcanic eruptions, wildfires, and windstorms), climate change (e.g., global warming and El Niño events), and anthropogenic activities (e.g., land reclamation, deforestation, grazing, and mowing) often facilitate the occupation and expansion of plants by creating bare patches (Table S1 in the Supplementary Materials) [30–33]. On the other hand, disturbances that result in habitat degradation, fragmentation, loss, and change in distribution range threaten plants that are sensitive to environmental changes [6,34,35]. Heavily disturbed environments generally include cutting blank, burned blank, desertified land, abandoned land, dumping sites, polluted lakes, heavily grazed grassland, and derelict mines (Table S1 in the Supplementary Materials). In contrast with disturbance, stressful environments (e.g., deep valley, cliff, treetop, and forest understory) might result in the suppression of plants to obtain water, sunlight, and nutrients [36,37]. Nevertheless, stressful environments provide stable conditions for plants to grow if they respond with an effective phenotypic plasticity strategy [38,39]. Comparisons of the adaptive capacity of alien and rare plants using biological and habitat characteristics in stressful and disturbed environments are limited.

We collected plant information, including dispersal strategy, the number of dispersal strategies of a plant, distribution spatial extent, life form, habitat type, the number of habitats of a plant, reproductive mode, and the number of sexual and asexual reproduction modes of a plant to assess the adaptive capacity of alien and rare plants in disturbed and stressful environments using the analytic hierarchy process. Our aim was to answer why the distribution of alien plants may tend to expand whereas that of rare plants tends to stay constant or shrink.

2. Materials and Methods

2.1. Biological Characteristics of Alien and Rare Plants

We retrieved all 562 alien plants from The Checklist of the Chinese Invasive Plants [40] and all 1898 rare plants recorded in the information system of the Chinese Rare and Endangered Plants (http://www.iplant.cn/rep/ (accessed on 30 October 2021)). The alien plants were defined as six invasive ranks, i.e., malignant invaders, serious invaders, local invaders, mild invaders, requiring further observation, and cultivated aliens, based on their
distribution spatial extent, distribution characteristics, and economic losses caused (Table S2 in the Supplementary Materials). The rare plants were categorized into eight extinction risk statuses, i.e., Extinct in the Wild (EW), Critically Endangered (CE), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), Data Deficient (DD), and Not Evaluated (NE), based on the International Union for Conservation of Nature (IUCN) Red List (Table S3 in the Supplementary Materials).

Based on previous reports, we listed five dispersal strategies (by five dispersal agents) for alien and rare plants: autochory (by weight, elasticity, blasting force, etc. without agents), anemochory (by wind), hydrochory (by water), zoochory (by animals), and anthropochory (by humans) (Table S4 in the Supplementary Materials) [16,41,42]. Dispersal strategies and the number of dispersal strategies of alien and rare plants were determined based on morphological traits of diaspores, published literature, and Baidupedia (https://baike.baidu.com (accessed on 31 October 2021)). The Flora of China (http://www.iplant.cn/foc/ (accessed on 30 October 2021)), Diaspore Information Database from the Royal Botanic Gardens (http://data.kew.org/sid/ (accessed on 11 November 2021)), and the database of plants from the United States (https://plants.usda.gov/java/ (accessed on 22 October 2022)) were used to collect the diaspore morphological traits of alien and rare plants. We defined the percentage of dispersal strategy as the total number of each dispersal strategy to the total number of five dispersal strategies in all species of alien or rare plants.

Based on the database of Flora of China and Baidupedia, the sexual and asexual reproduction modes of the alien and rare plants were categorized into five modes: (1) spores or seeds, (2) ramets, (3) cutting, layering, or grafting (human-mediated reproduction mode applied to cultivated alien plants), (4) rhizome, and (5) budding. We classified the number of sexual and asexual reproduction modes of a plant into four categories: one, two, three, and above three modes. We defined the percentage of sexual and asexual reproduction modes as the total number of each reproduction mode to the total number of sexual and asexual reproduction modes in all species of alien or rare plants. Based on the Flora of China database, alien and rare plants were classified into five life forms: annual and biennial herb, perennial herb, vine, shrub, and tree [43–45].

2.2. Habitat Characteristics of Alien and Rare Plants

According to the Flora of China, habitats of alien and rare plants can be grouped into 10 types from dry to wet conditions: (1) deserts or desert steppes, (2) steppes or dry hillsides, (3) waysides, near villages or wastelands, (4) farm lands, (5) meadow steppes or grasslands, 6) exposed rocks and crevices or tree tops, (7) forest edges, shrublands, or jungles, (8) rivers, lake banks, or benches, (9) marshes, wet meadows, or paddy fields, and (10) in water. Many alien and rare plants live in various habitats. Therefore, the number of plant habitats was counted as an indicator to assess the adaptive capacity of the plant. We classified the number of plant habitats into four categories: one type, two type, three type, and above three type.

The geographical distributions of alien and rare plants in different counties, municipalities, provinces, and autonomous regions were collected from the Flora of China database (http://www.iplant.cn/foc/ (accessed on 22 October 2022)) and The Checklist of the Chinese Invasive Plants. The total distribution area of an alien or rare plant was calculated according to their geographical distributions. Based on our data, we defined a distribution area of less than $5 \times 10^4$ km$^2$ as county scale, $5–35 \times 10^4$ km$^2$ as municipal scale, $35–150 \times 10^4$ km$^2$ as provincial scale or autonomous regions, and more than $150 \times 10^4$ km$^2$ as the national scale.

2.3. Assessment of the Adaptive Capacities of Alien and Rare Plants in Disturbed and Stressful Environments

We established an index system using the plant biological and habitat characteristics (eight primary indicators) and their levels (41 secondary indicators) to assess the adaptive capacity of alien and rare plants (Figure S1 and S2, Table S5–S7 in the Supplementary Materials).
Materials). Using the analytic hierarchy process [46], comparing the relative importance of the primary indicators and their secondary indicators according to experts’ opinions, we established comparison matrices of the primary and secondary indicators using a numerical scale from 1 to 5 (Table S5 in the Supplementary Materials) in stressful (Equations (1)–(9) in the Supplementary Materials) and disturbed (Equations (10)–(18) in the Supplementary Materials) environments, respectively. Based on the comparison matrices, we calculated the weight vectors of primary and secondary indicators in stressful (Equations (20)–(28) in the Supplementary Materials) and disturbed (Equations (29)–(37) in the Supplementary Materials) environments, respectively. Scores of secondary indicators were calculated by multiplying the weight of the primary indicators with that of the secondary indicators (Equations (38) in the Supplementary Materials). The scores of secondary indicators are dimensionless and normalized corresponding to the biological and habitat characteristics of the alien and rare plants. Therefore, we defined the adaptive capacity of an alien or endangered plant as the score obtained by adding the corresponding scores of biological and habitat characteristics of plants in stressful and disturbed environments, respectively (Table S7 in the Supplementary Materials).

2.4. Data Analysis

The two-sample Kolmogorov–Smirnov (KS) test was used to analyze the consistency of distribution in the adaptive capacity of alien and rare plants in stressful and disturbed environments using R 4.1.2 (2021). One-way analysis of variance (ANOVA) and multiple comparisons (Duncan’s tests) were conducted to test differences of adaptive capacity of alien and rare plants using the “tidyverse” and “agricolae” packages in R. All data are presented as the mean values ± standard deviation (SD).

We used R to normalize the comparison matrix of the primary and secondary indicators in disturbed and stressful environments to obtain the maximum eigenvalues of the matrix, to test the consistency of the comparison matrix, and to calculate the weight vector of primary and secondary indicators in disturbed and stressful environments.

Histograms of the percentage of dispersal strategy, number of dispersal strategies of a plant, reproductive mode, number of sexual and asexual reproduction modes of a plant, life form, habitat type, number of habitats of a plant, and distribution spatial extent of the alien and rare plants were illustrated using the ggplot2 package in R. We used the estimated standard error of rate (1) to estimate the standard error of the percentages.

\[ S_p = \sqrt{\frac{p(1-p)}{n}} \]  

Here, \( S_p \) is estimated standard error of rate; \( p \) is sample rate; \( n \) is sample size.

3. Results

3.1. Biological Characteristics of Alien and Rare Plants

Anthropochory, zoochory, and autochory were the main dispersal strategies, accounting for 60.3%, 19.1%, and 17.0% of alien plants, and 52.5%, 4.8%, and 41.1% of rare plants, respectively. The percentages of anthropochory and zoochory in alien plants were higher than those in rare plants. However, the percentage of autochory in rare plants was higher than that in alien plants (Figure 1a,b).
Sexual reproduction (71.7%) was the dominant reproduction mode in alien plants (Figure 2c). In contrast, most rare plants used two reproduction modes (i.e., coexistence of sexual and asexual reproduction modes, 73.2%) (Figure 2d).

Higher proportion of alien species have multiple dispersal modes. For example, most alien species (71.7%) use more than four dispersal strategies (Figure 1c), while the vast majority of rare plants use up to three dispersal strategies (92.3%) (Figure 1d).

Spores or seeds (72.9%) were the main reproduction modes of alien plants (Figure 2a), whereas spores or seeds (48.1%) and ramets (32.8%) were the main reproduction modes of rare plants (Figure 2b).

Figure 1. Percentage of dispersal strategies and the number of dispersal strategies of a plant. Percentage of dispersal strategy of alien plants (a) and rare plants (b); percentage of the number of dispersal strategies of a plant of alien plants (c) and rare plants (d). Aut, autochory; Ane, anemochory; Hyd, hydrochory; Zoo, zoochory; Ant, anthropochory; One or two, one or two modes; Three, three modes; Four, four modes; Above three, more than four modes. Error bars represent standard error.

Figure 2. Percentage of reproduction modes and the number of reproduction modes of a plant. Percentage of reproductive mode of alien plants (a) and rare plants (b); percentage of the number of reproduction modes of a plant of alien plants (c) and rare plants (d). Sp or Se, spore or seed; Ram, ramet; Cu or La or Gr, cutting or layering or grafting; Rhi, rhizome; Bud, budding; One, one mode; Two, two modes; Three, three modes; Above three, more than three modes. Error bars represent standard error.
Annual and biennial herbs as well as perennial herbs were the main life forms (accounting for 80.2% in total) in alien plants (Figure 3a), whereas perennial herbs (80.6%) and trees (10.8%) were the main life forms in rare plants (Figure 3b).

**Figure 3.** Percentage of life forms of alien (a) and rare plants (b). An and Bi, annual and biennial herb; Per, perennial herb; Vin, vines; Shr, shrubs; Tre, trees. Error bars represent standard error.

### 3.2. Habitat Characteristics of Alien and Rare Plants

Alien plants are mainly found on the wayside, near villages or wasteland (C, 30.8%); farmland (D, 30.2%); and forest edges, shrubland, or jungle (G, 17.8%) (Figure 4a), while rare plants are mainly found in exposed rocks and crevices or on tree tops (F, 35.6%), and forest edges, shrubland, or jungle (G, 52.9%) (Figure 4b). Both alien and rare plants tend to occupy only a few habitats (up to two, summed percentages 70.8% and 87.8%, respectively) (Figure 4c,d).

**Figure 4.** Percentage of habitat types and the number of habitats of a plant. Percentage of habitat type of alien (a) and rare plants (b); percentage of the number of habitats of a plant of alien (c) and rare plants (d). A, desert or desert steppe; B, steppe or dry hillside; C, wayside, near the village or wasteland; D,
farm land; E, meadow steppe or grassland; F, exposed rocks and crevices or tree top; G, forest edge, shrubland, or jungle; H, river, lake bank or bench; I, marshes, wet meadows or paddy field; J, in water; One, one type; Two, two types; Three, three types; Above three, more than three types. Error bars represent standard error.

The percentages of alien plants distributed on the provincial and national scales were 37.2% and 61.9%, respectively (Figure 5a), whereas rare plants were mainly distributed at the county scale (20.9%), municipal scale (29.4%), and provincial scale (38.0%), with only 11.6% at the national scale (Figure 5b).

3.3. Assessment of Adaptive Capacity of Alien and Rare Plants to Low and Highly Disturbed Environments

Significant differences in adaptive capacity ($p < 0.01$) were found across alien and rare plants in both stressful and disturbed environments. The adaptive capacity of alien plants (0.21) in stressful environments was significantly lower than that in disturbed environments (0.28) ($F = 1352, p < 0.01$). However, the adaptive capacity of the rare plants in stressful environments (0.22) was significantly higher ($F = 455.7, p < 0.01$) than that in the disturbed environments (0.20) (Figure 6). In a stressful environment, the adaptive capacity of rare plants was significantly higher than that of alien plants ($F = 25.3, p < 0.01$). In a disturbed environment, the adaptive capacity of rare plants was significantly lower than that of alien plants ($F = 2933, p < 0.01$) (Figure 6).
4. Discussion

4.1. Effect of Biological Characteristics on Adaptive Capacity of Alien and Rare Plants

Dispersal strategies are important for the adaptation of alien and rare plants to stressful and disturbed environments. Our results show that anthropochory is the most important dispersal strategy for alien and rare plants to adapt to disturbed environments (Figure 1). However, anthropochory in alien plants is mainly unintentional (e.g., hidden in goods, cars, hay, or accidentally mixed with grain) [47] and in rare plants it is intentional (e.g., sold for agriculture and gardening) because more than 60% of the rare plants are Orchidaceous and medicinal plants, which are often cultivated and traded. Zoorchory is used more by alien plants for diasporas with spiny or hooked appendages, facilitating spread in disturbed environments [16, 47]. The higher percentage of zoorchory in alien plants than in rare plants might be due to greater access to animals in their habitats. Autochory has a short dispersal distance, dispersed by gravity or plants themselves, and tends to be utilized by rare plants in stressful environments [47]. Alien plants tend to have multiple dispersal modes for long-distance dispersal to extend habitats [47], whereas rare plants tend to have fewer or shorter dispersal strategies for maintaining and adapting to stable and stressful environments [48].

Sexual reproduction modes are crucial for alien plants to expand in disturbed environments and asexual reproduction modes are crucial for rare plants to survive in stressful environments. Sexual reproduction increases offspring diversity (new genetic recombination), decreases mutational load, increases adaptive potential to environmental variation and disturbances, and increases dispersal potential for the colonization of new environments [22, 24, 49]. Asexual reproduction (clonal growth) increases reproductive assurance (persistence of successful genotypes) to colonize stressful environments [24, 49, 50]. A higher rate of sexual reproduction (spore or seed) and one reproductive mode are used by alien plants to adapt to a highly disturbed environment and spread to new habitats. Many of the alien species have both sexual and asexual reproduction modes, e.g., Sporobolus alterniflorus, Solidago canadensis, and Alternanthera philoxeroides [51]. In contrast, higher rates of asexual reproduction (nearly the same sexual reproduction) and two sexual and asexual reproduction modes are adopted by rare plants to adapt to stressful environments.

Plant life form (or growth form) plays an important role in plant adaptive strategies in response to climate variables, such as temperature or precipitation [25, 52]. Consistent with
our expectation, alien plants are characterized by a high proportion of annual and biennial herbs in disturbed environments [40,53]. Rare plants are characterized by more perennial herbs and trees in stressful environments [54]. Annual and biennial herbs, with light and large amounts of seeds, facilitate the spread and invasion of plants, whereas perennial herbs and trees, when accompanied by low germination [55,56] or underdeveloped embryo [57] of seeds, do not support plant invasion [40].

In summary, the effect of biological characteristics on the adaptive capacity of alien and rare plants can explain why habitat areas of alien plants tend to expand, while that of rare plants remain constant or shrinks.

4.2. Effect of Habitat Characteristics on Adaptive Capacity of Alien and Rare Plants

Our results show that most alien plants tend to live in disturbed habitats (e.g., waysides, wastelands, and farmlands), which is consistent with previous studies reporting that alien plants tend to invade highly disturbed habitats [29]. The capacity of alien plants to adapt to these habitats largely depends on their biological characteristics, for example, small seed mass, short juvenile stage, and rapid population growth [4,53]. Disturbances often facilitate the successful establishment and spread of alien species by creating open spaces or making resources available [32,33]. Therefore, the adaptive capacity of alien plants is higher (0.08, \( p < 0.01 \)) than that of native plants in highly disturbed habitats.

Our results suggest that rare plants tend to live in highly stressful habitats with limited light, water, nutrition, and space (e.g., exposed rocks and crevices, treetops, and jungles) [58,59]. Consequently, they have a reduced ability to adapt to changing environmental conditions resulting from climatic or anthropogenic disturbances (e.g., habitat degradation, fragmentation, and habitat migration) [6]. Therefore, rare plants may have a higher adaptive capacity in high-stress environments.

Our results show that alien plants tend to occupy more habitats than rare plants. Therefore, alien plants are multi-habitat species that can utilize and thrive in heterogeneous habitats [60]. In contrast, rare plants occur mostly in one or a few specific habitats with small populations [7]. Therefore, rare plants are at a greater risk of extinction once their habitat is in danger of degradation, fragmentation, and loss [7,61,62].

Our results show that many alien plants have the potential to spread over a considerable area (mostly beyond provincial and national scales), which is closely related to the invasiveness of those invasive alien plants [17,63]. Furthermore, intense, constant, and stretched anthropogenic disturbances may be important for the distribution of alien plants [64]. In contrast, rare plants mostly have a narrow distribution range (mostly below the provincial scale), which is often attributed to their vulnerability to climatic variation, habitat loss, overexploitation of resources, and competition with invasive species [35].

Plants might develop local adaptation and phenotypic plasticity to gain an advantage in surviving in heterogeneous environments, adapting to environmental stress and acquiring essential resources [65,66]. In general, phenotypic plasticity responses to environmental changes are followed by local adaptations [67]. Alien plants with higher adaptive capacity to highly disturbed environments than rare plants are able to thrive because they develop local adaptation (e.g., mostly zoochory and anthropochory in seed dispersal, one sexual reproductive mode, and annual and biennial herbs in life form) to acclimate to variable conditions [66,68]. In comparison, the higher adaptive capacity to a high-stress environment seen in rare plants might be due to local adaptation (e.g., largely autochory in seed dispersal and a high rate of clonal reproduction modes) to acclimate to stressful conditions [38,67]. In addition, rare plants tend to adapt to static stresses (e.g., barren, altitude, shade, and aridness), resulting in ecological specialization in stressful environments [38,69]. Alien plants have also been restrained in stressful environments; however, they adapt to such conditions not only through local adaption (genotype change) and phenotypic plasticity but also by migrating to survive, invade, and spread [70].
5. Conclusions

Assessment of the biological (e.g., dispersal strategy, reproductive mode, life form, etc.) and habitat (e.g., habitat type and distribution spatial extent) characteristics of alien and rare plants can demonstrate their adaptive capacity in stressful and disturbed environments. We found alien plants gain advantages in disturbed environments and become restricted in stressful environments, whereas rare plants gain advantages in stressful environments and do not occupy disturbed environments. Understanding the biological and habitat characteristics of alien and rare plants, as well as their adaptive capacity, can help ecologists, conservationists, and policy makers assess and predict community dynamics. Such information is also critical in preventing the invasion of alien plants and protecting rare plants.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f13122005/s1, Table S1: Characteristics of disturbances and stresses in disturbed and stressful environments used in this study, Table S2: Definition of six invasive ranks and their perspective percentage of alien plant species in China (adapted from Zhou et al., 2020), Table S3: Categories of Chinese rare species (1898) based on International Union for Conservation of Nature (IUCN) Red List, Table S4: Five dispersal strategies and 21 dispersal modes of diaspores based on previous literature (Adapted from Zhou Q, 2020), Table S5: Numerical scale for pairwise comparison, Table S6: Random coincidence index value (RI), Table S7: Assessment indices system of adaptive capacity of alien and rare plants in stressful and disturbed environment and weight vector of primary and secondary indicators as well as score of the secondary indicators, Figure S1: Steps of analytic hierarchy process (AHP) method for evaluation of adaptive capacity of alien and rare plants to environment, Figure S2: Assessment indices system of adaptive capacity to environment.

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Conflicts of Interest: The authors declare that they have no competing interests.

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