RESEARCH

Role of plant functional traits in the invasion success: analysis of nine species of Asteraceae

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Abstract

Various attributes are hypothesized to facilitate the dominance of an invasive species in non-native geographical and ecological regimes. To explore the characteristic invasive attributes of the family Asteraceae, a comparative study was conducted among nine species of this family, co-occurring in the western Himalayan region. Based on their nativity and invasion status, the species were categorized as "*Invasive*", "*Naturalized*", and "*Native*". Fifteen plant functional traits, strongly linked with invasion, were examined in the test species. The analyses revealed a strong dissimilarity between all the plant functional traits (except leaf carbon [Leaf C]) represented by "Invasive" and "Native" categories and most of the traits (except leaf area [LA], leaf nitrogen [Leaf N], Leaf C, and leaf carbon-nitrogen ratio [C: N]) represented by the "Naturalized" and "Native" categories. Similarly, "Invasive" and "Naturalized" categories also varied significantly for most of the traits (except Leaf N, Leaf C, capitula per m² population [C_{m^2}], seeds per capitula [$S_{capitula}$], and seed mass). Invasive species are characterized by high LA, specific leaf area [SLA] and germination, and low C:N and leaf construction costs [LCC]. Most of the traits represented by native species justify their non-invasive behavior; whereas the naturalized species, despite having better size metrics (plant height), resource investment strategy (aboveground non-reproductive biomass [BNR], and aboveground reproductive biomass [BR]), and reproductive output (capitula per individual plant [C_{plant}], and seeds per individual plant [S_{plant}]) failed to invade, which implies that the role of these functional aspects in imparting invasion potential to a species is not consistent in all the ecosystems and/or phylogenetic groups. Results of PCA revealed that trait divergence plays a more imperative role in invasion success than naturalization in the species of the family Asteraceae. The present study is intended to refine the pre-generalized invasion concepts associated with family Asteraceae to ensure more accurate identification of the potential invaders and better management of the existing ones.

Keywords Compositae, Invasive plant species, Native species, Naturalized species, Plant functional traits, Trait divergence

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Background

Plant invasion is a key contemporary issue in community ecology, owing to its outrageous economic and ecological repercussions. It is a multistep process beginning with the 'introduction' of a plant or its propagule across a major geographical barrier, followed by its 'acclimatization' to the novel environment and 'naturalization' via independent reproduction for several generations [1]. Finally, it becomes 'invasive' by producing offspring in hefty numbers, surmounting the local dispersal barriers, and significantly expanding its distribution range [1]. Invasive species profoundly disrupt the balance of ecosystem by outcompeting native species for resources and altering soil properties [2–4]. These changes lead to a reduction in native species diversity, which can significantly affect ecosystem productivity and functionality [4]. The invasions often result in biotic homogenization, where the ecological uniqueness of habitats diminishes [5, 6]. This homogenization undermines the resilience of ecosystems, making them more susceptible to further invasions and environmental changes [7].

A global study has anticipated a total of 13,168 naturalized plant species (approximately 3.9% of the world's total extant flora) in 843 continental and island regions [8]. Recent estimates indicate that non-native plants currently account for more than 25% of island flora [9]. It is also estimated that 16% of the world's biodiversity hotspots, or close to one-sixth of the earth's surface, are at risk of invasion [10]. Asteraceae (1343 species) has the maximum contribution to the global naturalized alien flora, followed by Poaceae (1267 species) and Fabaceae (1189 species) [11]. Similarly, in India, a total of 471 naturalized alien species were reported (representing 2.6% of the total flora of India), with the maximum contribution of Asteraceae (75 species), Fabaceae (50 species), and Poaceae (36 species) [12].

Interactions between the characteristics of introduced species and the invaded habitat are one of the most crucial drivers of introduction-naturalization-invasion continuum [13]. Although chance and timing play a key role in the success of alien invasive species, it is not justified to say that invasions are entirely random events [14]. According to "*Ten's rule*", if only one-tenth of the species could survive at every step of the invasion process [15, 16], the taxon finally becoming invasive must possess some specific attributes that differentiate it from the rest of the introduced species. However, no single theory can justify the unconstrained dominance of an invasive species, and there are always interactions, interplay, and feedback among a suite of biological traits driving the entire process [17].

Efforts have been made to determine the set of traits that may stimulate or strengthen the invasive tendencies of an exotic plant species. Many attempts have been made to compare the organisms differing in the degree of invasiveness and a few such studies managed to outline the considerable attributes. The most important milestone in this direction was laid by Rejmánek and Richardson [18], who identified three significant characters (mean seed mass, minimum juvenile period, and mean interval between large seed crops) and their interrelationship as a screening tool for the detection of invasive woody angiosperms. Other researchers suggested that ecological [19], physiological [20], reproductive [21–23], and genomic [24, 25] factors are strongly linked to invasiveness and could be used for predicting the invasion success of exotic species.

The choice of comparators, however, is the most crucial step in such contemplative studies. A conceptual framework proposed by van Kleunen et al. [26] suggested that within an introduced range, studies involving parallel comparison among native species, invasive alien species, and non-invasive alien species might yield more informative insights regarding the determinants of invasiveness and could eliminate the biasness emanating while comparing only native vs. invasive alien species or invasive vs. non-invasive alien species. Another meta-analysis emphasized that such studies should consider the taxonomy, phylogeny, and growth stage of the comparator species to avoid spurious results [27]. It is also suggested that not only the traits of the most serious invaders are critical in understanding the complex mechanism of invasion, but studies considering the transition stages may help in deducing a better and stronger invasion theory [21].

There are two most common approaches used for trait-based studies, each with its own advantages and disadvantages. The first one involves meta-analysis of many invasive and non-invasive species, for which the information is generally collected from databases [28–30]. The second one outlines the similarities and dissimilarities among native, invasive, and non-invasive plant species based on the garden/field experiments [31–34]. Studies relying solely on the information obtained from the databases may involve large species datasets, but are restricted to relatively simple traits and lack sufficient precision. In contrast, studies based on field or garden experiments may not involve a large number of species due to several reasons, such as a deficit of con-generic or con-familial species within a suitable geographical range, varying growth seasons of the species, complexity in handling large replicates or datasets, etc. [27]. The most appropriate middle ground is to cross-validate the results obtained *via* large-scale database-oriented studies with the data collected at a local scale [21].

Following these rationales, a comparative study was undertaken amongst the nine con-familial plant species co-occurring in the western Himalayas with a common growth season but varying invasion status. Asteraceae

was selected as the target taxonomic family as it owns the largest share of naturalized and invasive species globally as well as in India [11, 12, 35]. It was hypothesized that certain attributes may facilitate the establishment and dominance of the members of Asteraceae. Suitable plant functional traits, proven to be strongly linked with invasiveness, were studied among the selected taxa to (i) figure out which biological characteristics provide a statistically sound explanation of the invasion success of the family Asteraceae and (ii) explore the interrelationship and response of different invasion categories (Invasive, Naturalized, and Native) in multiple trait spaces.

Methods

Study system

The study was conducted in Kangra district of Himachal Pradesh, India (Fig. 1). Geographically, the study area is situated in the Shiwalik and lower ranges of the western Himalayas within the latitudes and longitudes of 76°32′64″ E to 77°10′03″ E and 32°00′24″ N to 32°14′46″ N, respectively, and within an altitude of 1500 m to 1800 m above the mean sea level. It represents a subtemperate humid midhill agroclimatic zone, with an average annual temperature recorded at 18 ℃ and an average annual rainfall of around 2500 mm [36]. The average minimum temperature is recorded to be 11 ℃ during the winter season (mid-November to mid-March), and the average maximum temperature is around 29 ℃ during the summer season (April to June). The vegetation in the study area is composed of diverse life forms belonging to gymnosperms and angiosperms, represented by mixed forests of *Mangifera indica* L., *Pinus roxburghii* Sarg., *Populus ciliata* Wall. ex Royle, and *Quercus semecarpifolia* Sm. The limited proportion of land in the study area is used for agriculture, fodder production, tea cultivation, and grazing.

The region acts as a transitional zone between the Northwestern Plains and the mid- and higher Himalayan hills, making it an area with a high prevalence of exotic plant species within the Himalayan ecosystem [37]. The region's conditions are conducive for tropical invaders to gradually adapt to higher altitudes and expand their ranges upward. A total of 497 exotic species are recorded from the study area (Himachal Pradesh), of which the species belonging to the family Asteraceae, Poaceae, and Fabaceae are the most common [37]. Maximum species belong to the family Asteraceae (59 species), of which six are cultivated, three are casual, 18 are naturalized, 27 are invasive, and five of the species have a conflicted status [37]. Therefore, this region provides an ideal setting to investigate the traits of invasive, naturalized, and native species in this habitat. The coexistence of invasive, naturalized, and native species within the same area and growth season provides a valuable opportunity for studying species interactions.

Study species

Since Asteraceae contributes to the maximum alien and invasive flora in the study area [37–39], nine co-occurring herbaceous annuals of this taxonomic family with a similar growth season were selected for the study, i.e., *Parthenium hysterophorus* L., *Bidens pilosa* L., *Ageratum conyzoides* L., *Tagetes minuta* L., *Artemisia scoparia* Waldst. & Kitam., *Cirsium wallichii* DC., *Anaphalis royleana* DC., *Anaphalis adnata* Wall. ex DC., and *Aster peduncularis* Wall. ex Nees. The species were selected after careful consideration of several factors, including their ecological significance, potential for
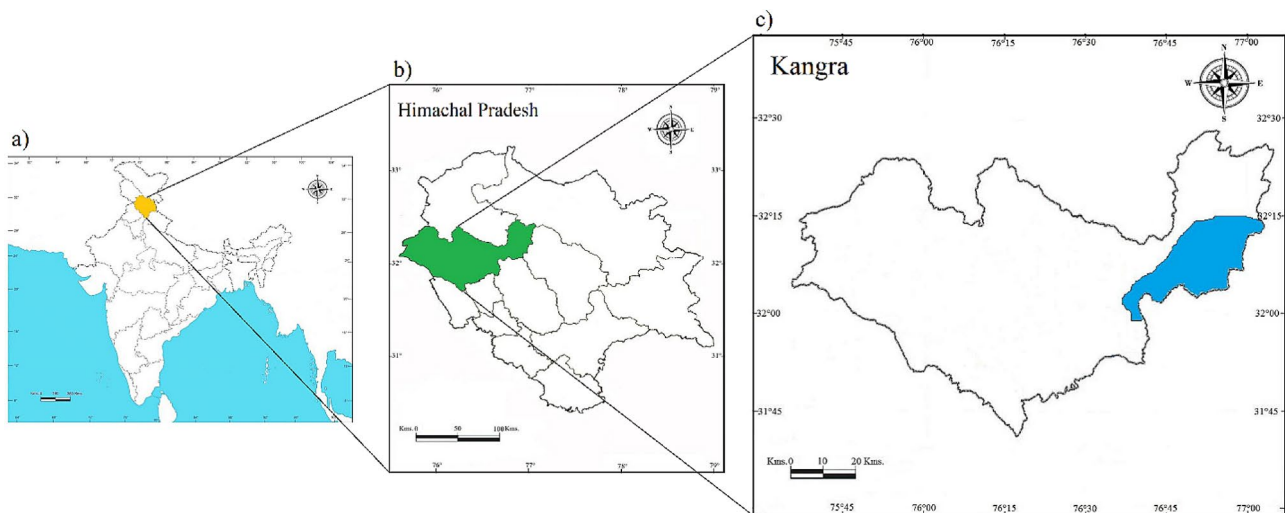

Fig. 1 (**a**) Map of India with state political boundaries representing the state of Himachal Pradesh (area shaded with yellow color), (**b**) map of Himachal Pradesh with district political boundaries representing the district of Kangra (area shaded with green color), and (**c**) map of Kangra representing the study area (area shaded with blue color)

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invasive behavior, and distribution within the study area. Our focus zeroed in on the prevalent invasive species in the study area, and the selection of species in other categories was based on their coexistence in both space and time with these invasive counterparts. While the selected invasive species are the most common invaders in the region, the species selected under naturalized and native categories are frequently observed along with these invaders within a particular growth season (July–October) in the study area. Thus, on both spatial and temporal scales, these nine species represent the best comparators within the selected phylogenetic group.

Among the selected taxa, *P. hysterophorus*, *B. pilosa*, and *A. conyzoides* belong to the tropical Americas and have a massive spread in the opted study area [37, 39]. Not only the northern part of India is affected by these weeds, but their spread can be witnessed throughout the country and in many other regions of Asia, Australia, and Africa [39, 40]. *T. minuta* is also a native to the southern USA and has been successfully established in the western Himalayas [37, 42]. *A. scoparia* and *C. wallichii*, on the other hand, are the natives of Asia (excluding the Indian subcontinent) that have been naturalized in the Shiwaliks and lower Himalayan ranges [37]. Despite their widespread occurrence, these weeds could neither flourish extensively like other exotic species nor be reported to have any significant impacts on biodiversity. Contrastingly, *A. royleana*, *A. adnata*, and *A. peduncularis* are native species of the Himalayan region [43–45]. Based on their nativity and distribution, *P. hysterophorus (Ph)*, *B. pilosa (Bp)*, and *A. conyzoides (Ac)* were categorized as "Invasive"; *T. minuta (Tm)*, *A. scoparia (As)*, and *C. wallichii (Cw)* as "Naturalized"; and *A. royleana (Ar)*, *A. adnata (Aa)*, and *A. peduncularis (Ap)* as "Native". The selected plant species were validated by Prof. Daizy R. Batish, and voucher specimens were deposited in the herbarium of Panjab University, India (PAN), and Botanical Survey of India, DehraDun, India (BSD) (Voucher# PAN 22311 [*Ph*]; PAN 22325 [*Bp*]; BSD 417 [*Ac*]; PAN 22469 [*As*]; PAN 22295 [*Tm*]; BSD 421 [*Cw*]; BSD 418 [*Ar*]; BSD 419 [*Aa*]; BSD 420 [*Ap*]). There was no need for permission because the plants grew wild in the designated sites or plots and were not on any private or government-recognized forest land.

Experimental design

The sampling was done on the plants growing under wild conditions using the random quadrat method during July–October 2020. For each taxon, quadrats of 1×1 m^2 were laid across the study area. The percent cover of each taxon varied between 25 and 75% in the established quadrats. For measurement of plant functional traits, 1–5 mature individuals (at peak flowering stage) per quadrat were randomly selected. Some of the traits were observed

and/or measured in the intact plants, whereas for assessing the traits related to seed biology, biomass estimations, and chemical characterization, the plant material and seeds were collected from the study area and examined in the laboratory at the Department of Botany, Panjab University, Chandigarh.

The soil samples from the top 15 cm layer were collected from each sampled quadrat for the estimation of pH, available nitrogen content, available phosphorus content, available potassium content, and percent saturation. The pH of the soil samples was confined between 5.9 and 6.5. Available nitrogen was observed in the range of 557.88–664.35 kg ha^{-1}, available phosphorus in the range of 23.00–48.69 kg ha^{-1}, and available potassium in the range of 388.46–512.27 kg ha^{-1}. The percent saturation of the soil samples varied from 59.9 to 71.98%.

Plant functional traits

Fifteen plant functional traits representing plant morphology (plant height [cm], leaf area [LA; cm^2], specific leaf area [SLA; cm^2 g^{-1}], and aboveground non-reproductive biomass [BNR; g]), leaf chemistry (leaf nitrogen [Leaf N; %], leaf carbon [Leaf C; %], leaf carbon-nitrogen ratio [C: N], and leaf construction costs [LCC; g glucose g^{-1}]), reproductive output (capitula per m^2 population [C_{m^2}], capitula per individual plant [C_{plant}], seeds per capitula [$S_{capitula}$], and seeds per individual plant [S_{plant}]), and reproductive fitness (aboveground reproductive biomass [BR; g], seed mass [g], and germination [%]) were examined in the test species as explained by Cornelissen et al. [46], Barthod and Epron [47], and Singh et al. [48]. The traits were selected based on sound ecological relevance and their association with invasiveness, as detailed in Table 1.

Plant height was measured as the distance between the topmost photosynthetic tissue of the plant and the ground level. LA was assessed by scanning the one-sided projected area of an average-sized fresh leaf and analyzing the image using *ImageJ* software version *k* 1.45, whereas SLA was estimated by dividing LA with its oven-dried biomass. For the dry weight/biomass estimations, samples were oven-dried at 60 °C for 72 h.

Leaf N and C were detected using the Flash 2000 Organic Elemental Analyzer (Thermofisher Scientific, USA), available at the Central Instrumentation Laboratory (CIL), Panjab University, Chandigarh, India. The instrument was calibrated three times using cystine and methionine and thereafter, the sample (in the form of dried leaf powder) stored in the tin container of an auto sampler was dropped into the combustion reactor. Upon experiencing an extremely oxidizing environment, tin triggered a strong exothermic reaction that led to the process of combustion. The resultant products (in the form of gaseous mixture) were conveyed across the

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Table 1 Ecological significance of the plant functional traits studied in the test species

Traits	Abbreviation	*n*	Units	Ecological significance
Plant morphology				
Plant height	-	150	cm	Associated with plant metabolic rate; helps in overcoming the competition for light [49]
Leaf area	LA	75	cm^2	Measures surface area for photosynthesis and transpiration; key component of leaf size-twig size spectrum [27, 50]
Specific leaf area	SLA	75	cm^2 g^{-1}	Important aspect of leaf economic spectrum; linked to relative growth rate [27, 50, 51]
Aboveground non-reproductive biomass	BNR	75	g	Explains biomass allocation patterns [27, 46]
Leaf chemistry				
Leaf nitrogen	Leaf N	9	%	Associated with photosynthetic capacity; key component of leaf economic spectrum [50]
Leaf carbon	Leaf C	9	%	Related to carbon inputs into soil, herbivory rate and biomass reproduction [52]
Leaf carbon-nitrogen ratio	C: N	9	-	Chemical indicator of nutritional value of the leaf [50]
Leaf construction costs	LCC	9	g glucose g^{-1}	Associated with relative growth rate; affects the energy demand and utilization [48, 51]
Reproductive output				
Capitula per m^2 population	C$_{m^2}$	30	-	
Capitula per individual plant	C$_{plant}$	75	-	Measures fecundity and ability of a species to expand its population size [21, 27]
Seeds per capitula	S$_{capitula}$	75	-	
Seeds per individual plant	S$_{plant}$	75	-	
Reproductive fitness				
Aboveground reproductive biomass	BR	75	g	Explains biomass allocation patterns [27, 46]
Seed mass	-	30	g	Aids seed dispersal; decides the production, dormancy, and germination of seeds [49]
Germination	-	30	%	Measures seed establishment, colonization, and regeneration [21, 27]

reactor and separated in the gas chromatographic column. The eluted gases were then conveyed to the thermal conductivity detector that generated the electrical signals processed by Eager 300 software, providing the percentage of C and N present in the sample. C: N was then obtained as a ratio of percent C to percent N. LCC was calculated using the given expression:

$$\text{LCC (g glucose per g)} = (-1.041 + 5.077\,C/\,[1-a])\,(1-a)$$

where 'C' is the carbon content (g g^{-1}) estimated by the loss on ignition method and 'a' is the ash content (g g^{-1}) determined by weighing the mass remained after combustion of leaf powder samples of the test plants in a muffle furnace (Narang Scientific Works, New Delhi, India) at 550 °C for 6 h.

The number of capitula produced by the total individuals of a species present in each quadrat and the number of capitula produced by individual plants were counted for all the studied taxa. Similarly, the number of seeds produced per capitula and the number of seeds produced per individual plant were counted for each taxon.

For estimating the biomass allocated to floral parts, samples were oven-dried at 60 °C for 72 h. For assessing the traits expressing seed biology, the collected seed lots were sun-dried and subjected to a short period of dry storage (30 days). A total of 1000 random, but healthy, seeds were selected for each taxon to determine the seed mass (100 seeds per replicate). Thereafter, 100 seeds per taxon were used to figure out their ability to germinate under in vitro conditions. For this, the sterilized and pre-imbibed seeds were placed in 15 cm diameter Petri dishes (ten seeds per Petri dish) lined with a thin layer of cotton wad and Whatman #1 filter circle and moistened with 10 ml of distilled water. The Petri dishes were placed in a growth chamber set at 25±2 °C temperature, a 16/8 h light/dark photoperiod, 75% relative humidity, and 240 µmol m^{-2} s^{-1} of photon flux density for 7 days. Thereafter, the percent seed germination was calculated as:

$$Germination\,\% = \frac{Number\ of\ seeds\ germinated}{Number\ of\ seeds\ sown} \times 100 \quad (1)$$

Statistical analysis

To validate the results statistically, the data were standardized using the z-score transformation. The Shapiro-Wilk test was used to ensure the normal distribution of

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data, whereas Levene's test was used to determine if different invasion categories have equal variances. Due to the heterogeneity of variances in the dataset, a Welch ANOVA was used to test the significance of plant functional trait means, followed by a pairwise comparison of the different invasion categories (Invasive, Naturalized, and Native) using a Games-Howell *post-hoc* test. A standardized principal component analysis (PCA) was also performed to explore categorical differences in multiple trait spaces using the *Factoextra* package. All the analyses were carried out in R version 4.1.0, and the results were considered significant at $p \leq 0.05$.

Results

All the traits representing plant morphology were statistically significant at $p \leq 0.05$, as determined using Welch's ANOVA (Table 2).

A pairwise comparison showed that the plant height, SLA, and BNR varied significantly ($p \leq 0.05$) among the three invasion categories, whereas LA did not vary significantly between the "Naturalized" and "Native" categories (Fig. 2). Species categorized as "Invasive" were characterized by high LA and SLA; those categorized as "Naturalized" were characterized by high plant height and BNR and low SLA; and those categorized as "Native" represented low plant height and BNR (Fig. 2).

Leaf chemistry also differed statistically at $p \leq 0.05$, except for leaf carbon content ($F_{welch} = 3.41$; $p=0.06$) (Table 2). Leaf N varied significantly at $p \leq 0.05$ only between "Invasive" and "Native", C: N between "Invasive" and "Naturalized", and "Invasive" and "Native", and LCC among all the three invasion categories (Fig. 3). Species categorized under "Invasive" had characteristically low C:

N and LCC, and those under "Naturalized" had high LCC (Fig. 3).

The reproductive output, measured in terms of C_{m^2}, C_{plant}, $S_{capitula}$, and S_{plant}, varied significantly at $p \leq 0.05$ as per Welsch's ANOVA (Table 2), whereas the pairwise comparison ruled out significant dissimilarity between the "Invasive" and "Naturalized" categories in the case of C_{m^2} and $S_{capitula}$ at $p \leq 0.05$ (Fig. 4). The species grouped under the "Naturalized" category had high output in terms of C_{plant} and S_{plant}; whereas the "Native" category was represented by high $S_{capitula}$ but low C_{m^2}, C_{plant} and S_{plant} (Fig. 4).

The traits studied for assessing the reproductive fitness of the test species also varied significantly at $p \leq 0.05$ (Table 2). Except for seed mass, which did not vary significantly between "Invasive" and "Naturalized", all the other traits (BNR and germination) differed significantly at $p \leq 0.05$ among all the invasion categories (Fig. 5). The species grouped under the "Invasive" category can be distinguished based on high germination, and those under the "Naturalized" category can be differentiated based on high BR (Fig. 5). In contrast, low BR, seed mass, and germination were the characteristic traits of species categorized as "Native" (Fig. 5).

Standardized PCA was used to demonstrate the correlation among selected plant functional traits and the arrangement of different invasion categories in the trait space (Fig. 6). Since the first two principal components (PC1 and PC2) explained 75.1% of the total variance in the dataset, the results of PCA are presented as a biplot (Fig. 6). The first principal component (PC1) accounted for 43.0% of variation and was associated with high positive loadings (>0.5) of SLA and high negative loadings (> −0.5) of BNR, Leaf C, LCC, C_{m^2}, C_{plant}, S_{plant}, and BR

Table 2 Results of Welch's ANOVA applied to the plant functional trait means studied in the three invasion categories, i.e., invasive, naturalized, and native (each represented by three taxa of the family Asteraceae). For abbreviations, see Table 1

| Traits	Mean ± SE			n_{obs}	F_{welch}	*p*-value
	Invasive	**Naturalized**	**Native**			
Plant height	117.12 ± 4.13	150.67 ± 4.75	45.56 ± 1.23	450	342.58	0.000
LA	41.78 ± 2.38	14.8 ± 1.18	12.6 ± 1.12	225	63.43	0.000
SLA	352.55 ± 19.89	190.97 ± 5.52	250.34 ± 15.64	225	34.62	0.000
BNR	13.79 ± 1.3	34.03 ± 2.56	2.36 ± 0.21	225	111.53	0.000
Leaf N	26.4 ± 0.09	6.98 ± 0.19	4.79 ± 0.22	27	12.87	0.001
Leaf C	9.14 ± 0.6	8.78 ± 1.06	7.93 ± 0.47	27	3.41	0.060
C: N	40.3 ± 0.1	43.03 ± 0.08	41.98 ± 0.14	27	14.76	0.000
LCC	4.42 ± 0.08	4.9 ± 0.08	5.32 ± 0.03	27	15.50	0.000
C_{m^2}	6686.4 ± 1644.1	70,048 ± 18,311	598.17 ± 95.01	90	15.90	0.000
C_{plant}	997.07 ± 205.72	13,190 ± 2184.1	201.91 ± 29.11	225	27.56	0.000
$S_{capitula}$	43.45 ± 3.91	40.8 ± 5.69	58.72 ± 2.37	225	8.14	0.000
S_{plant}	9481.2 ± 928.8	61,742 ± 9357	12,460 ± 2046.7	225	11.83	0.000
BR	5.52 ± 0.75	13.08 ± 1.31	0.52 ± 0.05	225	67.24	0.000
Seed mass	0.09 ± 0.01	0.07 ± 0.01	0.03 ± 0.00	90	28.54	0.000
Germination	61.67 ± 3.62	30.33 ± 1.89	19.67 ± 3.09	90	41.12	0.000
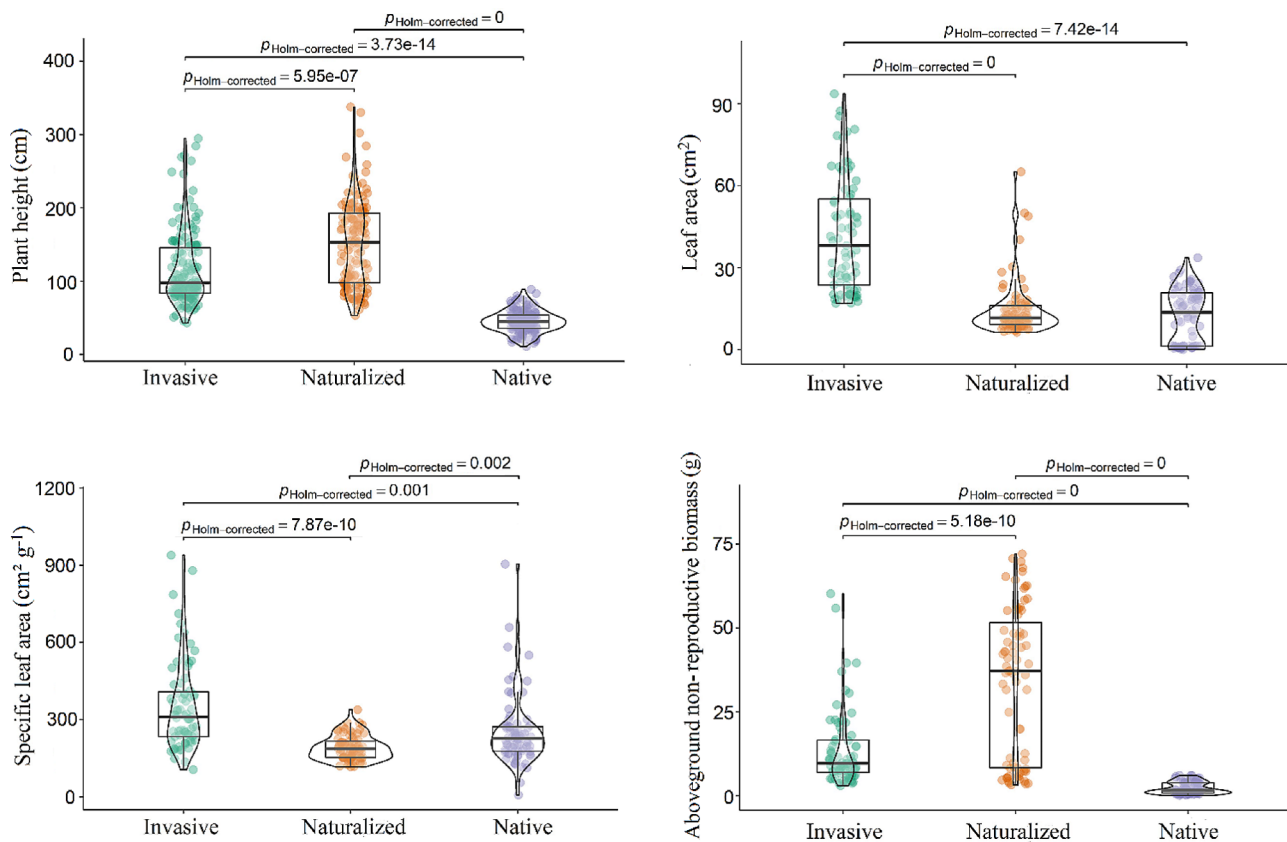
Fig. 2 Violin plots representing pairwise comparison of the plant morphological traits among the three invasion categories, i.e., Invasive, Naturalized, and Native (each represented by three taxa of the family Asteraceae). P_{Holm} values over the plots represent the significance level of dissimilarity between the bracketed invasion categories at $p \leq 0.05$ applying Games-Howell *post-hoc* test
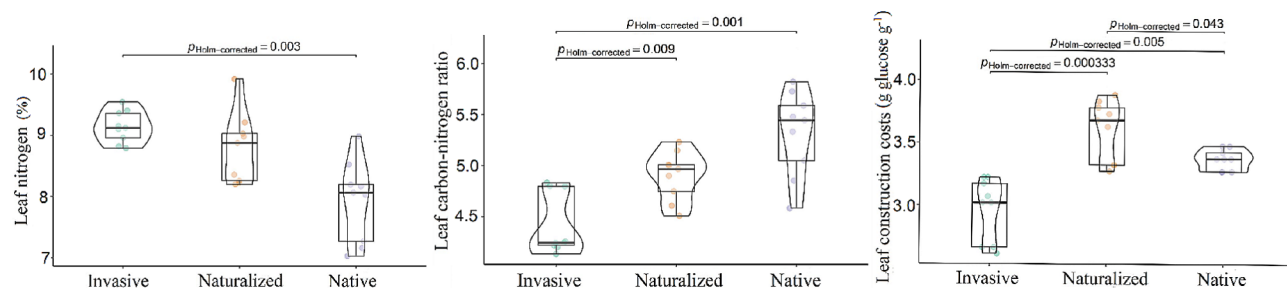

Fig. 3 Violin plots representing pairwise comparison of the leaf chemical traits among the three invasion categories, i.e., Invasive, Naturalized, and Native (each represented by three taxa of the family Asteraceae). P_{Holm} values over the plots represent the significance level of dissimilarity between the bracketed invasion categories at $p \leq 0.05$ applying Games-Howell *post-hoc* test

(Fig. 6). The second principal component (PC2) explained 32.1% of variation, and the axis was associated with high positive loadings (>0.5) of plant height, LA, SLA, leaf N, seed mass, and germination, and high negative loadings (> −0.5) of C: N, and LCC (Fig. 6). The relative position of each invasion category to one another and with respect to the traits provided the functional profile of species clustered under these categories (Fig. 6). Confidence ellipses indicated a significant difference between the "Invasive" and "Native" categories, which were prominently

separated across the biplot primarily based on LA, SLA, seed mass, and germination (Fig. 6). On the other hand, overlapping confidence ellipses indicated that the species belonging to the "Naturalized" category depicted a wide range of functional trait spectra and were functionally alike to the species of both the "Invasive" and "Native" categories (Fig. 6).
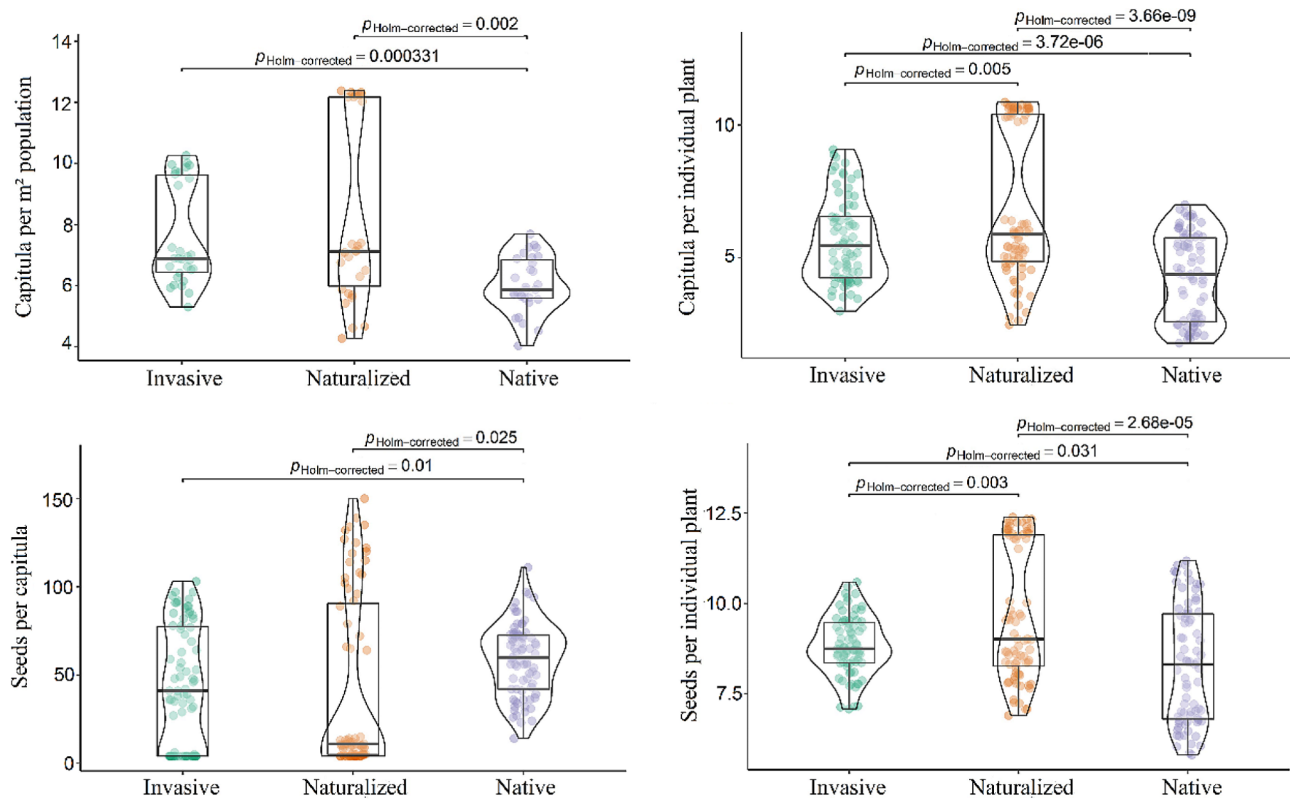
Fig. 4 Violin plots representing pairwise comparison of the reproductive output among the three invasion categories, i.e., Invasive, Naturalized, and Native (each represented by three taxa of the family Asteraceae). P_{Holm} values over the plots represent the significance level of dissimilarity between the bracketed invasion categories at $p \leq 0.05$ applying Games-Howell *post-hoc* test
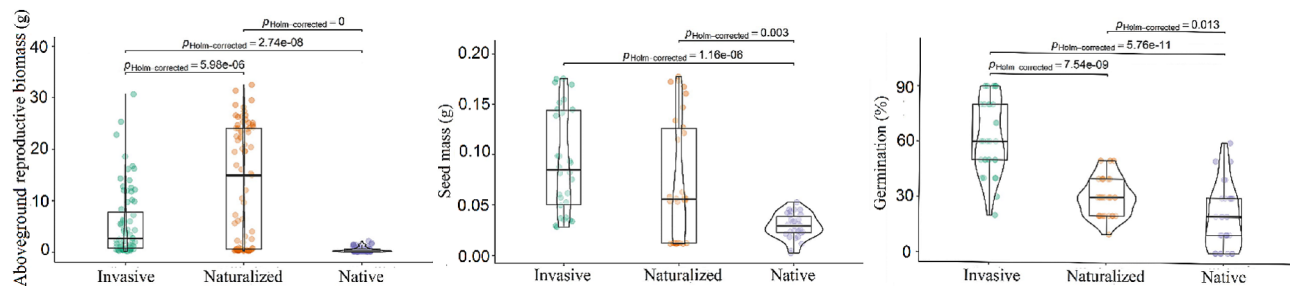

Fig. 5 Violin plots representing pairwise comparison of the reproductive fitness among the three invasion categories, i.e., Invasive, Naturalized, and Native (each represented by three taxa of the family Asteraceae). P_{Holm} values over the plots represent the significance level of dissimilarity between the bracketed invasion categories at $p \leq 0.05$ applying Games-Howell *post-hoc* test

Discussion

Asteraceae is one of the largest and most diverse families of angiosperms, harboring the world's worst weeds and invasive species [53, 54]. A few studies have attempted to highlight the characteristic traits associated with the naturalized and invasive members of this family. Advanced reproductive biology, particularly fruit heteromorphism, has previously been associated with the greater naturalization success of Asteraceae as compared to the other taxonomic families [55]. Most of the invasive members of this family also demonstrate self-fertilization [56]. A recent study by Li et al. [57] relates leaf construction

costs (LCC) with the expansion of exotic invasive flora of Asteraceae in the coastal wetlands of the Guangdong-Hong Kong-Macau Bay Area, China. Common genomic responses by several invasive taxa of this family also suggest the possibility of evolutionary adaptations in the species during their introduction and/or spread [58].

Our study provides some interesting insights into the functional trait variations within this family. The analyses revealed a strong dissimilarity between all the plant functional traits (except Leaf C) represented by "Invasive" and "Native" categories and most of the traits (except LA, Leaf N, Leaf C, and C: N) represented by "Naturalized"
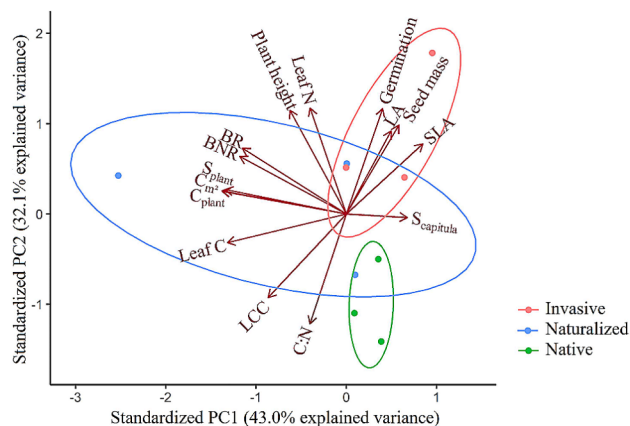
Fig. 6 Biplot of standardized Principal Component Analysis (PCA) representing plant functional trait responses in the three invasion categories, i.e., Invasive, Naturalized, and Native (each represented by three taxa of the family Asteraceae). Separable confidence ellipses indicate the significant difference between the invasion categories, whereas overlapping confidence ellipses do not differ significantly. For abbreviations, see Table 1

and "Native" categories. Similarly, the "Invasive" and "Naturalized" categories also varied significantly for most of the traits (except Leaf N, Leaf C, C_{m^2}, $S_{capitula}$, and seed mass). The results indicate remarkable differences in the functional abilities of phylogenetically related species, and there is a strong possibility that these functional variations may define the invasive potential of members of Asteraceae.

We established that the selected invasive species are characterized by high LA, SLA, and germination and low C: N, and LCC. A large section of invasion biology literature corroborates our observations. In accordance with our study, invasive species are frequently associated with higher LA and SLA [29, 34, 41, 59–62]. Higher LA offers the plant a larger surface area to carry out photosynthetic activities [29, 62, 63]. On the other hand, SLA regulates the relative growth rate, resource capturing, and many other physiological functions in plant species [60, 62, 63]. Gallagher et al. [49] even emphasized adding SLA as the screening parameter in weed risk assessment procedures. Likewise, high percent germination fosters the ability of an alien species to occupy available vacant niches, thus expediting its progress at every step of the invasion process [64]. C:N, on the other hand, is a chemical indicator of the nutritional value of leaves and its decrease accelerates the photosynthetic activities in the plant [65, 66]. However, decreased values of C:N also led to increased palatability, and therefore, the species must be released from its natural enemies to afford the benefits associated with this functional trait [50]. Lower LCC, on the other hand, decreases resource allocation to expensive structural defenses while saving energy for growth and reproduction [29, 67]. Reports also suggest that lower

construction costs may enhance species abundance and, hence, their invasion success [57].

In contrast, high $S_{capitula}$ and low plant height, BNR, C_{m^2}, C_{plant}, S_{plant}, BR, seed mass, and germination were the characteristic traits of species categorized as "Native". Most of these traits imply the non-invasive behavior of these species. Although a higher number of seeds per capitula represents better reproductive output and low seed mass is a facilitating factor for wind-dispersed seeds, these few characteristics cannot assist the spread of these species in larger areas. This is particularly true when the rate of germination has been the lowest in "Native" among the three categories. This justifies the fact that the selected native species have not been reported as naturalized or invasive elsewhere in the world.

In another observation, it was noted that the species under the "Naturalized" category were distinguishable based on high plant height, BNR, LCC, C_{plant}, S_{plant}, and BR, and low SLA. Interestingly, the naturalized species have performed better than "Native" and "Invasive" for certain traits, particularly those related to size metrics (plant height), resource investment strategy (BNR and BR), and reproductive output (C_{plant} and S_{plant}). However, these traits varied from those of the invasive species, which implies that they are not indicative of species' invasiveness in all ecosystems and/or phylogenetic groups. In accordance with our study, Hamilton et al. [68] also suggested that plant height could not explain the unique variation in invasion success among non-native species of eastern Australia on a regional or continental scale. Low plant height was also observed to confer invasiveness in the exotic species of the windy sub-Antarctic region [31]. Similarly, studies have also found that the competitive advantages of invasive species are associated with requirement-based shifts rather than a constant increase in biomass allocation patterns [69]. In addition, plant height and biomass investment also show plasticity in response to environmental conditions, particularly in high altitudinal regions [70, 71]. On the other hand, high reproductive output might be an important factor for invasion; however, in the absence of successful germination (as witnessed in the present study), it may fail to facilitate the geographic expansion of a species [33, 72].

The results of PCA clearly align with those of ANOVA, explaining that the species in different invasive categories are functionally divergent; however, in addition to that, the biplot explained that the naturalized species depict a wide range of functional trait spectra and share similarities with both "Invasive" and "Native" categories. The broad array of traits exhibited by naturalized species represents both functional similarity and distinctiveness from the resident plant communities. A similar conundrum has been presented by Darwin's opposing hypotheses: '*preadaptation hypothesis*' stating that pre-adapted

traits in an exotic species would be crucial for environmental filtering and its survival in a particular habitat and '*naturalization hypothesis*' stating that trait disparities in an exotic species allow it to successfully establish via niche differentiation and competitive exclusion [73, 74]. Both the hypotheses have been accepted in the invasion ecology and both the mechanisms function across all scales and situations [73–77]. Our study implies that both environmental filtering and competitive exclusion can facilitate the colonization of exotic Asteraceae species. On the contrary, the functional disparities observed in the species grouped as "Invasive" imply that functionally unique naturalized species might have maximal access to unused niche opportunities in the introduced ecosystem, which may facilitate their dominance and range expansion [31]. This signifies that trait divergence acquired inherently or via plasticity in response to environmental and anthropogenic factors plays a more imperative role in invasion success than naturalization in the family Asteraceae.

The substantial research has been conducted on plant functional traits in invasive species. However, these studies are scarce in the Himalayan ecosystem. Therefore, the present study provides significant insights into the mechanisms driving invasiveness within the family Asteraceae in the Himalayan ecosystem. The findings underscore the importance of trait-based monitoring of invaders in the Himalayan ecosystem. The traits characteristically shown by invasive species, such as high LA, SLA, and germination rates and low C: N, and LCC, can serve as a framework for future prediction of potential invaders, helping to refine and validate management strategies across a broader spectrum of plant species and habitats. And these findings will support early detection, improve risk assessments, and implement more effective management practices. The current study also provides a base for future studies aiming to explore functional traits, adaptation strategies, and species interactions in the context of invasive species in the Himalayan region.

Conclusions and future recommendations

The present study intended to refine the pre-generalized invasion concepts associated with family Asteraceae, thus ensuring the more accurate identification of the potential invaders and better management of the existing ones. Three significant conclusions can be drawn from the results of our study. First, the selected invasive species were characterized by high LA, SLA, and germination and low C: N, and LCC, and these traits can be used to anticipate the potential invaders of the family Asteraceae. Second, most of the traits represented by native species justify their non-invasive behavior, whereas the naturalized species, despite having better size metrics, biomass allocation and reproductive output failed to invade,

which implies that the role of these functional aspects in imparting invasion potential to a species is not consistent in all ecosystems and/or phylogenetic groups. Third, trait divergence plays a more imperative role in invasion success than naturalization in the family Asteraceae.

However, it is important to mention that the given conclusions are obtained from a small dataset in a limited study system and are thus only meant to point out the possibilities associated with the characteristic invasive traits of the family Asteraceae. Further, some of the functional traits might be inconsistent with the literature due to other niche-related effects that have not been captured in our study. Therefore, the efficacy of these results needs to be tested over a wide range of the invasive species and in a broader array of ecological conditions. Further, we believe that apart from establishing the universal characteristics that could explain invasive abilities of much larger groups of species, these characters should also be distinguished based on phylogenetic classes, orders, and families, which is rather easier and might yield more robust and widely applicable results.

Author contributions
DRB, RKK, and HPS: Conceptualization, Project leader; DRB, SK, RKK: Design of work; AK, AS: Field studies, Data collection; AK, AS, and SK: Data analysis; AK, AS, SA, and MHS: Data interpretation and modelling; MA, AK and AS: Figure preparation; AK, AS, RKK, MHS, and SA: Manuscript preparation; HPS, DRB, SK, and MHS: Manuscript editing; MHS: Fund procurement. All authors reviewed the manuscript.

Data availability
Data shall be provided by the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Since the collected plants were growing wild in the selected sites/plots and these were not in any private or government recognized forest land, no permission is required.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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