ABSTRACT: The species richness of naturalized flora in Taiwan has continued to increase over the past decade. To understand the recent dynamics of naturalization, we updated the checklist of naturalized plants and investigated their chronology, taxonomic distributions, life histories, origins, and invasive risks. One hundred thirty-five species were newly added, and 58 species were excluded owing to a lack of clear evidence of naturalization. The number of naturalized species per decade has gradually increased, peaking in the 2000s (144 species), and declining remarkably in the 2010s (63 species). Poaceae, Asteraceae, and Fabaceae were the most species-rich families, consistent with the global patterns of naturalized alien flora. These exotic species were primarily perennial herbs, followed by annual herbs and shrubs. America has been the most consistent source of naturalized species over the past 160 years. Although the naturalization rate has decreased in the last decade, a few potential invaders (i.e., species with extremely high risk scores) are still worthy of further monitoring and management.

KEY WORDS: Exotic species, invasive species, islands, life history, naturalized species, regional flora, taxonomical distribution.

INTRODUCTION

Human activities are causing increasing similarities in species composition among biological communities worldwide by transporting and introducing species out of their natural ranges and across biogeographic barriers. Among the species introduced to new regions, a proportion of them establish viable populations and a small subset becomes invasive, exerting strong effects on ecosystem processes in their new environment (Thompson et al., 1995; Rejmanek and Richardson, 1996; Richardson and Pyšek, 2012). Naturalization has been recognized as the first phase of biological invasions. The biological attributes, geographic distribution, and chronographic information of naturalized flora provide insights into the overall patterns of potential invaders (Wu et al., 2004a; Pyšek et al., 2010; Essl et al., 2020).

In Taiwan, the checklist of naturalized flora was first compiled in 2004 (Wu et al., 2004b) and then updated in 2010 (Wu et al., 2010), which cataloged 624 naturalized species belonging to 371 genera and 87 families. The average naturalization rate was 4.2 species/year from 1860 to 2008, with a much higher rate (12.8 species/year) observed between 2002 and 2008. The naturalized species mainly comprise herbaceous plants (approximately 80%; 486 species), followed by shrubs and vines. Poaceae, Fabaceae, and Asteraceae are the most species-rich families in naturalized flora. Most species naturalized in Taiwan originated in America, followed by Asia and Europe. Because the number of species naturalized in Taiwan has continued to increase in the past decade (e.g., Su and Hassemer, 2019; Taiwan Pteridophyte Group, 2019; Liao et al., 2020), we decided to update the checklist of naturalized flora by reviewing recent reports on naturalized plants between 2009 and 2020 and verifying the naturalization status of all species in the list. We also aimed to examine the life forms, habits, and origins of naturalized species, and investigate the temporal variation in naturalization rates over the past 160 years to understand the dynamics of naturalization.

MATERIALS AND METHODS

Study area

Taiwan is a subtropical island located in the Western Pacific Rim. This island is approximately 36,000 km² in area, two-thirds of which is covered by hills and mountains that are 500–3,952 m high. The varying climate along the altitudinal gradient supports evergreen broadleaf forests below ca. 1000 m, mixed forests at ca. 1,000–2,500 m, and evergreen coniferous forests and subalpine grasslands above ca. 2,500 m a.s.l. More than 4,200 native and naturalized plant species have been reported in Taiwan, and about a quarter of them are endemic to Taiwan (Hsieh, 2002).

Naturalized species

To update the previously compiled checklist of naturalized flora in Taiwan (Wu et al., 2004b; Wu et al., 2010), we reviewed all relevant journal articles and government publications and documents between 2009 and 2020, including the Red List of Vascular Plants in Taiwan, 2017 (Editorial Committee of the Red List of Vascular Plants of Taiwan, 2017). We compiled all species exotic to Taiwan, designated as naturalized, escaped after cultivation, or invasive. We then verified the naturalization status of these alien species by reviewing the records from three main herbaria (TAI,
We did not consider introduced or cultivated species as naturalized species if there was no evidence of escape. The records of naturalized plant species mentioned in the non-peer-reviewed literature or amateur records were not considered. We also excluded species with unreliable records from the previous checklist according to the following criteria: (1) the species were considered native species in the peer-reviewed literature; (2) there was no peer-reviewed literature that described the species as naturalized species, and the geographic distribution of this species is close to Taiwan; and (3) it is a cultivar.

For each naturalized species, we obtained its life form, habit, origin, year of the first record, mode or purpose of introduction, and global risk score from Randall (2017) (Table S1). We defined the year of the first record as the year of its first herbarium record or first documentation. The global weed risk score was obtained from Randall (2017), who considered the primary pathways by which plants enter new regions, the major dispersal mechanisms from an initial point of establishment, and the potential impact of the weeds. The risk score ranges from 0 to 64 and can be classified into four levels: low (>0–6), medium (7–15), high (16–31), and extremely high (32–64) (Randall, 2016).

The family names used in the following analysis and Table S1 and S3 are based on Pteridophyte Phylogenetic Group I (PPG I, 2016) and Angiosperm Phylogeny Group IV (APG IV, 2016). The family names used in the Flora of Taiwan are also provided in the Supplement for the sake of convenience, allowing readers to track the plant names used in the previous catalogs.

RESULTS AND DISCUSSION

Accumulation of naturalized flora

The updated checklist of naturalized flora in Taiwan included 695 species from 400 genera and 95 families (Table S1), 135 of these species were newly added. Among these additional species, only 79 species were naturalized after 2009; the other 56 species were naturalized before 2009 but documented after 2009. The accumulation of naturalized plants between 2001 and 2010 was much faster than that at any other time interval over the past 160 years (Fig. 1A). The number of naturalized species per decade increased gradually from 1961 to 2000, peaked in the 2000s (144 species), and declined remarkably after 2010 (Fig. 1B). From 2011 to 2020, the first records of 63 species were documented. Notably, we also updated the scientific names of 61 species according to the Catalogue of Life in Taiwan (Chung and Shao, 2021) and the World Flora Online (http://www.worldfloraonline.org) in the newly compiled checklist (Table S2).

We did not include 49 species listed in the Red List of Vascular Plants of Taiwan, 2017 (Editorial Committee of the Red List of Vascular Plants of Taiwan, 2017) because no peer-reviewed literature has documented their morphology, habits, habitats, geographic distribution, illustrations, and citations of herbarium collections. We placed these species in Table S3 because their naturalization status was uncertain.

We excluded 58 species from the 2010 checklist because there was no clear evidence of their naturalization (Table S4). Most of these species are annual or perennial herbs. The first records of three-quarters of the excluded species were documented before 1940, and there was no peer-reviewed literature that regarded them as naturalized species. Additionally, their geographic distribution was primarily in regions close to Taiwan. For example, Heliotropium indicum (Boraginaceae) was first documented by Forbes and Hemsley (1890) and is widely distributed in tropical Asia. Likewise, Capsella bursapastoris (Brassicaceae) was first recorded by Matsumura and Hayata (1906) and is of wide-distribution in Asia, Europe, and Africa with numerous specimens collected in China, Japan, and Taiwan. Another example is Sapium sebiferum (Euphorbiaceae), which was reported by Forbes and Hemsley (1894) and is widely distributed in Southern China. Moreover, some species have been described as native species in peer-reviewed literature [e.g., Acmella paniculata (Asteraceae) in Chung et al. (2008), Neptunia gracilis (Fabaceae) in Huang and Huang (1996), and Limnophila heterophylla (Scrophulariaceae) in Yang and Yen (1997)]. The reasons of exclusion from the checklist for each species are listed in Table S4.

Several factors may explain the naturalization rate changes observed since the 1960s, including economic
development and increasing international trade. At both regional and global levels, the richness of alien plants increases with the gross domestic product (GDP) or per capita GDP (Liu et al., 2005; Hulme, 2009; Pyšek et al., 2017), which reflects the levels of international trade and infrastructure (Levine and D’antonio, 2003; Hulme, 2009; Pyšek et al., 2010). Thus, economic development may contribute to the accumulation of naturalized flora in Taiwan. The substantial increase in the number of naturalized species in the 2000s might be associated with the country’s entry into World Trade Organization in 2002 and the warming relationships between Taiwan and China (Wu et al., 2010). However, the naturalization rates have been proposed to decrease after a certain threshold GDP because most developed economies allocate additional resources to biosecurity (Pyšek et al., 2017); this finding could explain the decrease in the number of naturalized species after 2010.

**Taxonomic distributions**

In our updated checklist, Poaceae was the most species-rich family (97 species), followed by Asteraceae (93 species), Fabaceae (79 species), Solanaceae (30 species), and Convulvulaceae (27 species) (Fig. 2A). These five families constitute nearly half (47%) of the naturalized flora in Taiwan. Except for Solanaceae, the remaining four families plus Malvaceae were the primary contributors to the newly added naturalized species in this study (Fig. 2A). The dominant genera remained the same over the past decade as that in the previously compiled checklist; these genera include *Ipomoea, Solanum, Amaranthus, Crotalaria, Paspalum*, and *Senna* (Fig. 2B).

The major families of naturalized flora in Taiwan are in agreement with the global patterns of naturalized alien flora (Pyšek et al., 2017). Although the dominance of Asteraceae in Taiwan reflects its global species richness, Poaceae and Fabaceae are usually over-represented among the species-rich families in the naturalized flora. In addition to these three families, Convulvulaceae and Malvaceae have been particularly abundant among the naturalized species on islands (Pyšek et al., 2017). The over-representation of Convulvulaceae is primarily due to the large genus *Ipomoea*, whose phenology and breeding systems may contribute to its success at naturalization in Taiwan (Chao et al., 2019).

Among the newly added members of the naturalized flora, most of the genera (95 out of 112) and families (27 out of 52) contained only one naturalized species. Furthermore, 29 genera and one family (Linaceae) were new to Taiwan. The species belonging to such exotic genera may experience less competition because they do not interact with native congeners (Wu et al., 2004a) or less herbivory than naturalized species closely related to natives (Hill and Kotanen, 2009). In contrast, *Eriochloa,
Hibiscus, Merremia, Urochloa, and Utricularia were the only five genera with more than two new naturalized species. Insufficient taxonomic efforts may delay the documentation processes for these naturalized plants of these taxa. Nevertheless, these neglected genera highlight another aspect of potential invaders and deserve more attention.

Life histories and origins
The naturalized flora was primarily represented by perennial herbs (44.0%), followed by annual herbs (28.0%), shrubs (9.2%), trees (5.9%), and perennial vines (5.6%) (Fig. 3). Most naturalized species are from America, followed by Asia, Africa, and Europe. America has been the most consistent contributor of naturalized species over the past 160 years (Fig. 4). The major life histories and origins of naturalized species remained unchanged from those recorded in the previously compiled checklist, suggesting that the environment and climate in Taiwan favor certain groups of alien plants (Wu et al., 2010). The over-representation of perennial herbs can be related to a few typical traits, such as greater dispersal ability, seed bank formation ability, and short generation time (Pyšek and Hulme, 2005; Gioria and Pyšek, 2016). The geographic origins of the naturalized plants in Taiwan are also relatively similar to those of the naturalized plants in neighboring regions, such as Japan, Hong Kong, and China (Corlett, 1992; Miyawaki and Washitani, 2004; Jiang et al., 2011; Ryu et al., 2017). Such a high proportion of species originating from America may be due to similar climate between Taiwan and Tropical America. Furthermore, a high exchange of trade between Taiwan and neighboring regions could be attributable to the increased proportion of naturalized plants shared by Taiwan with China and Japan (Wu et al., 2010).

Potential risk of weedingness
Global weed risk scores were available for 548 of 695 (79%) naturalized species. Among them, 40% of the species had high to extremely high risk scores (>15). Leucaena leucocephala (Fabaceae), the species with the highest risk score (64), was first recorded in Taiwan in 1916 (Fig. 5). The median values of the weed risk scores of the naturalized species in Taiwan gradually decreased from 1951 to 2020 (Fig. 5), but there were still a few species with extremely high risk scores (>30) introduced after 1991, which might be potential invaders in Taiwan. Ninety-eight naturalized plant species were also listed in the global invasive species database, and four of them (Cecropia peltata, Cirsium vulgare, Sagina procumbens, and Solanum viarum) were naturalized after 2010 (Table S1). Because these species may still be in the early phase of plant invasion and might have potential environmental and economic impacts in Taiwan in the near future, long-term monitoring and proper management plans for these species are urgently needed.
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LITERATURE CITED


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