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Rapid monitoring of *Ambrosia artemisiifolia* in semi-arid regions based on ecological convergence and phylogenetic relationships

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Rapid monitoring and early elimination are important measures to control the spread of invasive plants. *Ambrosia artemisiifolia* is a globally distributed harmful invasive weed. The aim of this study was to clarify the invasion habitat preferences of *A. artemisiifolia* and the interspecific associations or phylogenetic relationships between this and native species in the Yili River Valley of Xinjiang, China. We identified the preferred habitat types of *A. artemisiifolia*, and investigated the composition and distribution of native species at the early stage of invasion by targeted sampling at 186 sites. By comparing the associations and phylogenetic distance between *A. artemisiifolia* and native species with those in Xinjiang and worldwide, we assessed the feasibility of using native species as indicators for rapid monitoring of *A. artemisiifolia*. *A. artemisiifolia* displayed an obvious invasive preference for semi-arid areas, particularly road margins (27.96%), forest (21.51%), farmland (19.35%), wasteland (12.37%), residential areas (10.75%), and grassland (8.06%). The composition and distribution of native species were similar across habitats, with more than 50% co-occurrence of *A. artemisiifolia* with *Setaria viridis*, *Poa annua*, *Arrhenatherum elatius*, *Artemisia annua*, *Artemisia vulgaris*, *Artemisia leucophylla*, *Cannabis sativa*, and *Chenopodium album*. *A. artemisiifolia* was more likely to show co-occurrence with closely related species. Overall, 53.85% of the above indicator native species with high co-occurrence were widely distributed in the potential suitable areas for *A. artemisiifolia* in Xinjiang. Globally, the species with the highest occurrence belonged to the genera *Chenopodium* (58%), *Bromus*, *Poa*, *Setaria*, and *Trifolium* (>40%). Therefore, native species with the strong association and phylogenetic distant relationship to *A. artemisiifolia* can be employed as indicators for rapid and accurate monitoring in semi-arid areas.

KEYWORDS

***Ambrosia artemisiifolia*, invasive species, interspecific association, Darwin's naturalization hypothesis, Darwin's pre-adaptation hypothesis, early stage**

Introduction

Alien plant invasion can be roughly divided into three stages: introduction, colonization, and naturalization (Radosevich, 2007). Accurate monitoring at an early stage is essential for immediate detection and effective prevention and control of invasive plants. At present, the monitoring of alien invasive plants relies mainly on inefficient manual large-scale screening (Richter et al., 2013). Although hyperspectral data monitoring has been proposed as an alternative, the corresponding results are strongly affected by source data and model accuracy, on top of elevated operational costs (Thamaga and Dube, 2018; Al-Lami et al., 2021). Because the early invasive population is difficult to spot due to low density and patchy or sporadic distribution, attempts should focus on rapid, efficient, and low-cost invasive species monitoring technology in the early stage.

The growth and distribution of invasive plants depend on the environment. Understanding habitat requirements and species distribution is essential for the successful monitoring and effective control of alien species (Hauser and McCarthy, 2009; Giljohann et al., 2011). Although the introduction and diffusion of alien species are random and the habitats they colonize are very diverse, interactions with abiotic and biotic factors will define a preference for certain habitats, especially during establishment and population expansion (Hejda et al., 2015; Andelkovic et al., 2022). At a local scale, habitat type is the best predictor of plant invasion, trumping the importance of propagule pressure and climate (Chytrý et al., 2008a,b, 2009). Therefore, it is crucial to identify suitable or preferred habitat characteristics of alien species, and conduct a census in these habitats to enable rapid monitoring.

Interaction with native species plays an important role for individual survival and population growth of invasive plants, overcoming the constraints of abiotic factors and propagule pressure (Thomaz and Michelan, 2011; Waller et al., 2016). On the one hand, alien species usually show positive interspecific associations with widespread native species in specific habitats (Fridley et al., 2007; Lei et al., 2018). On the other hand, Darwin noted how the relationship between alien and native species affected the successful naturalization of the former (Darwin, 1929). According to this simple methodological framework, the relationship between alien and native species can be used to predict which species are prone to invasion in which ecosystems (Procheş et al., 2010).

Furthermore, regular changes to interspecific associations and kinship between invasive and native species could potentially define some general rules governing specific invasion trends, leading to common indicator species. These could be employed as search tools for alien species in targeted rapid monitoring.

The invasive annual herbaceous species *Ambrosia artemisiifolia* has become a global problem, particularly in Europe and China. Crop yields are reduced in the invaded areas, and the large amount of pollen produced is harmful to human health (Essl et al., 2015; Hamaoui-Laguel, 2018). *A. artemisiifolia* is strongly competitive. When exposed to water and nitrogen stress, it responds by adjusting biomass allocation and by making other phenotypic plasticity changes, which makes it highly adaptable to habitats likely to be invaded (Leskovšek et al., 2012a,b). This species, thus, has a wide range of suitable habitat types, including croplands, transportation corridors, wastelands, and riparian areas (Montagnani et al., 2017). Therefore, it is necessary to identify the preferred habitats of *A. artemisiifolia* and then use indicator species to rapidly and effectively monitor these habitats to carry out prevention and control as early as possible.

Ambrosia artemisiifolia is widely distributed in northeast, north, and south China (Feng et al., 2012; Xing, 2012; Liu, 2019). Previously, we found that Yili Valley, located in the arid and semi-arid Xinjiang Province of China, was first invaded by *A. artemisiifolia* in 2010 (Dong et al., 2020). In this study, we investigated the community invaded by *A. artemisiifolia* in the Yili Valley to identify the preferred habitat of this species in semi-arid regions. Moreover, we evaluated the interspecific associations between *A. artemisiifolia* and native species in each invasive habitat, as well as the corresponding phylogenetic relationship. Finally, we used this information to determine whether the indicator species of Yili Valley could be employed as universal predictors for all of Xinjiang and global distribution areas of *A. artemisiifolia*. As an overall objective, this study is expected to aid the rapid monitoring of *A. artemisiifolia* in semi-arid areas.

Materials and methods

Study area

The Yili Valley (42°14′–44°53′N, 80°09′–84°56′E) lies in the westernmost part of the Tianshan Mountain Range of Xinjiang. The Valley comprises 56,400 km^2, and has a continental temperate arid climate. The region has an average annual temperature of 10.4°C and precipitation of 417.6 mm. In grassland habitats, which represent the wettest area in Yili River, precipitation can reach 500 mm annually. The Yili Valley, with its rich plant diversity and extensive seed dispersal via canals, cattle, sheep, and tourists, provides favorable conditions for the invasion and rapid spread of alien species (Jia et al., 2011).

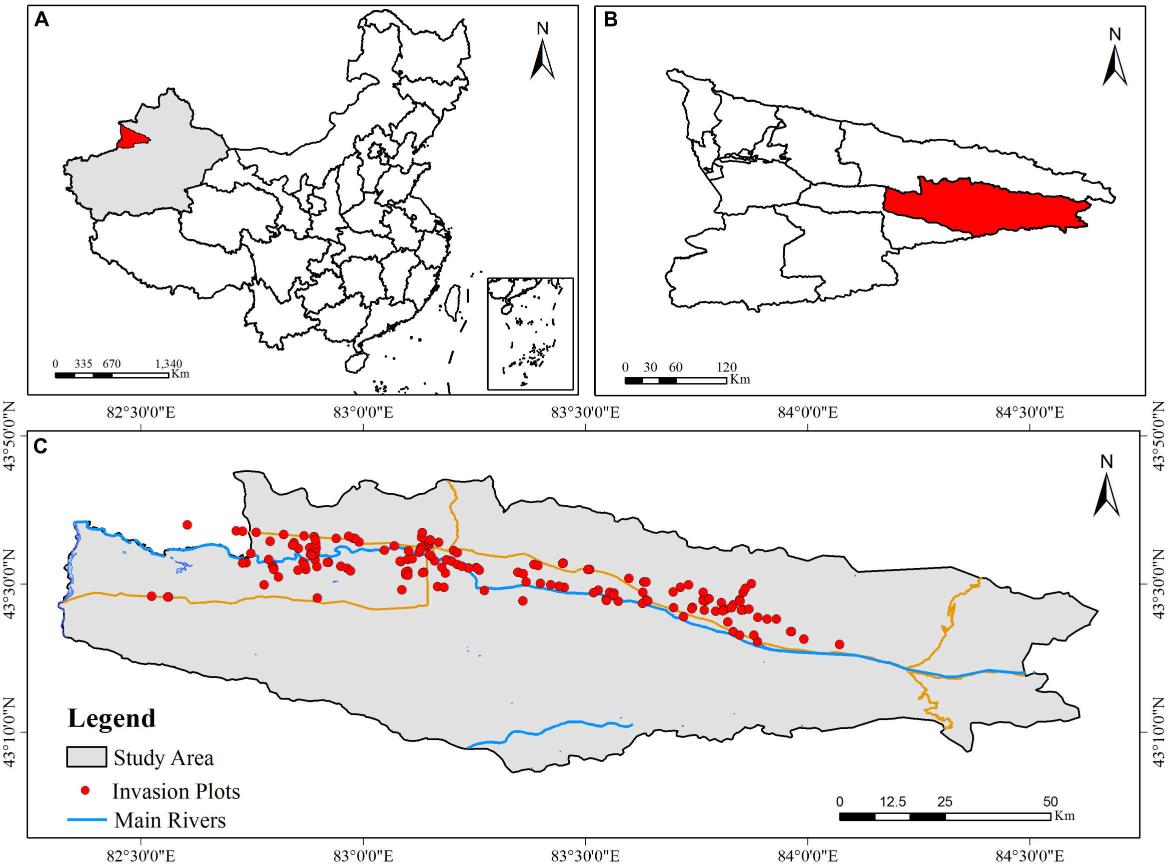

FIGURE 1
Distribution points of *Ambrosia artemisiifolia* invasion communities in the study area. **(A)** The semi-arid regions Xinjiang is located in northwest of China. **(B)** The Yili Valley is located in northwest of Xinjiang. **(C)** Study area in the Yili Valley.

Experimental design and statistical analysis

Habitat investigation and sample setup of *Ambrosia artemisiifolia* invasion

In August 2020, all communities at the initial stage of invasion by *A. artemisiifolia* (≤20% population coverage) were surveyed (Fenesi et al., 2015). Each invasive community was considered an invasion point, which was demarcated by latitude and longitude based on GPS data, as well as by habitat type (**Figure 1**).

Observation plots were set up in the areas of *A. artemisiifolia* distribution within each habitat. Continuous or discontinuous 2 m × 2 m squares were used to cover the distribution of *A. artemisiifolia*. Species frequency was defined as the number of squares with a particular species/total number of squares × 100%. After the species frequency calculation of a certain habitat samples was completed, the species frequency of all samples in the habitat were regarded as repeated, and the mean and standard deviation were calculated as the species frequency of the habitat type.

There were some alien species (such as *Conyza canadensis*) that, according to our observations, were successfully naturalized in the study area. These species did not cause harm, and their distribution was stable and common. Therefore, we considered these as native species during our statistical analysis.

For species that could not be accurately identified in the field, plants were collected and identified in the laboratory. Growth forms and species taxonomy were identified according to descriptions in the Flora of China (Chinese Academy of Sciences Flora of China Editorial, 1998), Flora of Xinjiang (Editorial Committee of Xinjiang Flora, 1992–2011).

Interspecific associations between *Ambrosia artemisiifolia* and native species in the Yili Valley

Interspecific association reflects the coexistence of two species. A strong interspecific association indicates that ecological demand and habitat selection of *A. artemisiifolia* and native species have strong convergence and divergence.

The χ^2 statistic, association coefficient (AC), percentage of co-occurrence (PC), Ochiai index (OI), and dice index (DI) were used to determine the associations and co-occurrence probability between *A. artemisiifolia* and native species. To avoid bias introduced by rare species, taxa with a frequency < 10% were excluded from the analysis.

A 2×2 contingency table was constructed to show the coexistence interspecific associations between *A. artemisiifolia* and native species. The significance of interspecific associations were assessed by chi-square tests with Yates correction as follows:

$$\chi^2 = \frac{N\left[\left(|ad - bc|\right) - 0.5N\right]^2}{(a+b)(c+d)(a+c)(b+d)} \tag{1}$$

Each *A. artemisiifolia* invasion point was taken as the unit of calculation, with N representing the total number of *A. artemisiifolia* invasion points, a the number of points in which two species co-occurred, b and c the number of points in which only one species occurred, and d the number of points in which none of the species occurred. For $n = 1$ degrees of freedom, the interspecific association of each species pair was non-significant if $\chi^2 < 3.841$ ($P > 0.05$), significant if $3.841 < \chi^2 < 6.635$ ($0.01 < P < 0.05$), and highly significant if $\chi^2 > 6.635$ ($P < 0.01$). A positive association was indicated if $ad > bc$, and a negative association was indicated if $ad < bc$. The χ^2 statistic could objectively and accurately reflect the significance of association between species pairs, but it could not quantify the closeness of this association.

The AC can further reflect the degree of interspecific associations, but it tends to exaggerate the significance of such associations in the absence of both species. The AC is calculated as follows:

$$\text{If } ad \geq bc,\ \text{AC} = (ad - bc)/[(a+b)(b+d)] \tag{2}$$

$$\text{If } bc > ad \text{ and } d \geq a,\ \text{AC} = (ad - bc)/[(a+b)(a+c)] \tag{3}$$

$$\text{If } bc > ad \text{ and } d < a,\ \text{AC} = (ad - bc)/[(b+d)(d+c)] \tag{4}$$

The AC range is $[-1, 1]$, and the closer it is to 1, the stronger is the positive association between species; whereas a value close to -1 indicates a strong negative association. AC = 0 indicates complete independence between species.

The PC reflects the degree of positive association between species, but tends to exaggerate the role of a, b, and c in the determination of association. The formula is PC = a/(a+b+c). The PC range is [0, 1]; the closer the value is to 1, the higher is the degree of positive connection, and the more likely two species are to appear or not together. Consequently, the ecological habitats and environmental requirements of the two species become more consistent.

The OI and DI can accurately reflect the probability and degree of association between different species pairs, and overcome the deviation caused by the large influence of d on the point AC. They are calculated as follows:

$$\text{OI} = \frac{a}{\sqrt{(a+b)(a+c)}} \tag{5}$$

$$\text{DI} = \frac{2a}{2a+b+c} \tag{6}$$

The range of these two indices is [0, 1]; the closer either of them is to 1, the higher is the degree of positive association between species pairs, and the higher is the probability of co-occurrence.

Phylogenetic relationship between *Ambrosia artemisiifolia* and native species in the Yili Valley

The *PhyloMaker* package in R was used to generate a phylogenetic tree framework, with the phylogenetic clade based on the APG classification system. The latter was done after the list of all families and species obtained from the survey was corrected in R 4.1.3 The phylogenetic distance (PD) between the invader and resident species in a recipient community was used as a metrics to represent their phylogenetic relatedness (Feng and Fu, 2008; Tretyakova et al., 2021). PD values were calculated uniformly for all indigenous species, regardless of habitat, using the *picante* package in R.

Distribution and representativeness of indicator species from the Yili Valley in potential suitable areas of Xinjiang

The classification of potential suitable areas of *A. artemisiifolia* plays an important role in early warning and effective monitoring. Through the Maxent model, Ma et al. (2020) used environmental factors, including climate data (precipitation and temperature); soil data; land use data; and altitude, slope, and aspect data, to identify the 13 areas listed in this study that are potentially suitable for *A. artemisiifolia*. The Flora of Xinjiang (Editorial Committee of Xinjiang Flora, 1992–2011) was consulted to check whether indicator species from the Yili Valley were distributed in all potential suitable areas for *A. artemisiifolia* in Xinjiang, and their proportion was calculated. Determining whether the main habitat types of the species recorded in the Flora were similar to those of indicator species could attest to the universality and representativeness of such species across Xinjiang.

TABLE 1 Distribution frequency (Mean ± SD) of native species in *Ambrosia artemisiifolia* invasive communities in the Yili Valley.

Habitat types	Species	Frequency/%	Species	Frequency/%	Species	Frequency/%	Species	Frequency/%
Grassland	*Poa annua*	100 ± 0	*Cannabis sativa*	70 ± 16.12	*Artemisia vulgaris*	60 ± 10.12	*Achnatherum splendens*	33.33 ± 18.86
	Setaria viridis	98.18 ± 5.75	*Trifolium*	70 ± 10	*Eragrostis pilosa*	60 ± 0	*Arctium lappa*	20 ± 0
	Polygonum aviculare	90 ± 10	*Plantago asiatica*	70 ± 10	*Lagedium sibiricum*	60 ± 0	*Phragmites australis*	20 ± 0
	Eleusine indica	85 ± 16.58	*Artemisia annua*	67.27 ± 15.43	*Geranium wilfordii*	53.33 ± 9.43	*Carduus nutans*	20 ± 0
	Medicago sativa	80 ± 0	*Artemisia leucophylla*	67.27 ± 15.43	*Polygonum lapathifolium*	50 ± 10	*Achillea millefolium*	20 ± 0
	Sonchus oleraceus	80 ± 0	*Festuca elata*	60 ± 14.14	*Xanthium sibiricum*	44 ± 8		
	Conyza canadensis	75 ± 8.66	*Elymus dahuricus*	60 ± 0	*Daucus carota*	40 ± 0		
	Chenopodium album	70 ± 15.27	*Cirsium japonicum*	60 ± 0	*Lepidium apetalum*	40 ± 0		
Farmland	*Bromus japonicus*	88.7 ± 17.52	*Conyza canadensis*	56 ± 8	*Medicago sativa*	46.67 ± 9.43	*Sonchus oleraceus*	30 ± 10
	Polygonum aviculare	80 ± 21.91	*Artemisia vulgaris*	56 ± 7.12	*Sonchus oleraceus*	46.67 ± 24.94	*Phragmites australis*	30 ± 10
	Setaria viridis	79.2 ± 16.47	*Festuca elata*	50 ± 3	*Taraxacum mongolicum*	40 ± 0	*Abutilon theophrasti*	26.67 ± 9.43
	Artemisia annua	67.14 ± 9.58	*Echinochloa crus-galli*	48.57 ± 14.57	*Xanthium sibiricum*	36 ± 8	*Achnatherum splendens*	20 ± 0
	Trifolium	64 ± 23.32	*Plantago asiatica*	48 ± 9.8	*Geum aleppicum*	33.33 ± 9.43	*Chrysopogon aciculatus*	20 ± 0
	Eleusine indica	64 ± 19.6	*Arrhenatherum elatius*	48 ± 20.4	*Cannabis sativa*	32.31 ± 14.76	*Arctium lappa*	20 ± 0
	Chenopodium album	57.5 ± 6.61	*Geranium wilfordii*	48 ± 9.8	*Lagedium sibiricum*	30 ± 10	*Polygonum lapathifolium*	20 ± 0
	Artemisia leucophylla	56.5 ± 7.23	*Eragrostis pilosa*	46.67 ± 9.43	*Polygonum plebeium*	30 ± 10	*Galium paradoxum*	20 ± 0
Forest	*Bromus japonicus*	97.33 ± 6.8	*Chenopodium album*	69.33 ± 14.36	*Sonchus oleraceus*	60 ± 0	*Xanthium sibiricum*	36.36 ± 11.5
	Setaria viridis	87.5 ± 13.92	*Plantago asiatica*	67.06 ± 16.72	*Taraxacum mongolicum*	55 ± 8.66	*Polygonum plebeium*	35 ± 16.58
	Conyza canadensis	87.5 ± 9.68	*Artemisia leucophylla*	65.56 ± 16.06	*Festuca elata*	53.33 ± 9.42	*Polygonum lapathifolium*	35 ± 8.66
	Geranium wilfordii	80 ± 16.33	*Artemisia vulgaris*	62.14 ± 16.31	*Melilotus officinalis*	50 ± 10	*Arctium lappa*	33.33 ± 9.43
	Poa annua	80 ± 0	*Medicago sativa*	60 ± 12.65	*Elymus dahuricus*	50 ± 10	*Cirsium japonicum*	30 ± 10
	Polygonum aviculare	76 ± 23.32	*Echinochloa crus-galli*	60 ± 12.65	*Cannabis sativa*	48.75 ± 14.09	*Daucus carota*	26.67 ± 9.43
	Eleusine indica	73.33 ± 9.43	*Eragrostis pilosa*	60 ± 0	*Sophora alopecuroides*	40 ± 0	*Achnatherum splendens*	20 ± 0
	Trifolium	71.67 ± 15.18	*Chrysopogon aciculatus*	60 ± 16.33	*Phragmites australis*	38.33 ± 9.86	*Urtica fissa*	20 ± 0
Road margins	*Sophora alopecuroides*	96.67 ± 7.45	*Chenopodium album*	81.43 ± 15.97	*Artemisia annua*	62 ± 16.61	*Lagedium sibiricum*	48.57 ± 9.9
	Geranium wilfordii	93.33 ± 9.43	*Eragrostis pilosa*	80 ± 14.14	*Taraxacum mongolicum*	60 ± 20	*Arctium lappa*	41.67 ± 9.86
	Arrhenatherum elatius	92.65 ± 9.64	*Festuca elata*	80 ± 17.89	*Artemisia leucophylla*	56 ± 15	*Polygonum hydropiper*	40 ± 0
	Setaria viridis	91.74 ± 12.91	*Juncus bufonius*	80 ± 28.28	*Polygonum lapathifolium*	56 ± 15	*Daucus carota*	40 ± 0
	Polygonum aviculare	90 ± 19.15	*Trifolium*	74.29 ± 11.78	*Sonchus oleraceus*	54.29 ± 9.04	Achnatherum splendens	26.67 ± 9.43

(*Continued*)

TABLE 1 (Continued)

Habitat types	Species	Frequency/%	Species	Frequency/%	Species	Frequency/%	Species	Frequency/%
	Eleusine indica	90 ± 17.32	*Plantago asiatica*	69.41 ± 19.55	*Artemisia vulgaris*	52 ± 9.8		
	Echinochloa crus-galli	82.86 ± 7	*Medicago sativa*	67.27 ± 17.63	*Phragmites australis*	52 ± 9.8		
	Conyza canadensis	82.22 ± 17.5	*Cannabis sativa*	63.08 ± 18.14	*Xanthium sibiricum*	49.41 ± 15.52		
Residential area	*Setaria viridis*	97.89 ± 6.14	*Polygonum aviculare*	93.75 ± 9.27	*Geranium wilfordii*	60 ± 20	*Melilotus officinalis*	42.86 ± 9.43
	Arrhenatherum elatius	97.5 ± 6.61	*Eleusine indica*	90 ± 10	*Medicago sativa*	57.5 ± 12	*Sonchus oleraceus*	40 ± 0
	Echinochloa crus-galli	96 ± 8	*Chenopodium album*	84 ± 15	*Polygonum lapathifolium*	52 ± 9.8	*Achnatherum splendens*	33.33 ± 9.43
	Conyza canadensis	95 ± 8.66	*Cannabis sativa*	80 ± 16.33	*Xanthium sibiricum*	50 ± 10		
Residential area	*Artemisia leucophylla*	95 ± 8.66	*Trifolium*	77.5 ± 21.07	*Arctium lappa*	46.67 ± 9.43		
	Artemisia annua	95 ± 8.66	*Plantago asiatica*	61.82 ± 13.36	*Cirsium japonicum*	46.67 ± 9.43		
Wasteland	*Setaria viridis*	98.1 ± 5.87	*Taraxacum mongolicum*	90 ± 9.27	*Plantago asiatica*	57.78 ± 11.33	*Xanthium sibiricum*	42.5 ± 6.61
	Eleusine indica	98 ± 6	*Conyza canadensis*	80 ± 16.33	*Artemisia vulgaris*	50 ± 10	*Arctium lappa*	40 ± 0
	Polygonum aviculare	96 ± 8	*Festuca elata*	80 ± 16.33	*Phragmites australis*	50 ± 10	*Cirsium japonicum*	33.33 ± 9.43
	Trifolium	96 ± 8	*Chenopodium album*	77.5 ± 21.07	*Sonchus oleraceus*	50 ± 10		
	Geranium wilfordii	95 ± 8.66	*Artemisia annua*	63.08 ± 17.27	*Polygonum lapathifolium*	46.67 ± 9.43		
	Arrhenatherum elatius	93.75 ±	*Cannabis sativa*	60 ± 18.52	*Polygonum hydropiper*	46.67 ± 9.43		

Prevalence and representation of indicator and native species of the Yili Valley in major invasive areas of *Ambrosia artemisiifolia* across the world

To assess the difference and similarity of species composition between indicator species in the Yili Valley and native species in the main worldwide invasion areas of *A. artemisiifolia*, we search the literatures of associated species in the world's recorded *A. artemisiifolia* distribution areas and count the native species present in the literatures (Igrc et al., 1995; Song and Prots, 1998; Makra et al., 2005; Brandes and Nitzsche, 2006; Fumanal et al., 2006; Essl et al., 2009; Gajnik and Peternel, 2009; Galzina et al., 2010; Patracchini and Ferrero, 2011; Puc and Wolski, 2013; Csontos et al., 2015; Gentili et al., 2016; Romain et al., 2016; Abramova, 2018; Chadaeva et al., 2018; Mang et al., 2018; Gusev, 2019; Petrova, 2019; Pinke et al., 2019).

To prevent discrepancies arising from different classification methods, the genera of recorded species were used to calculate the number of references for the occurrence of a species (i.e., the occurrence frequency of the species relative to the total number of references, which was 19). By arranging the frequency of each species, the similarity between the identified indicator species and the associated species of *A. artemisiifolia* was determined. This calculation defined the universality and representativeness of the species in present global distribution areas of *A. artemisiifolia*.

Results

Habitat types and species composition of *Ambrosia artemisiifolia* in the Yili Valley

A total of 186 invasion sites of *A. artemisiifolia* in the Yili Valley were cataloged. The invasive communities encompassed six habitat types: road margins (52), forest (40), farmland (36), wasteland (23), residential area (20), and grassland (15). *A. artemisiifolia* could not be found in other habitats, suggesting clear habitat preference for invasion.

Composition and distribution frequency of native species were similar across all habitats (**Table 1**). Specifically, 17 species were common in all habitats; they accounted for 60.71% of grassland species, 53.13% of farmland species, 56.67% of forest species, 60.71% of road margins species, 77.27% of residential area species, and 80.95% of wasteland species.

The most frequent grass species were *Setaria viridis*, *Poa annua*, *Bromus* spp., *Arrhenatherum elatius*, *Echinochloa crus-galli*, *Eleusine indica*, and some *Artemisia* species. Other common species were *Chenopodium album*, *Plantago asiatica*, *C. canadensis*, *Cannabis sativa*, and *Trifolium* spp. These results pointed to similar species composition and distribution in the habitats invaded by *A. artemisiifolia* (**Table 1**).

Interspecific associations between *Ambrosia artemisiifolia* and native species

No significant interspecific association between *A. artemisiifolia* and native species could be detected in all habitats. *S. viridis*, *P. annua*, and *Bromus* spp. correlated positively with *A. artemisiifolia* in all habitats; whereas *A. elatius* did so only in road margins, residential areas, and wasteland. *Artemisia annua*, *Artemisia vulgaris*, and *Artemisia leucophylla* showed similar association characteristics and were positively associated with *A. artemisiifolia* in all habitats. Instead, *C. sativa* exhibited positive association with *A. artemisiifolia* in farmland and grassland, but a negative association in other habitats. A negative association was observed also between *C. album* and *A. artemisiifolia* in all habitats (**Table 2**).

The PC of *A. artemisiifolia* and native species in different habitats was above 50% and reached up to 96.2% for *S. viridis*, *P. annua*, *Bromus* spp., *A. annua*, *A. vulgaris*, and *A. leucophylla* in all habitats. The PC of *A. elatius* in road margin, residential area, and wasteland habitats were above 60%, with a peak of 95.2%. Except for wasteland, the OI and DI values of *C. sativa* surpassed 60% in all habitats; whereas those of *C. album* were greater than 50% in all habitats (**Table 3**).

Various native species and *A. artemisiifolia* showed different PC due to different habitats (**Table 3**). The PC of *A. artemisiifolia* and *Xanthium sibiricum* in farmland reached 68.1%, that of *Bromus* spp. in forest reached 77.8%, that of *Trifolium* reached 56.3%, that of *E. indica* in wasteland reached 68.1%, and that of *P. asiatica* reached 59.3%.

Phylogenetic relationship between *Ambrosia artemisiifolia* and its native companion species

The greatest PD (376.57 MA) was observed between *A. artemisiifolia* and species of the Gramineae family with elevated PC, such as *S. viridis*, *P. annua*, and *Bromus* spp. The PD between *A. artemisiifolia* and *C. album*, *C. sativa*, and *Trifolium* spp. increased over time, with the proportion of species showing a distant relationship being greater in the early stages of *A. artemisiifolia* invasion (**Figure 2**).

Indicator species in the potential habitat of *Ambrosia artemisiifolia* in Xinjiang

Poa annua, *C. album*, *Trifolium* spp., and *A. elatius* are widespread in Xinjiang, and their distribution area covered 100% of the potential suitable areas of *A. artemisiifolia* in this region. The distribution of *A. annua* showed a 46.15% overlap with potential suitable areas of *A. artemisiifolia* in Xinjiang, including severe, moderate, and mildly suitable areas. The degree of overlap between *A. artemisiifolia*, *Bromus* spp., *S. viridis*, *A. leucophylla*, and *P. asiatica* was only 30.77%, decreasing further to 15.38% for *C. sativa*, *X. sibiricum*, and *E. indica*. Notably, the habitats defined by each indicator species were similar to the main habitat types in the suitable area, especially in farmland, forest, road margins, and wasteland (**Table 4**).

Representation of indicator species from the Yili Valley in global distribution areas of *Ambrosia artemisiifolia*

In terms of species composition, 13 families (72.22%), 31 genera (61.76%), and 22 species (39.29%) were shared between the native species of the Yili Valley and those of areas currently infested by *A. artemisiifolia* across the world (**Table 5**). Among them, species belonging to the Gramineae and Compositae families accounted for the largest share. These common species had a high frequency of distribution in the Yili Valley.

Among all indicator species, *C. album* had the highest frequency of occurrence (58%); whereas species belonging to the *Bromus*, *Poa*, *Setaria*, and *Trifolium* genera appeared more than 40% of the time (**Table 5**).

Discussion

Ambrosia artemisiifolia shows obvious habitat preference when invading a semi-arid area

The successful establishment of alien invasive species is determined by the fluctuation of abiotic environmental factors, propagule pressure, and the interaction between species (Pysek and Chytry, 2014). Habitat conditions play a fundamental role by influencing the invasion process and the composition of

TABLE 2 Association coefficient (AC) between native species and *Ambrosia artemisiifolia* invasive habitat community in the Yili Valley.

Habitat types	Species	AC	Species	AC	Species	AC	Species	AC
Grassland	*Poa annua*	0.346	*Xanthium sibiricum*	−0.227	*Trifolium*	−0.393	*Achillea millefolium*	−0.433
	Setaria viridis	0.292	*Eleusine indica*	−0.292	*Elymus dahuricus*	−0.393	*Eragrostis pilosa*	−0.433
	Artemisia annua	0.292	*Festuca elata*	−0.292	*Polygonum lapathifolium*	−0.393	*Arctium lappa*	−0.433
	Artemisia vulgaris	0.292	*Conyza canadensis*	−0.292	*Plantago asiatica*	−0.393	*Cirsium japonicum*	−0.433
	Artemisia leucophylla	0.292	*Medicago sativa*	−0.292	*Daucus carota*	−0.433	*Phragmites australis*	−0.433
	Cannabis sativa	0.227	*Lagedium sibiricum*	−0.346	*Carduus nutans*	−0.433		
	Chenopodium album	−0.15	*Geranium wilfordii*	−0.346	*Lepidium apetalum*	−0.433		
	Polygonum aviculare	−0.227	*Achnatherum splendens*	−0.346	*Sonchus oleraceus*	−0.433		
Farmland	*Setaria viridis*	0.462	*Echinochloa crus-galli*	−0.3	*Chrysopogon aciculatus*	−0.391	*Festuca elata*	−0.44
	Bromus japonicus	0.417	*Polygonum aviculare*	−0.364	*Achnatherum splendens*	−0.391	*Lagedium sibiricum*	−0.44
	Artemisia annua	0.067	*Trifolium*	−0.364	*Sonchus oleraceus*	−0.413	*Sonchus oleraceus*	−0.44
	Artemisia vulgaris	0.067	*Eleusine indica*	−0.364	*Medicago sativa*	−0.413	*Polygonum plebeium*	−0.44
	Artemisia leucophylla	0.067	*Plantago asiatica*	−0.364	*Eragrostis pilosa*	−0.413	*Phragmites australis*	−0.44
	Cannabis sativa	0.067	*Arrhenatherum elatius*	−0.364	*Geum aleppicum*	−0.413	*Galium paradoxum*	−0.44
	Xanthium sibiricum	−0.176	*Geranium wilfordii*	−0.364	*Abutilon theophrasti*	−0.413	*Polygonum lapathifolium*	−0.44
	Chenopodium album	−0.263	*Conyza canadensis*	−0.364	*Arctium lappa*	−0.413	*Taraxacum mongolicum*	−0.462
Forest	*Setaria viridis*	0.439	*Trifolium*	−0.29	*Taraxacum mongolicum*	−0.422	*Festuca elata*	−0.439
	Poa annua	0.403	*Phragmites australis*	−0.229	*Cirsium japonicum*	−0.422	*Chrysopogon aciculatus*	−0.439
	Bromus japonicus	0.383	*Xanthium sibiricum*	−0.26	*Achnatherum splendens*	−0.422	*Eragrostis pilosa*	−0.456
	Artemisia leucophylla	0.026	*Conyza canadensis*	−0.339	*Polygonum lapathifolium*	−0.422	*Melilotus officinalis*	−0.456
	Artemisia vulgaris	0.026	*Arctium lappa*	−0.383	*Polygonum plebeium*	−0.422	*Urtica fissa*	−0.456
	Plantago asiatica	−0.026	*Echinochloa crus-galli*	−0.403	*Eleusine indica*	−0.439	*Sonchus oleraceus*	−0.456
	Cannabis sativa	−0.075	*Polygonum aviculare*	−0.403	*Geranium wilfordii*	−0.439	*Elymus dahuricus*	−0.456
	Chenopodium album	−0.119	*Medicago sativa*	−0.403	*Daucus carota*	−0.439	*Sophora alopecuroides*	−0.456
Road margins	*Arrhenatherum elatius*	0.45	*Chenopodium album*	−0.313	*Taraxacum mongolicum*	−0.402	*Geranium wilfordii*	−0.461
	Setaria viridis	0.415	*Trifolium*	−0.313	*Echinochloa crus-galli*	−0.415	*Juncus bufonius*	−0.461
	Artemisia annua	0.113	*Eleusine indica*	−0.345	*Sonchus oleraceus*	−0.415	*Achnatherum splendens*	−0.461
	Artemisia vulgaris	0.113	*Polygonum aviculare*	−0.345	*Lagedium sibiricum*	−0.415	*Daucus carota*	−0.471
	Artemisia leucophylla	0.113	*Arctium lappa*	−0.345	*Sophora alopecuroides*	−0.427	*Polygonum hydropiper*	−0.481
	Cannabis sativa	−0.018	*Medicago sativa*	−0.36	*Polygonum lapathifolium*	−0.439		
	Plantago asiatica	−0.257	*Phragmites australis*	−0.375	*Eragrostis pilosa*	−0.45		
	Xanthium sibiricum	−0.257	*Conyza canadensis*	−0.389	*Festuca elata*	−0.45		
Residential area	*Setaria viridis*	0.364	*Phragmites australis*	−0.222	*Achnatherum splendens*	−0.364	*Cirsium japonicum*	−0.417
	Arrhenatherum elatius	0.3	*Trifolium*	−0.222	*Conyza canadensis*	−0.364	*Medicago sativa*	−0.417
	Artemisia annua	0.125	*Xanthium sibiricum*	−0.3	*Eleusine indica*	−0.364	*Polygonum lapathifolium*	−0.417
Residential area	*Artemisia leucophylla*	0.125	*Echinochloa crus-galli*	−0.3	*Polygonum aviculare*	−0.364	*Sonchus oleraceus*	−0.417
	Cannabis sativa	0	*Plantago asiatica*	−0.3	*Geranium wilfordii*	−0.364		
	Chenopodium album	−0.125	*Melilotus officinalis*	−0.3	*Arctium lappa*	−0.364		
Wasteland	*Setaria viridis*	0.405	*Chenopodium album*	−0.219	*Geranium wilfordii*	−0.375	*Taraxacum mongolicum*	−0.432
	Arrhenatherum elatius	0.265	*Xanthium sibiricum*	−0.219	*Trifolium*	−0.375	*Sonchus oleraceus*	−0.432
	Artemisia annua	0.107	*Cannabis sativa*	−0.265	*Festuca elata*	−0.405	*Arctium lappa*	−0.432
	Artemisia vulgaris	0.107	*Conyza canadensis*	−0.306	*Polygonum hydropiper*	−0.405		
	Eleusine indica	−0.107	*Phragmites australis*	−0.342	*Polygonum lapathifolium*	−0.405		
	Plantago asiatica	−0.167	*Polygonum aviculare*	−0.342	*Cirsium japonicum*	−0.405		

TABLE 3 Common percentages of native species and *Ambrosia artemisiifolia* invasive habitat communities in the Yili Valley.

Habitat types	Species	PC	OI	DI	Species	PC	OI	DI	Species	PC	OI	DI
Grassland	***Poa annua***	75	85.9	85.7	*Festuca elata*	25	46.2	40	*Daucus carota*	6.3	18.3	11.8
	Setaria viridis	68.8	82	81.5	*Conyza canadensis*	25	46.2	40	*Carduus nutans*	6.3	18.3	11.8
	Artemisia annua	68.8	82	81.5	*Medicago sativa*	25	46.2	40	*Lepidium apetalum*	6.3	18.3	11.8
	Artemisia vulgaris	68.8	82	81.5	*Lagedium sibiricum*	18.8	38.7	31.6	*Sonchus oleraceus*	6.3	18.3	11.8
	Artemisia leucophylla	68.8	82	81.5	*Geranium wilfordii*	18.8	38.7	31.6	*Achillea millefolium*	6.3	18.3	11.8
	Cannabis sativa	62.5	77.8	76.9	*Achnatherum splendens*	18.8	38.7	31.6	*Eragrostis pilosa*	6.3	18.3	11.8
	Chenopodium album	37.5	58.6	54.5	*Trifolium*	12.5	29.8	22.2	*Arctium lappa*	6.3	18.3	11.8
	Polygonum aviculare	31.3	52.7	47.6	*Elymus dahuricus*	12.5	29.8	22.2	*Cirsium japonicum*	6.3	18.3	11.8
	Xanthium sibiricum	31.3	52.7	47.6	*Polygonum lapathifolium*	12.5	29.8	22.2	*Phragmites australis*	6.3	18.3	11.8
	Eleusine indica	25	46.2	40	*Plantago asiatica*	12.5	29.8	22.2				
Farmland	***Setaria viridis***	92.6	96.2	96.2	*Eleusine indica*	25.9	48.5	41.2	*Abutilon theophrasti*	14.8	35.1	25.8
	Bromus japonicus	85.2	92.1	92	*Plantago asiatica*	25.9	48.5	41.2	*Arctium lappa*	14.8	35.1	25.8
	Artemisia annua	51.9	70.9	68.3	*Arrhenatherum elatius*	25.9	48.5	41.2	*Festuca elata*	11.1	29.4	20
	Artemisia vulgaris	51.9	70.9	68.3	*Geranium wilfordii*	25.9	48.5	41.2	*Lagedium sibiricum*	11.1	29.4	20
	Artemisia leucophylla	51.9	70.9	68.3	*Conyza canadensis*	25.9	48.5	41.2	*Sonchus oleraceus*	11.1	29.4	20
	Cannabis sativa	51.9	70.9	68.3	*Chrysopogon aciculatus*	18.5	40	31.3	*Polygonum plebeium*	11.1	29.4	20
	Xanthium sibiricum	48.1	68.1	65	*Achnatherum splendens*	18.5	40	31.3	*Phragmites australis*	11.1	29.4	20
	Chenopodium album	33.3	55.8	50	*Sonchus oleraceus*	18.5	40	31.3	*Galium paradoxum*	11.1	29.4	20
	Echinochloa crus-galli	29.6	52.3	45.7	*Medicago sativa*	14.8	35.1	25.8	*Polygonum lapathifolium*	11.1	29.4	20
	Polygonum aviculare	25.9	48.5	41.2	*Eragrostis pilosa*	14.8	35.1	25.8	*Taraxacum mongolicum*	7.4	22.6	13.8
	Trifolium	25.9	48.5	41.2	*Geum aleppicum*	14.8	35.1	25.8				
Forest	***Setaria viridis***	88.9	94.2	94.1	*Conyza canadensis*	16.7	38.3	28.6	*Geranium wilfordii*	5.6	19.5	10.5
	Poa annua	83.3	91.1	90.9	*Arctium lappa*	13.9	34.5	24.4	*Daucus carota*	5.6	19.5	10.5
	Bromus japonicus	62.5	77.8	76.9	*Echinochloa crus-galli*	11.1	30.2	20	*Festuca elata*	5.6	19.5	10.5
	Artemisia leucophylla	50	69.8	66.7	*Polygonum aviculare*	11.1	30.2	20	*Chrysopogon aciculatus*	5.6	19.5	10.5
	Artemisia vulgaris	47.2	69.8	66.7	*Medicago sativa*	11.1	30.2	20	*Eragrostis pilosa*	2.8	12	5.4
	Plantago asiatica	47.2	67.7	64.2	*Taraxacum mongolicum*	8.3	25.4	15.4	*Melilotus officinalis*	2.8	12	5.4
	Cannabis sativa	44.4	65.6	61.5	*Cirsium japonicum*	8.3	25.4	15.4	*Urtica fissa*	2.8	12	5.4
	Chenopodium album	41.7	63.4	58.8	*Achnatherum splendens*	8.3	25.4	15.4	*Sonchus oleraceus*	2.8	12	5.4
	Trifolium	33.3	56.3	50	*Polygonum lapathifolium*	8.3	25.4	15.4	*Elymus dahuricus*	2.8	12	5.4
	Phragmites australis	30.6	53.7	46.8	*Polygonum plebeium*	8.3	25.4	15.4	*Sophora alopecuroides*	2.8	12	5.4
	Xanthium sibiricum	22.2	45.1	36.4	*Eleusine indica*	5.6	19.5	10.5				
Road margins	***Arrhenatherum elatius***	90.7	95.2	95.1	*Eleusine indica*	22.2	45.7	36.4	*Sophora alopecuroides*	11.1	31.2	20
	Setaria viridis	85.2	92.2	92	*Polygonum aviculare*	22.2	45.7	36.4	*Polygonum lapathifolium*	9.3	28	16.9
	Artemisia annua	55.6	74	71.4	*Arctium lappa*	22.2	45.7	36.4	*Eragrostis pilosa*	7.4	24.6	13.8
	Artemisia vulgaris	55.6	74	71.4	*Medicago sativa*	20.4	43.6	33.8	*Festuca elata*	7.4	24.6	13.8
Road margins	***Artemisia leucophylla***	55.6	74	71.4	*Phragmites australis*	18.5	41.4	31.3	*Geranium wilfordii*	5.6	20.6	10.5
	Cannabis sativa	48.1	68.7	65	*Conyza canadensis*	16.7	39.1	28.6	*Juncus bufonius*	5.6	20.6	10.5
	Plantago asiatica	31.5	55	47.9	*Taraxacum mongolicum*	14.8	36.6	25.8	*Achnatherum splendens*	5.6	20.6	10.5
	Xanthium sibiricum	31.5	55	47.9	*Echinochloa crus-galli*	13	34	23	*Daucus carota*	3.7	15.9	7.1
	Chenopodium album	25.9	49.7	41.2	*Sonchus oleraceus*	13	34	23	*Polygonum hydropiper*	1.9	9.7	3.6
	Trifolium	25.9	49.7	41.2	*Lagedium sibiricum*	13	34	23				
Residential area	***Setaria viridis***	76.9	87	87	*Xanthium sibiricum*	23.1	43.3	37.5	*Geranium wilfordii*	15.4	33.3	26.7
	Arrhenatherum elatius	69.2	82.2	81.8	*Echinochloa crus-galli*	23.1	43.3	37.5	*Arctium lappa*	15.4	33.3	26.7
	Artemisia annua	53.8	71.4	70	*Plantago asiatica*	23.1	43.3	37.5	*Cirsium japonicum*	7.7	20.4	14.3
	Artemisia leucophylla	53.8	71.4	70	*Melilotus officinalis*	23.1	43.3	37.5	*Medicago sativa*	7.7	20.4	14.3
	Cannabis sativa	46.2	65.5	63.2	*Achnatherum splendens*	15.4	33.3	26.7	*Polygonum lapathifolium*	7.7	20.4	14.3
	Chenopodium album	38.5	58.9	55.6	*Conyza canadensis*	15.4	33.3	26.7	*Sonchus oleraceus*	7.7	20.4	14.3
	Phragmites australis	30.8	51.6	47.1	*Eleusine indica*	15.4	33.3	26.7				
	Trifolium	30.8	51.6	47.1	*Polygonum aviculare*	15.4	33.3	26.7				

(Continued)

TABLE 3 (Continued)

Habitat types	Species	PC	OI	DI	Species	PC	OI	DI	Species	PC	OI	DI
Wasteland	***Setaria viridis***	83.3	91	90.9	***Xanthium sibiricum***	33.3	55.6	50	*Festuca elata*	12.5	31.3	22.2
	Arrhenatherum elatius	66.7	80.9	80	*Cannabis sativa*	29.2	51.6	45.2	*Polygonum hydropiper*	12.5	31.3	22.2
	Artemisia annua	54.2	72.4	70.3	*Conyza canadensis*	25	47.3	40	*Polygonum lapathifolium*	12.5	31.3	22.2
	Artemisia vulgaris	54.2	72.4	70.3	*Phragmites australis*	20.8	42.6	34.5	*Cirsium japonicum*	12.5	31.3	22.2
	Eleusine indica	41.7	62.9	58.8	*Polygonum aviculare*	20.8	42.6	34.5	*Taraxacum mongolicum*	8.3	24.1	15.4
	Plantago asiatica	37.5	59.3	54.4	*Geranium wilfordii*	16.7	37.3	28.6	*Sonchus oleraceus*	8.3	24.1	15.4
	Chenopodium album	33.3	55.6	50	*Trifolium*	16.7	37.3	28.6	*Arctium lappa*	8.3	24.1	15.4

Species in bold are indicator species.

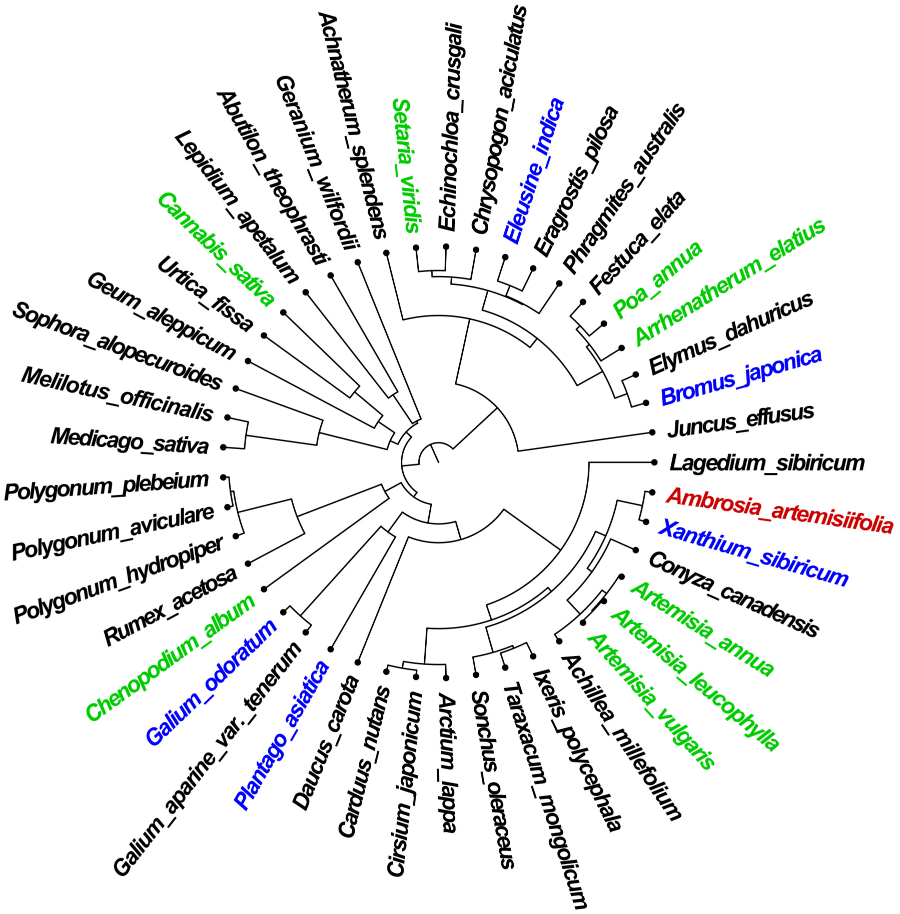

FIGURE 2
Phylogenetic distance between *Ambrosia artemisiifolia* (red-colored) and native species in the study area. Green-colored species are the indicator species present in all habitat types. Blue-colored species are indicator species that occur only in a particular habitat type.

native species, thus defining the relationship between the latter and the invaders, as well as the spread and harm caused by these (Catford et al., 2012; Hejda et al., 2015).

Water is an important factor affecting species distribution. Indeed, precipitation contributes more than 50% to the potential distribution of *A. artemisiifolia* (Ma et al., 2020; Liu et al., 2021). Precipitation above 280 mm promoting growth and propagation of *A. artemisiifolia*. Precipitation in most areas of The Yili Valley is above 280 mm; while the average precipitation in Xinyuan County, where *A. artemisiifolia* is particularly abundant, is 417 mm (Dong et al., 2020). Therefore, in low-lying areas, such as grassland, farmland, and road margins, the water supply can meet the needs for germination, growth, and reproduction of *A. artemisiifolia*

TABLE 4 Distribution of indicator species in potential suitable areas of *Ambrosia artemisiifolia* in Xinjiang.

Species	Suitable areas of major distribution	Proportion of suitable area/%	Habitat types in the suitable area
Setaria viridis	Wide distribution	100	**Farmland**, **Wasteland**, **Road margins**
Chenopodium album	Wide distribution	100	**Farmland**, Canal, **Wasteland**
Trifolium	Wide distribution	100	Valley, **Forest**
Arrhenatherum elatius	Wide distribution	100	Valley, **Wasteland**, **Farmland**, **Road margins**, Valley meadow
Artemisia annua	Tarbagatay, Bortala, Altay, Changji, Aksu, Hetian	46.15	**Farmland**, Hillside, **Wasteland**, **Road margins**
Artemisia vulgaris	Tarbagatay, Altay, Urumqi, Turpan, Kashgar	38.46	**Grassland**, **Forest**, **Wasteland**, **Road margins**
Bromus japonicus	Tarbagatay, Bortala, Altay, Urumqi, Shihezi	38.46	**Farmland**, Canal
Poa annua	Tarbagatay, Altay, Urumqi, Aksu	30.77	Valley, **Forest**, **Farmland**
Artemisia leucophylla	Altay, Urumqi, Aksu, Kashgar	30.77	Hillside, **Forest**, Valley, **Road margins**
Plantago asiatica	Bortala, Changji, Urumqi, Aksu	30.77	Upland meadow, Alpine meadow, **Farmland**, Canal
Cannabis sativa	Tarbagatay, Altay	15.38	Valley, **Wasteland**, **Farmland**
Xanthium sibiricum	Urumqi, Yili	15.38	**Farmland**, Road margins, **Wasteland**
Eleusine indica	Bortala, Tarbagatay	15.38	**Farmland**, Road margins, **Wasteland**

The habitat type in bold is the same as that of the indicator species in Yili River Valley.

TABLE 5 Statistics of native species of *Ambrosia artemisiifolia* in the world distribution.

Genus	Frequency/%	Genus	Frequency/%	Genus	Frequency/%	Genus	Frequency/%
Chenopodium	58.33	*Arrhenatherum*	25	*Potentilla*	16.67	*Datura*	8.33
Medicago	50	*Festuca*	25	*Arctium*	8.33	*Kochia*	8.33
Bromus	41.67	*Taraxacum*	25	*Capsella*	8.33	*Oenothera*	8.33
Cirsium	41.67	*Daucus*	25	*Sonchus*	8.33	*Anthoxanthum*	8.33
Poa	41.67	*Melilotus*	25	*Galinsoga*	8.33	*Crepis*	8.33
Setaria	41.67	*Amaranthus*	16.67	*Galium*	8.33	*Picris*	8.33
Trifolium	41.67	*Centaurea*	16.67	*Abutilon*	8.33	*Senecio*	8.33
Lolium	41.67	*Polygonum*	16.67	*Forsythia*	8.33	*Rubus*	8.33
Achillea	33.33	*Bellis*	16.67	*Pisum*	8.33	*Sanguisorba*	8.33
Artemisia	33.33	*Cichorium*	16.67	*Cynodon*	8.33	*Stellaria*	8.33
Echinochloa	33.33	*Potentilla*	16.67	*Carex*	8.33	*Hordeum*	8.33
Lactuca	33.33	*Juncus*	16.67	*Digitaria*	8.33	*Phleum*	8.33
Convolvulus	33.33	*Lotus*	16.67	*Viola*	8.33	*Calamagrostis*	8.33
Conyza	25	*Erigeron*	16.67	*Sorghum*	8.33		
Plantago	25	*Xanthium*	16.67	*Arenaria*	8.33		

seeds, thereby ensuring successful settlement and population expansion. By simulating the effect of different precipitation levels on the growth of *A. artemisiifolia*, found that *A. artemisiifolia* was highly adaptable to drought (Leiblein and Lösch, 2011; Leskovšek et al., 2012a), explaining its widespread distribution in a habitat with little water such as wasteland. Temperature had no significant effect on the growth and distribution of *A. artemisiifolia* in the Yili Valley (Dong et al., 2020).

Although the habitats of *A. artemisiifolia* across the world are not exactly the same as those in this study, priority targeting of habitats preferentially invaded by *A. artemisiifolia* is the basis for rapid surveillance (Epanchin-Niell and Hastings, 2010). This study describes the habitats that may be preferred for invasion by *A. artemisiifolia* throughout the world.

The probability of co-occurrence between *Ambrosia artemisiifolia* and species with strong positive correlation and distant relationship is higher at the neighborhood scale

In this study, the invasive community of *A. artemisiifolia* was at the stage from establishment to population growth, and the association between *A. artemisiifolia* and other species were weak (**Table 2**). The lack of any significant association on the whole indicated that the current invasive community of *A. artemisiifolia* was in a dynamic succession process and had not yet stabilized (Liu et al., 2017). At this stage, interspecific competition was weak, meaning that native species ecologically similar to *A. artemisiifolia*, including *S. viridis*, *P. annua*, *A. elatius*, *A. annua*, *A. vulgaris*, *A. leucophylla*, *C. sativa*, and *C. album*, as well as other dominant native plants in the community, did not compete intensely for resources and exhibited a high PC (Lei et al., 2018).

At the same time, species related to *A. artemisiifolia* were detected in all habitats, indicating similar habitat selection and adaptation (Ozaslan et al., 2016). However, at the neighborhood scale (i.e., within the habitat sample in this study), the PC of *A. artemisiifolia* and other local related species, such as *X. sibiricum*., *Arctium lappa*, and *C. canadensis*, was below 50% and as low as 6.3% (**Table 3**). Only *Artemisia* species presented higher PC. All Asteraceae species accounted for a very small proportion of indicator species.

Darwin's naturalization and pre-adaptation hypotheses need not be mutually exclusive. Phylogenetic similarity may be both close and distant in the same system, as it may vary across spatial scales and at different stages of invasion (Diez et al., 2008; Procheş et al., 2010; Cadotte et al., 2018; Tretyakova et al., 2021). At fine spatial scales (in relation to plant size), one can expect closely related organisms to exist in mutually exclusive patterns due to competitive interactions. Species less closely related to the local community are more likely to coexist by minimizing competitive exclusion (Maitner et al., 2021). Li et al. (2015) found that the probability of invader establishment declined with increasing PD between the invader and residents; whereas the average size of surviving invader individuals increased with PD. Because of their adaptability to environmental conditions, successfully established *A. artemisiifolia* became more closely related to the community during the invasion stage, but grew phylogenetically more distant over time, as they were striving to replace closely related native plants (Ma et al., 2016). These studies suggest that the Darwin's pre-adaptation hypothesis is more applicable to large scales and early stages of establishment, while Darwin's naturalization hypothesis is applicable to neighborhood scales and late growth stages, which is similar to our results.

Indicator species are universal and representative

This study found a similar species composition of invasive communities across different habitats (**Table 1**). Native species were present in all invasive habitats except for some species, such as *Achillea millefolium*, *Sophora alopecuroides*, and *Melilotus* spp., in residential areas, grassland, and forest. Among widely distributed native species, *S. viridis*, *P. annua*, *A. elatius*, *A. annua*, *A. vulgaris*, *A. leucophylla*, *C. sativa*, and *C. album* exhibited positive correlation with *A. artemisiifolia* in all habitats and a high PC (**Tables 2**, **3**). These indicator species accounted for 33.33% of native species, whose distribution frequency was more than 50% in the grassland, 81.82% in the farmland, 42.86% in the forest, 26.09% in the road margins, 37.5% in the residential areas, and 37.5% in the wasteland. These species not only reflect the co-occurrence with *A. artemisiifolia*, but are also representative and universal in various habitats, as well as easy to locate and identify. In the same way, *X. sibiricum* in the farmland, *Bromus* in the forest, *Trifolium* in the wasteland, and *P. asiatica* are good indicators and representative of their respective habitats.

By comparing similarities between the distribution of indicator species in potential suitable areas of *A. artemisiifolia* in the Yili Valley and the main habitat types, we found that indicator species grew in all such areas. In Tarbagatay and Bortala, more than 80% of indicator species were present in each habitat. The Maxent model predicted that precipitation in these two areas could meet the demand of *A. artemisiifolia* (Ma et al., 2020). Grassland was the main habitat type in the potential distribution area within the Yili Valley. This suggests that the distribution of indicator species from the Yili Valley points to potential suitable areas of *A. artemisiifolia* throughout Xinjiang. Therefore, it is feasible to rapidly monitor *A. artemisiifolia* by targeting indicator species in preferred invasive habitats of semi-arid regions.

In this study, native species associated with *A. artemisiifolia* across the world were counted by genus, limiting the influence of taxonomic differences and distribution habitat heterogeneity on the results. Except for *C. sativa*, which appeared only in the Yili River Valley, other species were distributed in all areas invaded by *A. artemisiifolia*. *Setaria*, *Bromus*, *Elytrigia*, *Artemisia*, and other species presented a wide distribution range. These results provide guidance and a reference for the worldwide rapid monitoring of *A. artemisiifolia* invasion.

At the time of monitoring, the worldwide distribution of *A. artemisiifolia*, and the composition and distribution of native species varied across habitats. Additionally, habitats with indicator species may not necessarily contain *A. artemisiifolia* because of non-dispersal or unsuccessful establishment. However, our study provides a reference key for finding common dominant native species as monitoring clues for the preferred habitat of *A. artemisiifolia* invasion. This is particularly true of *Chenopodium* spp., whose PC was 58% in the presence of *A. artemisiifolia* and reached up to 63.4% in a forest habitat (**Table 3**). Such examples improve dramatically the surveillance at an early stage of the invasion process, thereby facilitating prevention and control efforts.

Conclusion

In semi-arid areas, the preferred habitat of *A. artemisiifolia* and the transmission channel to surrounding areas can be accurately monitored by looking at the indicator species, i.e., dominant native species with strong correlation and distant phylogenetic relationship to *A. artemisiifolia*. Building on the potential suitable areas for *A. artemisiifolia* predicted by the Maxent model, this study provides clues for improved monitoring of this invasive species, thus reducing costs. All *A. artemisiifolia* found during monitoring should be removed in a timely manner to prevent the species from quickly forming dense populations and causing further harm.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

WZ conceived this study, performed data analyses, and wrote the manuscript. MS, HW, XL, and PS collected data of this study. TL led and coordinated the project. All authors read and approved the final manuscript.

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Conflict of interest

Publisher's note

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