



## OPEN Impact of *Gaura parviflora* invasion on urban wilderness biodiversity: a campus green patch case study

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Urban wilderness has gradually emerged as a hot spot for urban ecological research due to its crucial role in maintaining urban ecosystem services and protecting biodiversity. Compared to natural areas, urban wildernesses are more susceptible to invasions by alien species, which pose a threat to the functionality of the urban ecosystem. Currently, our understanding of biodiversity within various types of urban wilderness is not comprehensive, and the laws governing biodiversity changes due to alien species invasions remain unclear. This study focuses on an abandoned grassland community on a campus in northern China, which has been invaded by the alien weed *Gaura parviflora*. The study measured the characteristics of the aboveground community and the soil seed bank, comparing and analyzing species composition, plant/seed density, species diversity, and similarity at different levels of invasion (uninvaded, moderately invaded, severely invaded). The findings indicate that the uninvaded abandoned grassland community is rich in species (with 32 species) and has significant recovery potential (with an average seed density of 11,671 seeds per square meter). The community harbors multiple alien invasive species both aboveground and within the soil seed bank, and its succession process is influenced by biological invasions and human disturbances. The invasion by *G. parviflora* alters the species composition of both the aboveground community and the soil seed bank, resulting in a significant increase in plant density within the aboveground community. Its impact on the soil seed bank varies with soil depth, leading to a notable decrease in seed density in the 0–5 cm layer compared to the 5–10 cm and 10–15 cm layers; while the Shannon-Wiener biodiversity index for the 0–5 cm and 10–15 cm layers is lower than that of the uninvaded and severely invaded plots. This study reveals that the campus abandoned grassland community faces a high risk of biological invasion, and the invasion by *G. parviflora* has a more significant impact on the soil seed bank than on the aboveground community, which could lead to substantial changes in community species composition and a loss of biodiversity in the soil seed bank. It is therefore strongly recommended that greater attention be given to the impact of biological invasions on seed banks within the management of campus wild ecosystems.

**Keywords** Invasion, Biodiversity, Urban wilderness, *Gaura. Parviflora*, Abandoned green patch

Given the rapid acceleration of the global urbanization process, the protection of urban ecosystem biodiversity has become a top protection priority<sup>1</sup>. Urban wilderness is the land<sup>2</sup> dominated by natural processes in the urban interior or surrounding areas. Urban wilderness has an important and unique value in reconnecting human and nature, promoting human physical and mental health, protecting biodiversity, and maintaining ecosystem services<sup>3</sup>.

Due to human development activities, urban areas experience a higher influx of these species compared to rural or natural areas<sup>4–6</sup>, and they become central to the introduction of alien species, which has significant impacts on biodiversity, ecosystem function, ecosystem services, and human well-being<sup>7,8</sup>. Our current understanding of the hazard situation and invasion mechanisms of many exotic plants is largely based on studies of aboveground vegetation<sup>9–12</sup>, however, less is known about the effects of biological invasion on community soil seed banks<sup>13,14</sup>. Studies have shown that the biological invasion of local plant communities leads to a decrease in biodiversity, an increase in the dominance of invasive species, and changes in the physiochemical properties of the soil environment<sup>15</sup>. However, the impact of invasive species on aboveground vegetation may differ from their effect on seed banks<sup>16–20</sup>. The soil seed bank refers to the total sum of all viable seeds present on the soil surface and within the soil. It connects the past, present, and future of plant communities, representing their potential

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regeneration capacity<sup>21</sup>. Studying the effects of biological invasion on the community soil seed bank can not only reveal the ecological impact and survival potential of alien species but also provide a reference for developing strategies to control biological invasions and restore local vegetation<sup>17,22,23</sup>.

In many ecosystems, alien invasive species impact the replenishment of the seed bank by hindering the growth of native plants. Simultaneously, the seeds of these invasive species infiltrate the soil seed bank, inevitably altering its size and the species composition<sup>24</sup>. Additionally, many invasive alien plants exhibit allelopathy<sup>25</sup>, which can result in the depletion of native plant seeds' vitality by inhibiting the germination of seeds in the soil seed bank, and may even cause the permanent disappearance of some occasional species. Then, how does the invasion of *Gaura parviflora* affect the biodiversity of urban wildness communities, and is there any difference in the influence on the aboveground community and the soil seed bank of different soil layers? Studying and answering these questions is helpful to enhance people's understanding of the invasion mechanism of *G. parviflora*, and provide theoretical guidance for urban management of alien species invasions.

In central and eastern China, *G. parviflora* is a harmful invasive weed<sup>26,27</sup>, commonly found in farmland, wetland, urban green spaces and residential areas. Native to North America, *G. parviflora* has been widely distributed in Japan, Australia, and South America<sup>10</sup> and was introduced to China as an ornamental plant in the early 1950s<sup>4</sup>. *G. parviflora* grows rapidly, reproduces quickly, and exhibits strong adaptability. It possesses allelopathic properties, often forming monodominant communities that harm the local ecosystem's ecological function, drawing the attention of Chinese scholars<sup>28,29</sup>. However, there are currently no published studies on the impact of *G. parviflora* on community biodiversity, particularly on seed banks.

This study examined a specific type of urban wildness, an abandoned weed patch on a campus in Shandong Province, Eastern China, which were invaded by *G. parviflora*. It was investigated what the characteristics of the aboveground community and soil seed banks were at different soil depths within weed communities experiencing varying degrees of invasion by *G. parviflora*. Our findings would reveal the impact of *G. parviflora* invasion on the biodiversity of urban abandoned grassland communities.

## Study site and methods

### Study site description

The study site is located on a campus in Jinan City, Shandong Province, in eastern China. It occupies an area of approximately 300 m<sup>2</sup> of abandoned grassland, bordered by a footpath and an plantation. This region falls within the warm temperate continental monsoon climate zone, characterized by four distinct seasons and abundant sunshine. The city's annual average temperature is 14.5 °C. December is the coldest month, with an average temperature of - 0.2 °C, while August experiences the highest temperatures, with an average of 26.4 °C. The average annual precipitation amounts to 718.4 mm.

The study plot's vegetation had been initially a weed community, indicating that it constitutes an organic assemblage formed through competition and adaptation among multiple weed populations. The weeds mentioned in this study refer to non-cultivated wild plants. Between 2013 and 2017, the land underwent successive plowing and was artificially planted with ornamental plants, including *Orychophragmus violaceus*, *Brassica napus*, and *Helianthus annuus*. Since 2018, the land has been left to rewild, reverting to a weed community. By the end of 2019, it was observed that *G. parviflora* had invaded from the footpath, establishing a monodominant community within the weed patch, with its distribution range expanding annually. Mowing had been conducted annually in June for the years 2020 and 2021.

### Sample setting

The study plot was divided into three zones based on the coverage of *G. parviflora*: the severely invaded zone (0–15 m southwest of the footpath, with an invasive species coverage greater than 60% in summer), the moderately invaded zone (16–22 m southwest of the footpath, with an invasive species coverage of 10–40%), and the uninvaded zone (22–25 m southwest of the footpath, with no invasive plant cover). The center of the severe invasion transect is located at 36.559534°N latitude and 116.805390°E longitude. The center of the moderate invasion transect is located at 36.559470°N latitude and 116.805305°E longitude. The center of the non-invasion transect is located at 36.559509°N latitude and 116.805244°E longitude. A transect was set in the center of each zone along the direction of the footpath, and three 1 m\*1m quadrats were set up at 3-meter intervals along each transect, excluding edge positions, resulting in a total of nine sample quadrats. The cover of *G. parviflora* in the uninvaded transect is 0 ± 0%, in the moderate invasion transect it is 22.5 ± 14.4%, and in the severe invasion transect it is 67.5 ± 8.5%.

### Aboveground community survey

The aboveground community survey was conducted on September 30, 2021, and the total coverage, the number of species and the coverage data of each quadrat were obtained.

### Experiment of soil seed bank

Four sample points were randomly set for each square, and 10 cm diameter soil drills were used at 0–15 cm, and 0–15 cm soil samples were mixed according to a total of 0–5 cm, 5–10 cm and 10–15 cm; and 27 soil samples were obtained from 9 sample squares.

The resulting soil samples were crushed, removed stone, roots and other debris, and were tilled in the germination plate keeping a thickness not more than 1 cm. The seed bank germination experiment was conducted in a solar greenhouse to maintain uniform temperature and light conditions<sup>30</sup>. Tap water was poured regularly to keep the surface moist to ensure saturated water supply conditions. The germination of species was counted every week. The seedlings that cannot be identified were moved out to cultivate individually until the

species could be identified. Experiment were continued until no new seedlings germinated for a consecutive week. Germination experiments were performed from October 2th to November 30th, 2021.

## Data analysis method

(1) Characteristics of aboveground community and soil seed bank of native weed communities.

The species names and densities of the aboveground community and the soil seed bank communities of the uninvaded weed community were statistically analyzed, along with their families, ecological types and reproductive characteristics. According to the ranking by individual density, the density of *Lagopsis supina* in the aboveground community is much higher than that of other species, accounting for 82.7% of the total number of individuals in the aboveground community. In the seed bank, the densities of *Eleusine indica*, *Digitaria sanguinalis*, and *Descurainia sophia* rank the top three, accounting for 56.8% of the total number of seeds in the seed bank.

It provided an overview of the species composition profiles of the native weed community and the vertical distribution characteristics of the seed bank before be invaded by *G. parviflora*.

(2) Effect of *G. parviflora* invasion on the aboveground plant density and belowground seed density of local weed communities.

The density of individuals aboveground and belowground in weed communities was calculated and compared across different levels of invasion.

(3) The impact of *G. parviflora* invasion on the biodiversity of above and belowground communities in local weed communities.

The number of species and the four  $\alpha$  biodiversity indices of aboveground community and soil seed bank were calculated separately. The invasion mechanism of *G. parviflora* was explored according to the difference of invasion impact on the different native species.

Community species richness was calculated using Margalef's index (d), species diversity by the Shannon-Wiener index (H), community dominance by Simpson's index (D), and community evenness by the Pielou evenness index (E)<sup>31</sup>. The calculation formulas are as follows:

$$\text{Species richness index } d = (S - 1)/\ln N \quad (1)$$

$$\text{species diversity index } H = - \sum P_i \ln P_i \quad (2)$$

$$\text{community dominance index } D = 1 - \sum P_i^2 \quad (3)$$

$$\text{community evenness index } E = H / \ln S \quad (4)$$

$P_i = N_i/N$ , where S represents the number of species, and N is the total number of individuals within the quadrat;  $N_i$  denotes the number of individuals of the i-th species within the quadrat,

(4) The similarity change of aboveground communities and soil seed bank of communities with different invasion degrees.

The Sørensen similarity coefficient difference between aboveground communities and soil seed banks was calculated and compared. The calculation formula for the coefficient is:

$$C_s = 2j/(a + b) \quad (5)$$

Where j represents the number of species shared between the aboveground community and the soil seed bank; a denotes the number of species in the aboveground community, and b denotes the number of species in the soil seed bank.

The data analysis was conducted using Excel and SPSS Statistics version 26.0. Each data bar in the subsequent graph represents the average value from duplicate treatments. The significance of differences between treatments was assessed using one-way ANOVA (Duncan's test,  $P < 0.05$ ) and was indicated by lowercase letters in graph.

## Results

### Profiles of the species composition of uninvaded weed communities on campus

See online appendix 1.

As indicated in online appendix 1, a total of 32 species were identified in the autumn aboveground vegetation and seed bank of campus weed communities not invaded by *G. parviflora*. The most prevalent families were Asteraceae with 6 species, Brassicaceae with 5 species, Poaceae and Amaranthaceae each with 3 species, while the remaining families had only a single species each. The plant density of the aboveground community was significantly lower than the belowground seed density (46:11,671 seeds/m<sup>2</sup>,  $N=3$ ), and 59% of the seeds were stored in the 0–5 cm soil layer. The dominant species in the aboveground community was *Lagopsis supina*, whereas the dominant species in the seed bank were *Eleusine indica*, *Digitaria sanguinalis*, and *Descurainia sophia*. The aboveground community included 2 alien species: *Erigeron annuus* and *Amaranthus spinosus*; the

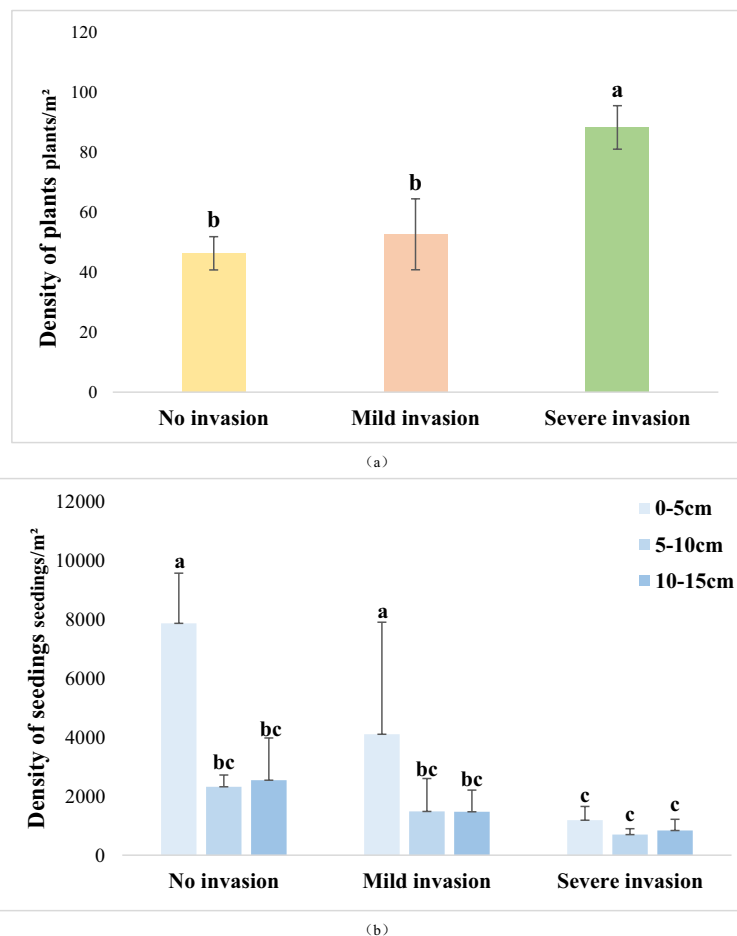
soil seed bank community included 6 alien species: *Lepidium apetalum*, *Sonchus wightianus*, *Veronica persica*, *Amaranthus blitum*, *Datura stramonium*.

Compared with the aboveground community, which had 9 species, the underground seed bank contained a more abundant variety of species, totaling 28. In aboveground communities, annual and perennial species were not significantly different, with 5 and 4 species, respectively. However, in the soil seed bank, there were more annual species than perennial species (18:10), and this trend was more pronounced in the middle and lowest layers of the soil (14:5 and 15:5). The aboveground weed community had tree seedlings of two species: *Morus alba* and *Melia azedarach*, whereas the seed bank was entirely composed of herbaceous species. Regarding fruit size, both the aboveground and soil seed bank species were predominantly those with seeds measuring 1–2 mm (6:9 and 16:27, respectively). The soil seed bank comprised five species with small seeds (fruit length less than 1 mm): *Portulaca oleracea*, *Artemisia annua*, *Mazus pumilus*, *Lepidium apetalum*, and *Datura stramonium*, which were absent from the aboveground community during autumn. When comparing the three soil layers (0–5 cm, 5–10 cm, 10–15 cm), small-seeded species were more abundant in the 0–5 cm and 5–10 cm layers (5:5:2), whereas seeds measuring 1–2 mm (15:10:13) and those larger than 2 mm (6:4:4) were more prevalent in the 0–5 cm layer. In the aboveground community, excluding trees, the ratio of herbaceous species maturing in autumn to those maturing in spring and summer was 5:2, while in the seed bank, the ratio was 18:9.

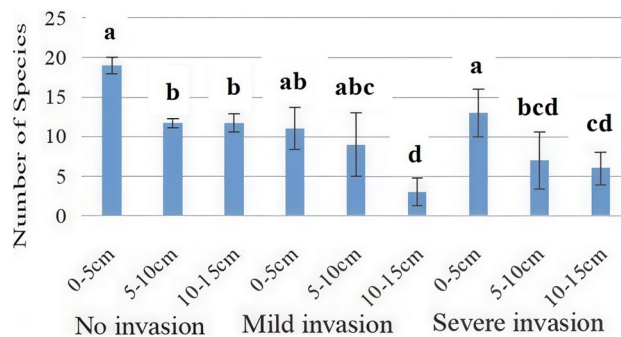
### Effect of invasion on the density of individuals in aboveground and belowground weed communities

Figure 1 showed that the aboveground plant density in the severely invaded community of *G. parviflora* is significantly higher than that in the uninvaded and moderately invaded communities, while the underground seed density was significantly higher in the uninvaded community than in the moderately and severely invaded communities.

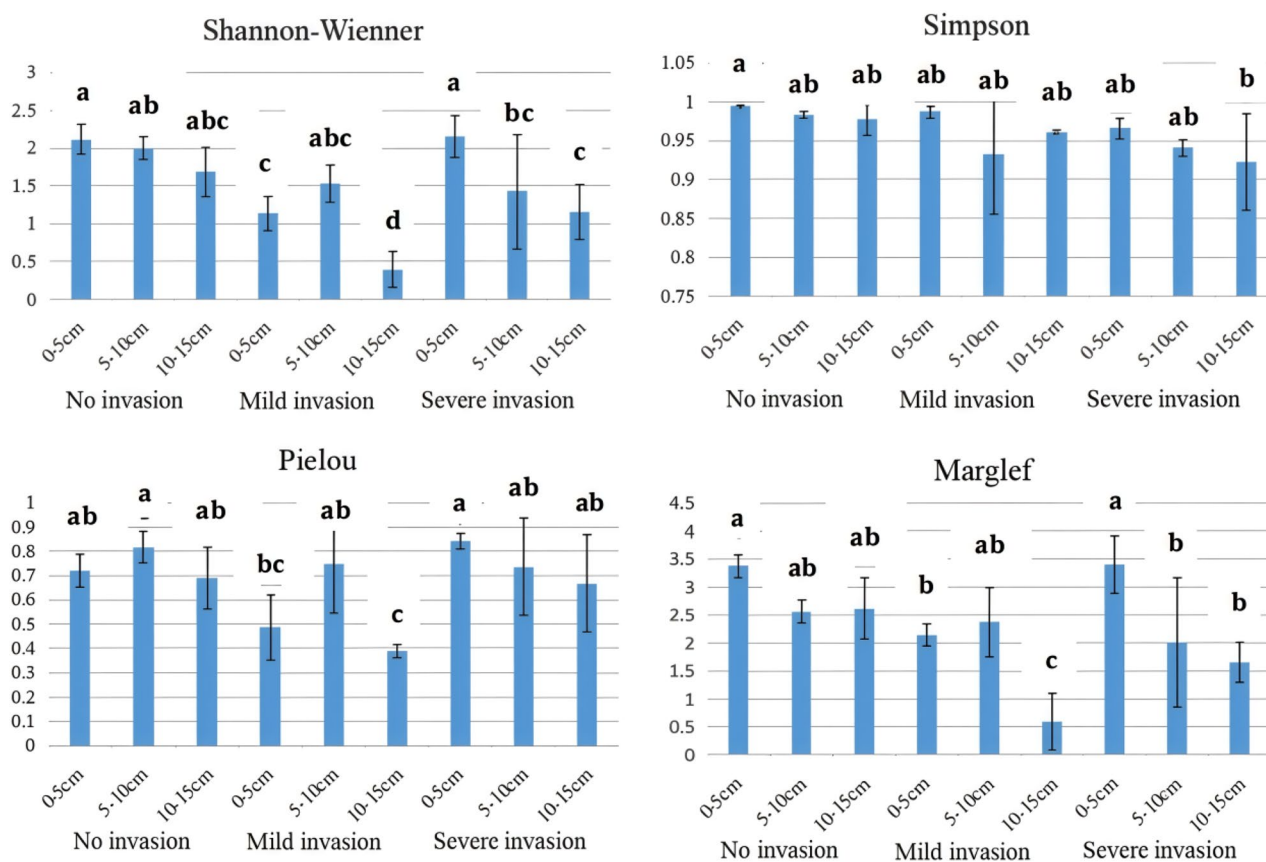
The seed density in the 0–5 cm layer was significantly higher than that of the other two soil layers; moreover, it decreased significantly with the aggravation of invasion. There was no significant difference between the 5–10 cm and 10–15 cm layers under different invasion degrees. These findings indicated that the invasion of *G. parviflora* would reduce the seed density in the 0–5 cm soil seed bank, leading to a change in the vertical distribution pattern of the soil seed bank.



**Fig. 1.** (a) Plant density of aboveground communities and (b) underground seed bank seed density (The different lowercase letters surrounding the bar indicate significant differences,  $N = 3$ ,  $P \leq 0.05$ ).



**Fig. 2.** Influence of the invasion intensity of *G. parviflora* on the number of species in soil seed bank of community (The different lowercase letters surrounding the bar indicate significant differences,  $N=3$ ,  $P \leq 0.05$ ).



**Fig. 3.** Influence of the invasion intensity of *G. Parviflora* on the biodiversity index of the soil seed bank in abandoned grassland communities on campus (The different lowercase letters surrounding the bar indicate significant differences,  $N=3$ ,  $P \leq 0.05$ ).

### Impact of invasion on the biodiversity of weed communities

The ANOVA analysis revealed no significant differences in the number of species or the four types of a biodiversity index within the aboveground weed communities across three levels of *G. parviflora* invasion ( $N=3$ ,  $P > 0.05$ ). However, the species composition had undergone significant changes. In the severely invaded communities, five species were unique: *Pharbitis nil*, *Pharbitis purpurea*, *Convolvulus arvensis*, *Inula japonica*, and *Chloris virgata*. Conversely, six species that were found in the uninvaded communities had been absent in the severely invaded ones: *Veronica persica*, *Lagopsis supina*, *Geranium wilfordii*, *Melia azedarach*, *Carex duriuscula*, and *Erigeron annuus*.

The invasion intensity significantly affected the species diversity within the weed community seed bank (see Figs. 2 and 3). The uninvaded community exhibited the greatest number of seed bank species. The Shannon-Wiener diversity index, species richness Margalef index, and Pielou's evenness index of the seed bank in the

moderately invaded community were all significantly lower than those in the uninvaded and severely invaded communities. The Simpson's dominance index in the severely invaded community was significantly lower than in the uninvaded and moderately invaded communities. Overall, the soil seed bank biodiversity was richest in the uninvaded community, followed by the severely invaded community, with the moderately invaded community having the lowest biodiversity.

The impact of invasion intensity on seed banks correlated with soil depth: the species count in the 0–5 cm and 10–15 cm soil layers of the uninvaded plot were significantly higher than in the other two plots. Although the species count in the 5–10 cm layer decreased with the intensity of invasion, the difference was not significant. The vertical distribution pattern of species counts was similar across the three invasion levels, with the 0–5 cm layer having the most species, the 10–15 cm layer the least, and no significant difference between the 5–10 cm and 15–20 cm layers.

The impact of invasion intensity on seed bank diversity also was associated with soil depth: within the 0–5 cm and 10–15 cm soil layers, the Shannon-Wiener index in uninvaded and severe invaded plots were markedly higher than those in moderately invaded ones. The surface layer of the seed bank in severe invaded plot exhibited a significantly higher Shannon-Wiener index compared to other layers, whereas no such differences were evident among the layers of the other two invasion levels.

The invasion intensity did not significantly affect the Simpson index of the different soil layers, and only the Simpson index of the 0–5 cm soil seed bank was significantly higher than that of the severely invaded 10–15 cm soil seed bank.

The Pielou's Evenness Index and Margalef's Richness Index of the seed banks in the 0–5 cm and 10–15 cm soil layers were significantly lower under moderate invasion compared to other invasion levels. The invasion intensity did not have a significant effect on the Pielou's Evenness Index for the 5–10 cm and 10–15 cm soil layers, nor on the Margalef's Richness Index for the 5–10 cm soil layer.

Overall, compared to other levels of invasion, the biodiversity of seed banks was lower at the moderate invasion level; the impact of invasion was more pronounced in the 0–5 cm soil layer compared to deeper soil layers; and there were differences in the impact of invasion on various biodiversity indices of the seed bank.

### Effect of invasion on the similarity between communities and soil seed banks

The Sørensen similarity between the community and the 0–15 cm soil seed bank was between 0.09 and 0.50 for different invasion intensity, and the average similarity between the uninvaded community and the seed bank was 0.24. Except for one sample in the moderately invaded community where the 10–15 cm layer of the soil seed bank had a medium similarity with the aboveground community in species composition (0.67), the indices of the rest of the samples were dissimilar. Although the results of the Anova analysis indicated that the impact of invasion intensity and soil layer depth on the similarity coefficient was not significant ( $N=3$ ,  $P>0.05$ ), the proportion of samples with an extremely low similarity between the 0–5 cm and 5–10 cm soil seed banks and the aboveground community was higher in the moderately and severely invaded communities (8:12) compared to the uninvaded community (0:6).

## Discussion

### Autumn community status of abandoned weeds on campus

Compared with artificial green space, urban wildness, as a product of natural succession, has relatively rich biodiversity and lower management costs<sup>32</sup>, which helps to promote urban biodiversity. In this study, the abandoned campus green space that underwent rewilding formed a weed community in autumn, with a total of 32 species existing both aboveground and belowground (Appendix 1). Among them, the number of species preserved in the soil seed bank was 2.7 times that of the aboveground community, with 22 species not present in the aboveground community. Excluding the 8 species that fruit in spring or summer, the remaining 14 species likely formed a dormant seed bank, a legacy of historical vegetation; the seed density preserved in the seed bank (11,671 seeds/m<sup>2</sup>) was 287 times that of the aboveground plant density (46 plants/m<sup>2</sup>). These findings highlight the significant, yet often overlooked, immense potential and unique value of the urban wildness soil seed bank in maintaining, protecting, and restoring urban biodiversity.

The vertical structure of the seed bank impacts seed longevity and germination, thereby influencing vegetation management strategies. Most studies have demonstrated a vertically decreasing distribution pattern of seeds in undisturbed soil profiles<sup>33</sup>. Corresponding research on urban vegetation has similarly revealed that the majority of seeds persist in surface soil layers<sup>34</sup>. In this study, the density of the seed bank in the soil surface of abandoned weed communities on campus not invaded by *G. parviflora* was significantly higher than in other layers. Different species exhibited distinct vertical distribution patterns (Appendix 1), which might be related to the shape, size, life cycle, quality, and dormancy characteristics<sup>35–37</sup> of the various species. Therefore, in urban vegetation management, special attention should be paid to protecting and rationally utilizing the surface soil seed bank of non-invaded weed communities. Prior to formulating restoration and conservation strategies for target species, it is essential to investigate the vertical distribution patterns of their seed banks in the soil profile.

At the study site, two species of tree seedlings were discovered in the aboveground community during autumn. The two tree species, *M. azedarach* and *M. Alba*, are local heliophilous tree species, indicating the potential next successional community type of the abandoned weed community. Within the same aboveground community during autumn, three exotic species—*Erigeron annuus*, *Amaranthus spinosus*, and *Robinia pseudoacacia*—were founded. However, they had few individuals aboveground and had not yet formed their soil seed banks. It is particularly noteworthy that *E. annuus* and *A. spinosus* are classified as Class 1 invasive weeds in China and have the potential to invade once they reach a certain population density<sup>38</sup>. The seed bank contained other three exotic species: *A. blitum*, *G. parviflora*, and *Veronica persica*. These findings indicate that the community has been invaded by exotic species for a significant period and continues to face the risk of invasion by new exotic

weeds, potentially experiencing reverse succession before transitioning to shrub-grasslands or heliophilous forests. Considering that artificial disturbances such as tillage management and human trampling near footpath may persist in the future, we believe that artificial disturbance and biological invasion will be significant factors influencing the direction of community succession. Therefore, for weed communities already invaded by alien species, it is recommended that landscape management authorities implement measures to reduce anthropogenic disturbances such as tilling and trampling. Concurrent monitoring of aboveground populations of the aforementioned invasive species and prompt removal of invasive plant propagules should be conducted. These actions will protect native plant diversity and facilitate positive community succession.

### Effect of exotic invasive weeds on campus weed community biodiversity

The effect of alien invasions on native communities varies depending on the invasive species, the type of community, and the habitat. For instance, the invasion by *Alternanthera philoxeroides* had diminished the biodiversity of freshwater wetland *Phragmites australis* communities and soil seed banks<sup>39</sup>; *Gumnera tinctoria* had decreased the biodiversity of grassland soil seed banks<sup>16</sup>; while *Spartina anglica* had increased the biodiversity of salt marsh communities<sup>40</sup>. In contrast, *Pennisetum ciliare* did not significantly alter the species richness of the aboveground grassland community or the density of native plant seeds in the soil seed bank after a decade<sup>41</sup>. These differences in the effects of invasive plants on seed banks indicates that biological invasion management should be customized to specific situations.

In this study, the invasion by *G. parviflora* increased significantly the plant density in the aboveground community and resulted in a substantial decrease in seed density within the soil seed bank (Fig. 1). However, when *G. parviflora* invaded with coverage between 10 and 40%, the species diversity of the soil seed bank, particularly in the 0–5 cm layer, was significantly reduced. The biological diversity index increased, becoming roughly comparable to that of the uninvaded soil seed bank at coverages over 60% (Fig. 3). Further analysis of the impact of invasion on the each species in soil seed bank revealed that the invasion led to a significant decrease in seed density in the 0–5 cm soil layer for species such as *Descurainia sophia*, *Trigonotis peduncularis*, *Digitaria sanguinalis*, *Lagopsis supina*, *Lepidium virginicum*, *Capsella bursa-pastoris*, *Amaranthus blitum*, and *Mazus pumilus* ( $N=3$ ,  $P \leq 0.05$ ) which had been high seed reserve in soil of uninvaded plot, and resulted in the disappearance of species with lower seed densities in the soil seed bank, such as *Mazus pumilus*, *Carex duriuscula*, *Cirsium arvense*, *Lysimachia clethroides*, *Brassica rapa* and *Artemisia capillaris*. In the soil seed bank of, severely invaded plot, species such as *Trigonotis peduncularis*, *Lagopsis supina*, *Ixeris polycephala*, *Artemisia selengensis*, *Oxalis corniculata*, *Potentilla chinensis*, and *Cynodon dactylon* disappeared, while new species such as *Datura stramonium* were joined. The reason might be that *G. Parviflora*, through competing for resources or exhibiting allelopathic effects, displaces local flora from their ecological niches, resulting in a diminished density of mature individuals among vulnerable native plants, alongside a reduction in their seed stock and vitality. Meanwhile, in the communities severely invaded by *G. parviflora*, new invasive species had settled down, and the interaction among these non-native species<sup>42,43</sup> need further research. These new invasive species were also responsible for the higher number of species and biodiversity index in the seed bank under severe invasion level compared to moderate ones. In any case, the presence of alien species such as *G. parviflora*, *Datura stramonium*, *Pharbitis purpurea* and *Veronica persica* in aboveground or underground communities indicates that the campus abandoned grassland community has a high risk of alien species invasion.

Given that the invasion of *G. Parviflora* has a significant impact on the soil seed bank, campus ecosystem managers should enhance the management of abandoned grasslands, incorporate the soil seed bank and aboveground community into the scope of biological invasion risk assessments, and coordinate prevention and control measures.

### Effect of *G. parviflora* invasion on the similarity between aboveground communities and soil seed bank

In published studies, some have shown a higher similarity between soil seed banks and ground vegetation, while others have shown a lower similarity<sup>44</sup>. The Sørensen similarity coefficient between soil seed banks and aboveground communities in three types of urban park green spaces in Beijing ranged from 0.10 to 0.18<sup>45</sup>; whereas in abandoned urban wetlands of Tianjin, this coefficient was 0.330<sup>46</sup>. These two cities and the city of Jinan where this study was conducted are located in the warm temperate zone of northern China. The weed communities in this study generally exhibited less similarity between aboveground community and underground seed banks. The difference between the 0–5 cm soil seed bank and the aboveground communities became more pronounced after the invasion by *G. parviflora*. The speculated reasons may include the reduction in seed supplementation from the aboveground vegetation to the upper seed bank of native plants due to the invasion of *G. parviflora*, the loss of seed vitality caused by the allelopathy of *G. parviflora*<sup>47</sup>, and the natural loss of seed vitality, which need to be proved by more studies.

### Conclusions

In summary, the abandoned grassland on campus not invaded by *G. parviflora* exhibits rich community biodiversity and restoration potential. Its aboveground and belowground communities consist of 32 species from 20 families, with low similarity between them. The average seed density was 11,671 seeds/m<sup>2</sup>, 59% of seeds are stored in 0–5 cm soil layer, the species composition analysis found that they are at high risk of alien species invasion, and the succession process was affected by human disturbance and biological invasion.

The invasion of *G. parviflora* has led to an increase in plant density within the aboveground community of abandoned campus grasslands, while the seed density in the topsoil (0–5 cm) seed bank had significantly decreased. The species composition of both aboveground and underground communities had been altered. The invasion had a more severe impact on soil seed bank biodiversity than on aboveground communities. The effect

was correlated with the soil layer, showing significant declines in species numbers in the 0–5 cm and 10–15 cm layers. In cases of moderate invasion, the 0–5 cm and 10–15 cm soil seed banks experienced the most significant loss in biodiversity. The invasion of *G. parviflora* impacted the succession process of the abandoned grassland community and its natural recovery capabilities. The study also revealed that four non-native species, including *G. parviflora*, have colonized aboveground or underground communities in campus abandoned grasslands, with some species already forming persistent seed banks.

The campus vegetation management department should prioritize addressing the impacts of biological invasions on soil seed banks. By first understanding the characteristics of target plant species' soil seed banks, appropriate strategies should be developed to prevent and control the invasion of alien plants in natural habitats. Concurrently, conservation and proper utilization of native species within the surface soil seed bank should be implemented.

## Data availability

Data are provided within the manuscript, and source data are available from the corresponding authors on request.

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## Author contributions

G.X. and L.X. wrote the main manuscript text. H.R. and Z.S. prepared the figures. J.C. collated the data. All authors reviewed the manuscript.

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## Declarations

## Competing interests

The authors declare no competing interests.

## Additional information

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