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Status, mechanism, suitable distribution areas and protection countermeasure of invasive species in the karst areas of Southwest China

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Biological invasion is one of the major threats to global biodiversity attracting a primary focus of scientific attention. During the past decades, due to the diversity and peculiarity of species, coupled with the vulnerable ecosystem, karst areas have received more and more attention. Numerous investigations and studies have confirmed that the karst areas in Southwest China are suffering from biological invasions under the intensified human activities and the climate change they caused. Despite some fundamental research on invasive species that has been conducted to understand the species and distribution in the karst areas, the mechanism of biological invasions and the response of karst ecosystem are still lack sufficient knowledge. In this paper, we summarized the habitat characteristics and invasion status of karst areas to biological invasions. This paper comprehensively analyzed the research results on biological invasions in karst areas to understand the status and development trends of biological invasions in the karst of China, so as to promote the relevant research on biological invasions in the karst areas. We found that the biological invasions in the karst areas were increasing with years. We also revealed the possible mechanism including competition, mutualism, allelopathy and phenotypic plasticity of biological invasion in karst by summarizing the relevant research results of in the karst areas. Moreover, the response of karst to biological invasion was described from the aspects of ecosystem, community, species and genetic levels, etc. By comparing the characteristics of invasive species that have been found in karst area, we analyzed the common characteristics including strong fecundity and rapid growth rate, strong environmental adaptability, strong phenotypic plasticity and high genetic diversity of the existing invasive species, we simulated and predicted the habitat of invasive species. Overall, we found three areas with high habitat suitability covering Chinese southwest Karst ecosystem, which include the southern Yunnan-Guizhou Plateau, foothill area on the Min-Yue-Gui and foothill area of southern Yunnan. It is also worth noting that the Sichuan Basin has a higher invasive risk compared to its surrounding Karst ecosystem, mainly because of the high habitat suitability of some invasive species. Therefore, we suggest that a general survey of alien invasive species in the karst areas of Southwest China should be carried out as soon as possible, focusing on the survey of the suitable areas of alien species for early warning. In addition, to establish a database of invasive alien species in the karst areas of southwest China, strengthen the monitoring of alien species, and evaluate the impact of invasive species in key areas on the biodiversity and ecosystem in the karst areas of Southwest China, so as to maintain the stability of cave biodiversity and the fragile ecosystem.

KEYWORDS

karst areas, invasive species, status quo, mechanism of biological invasions, potential distributions, countermeasures and proposals

Introduction

Biological invasion has been recognized as one of the main factors driving biodiversity declines, economic losses, and zoonotic disease emergences in the world (Pysek et al., 2020; Diagne et al., 2021; Zhang et al., 2022). By 2018, 667 invasive species had been recorded in China (Xu, 2018). Same as the "fully invasive species" in unified framework for biological invasions (Blackburn et al., 2011), these species with individuals reproducing, surviving and spreading at multiple sites have a serious impact. Biological invasion is a complex process that is influenced by various factors (Lake and Leishman, 2004; Geng et al., 2007). The invasiveness of alien species and the invasibility of the ecosystem being invaded are key factors for the successful invasion of alien species (Wang et al., 2015).

Southwest China's karst areas are the largest in the world and one of the hotspots of global biodiversity (Lu et al., 2013). The unique geological structure of karst areas has formed their unique habitats and provides rich ecological niches for the species in them (Xu, 2011). The characteristics of the karst ecosystem, such as shallow, calcium-rich soil and extensive caves, have led to the emergence of many unique and endemic species of plants and animals (Lu et al., 2013). Karst habitats in Southwest China are rich in rare, endangered and protected wildlife (Jiang, 2014; Shui, 2017). The specific habitat of karst not only promotes biodiversity but also determine the vulnerability of the ecosystem (Guo et al., 2011). For instance, the barren and easily erodible soil in the habitat is one of the major factors leading to the vulnerability of karst vegetation, which causes biodiversity decline and instability of the dynamic balance of the karst ecosystem (Jiang, 2014; Shui., 2017). Habitat disturbances in the karst area result from serious ecological disasters such as rocky desertification (Wang et al., 2004). Human activities also disturb habitat and will lead to biodiversity declines and biological invasions (Dukes and Mooney, 1999). For instance, land-use modifications significant affected biological invasion (Ficetola et al., 2010). Habitat loss facilitated the biological invasion of the American bullfrog (Rana catesbeiana) at Liuji Town, Jiangsu Province, China (Wang et al., 2022). At present, there are no relevant reports on the status and diffusion trend of biological invasion in the karst areas of Southwest China. The impact of biological invasion on the biodiversity of karst landforms has not attracted international attention. In this work, we collected, sorted and analyzed invasive species data in the karst areas of Southwest China, clarified the current status of biological invasion in those karst areas, and summarized the mechanism of biological invasion. We also put forward corresponding countermeasures and suggestions for the prevention and control of biological invasion in the karst areas of Southwest China.

Distribution and ecosystem characteristics of karst areas in southwest China

Distribution of karst areas in southwest China

The global extent of karst areas is approximately 2.2 million km^2 (Groves and Meiman, 2011), which accounts for approximately 12% of the world's total land area and provides drinking water to nearly 25% of the world's population. Karst ecosystems are an important part of the Earth's surface ecosystem (Goldscheider et al., 2020). Karst landforms in China are widely distributed and extensive. In particular, karst landforms in Southwest China are characterized by large area, rich biodiversity and a fragile ecosystem. (Lu et al., 2013). With the Yunnan-Guizhou Plateau as the core area, karst landforms in Southwest China are distributed in Guizhou, Yunnan, Sichuan and Chongqing (Jiang, 2014; Xu and Zhang, 2014). The Southwest karst region is the most well-known karst in the world, and its grassland ecosystem is vulnerable (Lu, 2012).

Ecosystem characteristics of karst areas in southwest China

The ecosystem of the karst areas in Southwest China are unique. The karst areas in Southwest China have a subtropical or tropical humid monsoon climate (Shui, 2017) and are warm in winter and hot in summer, with abundant annual rainfall but uneven seasonal distribution (Lu, 2012). In terms of habitat, the soil of the karst uplands is shallow and discontinuous, with a thick soil layer at the foot of the mountains and barren soil at the top, alkaline and calcium rich (Zhu, 2003). The different ecological niches such as stone crevices, caves, stone surfaces and soil layers have formed diversified small landforms in the karst areas in Southwest China (Jiang, 2014; Shui, 2017). For example, sinkholes provide refuge for many plants and caves combine with underground rivers to form a complex underground water system (Xiong, 2006). These isolated habitats provide rich ecological niches for organisms (Xu, 2011). In terms of plant species, the karst vegetation has evolved unique adaptive characteristics, including calcium and drought tolerance and strong roots, some of which can cling to rocks (Shui, 2017). These plant characteristics are due to strong water permeability and poor retention capacity of the shallow, calcium-rich, alkaline soil; fewer available water resources; and proclivity to drought of the karst landforms (Xiong, 2006; Shui, 2017). There are many unique cave animals and rock-dwelling animals in the karst areas due to the cave-rich ecosystems and special habitats, such as karst caves and underground water networks (Jiang, 2014). The uniqueness of karst plants also promotes the emergence of many unique and endemic species of animals in the ecosystem (Xu, 2011). Maolan Nature Reserve, for example, has more than 200 endemic species, including *Gekko liboensis*, *Nemacheilus liboensis*, *Sinocyclocheilus macrolepis* etc. (Jiang, 2014). Karst areas in Southwest China are rich in rare, endangered and protected wildlife. The unique karst habitats promote biodiversity and determine the vulnerability of their ecosystems. Once the karst landform is disturbed by human activities, serious ecological disasters such as rocky desertification occur easily (Wang et al., 2004; Guo et al., 2011; Xu and Zhang, 2014). Soil is one of the major factors among many leading to the vulnerability of karst ecosystems (Guo et al., 2011). For example, karst landforms in Southwest China have obvious seasonal droughts and weakly alkaline, high-calcium soil; the soil layer in many habitats is barren and easily erodible (Lu, 2012). These characteristics cause vulnerability of vegetation, which leads to the instability of the dynamic balance of the karst ecosystem.

Status quo of biological invasions in the karst areas of southwest China

Damage caused by biological invasion

In recent years, biological invasion caused by human activities have seriously affected the ecosystem in the karst areas of Southwest China. The species richness and diversity indexes of these areas are high. However, in recent years, these karst areas in Southwest China have suffered from serious biological invasion, which has decreased the biodiversity (Wang et al., 2004). Invasive species not only threaten the biodiversity of karst areas, but also may carry pathogens that threaten wildlife and human health (Zhang et al., 2022). Large numbers of invasive species were found in the karst areas of Guizhou, and malignant invasive species were found in more than 60% of survey sites (Yang et al., 2022). In the karst areas of Guizhou, the occurrence areas of invasive species *Ageratina adenophora*, *Alternanthera philoxeroides* and *Mikania micrantha* were 2,238, 79, and 1,467 km^2 respectively; and *Chromolaena odorata* has flooded the Nanpan River, Beipan River and Red River basins (Yang, 2020). After *Ageratina adenophora* and other invasive plants invaded the karst areas of Guizhou, the local biodiversity and the total number of soil animal groups decreased significantly, including a 41.3% decrease and 43.25% in grassland (Yang, 2020). As plant diversity decreases, herbivores lack food, and the food chain breaks down; thus, many karst endemic species have become endangered (Yang, 2020). In Caohai, Guizhou province, China, *Rana catesbiana* has occupied a niche and is proliferating (Liu and Li, 2009; Lv et al., 2020). The invasion of *Rana catesbiana* led to the extinction of *Cynops wolterstorffi* in Dianchi Lake, Yunnan Province (Li and Xie, 2004). Invasive species, such as *Pomacea canaliculata* and *Oreochromis nilotica*, are increasingly endangering the ecosystem in the karst areas of Guizhou, and in some areas invasive species are out of control (Qiu et al., 2019). The invasive species *Achating fulica* has endangered more than 200 species in Yunnan Province, posing a serious threat to local biodiversity (Li and Li, 2008). The impact of biological invasion on biodiversity in karst areas has not attracted broad international attention, but there are some case studies. For example, biological invasions have resulted in a significant reduction of biodiversity and total numbers of animal and plant groups and even endangered species (Jiang, 2014; Shui, 2017). The invasive plant *Aster subulatus* is one of the most harmful plants in nurseries and gardens in Southwest China, but the research on it is very limited (Pan et al., 2010). Therefore, biological invasions in the karst areas in Southwest China should receive more attention and research to prevent ecosystem degradation.

Invasive species

In recent years, the karst areas in Southwest China are suffering from serious biological invasion. To understand the status quo of biological invasion in these areas, we summarized the invasive species according to published literatures (Supplementary Table S1). A total of 172 invasive species were recorded, including 21 animal species (excluding insects) and 151 plants species. The 21 invasive animal species belonged to 16 families and six groups, of which fishes were the most abundant, with 12 species accounting for 57.14% of all species; mammals were the second abundant, with four species accounting for 19.05% of all species. Other groups had one or

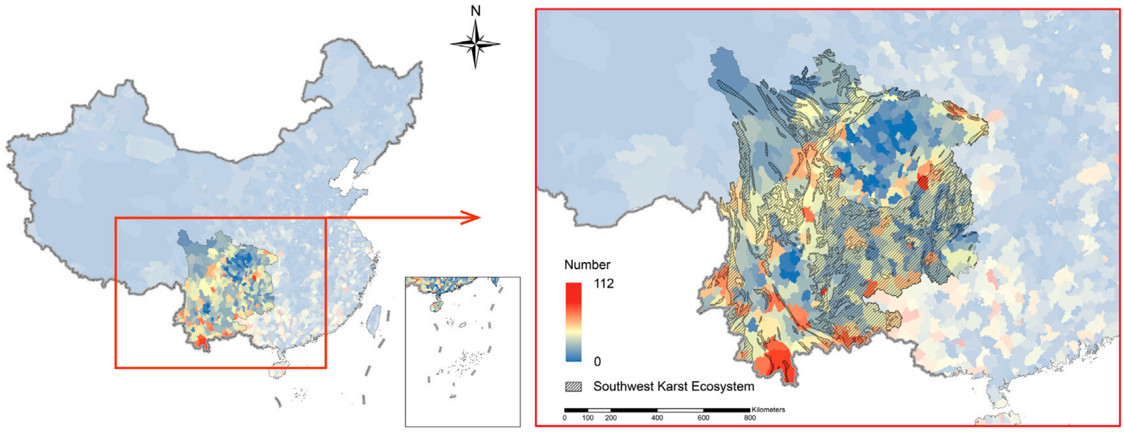

FIGURE 1
Richness of the typical invasive alien species among karst systems in southwest China. Blue represents counties with low richness, red represents counties with high richness. Crosshatch regions mean karst systems in southwest China.

two species. The 151 invasive plant species belonged to 36 families, of which Compositae was the most abundant, with 34 species accounting for 22.52% of all species; the second abundant was Leguminosae, with 19 species accounting for 12.58%. In addition, there are 14 species of Amaranthaceae accounting for 9.27% of all species and 13 species of Gramineae, accounting for 8.61% of all invasive species. Among the invasive plants, 32 species were malignant, 48 species were severe, 21 species were local, and 24 species were general. The malignant and severe invasive plants accounting for 52.98% of the total invasive plant species. Supplementary Table S1 showed that among the typical invasive animals in the karst areas of Southwest China, except for muroid, the other animal species were aquatic or amphibian. Among the invasive plants, *Ageratina Adenophora*, *Lantana camara*, *Alternanthera philoxeroides* and *Eichhornia crassipes* were hygrophytic species. These descriptions demonstrate that karst areas are being threatened by invasive species, especially some aquatic alien species, which have seriously affected the biodiversity of water ecosystems and the ecological safety in the karst areas. Effective measures are urgently needed to prevent and control invasive species.

Distribution of invasive species

We summarized the distribution of 151 invasive plant species and 21 invasive animal species with county-level resolution. For each animal species, we obtained information about their distribution from literatures. Because the data of most animal species' occurrence are only at the provincial level and some animal species, such as *Pomacea canaliculata*, *Pterygoplichthys pardalis* and *Rattus norvegicus* are widely distributed species, we believe that they are located in all counties of the recorded province. For plants, distribution data were extracted from the Invasive Plants module of the National Specimen Information Infrastructure (NSII) database. The Asteraceae family is widely distributed in all provinces including the karst areas, among which the most widely distributed species are *Bidens pilosa*, *Conyza canadensis*, *Crassocephalum crepidioides*, *Erigeron annuus* and *Galinsoga parviflora*. From Figure 1, it can be seen that there were more invasive species in the foothills area of the Min-Yue-Gui, Hengduan Mountain Area and Guizhou Plateau. The invasive species richness was low in Sichuan Basin and northwest Sichuan Province. We found that most species were not only distributed in the karst areas shown in Figure 1, but also distributed in other areas to varying degrees. For example, the adjacent Guangxi Province had a high invasive species richness, which might be related to the large karst area in this province.

Biological characteristics and mechanisms of invasive species in the karst areas of Southwest China

Biological invasion is a complex process and there are many factors affecting the spread of invasive species. The invasiveness of invasive species and the resistance to the invasion of the ecosystem are the key factors that determine the success of invasive species (Wang et al., 2015). Studies have shown that the invasiveness of invasive species is significantly related to its competitiveness, spatial growth ability, fecundity, resource utilization capacity and allelochemicals release etc. (Pyek and Richardson, 2007). The resistance to the invasion of the ecosystem is related to the species diversity and available resources of the local ecosystem (Lonsdale, 1999). During the process of biological invasion, alien species ensure their dominance in interspecific competition with local species especially for resources through the plasticity of their morphological characteristics, physiological characteristics and reproductive characteristics to enhance their invasiveness (Sodhi et al., 2019). In addition, alien species can increase their invasiveness by releasing allelochemicals that inhibit the growth of native species (Callaway and Ridenour, 2004). Generally, the biological invasion of alien species is the result of the combined action of different invasion methods.

Typical biological characteristics of invasive species

According to some studies, successful invasive species have several significant characteristics including high fecundity, strong environmental adaptability and high phenotypic plasticity (Mack et al., 2003). Among the 21 invasive animal species (insects excepted) in the karst areas of Southwest China, the successful invasive species had several significant characteristics in common. The first characteristic was omnivory (Table 1). Omnivorous alien species can find food and adapt to local environments rapidly. The American bullfrog (Rana catesbeiana) that invaded Yunnan, China, for instance, fed on more than 30 species from 10 taxonomic classes, including frogs native to Yunnan (Liu et al., 2015). *Procambarus clarkii*, which invaded Caohai, China, fed on plants, plankton, aquatic invertebrates, insects, etc. Its extensive diet contributed to maintaining and expanding the population (Tao, 2020). The second characteristic was strong fecundity (Table 1). Invasive animals showed strong fecundity. For example, each female American bullfrog laid 10,000 eggs at a time, with a survival rate of approximately 10% (Li and Xie, 2004). *Gambusia affinis* showed strong fecundity and high seasonal characteristics, which posed a serious threat to the survival of local fish in the areas invaded (Gao et al., 2019). The third characteristic was strong environmental tolerance with wide habitat adaptability (Cruz and Rebelo, 2007) (Table 1). *Procambarus clarkii* was highly adaptable to the hydrologic and temperature conditions of the new habitat (Gutiérrez-Yurrita et al., 1998), and it can reproduce in most water, even in the extreme environment of polluted water or the high-salinity water (Barbaresi and Gherardi, 2000). The last characteristic was high phenotypic plasticity (Table 1), which enables invasive animals to improve their adaptability to the environments. For example, *Gambusia affinis* had strong phenotypic plasticity, and environmental factors such as temperature, precipitation, altitude, salinity, electrical conductivity and dissolved oxygen all affected their life-history traits (Jourdan et al., 2016; Cheng et al., 2018). In addition, higher genetic diversity or genetic variation is beneficial to the adaptive evolution of invasive animals (Wang, 2015).

Among the 151 invasive, mostly herbaceous, plant species in the karst areas of Southwest China, the successful invasive species had several significant, common characteristics. The first characteristic was strong allelopathy (Table 1). For example, *Ageratum conyzoides*, *Parthenium hysterophorus* and *Lantana camara* have strong allelopathy (Kong et al., 2002). Studies have shown that *Lantana camara* and its extracts had allelopathic effects on seed germination and seedling growth of *Capsicum annuum*, *Brassica rapa* and *Brassica campestris*. The second characteristic was strong fecundity (Table 1). Table 1 shows that the invasive plants in the karst areas of Southwest China had strong fecundity, including vegetative propagation and sexual propagation. Some species had both propagation modes. For example, *Ageratum conyzoides* reproduced sexually in suitable conditions to ensure the variability of the population, and reproduced asexually under harsh conditions to ensure the fecundity of the species (Zhang et al., 2020). *Amaranthus spinosus* is a hermaphrodite angiosperms, with bisexual flowers and self-pollination. It can produce up to 10,000 seeds per plant and has strong fecundity (Li, 2016). The third characteristic was easy seed dispersal (Table 1). The reproductive strategy of annual invasive plants generally relies on the production of a large number of individuals to maintain the populations. This was usually manifested as a large number of seeds, while small seeds that spread easily by wind or river (Lu and Ma, 2005, 2006). For example, the seeds of *Bidens pilosa* and *Praxelis clematidea* were small, with long pappi and strong diffusibility in the wind (Zhong et al., 2016). The fourth characteristic was high phenotypic plasticity (Table 1). Phenotypic plasticity in plants plays an important role in the survival and maintenance of species under new environments and pressures by obtaining maximum fitness (Hendry, 2016). For example, *Alternanthera philoxeroides* showed high phenotypic plasticity in a variable environment (Geng et al., 2007). The last characteristic was higher genetic diversity or genetic variation. Most invasive plants in the karst areas of Southwest China have high genetic variation or diversity, such as *Praxelis clematidea*, *Amaranthus retroflexus*, *Amaranthus spinosus*, etc. (Chan and Sun, 1997; Li et al., 2007; Tang et al., 2009; Wang et al., 2015).

Ecosystem resistance to the invasive species

The ecosystem resistance to invasive species is related to available resources, species diversity, and human disturbance, etc. (Lonsdale, 1999). Biological invasions in the karst areas of Southwest China are related to available resources. If there are unused resources suitable for invasive species in the karst ecosystem, this is conducive to the early establishment of invasive species and to decreasing the ecosystem's resistance to invasion (Wan et al., 2015). For instance, in degraded karst sinkholes, invasive plants had fewer resources to use, which effectively reduced the invasion of *Ageratina adenophora*, resulting in different degrees of invasion in different karst habitats (Jiang et al., 2019). There were abundant aquatic plants and mosquitoes in the shallow lakes and wetlands in Caohai, Guizhou province, and the suitable conditions and available resources were conducive to the invasibility of the American bullfrog in this area (Lv et al., 2020). The species diversity of the karst ecosystem is also a factor affecting the degree of alien species invasion. For example, in western Panzhihua, Sichuan province, the higher species diversity of the shrub layer and the composition of the herb layer inhibited the invasion of *Ageratina adenophora*; the higher the species diversity of shrub layer, the lower the invasive degree of *Ageratina adenophora*, which was consistent with the diversity resistance hypothesis proposed by Albertson (1960).

TABLE 1 Main biological characteristics of invasive alien species in Karst areas of Southwest China.

	Group	Biological characteristics	Representative species	References
1	Invasive animals	Omnivorous feeding	*Rana catesbeiana, Procambarus clarkia, Pomacea canaliculata*	Liu et al. (2015); Marunouchi et al. (2003); Hofkin et al. (1992); Gutiérrez-Yurrita et al. (1998); Gherardi et al. (2001)
2		Strong fecundity and rapid growth rate	*Procambarus clarkia, Pomacea canaliculate, Gambusia affinis*	Barbaresi and Gherardi, (2000); Tanaka et al. (1999); Kai and Shi, (2017); Cheng et al. (2018)
3		Strong environmental adaptability	*Trachemys scripta elegans, Gambusia affinis*	Ramsay et al. (2007); Gao et al. (2019)
4		Strong phenotypic plasticity	*Pomacea canaliculate, Gambusia affinis*	Estebenet and Martín, (2002); Jourdan et al. (2016)
5		High genetic diversity	*Procambarus clarkia, Pomacea canaliculate*	Barbaresi et al., (2007); Xu et al., (2009); Yang et al. (2018)
6		Low genetic diversity	*Rana catesbeiana*	Austin et al., 2003; Bai et al. (2012)
7		Low genetic variation	*Rana catesbeiana*	(Austin et al., 2003; Bai et al. (2012)
8	Invasive plant	Strong allelopathy	*Amaranthus retroflexus, Amaranthus spinosus, Ageratum conyzoides, Aster subulatus, Bidens Pilosa, Erigeron canadensis, Conyza sumatrensis, Crassocephalum crepidioides, Chromolaena odorata, Dysphania ambrosioides, Avena fatua, Lantana camara*	Shahrokhi et al., (2011); Bakhshayeshan-Agdam et al., (2015); Macharia and Peffley, (1995); Kong et al., (1999); Kong et al., (2002); Sundufu and Shoushan, (2004); He et al., (2019); Zhang et al., (2016); Djurdjević et al., (2011); Wang et al., (2010); Wang et al., (2014); Zheng et al., (2015); Li et al., (2020); Liu et al., (2016)
9		Strong asexual reproduction ability and rapid growth rate	*Erigeron annuus, Parthenium hysterophorus, Praxelis clematidea, Oxalis corymbose, Lantana camara*	Fan et al., (2020); Adkins and Shabbir, (2014); Zhang et al., (2021); Sharma et al. (2008)
10		Strong sexual reproduction ability and rapid growth rate	*Conyza sumatrensis, Crassocephalum crepidioides*	Hao et al., 2009; Huang, (2008)
11		Strong ability of asexual and sexual reproduction	*Solidago canadensis, Phytolacca Americana, Eichhornia crassipes*	Xiao et al., (2019); Zhou et al., (2013); Huang and Ding, (2016)
12		Seeds spread easily	*Ageratum conyzoides, Ageratina Adenophora, Praxelis clematidea, Avena fatua*	Zhong et al., (2016); Lu and Ma, (2005); Lu and Ma, (2006); Intanon et al., (2020); Ņečajeva et al. (2021)
13		Strong environmental adaptability	*Erigeron canadensis, Ageratina Adenophora, Phytolacca Americana, Eichhornia crassipes*	Wang et al., (2021); Zhou et al., (2010); Dong et al., (2014); Teng et al. (2021)
14		strong phenotypic plasticity	*Alternanthera philoxeroides, Amaranthus retroflexus, Aster subulatus, Bidens Pilosa, Erigeron canadensis, Ageratina Adenophora, Parthenium hysterophorus*	Pan et al., (2006); Geng et al., (2007); Wang et al., (2015); Zhou et al., (2005); Pan Yumei et al., (2010); Pan et al., (2017); Mojzes et al., (2020); Zhao et al., (2012); Shi and Adkins, (2020)
15		High genetic diversity	*Amaranthus retroflexus, Amaranthus spinosus, Ageratum conyzoides, Erigeron annuus, Parthenium hysterophorus, Praxelis clematidea, Avena fatua*	(Suresh et al., 2013; Chan and Sun, 1997; Shukla et al., 2018; H. K. and N. T. H., 2017; Ni et al., 2009; Tang et al., 2009; Wang et al., 2015; Li et al. (2007)
16		Low genetic diversity	*Alternanthera philoxeroides, Chromolaena odorata, Eichhornia crassipes*	Wang et al., (2005); Ye et al., (2003); Yu et al., (2014); Li et al., (2006); Ren et al. (2005)
17		High genetic variation	*Erigeron canadensis, Erigeron annuus*	Marochio et al., (2017); Fernandes et al., (2015); Stratton, (1991)
18		Low genetic variation	*Praxelis clematidea, Eichhornia crassipes*	Wang et al., (2015); Zhang et al., (2010); Ren et al. (2005)

Ecosystem biodiversity is positively correlated with invasive species resistance. However, different conclusions were drawn about the impact of species diversity on ecosystem resistance to invasive species at different spatial scales. For example, at the scale of 25 m^2, the invasive degree of *Ageratina adenophora* was negatively correlated with local species diversity; at the scale of 400 m^2, there were both positive and negative correlations; and at the provincial scale, the invasive degree was positively correlated with the local biodiversity (Lu et al., 2008). In addition to the previously mentioned factors, human disturbance also affects the invasiveness of the karst ecosystem. With the intensification of human activities and global climate change, many natural ecosystems have been disturbed at various degrees. Excessive disturbance will lead to ecological imbalance and degradation, which will decrease the ecosystem resistance to invasion (Wan et al., 2015).

The mechanisms of alien species invasions

The main mechanisms of alien species invasion include competition, symbiosis, allelopathy and phenotypic plasticity. Compared with native species, invasive species have advantages in life-history traits, genetics and evolution (Callaway and Ridenour, 2004; Wan et al., 2015). The inherent superiority hypothesis holds that the successful invasion of some alien species is due to their morphological, physiological, ecological and other specific traits, which make them superior to other species in resource competition and environmental adaptation (Sax and Brown, 2000; Hufbauer and Torchin, 2008). Phenotypic plasticity in environmental adaptation is also an important strategy and mechanism for alien species invasion.

Species in the same ecological niche or trophic level compete for resources. Competition is an important way for native species to prevent biological invasion (Wan et al., 2015). For example, *Rana catesbeianus*can compete with native species in the same ecological niche of Caohai lake in Guizhou province for food and space resources because of their omnivory and large food intake (Liu and Li, 2009; Lv et al., 2020). Studies on the life-history traits of invasive plants showed that they had higher spatial growth capacity, resource utilization capacity, photosynthetic rate (Shen et al., 2011) as well as stronger fecundity (Qi et al., 2014). The height, specific leaf area, concentration of representative nutrients, and photosynthetic rate of invasive plants were significantly higher than those of native plants (Sodhi et al., 2019). These functional traits of invasive plants represent their efficient use of resources and contribute to their competitive ability and successful invasion (Lake and Leishman, 2004). Studies have shown that symbiosis is also a factor in plant invasion in the karst areas (Wan et al., 2015). The karst landforms have shallow and discontinuous soils that are calcium rich and nutrient poor, which determines their obvious spatial heterogeneity (Lu, 2012). These characteristics will significantly affect the development and distribution of plant populations (Qi et al., 2013). Most plants are symbiotic with arbuscular mycorrhizal (AM) fungi, which is highly adaptable in the heterogeneous habitat of karst landforms. Some research found that AM fungi can significantly improve the growth and nutrient use of the invasive plant *Bidens pilosa* in the karst areas and significantly improve its adaptability to the karst heterogeneous habitats (Xu, 2020). Some studies also found that mycorrhizal fungi can reduce the competitiveness of the native species *Kummerowia striata* and promote the invasion of *Solidago Canadensis* (Yang et al., 2014). Researchers have regarded invasive plants and AM fungi as a symbiotic relationship that facilitates invasion (Cui and He, 2009).

In addition to competition and symbiosis, invasive plants interact with native species by allelopathy. The allelopathy of invasive plants is mainly related to their rapid evolution and lack of coevolution with native plants. The new weapon hypothesis holds that an important reason for the success of alien plants is that they can release allelochemicals to inhibit the growth of native species (Callaway and Ridenour, 2004). A typical invasive weed in the Sichuan Basin, *Erigeron canadensis*, releases phenolic acid that can inhibit seed germination and seedling growth of species such as *Trifolium repens* (Djurdjević et al., 2011). The invasive weed *Parthenium hysterophorus* releases phenolic substances that inhibit the growth of *Brassica campestris*, *Brassica rapa* and *Brassica oleracea* seedlings (Singh et al., 2005). A tissue extract of the invasive weed *Amaranthus retroflexus* had allelopathic effects on the seed germination and growth of four important crops: cucumber (*Cucumis sativus*), alfalfa (*Medicago sativa*), kidney bean (*Phaseulus vulgaris*) and wheat (*Triticum aestivum*) (Bakhshayeshan-Agdam et al., 2015).

Phenotypic plasticity enables alien species to maintain high fitness in a variety of habitats, especially when the environment undergoes unsuitable changes. For example, the phenotypic plasticity of *Procambarus clarkii* is reflected in its feeding habits. An optimal feeding strategy can be achieved by adjusting feeding strategies at different times (Smart et al., 2002). Research found that in three different karst habitats, *Alternanthera philoxeroides* increased its adaptability to different habitats by changing a series of morphological characteristics and adjusting reproductive strategies (Zhang et al., 2017). The invasive species *Erigeron annuus* in Chongqing had strong phenotypic plasticity. In low-altitude areas, it adjusted a series of phenotypic traits to enhance ecological adaptability (Li, 2014). The most seriously invaded areas of *Ageratina adenophora* in China are in the Yunnan-Guizhou Plateau. Due to the large environmental differences between the invasion and origin, and the low genetic variation between and within populations in the invasion site, this species has

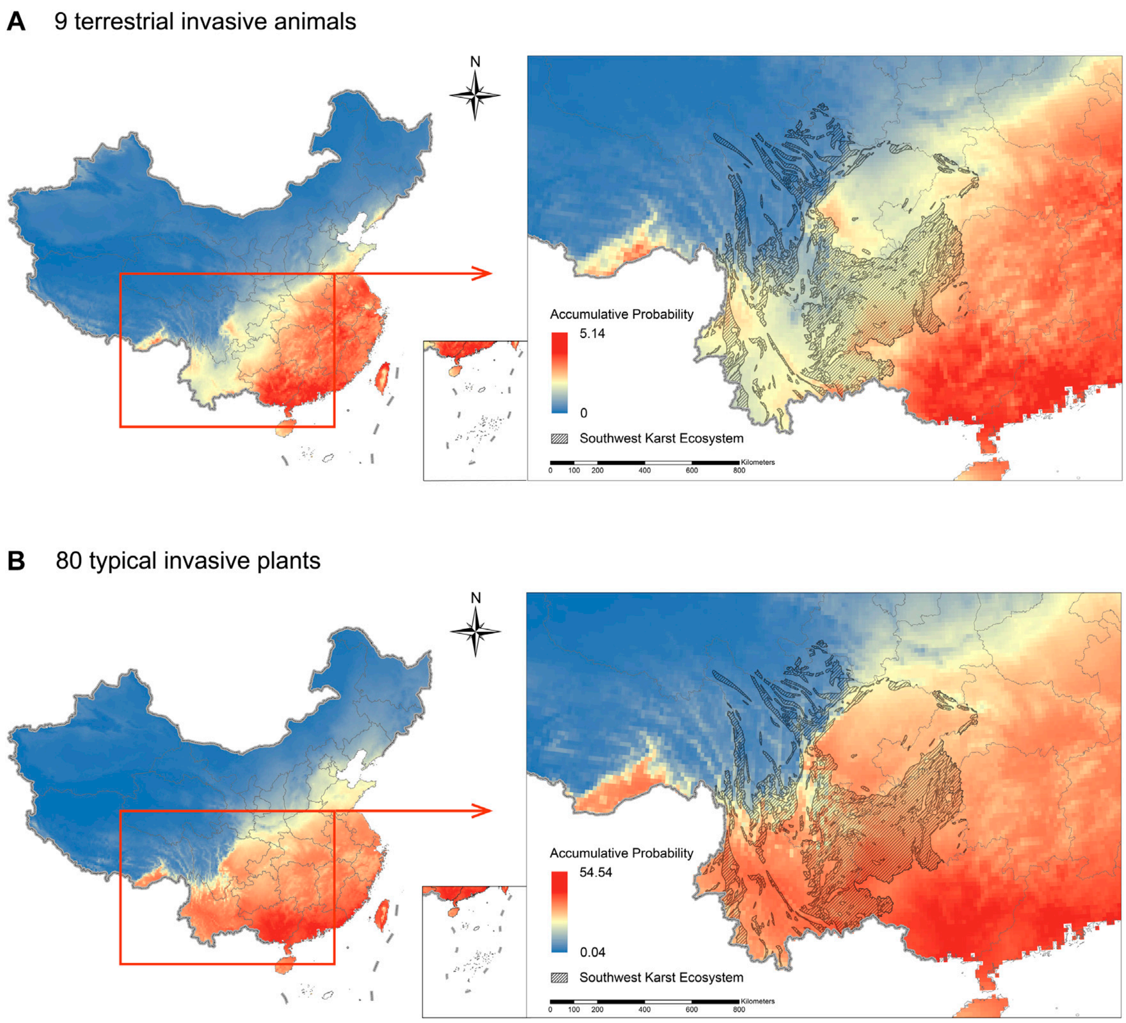

FIGURE 2
Accumulative potential distribution probability of typical invasive species in China predicted by the MaxEnt niche model. Blue represents grids with low probability which means low habitat suitability, red represents grids with high probability which means high habitat suitability. Crosshatch regions mean karst systems in southwest China.

great ecological adaptability (Sang et al., 2010), revealing the high phenotypic plasticity of its functional traits. That is the main strategy for its invasion of China (Zhao et al., 2012). This overview indicates that the main mechanisms of biological invasion in the karst ecosystems of Southwest China are competition, symbiosis, allelopathy and phenotypic plasticity.

Suitable habitats of invasive species in the karst areas of Southwest China

We collected global presence records for nine terrestrial invasive animal species and 80 malignant and severe invasive plant species (Supplementary Table S1) from the Global Biodiversity Information Facility (GBIF) and the citizen science database iNaturalist. Elevation data and 19 bioclimatic variables such as annual mean temperature are obtained from the WorldClim Climate Database (www.worldclim.org). The global potential habitat suitabilities for 89 invasive species were calculated by the maximum entropy niche model, using the software MaxEnt 3.4.4 and combined with these 20 environmental variables. For models of all species, the average training area under the curve (AUC) ranged from 0.656 to 0.99 (mean: 0.869; standard deviation: 0.076). Because of the need to use different model variables, aquatic invasive animals are not considered in this part. Habitat suitability in each grids were calculated as the accumulative distribution probabilities of these invasive species. A higher habitat suitability value for a given grid cell indicates a higher relative probability of invasion.

Except for two human-associated species, *Mus musculus* and *Rattus norvegicus*, the other seven invasive animal species had low habitat suitability in the karst area (Figure 2A.). For invasive plants, we found three areas with high habitat suitability, including the southern Yunnan-Guizhou Plateau, the Min-Yue-Gui foothills and the foothill of southern Yunnan. It can be observed from Figure 2 that, consistent with the current distribution pattern shown in Figure 1, the habitat suitability of 80 typical invasive species is highest in Guangxi Province adjacent to the study area and in Guangdong Province, which is at the same latitude. *Amaranthus lividus*, *Amaranthus viridis*, *Amaranthus spinosus*, *Conyza bonariensis* and *Pharbitis nil* have the largest suitable habitats areas in eastern and central China. In addition, the Sichuan Basin has a higher invasive risk compared to the surrounding karst areas, mainly because of the high habitat suitability of *Amaranthus lividus*, *Conyza bonariensis*, *Pharbitis nil*, *Pharbitis purpurea* and *Solanum khasianum*.

The Maxent model was used to predict the suitable distribution areas of *Alternanthera philoxeroides* in China, which were mainly distributed in tropical, subtropical and southeast warm temperate regions of China. In addition, high-suitability areas were mainly located in Guangxi, Shanghai, Jiangsu, Sichuan provinces and in Chongqing, where invasive species exhibit continuous expansion (Yan et al., 2020).

Countermeasures and suggestions

The plant communities in the karst areas of southwest China show complex and diverse species compositions, high species richness, and high diversity indexes and occupy important position in the global karst ecosystem. However, biological invasion caused by human activities has seriously affected the ecosystem of the karst areas in Southwest China in recent years. To effectively prevent and control biological invasion in this area, some countermeasures and suggestions are put forward as follows. It is necessary to conduct a survey of invasive species in the karst areas of Southwest China. A systematic survey of invasive species has not been carried out although there are many invasive species in the karst areas. We suggest that a survey of invasive species in the karst areas of Southwest China be conducted as soon as possible, especially in the important wetlands, plateaus, basins, and other suitable distribution areas. We must obtain the information of invasive species types, quantities, and key areas threatened to facilitate the development of an early warming and protection strategy. Moreover, for our models' results, the ROC analyses show fairly good performance by MaxEnt for training AUC values. But the high AUC values may result from the arbitrary selection of pseudo-absence data (Phillips et al., 2009; VanDerWal et al., 2009; Liu et al., 2011). The accurate presence-absence data is the key to further modeling.

It is necessary to establish a database of invasive species and a monitoring and early warning system for invasive species in the karst areas of Southwest China. Timely supplement and improvement of the database should be part of the follow-up investigation and research, to provide a basis for the establishment of the monitoring and early warning system. We also suggest increased monitoring of invasive species in the karst areas of Southwest China and evaluation of the impact of invasive species on local biodiversity and ecosystem in key areas. Concurrently, the key invasive species' habitat suitability should be simulated, so that species with a serious expansion trend can be monitored, warned against and controlled.

The last suggestion is to protect and improve the biodiversity of native species in the karst areas of Southwest China. We suggest strengthening the relevant research on the ecological characteristics of native species and restoring suitable ecosystem structures and functions to establish a benign successive ecological community and provide a basis for scientific replacement control of invasive species. In the prevention and control of alien plants, replacement control is a method that uses plants with ecological and economic value to replace invasive plants according to the succession rule of a plant community. We suggest strengthening the research on the ecological characteristics of native species, and giving full consideration to plant replacement restoration technologies in the prevention and control of alien species.

Author contributions

YL and JC designed the article; YL, TS, YL and LF collected the data and information; TS, YL and YH drew the figures; YL and JC wrote the manuscript. All authors have read and agreed to the published version of the manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2022.957216/full#supplementary-material

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