Journal of Environmental Management 241 (2019) 187–197

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

Phenotypic variations alter the ecological impact of invasive alien species: Lessons from *Parthenium hysterophorus*

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ARTICLE INFO

Keywords:
Ecological indices
Invasive
Morphotypes
Parthenium
Soil chemistry

ABSTRACT

Invasive plant species constantly adjust their behavior with ecological shifts by virtue of phenotypic plasticity and/or local adaptations. Changes in the phenotype of an invasive species may also trigger variations in its community level impacts, which is an acceptable, yet unexplored aspect of invasion biology. Our study attempts to fill important knowledge gaps on the basic behavior and ecological interactions of invasive species. *Parthenium hysterophorus*, a widely distributed invasive alien species of tropical and sub-tropical regions, was evaluated for variations in its morpho-functional traits and ecological performance at a common spatial and temporal scale. Field surveys were conducted in Chandigarh, India, in five sites identified as invaded with *P. hysterophorus*. Individuals of *P. hysterophorus* randomly sampled from these sites, showed from trait analyses that the population is differentiated into two morphotypes, P_A and P_B. Morphotype P_B exhibits traits comparable to the shrub life-form in terms of woody stem (with higher stem circumference [+32.26%], stem specific density [+128.57%], twig dry matter content [+25.15%]); profuse branching (+46.38%); larger canopy (+91.16%); and better reproductive output (+190.29%) compared to P_A. P_A, on the other hand, reflected herbaceous characteristics with greater leaf area (+67.58%) and higher content of chlorophyll (+21.92%) compared to P_B. Based on these morphotypes, the plots were divided into three invasion categories: areas invaded by P_A [IP_A], areas invaded by P_B [IP_B] and uninvaded areas [UI]. Ecological indices and soil chemical properties were compared across IP_A, IP_B and UI. Shannon's index ($p < 0.001$), evenness index ($p = 0.008$), and richness index ($p < 0.001$) were significantly lower in IP_B compared to IP_A. UI areas were found to have higher soil pH, phenolics, organic matter, and concentrations of N, P and K, compared to IP_A and IP_B, but lower Ca and Mg. Results suggest that phenotypic variations within population of *P. hysterophorus* regulate its ecological impact on associated vegetation. Conservation managers would benefit from studying its invasion patterns and identifying the morphotype with higher ecological impact to prioritize management efforts. Monitoring these behavioral and ecological patterns in *P. hysterophorus* over the long-term may also help in anticipating challenges to preventive measures.

1. Introduction

Due to an upsurge in international trade, transport and tourism, decades post 1950's have witnessed an exponential increase in human mediated accidental or intentional migration of non-indigenous plant species (Hulme, 2009). A small fraction of these non-indigenous species, capable of surviving the series of biotic and abiotic barriers offered by the novel habitat and holding the potential to cause evident impact both in ecological and economic terms, is defined as 'invasive species' (Richardson et al., 2000; Canning-Clode, 2015; Shackleton et al., 2019). Upon experiencing any sort of divergence in the environmental conditions, an invasive plant species explores every possibility of adaptation, be it phenotypic plasticity or adaptive evolution, to ensure its survival and dominance (Davidson et al., 2011; Oduor et al., 2016). Sometimes, these adaptations are taken up to the next level resulting in the formation of ecophenes or ecotypes or even ecospecies (Anderson and Treshow, 1980).

Along with plastic or evolutionary diversification, the possibility of associated changes in the ecological impact of invasive plant species cannot be denied (Oduor et al., 2016). The impact of invasive plant

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https://doi.org/10.1016/j.jenvman.2019.03.129
Received 21 December 2018; Received in revised form 28 March 2019; Accepted 29 March 2019

species on community/landscape ecology is witnessed by a number of studies, some of them providing ample evidence regarding the displacement and extinction of native species (Baider and Florens, 2011; Vilà et al., 2011; Simberloff et al., 2013; Kuebbing et al., 2014). The extent to which local adaptations can influence the community level impacts of invasive plant species is not much understood (Oduor et al., 2016). But despite the limited studies, it can still be interpreted that the ecological consequences borne out of phenotypic plasticity or adaptive evolution in invasive species could be more extensive (Grosholz, 2002). Furthermore, with the spiking of various natural and anthropogenic disturbances (climate warming, enhanced nitrogen and CO_2 emission, deforestation, habitat fragmentation, changes in land use pattern, population explosion, and rapid economic development), invasion dynamics are rapidly changing (Chown et al., 2007; Carboni et al., 2018). A regular check on the performance of invasive alien species is therefore necessary, not only to facilitate management strategies, but also to trace evolutionary adaptations acquired by the species over time and in response to raging climatic catastrophes.

Parthenium hysterophorus L. (Asteraceae) is an aggressive invader of agricultural fields, wastelands, degraded forests and disturbed sites in tropical and sub-tropical countries (Batish et al., 2012; Adkins and Shabbir, 2014). It is a native of the Americas (Gulf of Mexico and Southern USA) and has accidentally been introduced in different parts of the world including South Asia, Southeast Asia, Middle East Asia, Australia, Oceania and Africa (Adkins and Shabbir, 2014). In India, *P. hysterophorus* has been continuously spreading after it was introduced along with food grain lot in Maharashtra in 1950s (Kohli and Rani, 1994). Its troublesome impacts on human health, livestock, crop production and biodiversity are well documented (Bajwa et al., 2016). The invasive plant has dominated various landscapes owing to its high reproductive ability, wide range of ecological adaptations, phenotypic plasticity, and allelopathic properties (Kohli and Rani, 1994). Invasion potential of *P. hysterophorus* is projected to amplify in response to climate change (Shrestha et al., 2015) with a strong possibility of its expansion across southeast Asia, sub-Saharan Africa, temperate northern hemisphere and high elevation equatorial regions (McConnachie et al., 2011; Kriticos et al., 2015; Mainali et al., 2015).

The present study was conducted based on the literature reports indicating the presence of morpho-variants in the population of *P. hysterophorus* in Chandigarh, India, where its establishment goes back to late 1970's (Singla, 1998). We hypothesized that these phenotypic variations in the plant may indicate a higher level of adaptations and could possibly regulate the ecological impact of the invasive plant. Understanding the behavioral patterns of *P. hysterophorus* may help in re-considering its management options, predicting its potential spatial inclinations and tracing the evolutionary changes acquired by the plant over time. Keeping this rationale in mind, a study was planned on the basis of visual observations and literature records to investigate: a) the extent of phenotypic variability persisting within the population of *P. hysterophorus* in Chandigarh, India, and b) if its impact on associated floristic diversity and soil chemical properties is regulated by these behavioral changes.

2. Material and methods

2.1. Study site

Chandigarh, a Union Territory of India (76°47′14″E, 30°44′14″N; 304–365 m above mean sea level; area: 114 km^2), was selected for the study considering its intermittent geographical location between the terrestrial and hilly ranges and the long invasion history of *P. hysterophorus* in the region (Fig. 1). The study area is located in the foothills of Shiwalik belt of the Himalayas and is known to be a well-planned city (Kohli et al., 2000, Fig. 1). Chandigarh experiences cold dry winter from November to January (temperature range 1 °C–16 °C); hot summer from April to July (27 °C–44 °C); and sub-tropical monsoon from July to September with mean annual precipitation of 1110.7 mm (Chandigarh Administration, 2018). These climatic conditions are appropriate to shelter *P. hysterophorus*, and the continuous increase in annual mean minimum temperature as seen from 1954 to 2010 (Chandigarh Action Plan, 2018) makes it a more favorable habitat for the invasive plant (Tamado et al., 2002; Kaur et al., 2017). *P. hysterophorus* prefers to grow in the fallow agricultural fields, grasslands, pastures, wastelands, roadsides, degraded forests and disturbed areas (Bajwa et al., 2016). Due to urban sprawling, the sub-urban areas located on the periphery of the city witness continuous anthropogenic disturbances, habitat degradation and inadequacy of management efforts and thus serve as suitable niches for different invasive species (Sharma et al., 2017, Fig. 1). Surveys of the study area have shown invasion by *Lantana camara*, *Ageratum conyzoides*, *Hyptis suaveolens*, etc., along with *P. hysterophorus*, with some having been introduced accidentally, while others were deliberate ornamental introductions (Fig. 1).

2.2. Experimental design

Field surveys were carried out in the mature plants of *P. hysterophorus* (at post flowering BBCH stage 65/605; Kaur et al., 2017). The study was conducted during peak flowering season spanning July to September (Kaur et al., 2017) in 2015, 2016 and 2017. Preliminary data of 2015 and 2016 were used to design hypothesis and experiment, and data of 2017 were used for statistical analysis and presented in the study. Five sub-urban locations, marked as “study sites”, were selected based on (i) heavy infestations of *P. hysterophorus* and (ii) unevenness in the appearance and behavior of its individuals. A total of 64 plots of size 10 × 10 m were set up in these five study sites at a minimum distance of 500 m from each other. Each plot consisted of a dense monoculture of *P. hysterophorus* with identical individuals along with an uninvaded patch of vegetation. Morpho-functional traits were compared statistically between the individuals of different plots and accordingly the plots were clustered under different groups (Fig. 1).

For the vegetational and soil analysis, three quadrats of 2 × 2 m were randomly laid within each plot with two quadrats having $> 75\%$ cover of *P. hysterophorus*, to serve as the invaded quadrats and one quadrat having $< 10\%$ cover of *P. hysterophorus*, to serve as uninvaded quadrat (Fig. 1).

2.3. Morpho-functional traits

Individuals of *P. hysterophorus* were randomly sampled from each plot (10 individuals per plot) for assessing 20 morphological and functional traits (plant height [cm]; stem circumference [cm]; number of lateral branches; number of higher order branches; number of leaves; leaf size [length: width]; number of capitula; canopy cover [cm^2]; total chlorophyll content [$\mu g\ mg^{-1}$ d. wt.]; total carotenoid content [$\mu g\ mg^{-1}$ d. wt.]; stem specific density [$mg\ mm^{-3}$]; twig dry matter content [$mg\ g^{-1}$]; leaf area [cm^2]; specific leaf area [$mm^2\ mg^{-1}$]; leaf dry matter content [$mg\ g^{-1}$]; root-shoot ratio; biomass allocated to leaves, stem, capitula and roots [g]). The selected traits are related to basic morphology, functional aspects and reproductive success of plants and have strong ecological and evolutionary importance (Sultan, 2000; Cornelissen et al., 2003). Also, most of these traits are reported to exhibit plasticity in context of *P. hysterophorus* (Singla, 1998; Annapurna and Singh, 2003).

Among these traits, total chlorophyll content and total carotenoid content were estimated according to the method described by Sidhu et al. (2017). Twenty five milligrams of fresh leaf sample were incubated in 4 ml of dimethyl sulphoxide (DMSO) at 60 °C for 1 h. Thereafter, the absorbance of the solution was read on Shimadzu UV-1800 double beam spectrophotometer at 645 nm, 663 nm and 470 nm taking DMSO as blank. Further calculations were performed as per following equations:

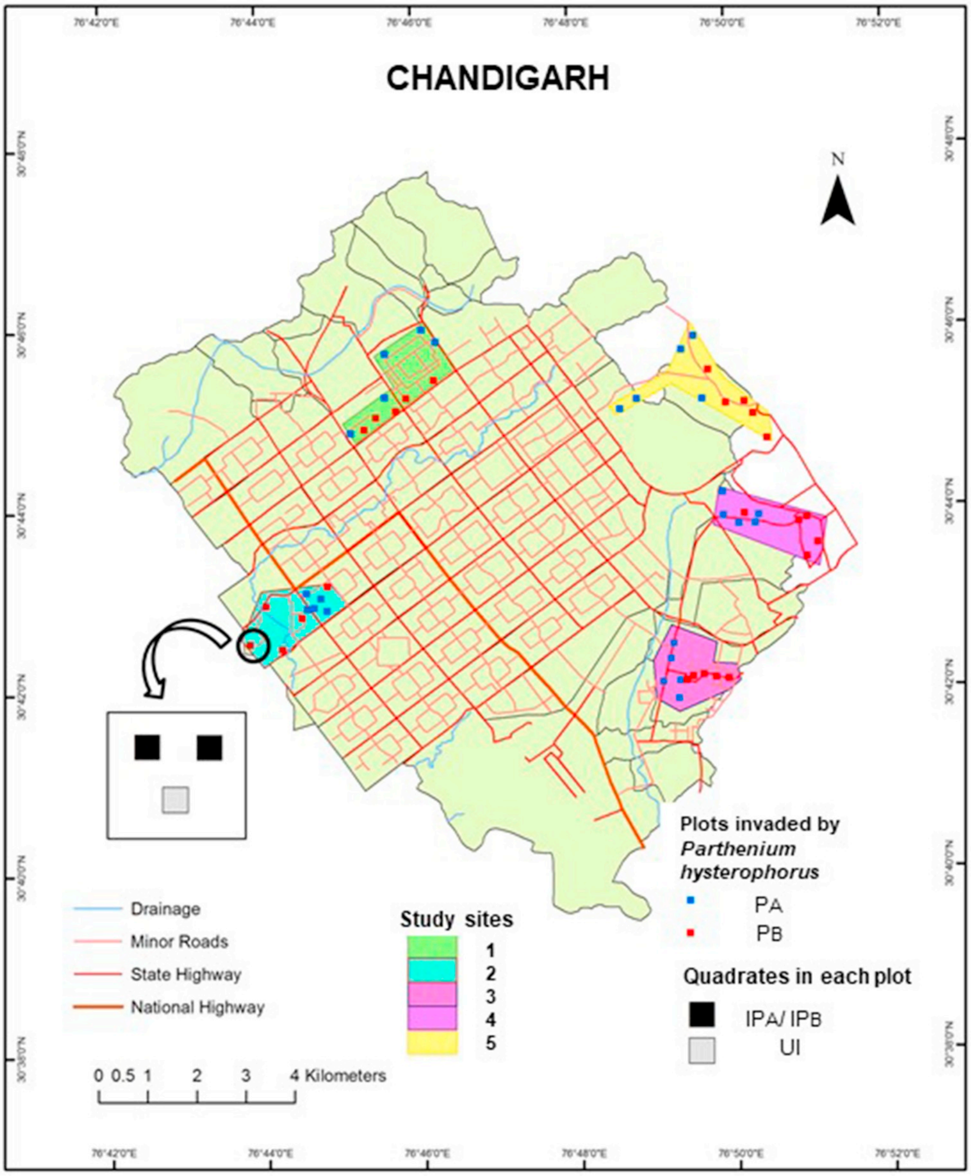

Fig. 1. Map of the study area prepared using *Thirdly ArcGis* 10.4 software. Different colors were used to differentiate the five study sites. P_A and P_B represent two different morphotypes of *Parthenium hysterophorus*. UI represents uninvaded plots, and IP_A and IP_B represent plots invaded by P_A and P_B, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

$$\text{Total chlorophyll content} = (6.45 \times A_{663}) + (17.72 \times A_{645})$$

$$\text{Chlorophyll a } (\text{Chl}_a) = (10.63 \times A_{663}) - (2.39 \times A_{645})$$

$$\text{Chlorophyll b } (\text{Chl}_b) = (20.11 \times A_{645}) - (5.18 \times A_{663})$$

$$\text{Total carotenoid content} = (1000 - A_{470} - 3.27 \times \text{Chl}_a - 104 \times \text{Chl}_b)$$

where A_{663}, A_{645} and A_{470} are the absorbance at 663 nm, 645 nm and 470 nm, respectively.

The remaining morphological/functional traits were determined as per Cornelissen et al. (2003). Canopy cover was estimated as area of the ground covered by vertical projections of the outmost boundary of plant foliage. Stem specific density was calculated by dividing oven dried mass of stem section from its volume which was measured when the stem section was fresh. Twig dry matter content was measured as the ratio of biomass of the terminal twig of plant to its fresh mass. Leaf area was measured by scanning the leaf and analyzing the image using ImageJ software version k 1.45. Specific leaf area was calculated as one-sided area of a fresh leaf divided by its biomass. Leaf dry matter content was measured as the ratio of biomass of a leaf to its fresh mass. Root-shoot ratio was determined as the ratio of total root dry weight to the total shoot dry weight. For the dry weight/biomass estimations, samples were oven dried at 60 °C for 72 h.

2.4. *Vegetation analysis*

For this, all flowering species encountered in the invaded and uninvaded quadrats of all the studied plots were identified and a herbarium was deposited in the Department of Botany, Panjab University, Chandigarh, India. An inventory was prepared listing the names and families of the species (Plant list, 2018) and classifying them according to their nativity (GRIN, 2018). All identified and sampled individuals within each quadrat were counted, with density and abundance of species subsequently determined. For counting the clonal species, a ramet was considered a unit. Density was estimated as total number of individuals of a species per total number of quadrats and abundance as total number of individuals of a species per total number of quadrats in which that species was present. The ecological indices such as Shannon's Index of diversity (H'), Simpson's Index of dominance (λ), Richness Index (R) and Evenness Index (E) were also calculated on the basis of species density as explained by Sharma et al. (2017).

$$H' = -\sum_{i=1}^{S} (ni/N)\ln(ni/N)$$

$$\lambda = \sum_{i=1}^{S} (ni/N)^2$$

$$R = \frac{S-1}{\log N}$$

$$E = \frac{H'}{\ln S}$$

where, ni = number of individuals of ith species, N = total number of individuals of all the species, and S = total number of species.

2.5. Soil analysis

Soil samples were collected after removing surface litter/humus up to 15 cm depth (one sample per quadrat). The soil samples (Psammentic hapludalf in nature) were shade-dried, sieved through a mesh with pore size 2 mm and stored in air tight bags prior to the analysis of various soil chemical properties. The pH of the samples was determined using 2:1 ratio of soil and deionized water with pH meter (Ecoscan CON 5, Eutech Instruments Pvt. Ltd., Singapore).

Phenolic content (Ph) was assessed according to Batish et al. (2006). For this, 1 ml of the soil extract (prepared in a ratio of 1:5) was added to 1:1 Folin-Ciocalteu reagent (v/v) with constant shaking. Thereafter, the reaction mixture was supplemented with 1 ml of 20% Na_2CO_3 and incubated at room temperature under dark conditions for 30 min. After incubation, the reaction mixture developed a blue color, absorbance of which was read at 700 nm against ferulic acid as standard and expressed as µg mg^{-1}.

Organic matter (OM), available nitrogen content (N), available phosphorus (P), available potassium (K), calcium (Ca) and magnesium (Mg) were estimated as per the methods given in Allen (1989).

For determining OM, 1 g of dry soil sample was taken in Erlenmeyer flask and 10 ml of 1 N $K_2Cr_2O_7$ and 20 ml of concentrated H_2SO_4 were added to it. After 30 min, 200–225 ml of distilled water, 10 ml of 85% *ortho*-phosphoric acid and 1 ml of diphenylamine indicator were also added. The contents of the flask (blue in color) were titrated against N/2 $FeSO_4.7H_2O$ until the green color appeared.

$$\text{OM (\%)} = \left(\frac{\text{Volume of 1 N } K_2Cr_2O_7 - \left(\frac{\text{volume of N/ 2 } FeSO_4\cdot 7H_2O}{2}\right)}{\text{Weight of the soil}} \times 0.003 \times 100\right) \times 1.724$$

To estimate N, Kjeldahl distillation apparatus was used. Twenty grams of dry soil were transferred to Kjeldahl distillation flask and 20 ml of distilled water, 100 ml of 0.32% $KMnO_4$ and 100 ml of 2.5% NaOH were added to it along with a few glass beads and 5–7 ml liquid paraffin (to avoid bumping of the solution). The flask was fitted in the apparatus and the end of the delivery was dipped in a conical flask containing 20 ml of 0.02 N H_2SO_4 and 2-3 drops of methyl red indicator. Tap water was run through a condenser and contents of the distillation flask were heated. Pure ammonia gas was collected in the conical flask and titrated against 0.02 N NaOH until pink color of the solution turned yellow.

$$\text{N (kg/ha)} = (\text{Volume of 0.02N } H_2SO_4 - \text{Volume of 0.02N NaOH}) \times \text{Weight of the soil}$$

For the detection of P, 2.5 g of dry soil sample were taken in a 250 ml stoppered flask along with a small amount of Darco G. 60 and 50 ml of 0.5 M $NaHCO_3$ (pH = 8.5). The contents were shaken for 30 min and filtered through Whatman filter paper # 41. Five milliliters of the filtrate were transferred to a 25 ml volumetric flask and carefully acidified to pH 5 using 5 N H_2SO_4. After diluting the contents with 20 ml of distilled water, 4 ml of 0.5% ascorbic acid solution prepared in ammonium molybdate reaction mixture were added and final volume was made 25 ml. The contents were shaken and after 10 min, the intensity of blue color was read in a spectrophotometer at 660 nm against KH_2PO_4 as standard and the final value was expressed as kg ha^{-1}.

For the determination of K, 5 g of soil sample were added to 25 ml of ammonium acetate solution (pH = 7). The contents were shaken for 5 min and filtered through Whatman filter paper # 40. The filtrate was subjected to the flame photometer against KCl as standard and the final value was expressed as kg ha^{-1}.

For estimating Ca and Mg, to 5 ml of the soil extracts prepared in a ratio of 1:5 (w/v), were added 20 ml of distilled water and 3-4 drops of Eriochrome Black T indicator. The wine-red colored solution was then titrated against 0.01 N EDTA until it turned blue.

$$\text{Ca + Mg (\%)} = \frac{\frac{\text{Volume of EDTA}}{\text{Volume of soil extracts}}}{2} \times 10$$

For determining Ca only, 5 ml of the soil extracts prepared in a ratio of 1:5 (w/v) were taken in a conical flask and added 20 ml of distilled water, 0.25 ml of 4 N NaOH and 50 mg of ammonium purpurate indicator. The contents were titrated against 0.01 N EDTA until the orange color of the solution turned purple.

$$\text{Ca (\%)} = \frac{\frac{\text{Volume of EDTA}}{\text{Volume of soil extracts}}}{2} \times 10$$

$$\text{Mg (\%)} = (\text{Ca + Mg}) - \text{Ca}$$

2.6. Statistical analyses

For estimating variations in the morphological and functional traits within the population of *P. hysterophorus*, a ‘plot’ was considered a unit. Mean values of the morpho-functional parameters studied in the 10 individuals of *P. hysterophorus* sampled from each plot were subjected to UPGMA hierarchical clustering. The operation was performed using PAST software ver. 2.17 and the outcome, generated in form of a dendrogram, clustered the similar/dissimilar plots on the basis of Euclidean distance, calculated by the formula, $ED_{jk} = \sqrt{\Sigma}\ (x_{ij}\text{-}x_{ik})^2$, where ED_{jk} is the Euclidean distance between the sampling units j and k (in this case referred to any two random plots) and x_{ij} and x_{ik} is the value of ith parameter in j and k, respectively. On the basis of clustering of the studied plots, two groups among the invasive plant population were identified, tagged as P_A and P_B. Moreover, the morphological and functional traits were subjected to backward model elimination using R software ver.3.4.1 to figure out the parameters that contribute most significantly in grouping of the invasive plant population.

For the vegetation and soil analysis, different invasion categories were established, i.e. areas invaded by P_A [IP_A], areas invaded by P_B [IP_B] and Uninvaded areas [UI]. Invaded quadrats, established in the plots clustered under P_A and P_B, were included in IP_A and IP_B, respectively, whereas the uninvaded quadrats established in all the studied plots were included in UI. The five study sites were used as the replicates. The effect of these invasion categories was then assessed on various ecological indices (H', λ, R, and E).

Since the data was continuous with three independent groups and independent observations, it was subjected to ANOVA and Tukey's *post-hoc* test to determine the significance levels of different comparisons in case of normally distributed data (checked using Shapiro-Wilk test of normality) without any outliers as observed in the H', λ, and E. On the other hand, data showing deviation from normality with significant outliers (as is the case with R) were analyzed using Kruskal-Wallis H

Test, followed by *post-hoc* analysis using Mann-Whitney U Test. Sørenson's similarity coefficient (Sørenson, 1948) was also used to indicate the possible similarities in the floristic assemblages among the invasion categories. In order to maintain uniformity (homogeneity of variances) during the statistical analysis, data from only 10 plots per site was processed to study the ecological impact, eliminating the plots where the vegetation was relatively sparse. All the calculations were performed using MS Excel (Microsoft office 2016) and the analysis was carried out in SPSS ver. 16.0.

The structure of species composition was determined using the gradient length of DCA (Detrended Correspondence analysis) axis which was greater than 4, thereby indicating the unimodal distribution of data. Therefore, constrained multivariate analysis of data (Canonical Correspondence Analysis [CCA]) was carried out on the plot-by-species community data matrix (based on species density) using XLSTAT ver.2018.3. The CCA map/ordination diagram thus obtained described the pattern of variation in the community composition along the environmental variables (soil chemical properties, i.e., pH; Ph; OM; N; P; K; Mg; and Ca). The significance of the results was obtained using 10,000 permutations of the original dataset at $p \leq 0.05$.

3. Results

3.1. Morpho-functional differences in the population of *P. hysterophorus*

The hierarchical clustering assembled the similar and dissimilar plots, thus identifying the two major groups present within the population of *P. hysterophorus*, tagged as morphotype A (P_A) and morphotype B (P_B) (Fig. 2). Of the 64 plots subjected to hierarchical clustering, 31 plots were clustered under P_A and 33 plots under P_B (Fig. 2). Eleven of the twenty morphological and physiological parameters compared for both the morphotypes (P_A and P_B) [stem circumference; number of higher order branches; number of capitula; canopy cover; total chlorophyll content; stem specific density, twig dry matter content; leaf area and biomass allocated to leaves, stem, and capitula] were found to be statistically significantly different at $p < 0.05$ using backward model elimination (Table 1). P_A was visibly more greenish in appearance with herbaceous stem, larger leaf area (+67.58%) and higher chlorophyll content (+21.92%) compared to P_B. On the other hand, P_B possessed traits similar to the shrub life form as established from the woody stem with profuse branching (+46.38%), greater stem circumference (+32.26%), higher stem specific density (+128.57%), higher twig dry matter content (+25.15%), and larger canopy cover (+91.16%) compared to P_A. P_B was found to be more gregarious with higher reproductive output (+190.29%) than P_A, and the biomass assigned to capitula was also greater in P_B than P_A by 82.85%. Patterns of biomass allocation to the aboveground vegetative parts also varied between the two morphotypes, with a stem: leaf ratio of 1.5 in P_A and 3.4 in P_B (Table 1).

3.2. Effect of morphotypes on floristic diversity

The three invasion categories, thus established in the studied plots *i.e.* areas invaded by P_A [IP_A], areas invaded by P_B [IP_B] and Uninvaded areas [UI], were compared for their vegetational patterns. A total of 92 plant species (including *P. hysterophorus*) were recorded in all the three invasion categories, of which 55 were native (originated in Indian subcontinent), 35 were alien, whereas 2 species had unknown/controversial place of origin (Table S1; supplementary information). Some of the alien species were invasive, while others were non-invasive in the region. A similarity of 70.42% was recorded between UI and IP_A, whereas in case of UI and IP_B and IP_A and IP_B, it was recorded to be 65.55% and 67.89%, respectively. A total of 9 alien and 11 native species were exclusively present in UI plots that were not recorded while sampling the invaded plots. Similarly, IP_A exclusively inhabited 12 species (1 alien, 11 native), but no such species association was recorded in IP_B. Moreover, UI and IP_A shared 17 species (6 alien; 11 native); UI and IP_B shared 6 species (2 alien, 4 native) and IP_A and IP_B shared 4 species (all alien), whereas 33 species (13 alien, 20 native) were common to all invasion categories (Fig. 3).

Significant difference in the Shannon's index of diversity ($p < 0.001$) and evenness index ($p = 0.008$) was observed between UI and IP_B as well as IP_A and IP_B, but the Simpson's index representing dominance of an individual species differed significantly only between UI and IP_B ($p = 0.003$). Margalef's richness index, on the other hand, varied among all the three invasion categories ($p < 0.001$) (Fig. 4). A difference in the percent reduction of native and alien species, in terms of abundance and number of plant species, was also recorded between the invasion categories. A reduction of 15% and 49.88% in the abundance of alien species was noticed in case of IP_A and IP_B, respectively, compared to UI. However, the decline in the abundance of native species is quite high with 60.28% reduction in case of IP_A and 69.62% reduction in case of IP_B with respect to UI. Similar results were observed for the total number of species with IP_A and IP_B reflecting

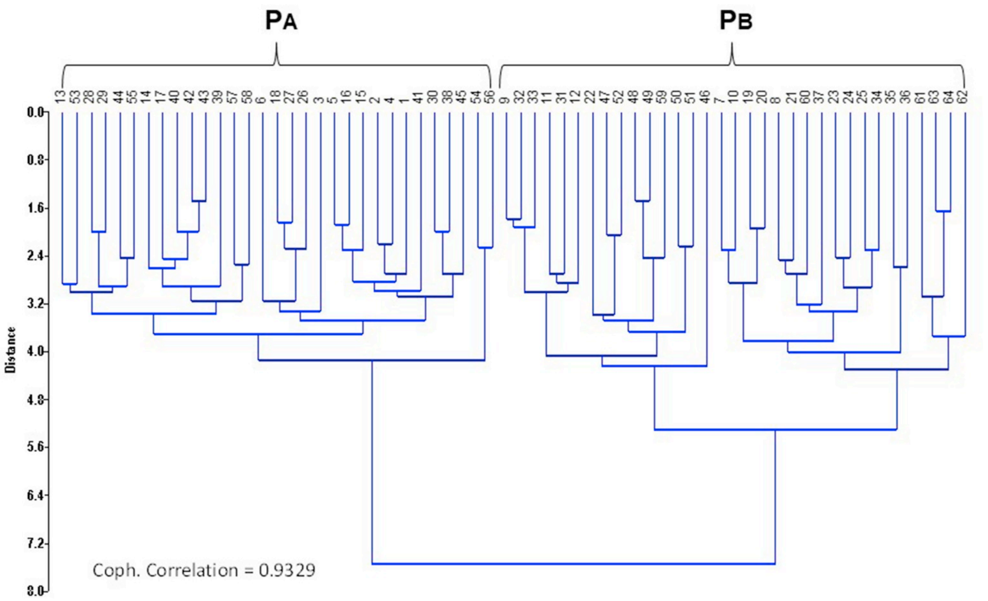

Fig. 2. Dendrogram representing hierarchical clustering of the studied plots (numbered from 1 to 64) on the scale of Euclidean distance. The clustering is based on the morphological and functional traits measured in the individuals of *Parthenium hysterophorus*. Cophenetic (Coph.) correlation measures how precisely the dendrogram represents the dissimilarities among observations. P_A and P_B represent two different morphotypes of *Parthenium hysterophorus*, identified on the basis of clustering.

Table 1
Morphological and functional traits studied in the two groups of morphotypes (P_A and P_B) of *Parthenium hysterophorus* identified using the hierarchical clustering approach using the same parameters.

	P_A	P_B	*t*-value
Morphological traits			
Plant height (cm)	38.97 ± 1.12	36.2 ± 1.98 (−7.11%)	–
Stem circumference (cm)	2.17 ± 0.14	2.87 ± 0.15 (+32.26%)	3.446**
Number of lateral branches	11.49 ± 0.21	11.08 ± 0.39 (−3.57%)	–
Number of higher order branches	36.52 ± 0.67	53.46 ± 1.51 (+46.38%)	9.813***
Number of leaves	12.6 ± 0.23	12.15 ± 0.4 (−3.57%)	–
Leaf size (length: width)	1.68 ± 0.06	1.74 ± 0.05 (+3.57%)	–
Number of capitula	2505.8 ± 117.17	7274 ± 204.77 (+190.29%)	2.105*
Canopy cover (cm^2)	56.05 ± 1.43	107.12 ± 2.6 (+91.16%)	2.069*
Functional traits			
Total chlorophyll content ($\mu g\ mg^{-1}$ d. wt.)	8.21 ± 0.07	6.41 ± 0.12 (−21.92%)	2.036*
Total carotenoid content ($\mu g\ mg^{-1}$ d. wt.)	2.49 ± 0.03	1.71 ± 0.05 (−31.32%)	–
Stem specific density ($mg\ mm^{-3}$)	0.07 ± 0.01	0.16 ± 0.01 (+128.57%)	2.001*
Twig dry matter content ($mg\ g^{-1}$)	230.81 ± 2.22	288.85 ± 1.47 (+25.15%)	5.435***
Leaf area (cm^2)	75.7 ± 2.62	24.54 ± 4.73 (−67.58%)	−8.736***
Specific leaf area ($mm^2\ mg^{-1}$)	17.99 ± 1.35	20.76 ± 2.31 (+15.4%)	–
Leaf dry matter content ($mg\ g^{-1}$)	216.54 ± 11.4	192.13 ± 10.7 (−11.27%)	–
Root-shoot ratio	0.19 ± 0.06	0.11 ± 0.04 (−42.10%)	–
Biomass allocated to leaves (g)	19.29 ± 0.41	14.54 ± 0.47 (−24.62)	−2.228*
Biomass allocated to stem (g)	29.94 ± 1	49.88 ± 0.98 (+66.6)	2.056*
Biomass allocated to capitula (g)	7.23 ± 0.24	13.22 ± 0.24 (+82.85)	3.062**
Biomass allocated to roots (g)	9.95 ± 0.46	8.57 ± 0.4 (−13.87%)	–

Data presented as mean ± SE (*df* = 24). Value in the parenthesis represents percent change (+, increase; −, decrease) in P_B with respect to P_A. *t-value* and its significance was computed using backward model elimination (*$p \le 0.05$; **$p \le 0.01$; ***$p \le 0.001$).

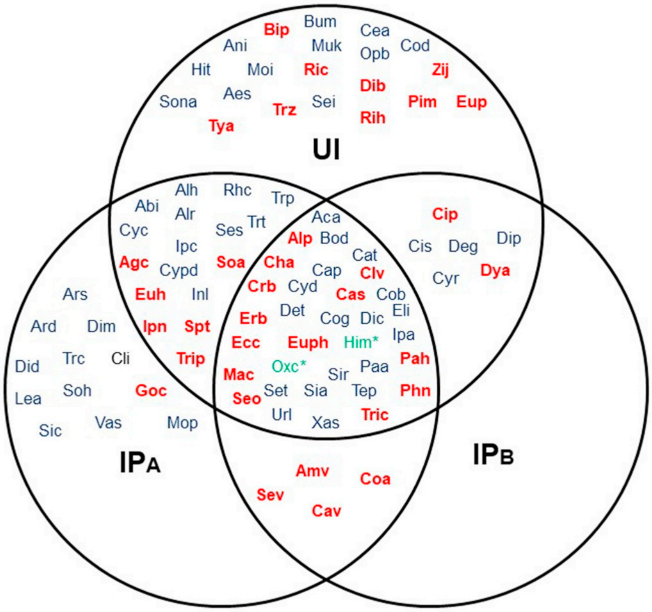

Fig. 3. Venn diagram showing the distribution of plant species in three invasion categories, designed manually in MS PowerPoint on the basis of calculations performed in MS excel (Microsoft office 2016). UI represents uninvaded plots and IP_A and IP_B represent plots invaded by two different morphotypes of *Parthenium hysterophorus*. Species names are abbreviated (see Table S1, supplementary information, for full names). Abbreviations in blue color (non-bold) symbolize native species, red color (bold) symbolize alien species, and green color (marked with *) symbolize species with unknown/controversial distribution. The species nativity was checked from GRIN (available at https://www.ars-grin.gov; accessed on 03/05/2018). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

17.46% and 44.44% reduction in alien species, respectively, and 35.58% and 59.62% reduction in native species, respectively, compared to UI (Table 2).

3.3. *Effect of the morphotypes on community composition and soil chemical properties*

Constrained CCA analysis corresponded to the 71.56% of the total inertia, represented by eight ordination axes (F1-F8). From the eigenvector analysis, it was established that F1 carried the maximum percent of the constrained inertia (40.32%), followed by F2 (22.46%), F3 (18.99%), F4 (5.63%), F5 (4.72%), F6 (3.79%), F7 (2.45%), and F8 (1.64%). Since the first two axes (F1 and F2) could explain 62.78% of the total inertia, the results of CCA are described as 2-dimensional ordination diagram/CCA map, analyzing the relationship among invasion categories, species and soil variables (Fig. 5). The data was found to be statistically significant at $p = 0.026$ with a pseudo F-value of 1.887 upon 10,000 permutations, thus indicating that the invasion categories/species are linearly related to the soil variables. The ordination diagram showed that the sites representing UI were distinguishable from the sites of IP_A and IP_B, whereas the latter two invasion categories were intermingled with each other. This confirmed that the soil variables vary between UI and IP_A/IP_B but not between IP_A and IP_B. Species association with IP_A and IP_B was remarkably less, but the soil nutrient composition was enhanced in these invasion categories, except for Mg and Ca. The majority of species was concentrated in the centre of the diagram or away from the vectors, indicating their preference for moderate/low levels of nutrients in the soil. The species sensitive to the higher level of nutrients, pH and phenolics were found to include the alien species (*Corchorus aestuans* [Coa]; *Parthenium hysterophorus* [Pah]; *Setaria verticillata* [Sev]; *Amaranthus viridis* [Amv]; *Calyptocarpus vialis* [Cav]) (Fig. 5; Table S1; supplementary information).

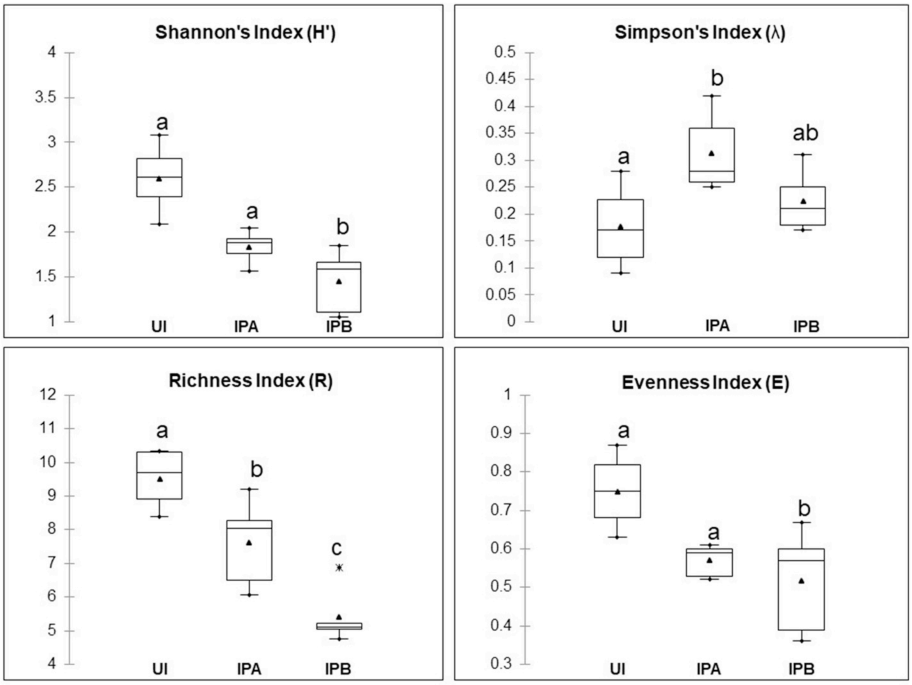

Fig. 4. Box plots representing the ecological indices (based on species density) recorded in three invasion categories, prepared in XLSTAT ver. 2018.3 (Vertical lines/whiskers represent the minimum to maximum range; horizontal lines represent 1st quartile, median and 2nd quartile; triangles represent mean and asterix represents the outliers). UI represents uninvaded plots and IP_A and IP_B represent plots invaded by two different morphotypes of *Parthenium hysterophorus*. Different alphabets symbolize significant difference among the three invasion categories at $p \leq 0.05$ using Tukey's test for H', λ, and E and Mann-Whitney U Test for R.

Table 2

Abundance and number of plant species of the native and alien species (including *Parthenium hysterophorus*) in three invasion categories. UI represents uninvaded plots and IP_A and IP_B represents plots invaded by two different morphotypes of *P. hysterophorus*.

	Abundance			Number of plant species		
	UI	IP_A	IP_B	UI	IP_A	IP_B
Alien species	108.8 ± 26.26	92.48 ± 16.58 (15.00%)	54.53 ± 8.48 (49.88%)	12.6 ± 1.36	10.4 ± 0.81 (17.46%)	7 ± 0.32 (44.44%)
Native species	282.44 ± 23.31	112.19 ± 12.74 (60.28%)	85.81 ± 9.79 (69.62%)	20.8 ± 1.16	13.4 ± 1.83 (35.58%)	8.4 ± 0.93 (59.62%)

Data presented as mean ± SE. Value in the parenthesis represents percent reduction with respect to UI.

4. Discussion

4.1. Diversity in the population of P. hysterophorus

This study revealed the presence of highly significant morpho-functional dissimilarities within the population of *P. hysterophorus*. The findings not only confirmed the presence of morphological variations as suggested by earlier findings of Singla (1998), but also provided an insight into the functional disparities between these morphotypes. Previously, the invasive plant morphotypes have been classified as 'tall type' (resembling to morphotype A [P_A] in our study) and 'bushy type' (resembling to morphotype B [P_B] in our study) (Singla, 1998). Both types of plants were found to be co-existing but with a remarkable differentiation in the size, habit, leaf segmentation and duration of vegetative and reproductive phases.

Superior leaf characteristics in terms of larger leaf area and higher chlorophyll content in P_A suggest the better photosynthetic ability of its individuals, which is a sign of resource rich environment (Cornelissen et al., 2003). Specific leaf area (SLA) is an important leaf trait with a significant role in plant metabolism, and tends to be higher in most invasive species (Feng et al., 2008; Gallagher et al., 2015). However, SLA was found to not vary between the morphotypes, such that other parameters (leaf area and photosynthetic pigments) were considered to compare the photosynthetic ability of P_A and P_B. On the other hand, profuse branching, greater stem circumference, higher stem specific density, higher twig dry matter content and larger canopy cover indicated the mechanical strength, safety of hydraulic transport, and resistance to damage from pests or pathogens in P_B, pointing towards the possibility of prevalence of harsh environmental conditions or biotic/abiotic stresses (Zanne and Falster, 2010). The biomass allocation patterns revealed that the individuals of P_A focused on better vegetative growth, whereas in case of P_B, the invasive plant tends more towards enhancing reproductive output. The variations in morphological and functional traits observed during the study, indicate that the invasive plant can exploit the competitive advantages afforded by each of these traits, depending upon requirements.

Phenotypic plasticity in *P. hysterophorus* has been shown by the altered behavior of the plant in response to varying soil conditions (Annapurna and Singh, 2003), wide temperature range (Kaur et al., 2017), and pollution stress (Kadam et al., 2009). Our study adds to existing literature because our data was collected from a common area and in a single time period, ruling out the involvement of any major climatic/geographical changes. This has allowed for an assessment of the effects of microclimatic and local habitat conditions on phenotypic plasticity. Singla (1998) described that the bushy morphotype (corresponds to P_B) tends to inhabit relatively drier areas, disturbed habitats, wastelands, roadsides, and railway tracts, etc., whereas tall morphotype (corresponds to P_A) was confined to agricultural lands, garden areas, construction sites and along the water channels. Kaur et al. (2017) also found that the season of germination of *P. hysterophorus* affected its phenological aspects. Therefore, it can be speculated that temperature/humidity/precipitation based changes in the maternal environment at the time of its germination or early growth period may also decide the resource allocation patterns and the functional behavior of the invasive plant (Lu et al., 2016).

Multiple introductions of a species can contribute to heterogeneity

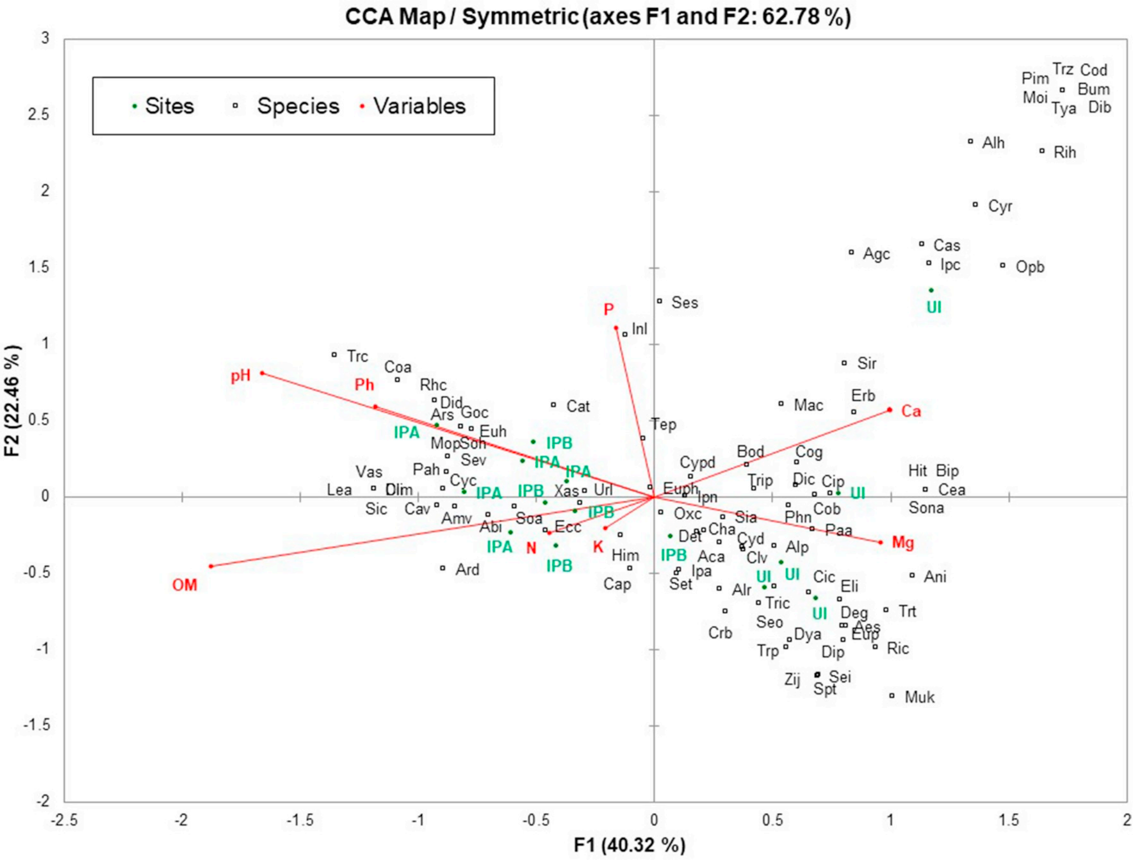

Fig. 5. Ordination diagram (Map) generated by canonical correspondence analysis. The figure illustrates the pattern of distribution of plant species (based on species density) and different invasion categories (sites) along the environmental variables, i.e. the soil chemical properties (pH; phenolics [Ph]; organic matter [OM]; available nitrogen [N]; available phosphorus [P]; available potassium [K]; magnesium [Mg]; and calcium [Ca]). UI represents uninvaded plots and IP_A and IP_B represent plots invaded by two different morphotypes of *Parthenium hysterophorus*. Species name are abbreviated (see Table S1, supplementary information for full names).

in its phenotypic behavior (Oduor et al., 2016), as is the case with *P. hysterophorus*' multiple introductions in India (Adkins and Shabbir, 2014). Two biotypes of the invasive plant in Australia, distinguished on the basis of their separate introductions, are reported to show variable morphology, physiology, and biochemistry (Bajwa et al., 2017). On the other hand, polyploidy and hybridization are also known to have a strong influence on the invasiveness of a species (Lee, 2002; Pandit et al., 2011). Both these factors are suggested to be a reason behind the diversity among South American populations of *P. hysterophorus* (Picman and Towers, 1982). However, in India, literature in this context is currently lacking.

4.2. Ecological impacts of morphotypes of *P. hysterophorus*

Ecological indices are the most widely used estimators of community structure, particularly in relation to invasion ecology (Karydis and Tsirtsis, 1996), with published examples in Hulme and Bremner (2006), Hejda et al. (2009) and Hejda et al. (2017). In our study, the significant alterations in *H′*, λ, *R* and *E* indices show the strong ecological impact of *P. hysterophorus* on local vegetation. Morphotype P_B was found to have a more pronounced effect on *H′*, *R* and *E*, compared to P_A, suggesting that phenotypic variations can influence the invasion potential of *P. hysterophorus*. In the case of λ, the non-significant difference obtained between UI/IP_A and IP_B is justified as the dominance of *P. hysterophorus* in IP_B can be explained better by its biomass rather than the density (Wasof et al., 2018). Sørenson's index also revealed a higher similarity in the species composition between UI and IP_A than UI and IP_B, which shows that the individuals of morphotype P_B have brought more evident changes in the vegetation patterns. Previously, studies have reported shifts in the floral composition upon the invasion by *P. hysterophorus* (Grice, 2006; Shabbir and Bajwa, 2006; Timsina et al., 2011). Our study align with published literature except in the case of Timsina et al. (2011) who reported that even if species composition was affected because of invasion by *P. hysterophorus*, species diversity was enhanced. Our study area and that in Timsina et al. (2011) differ in geographic, climatic and topographic conditions which can account for variation in the floral composition. Moreover, the effect of an invasive plant on species diversity of a region is driven by factors like interactions among the plant species, variation in the heights of invasive and native plants, and the spread extent of invasive plants (Hejda et al., 2009).

Invasive species can use mechanisms such as increased above-ground biomass production, decreased space/light/nutrient availability, and allelopathy, to exclude native plant species (Kuebbing et al., 2014). These factors can also be at play in our study site given the remarkable reduction in native species in the presence of both morphotypes. On the other hand, a few alien species were found to be exclusively associated with the invaded quadrats, i.e., *Gomphrena celosioides* (Goc), *Amaranthus viridis* (Amv), *Corchorus aestuans* (Coa), *Setaria verticillata* (Sev), and *Calyptocarpus vialis* (Cav). Some of these species had conspicuously high density, particularly in IP_B. Theory of invasional meltdown is, therefore, applicable in this context, where an invasive species promotes the other non-native species or *vice-versa* (Simberloff and von Holle, 1999).

The above-ground shifts in vegetation patterns are also governed by permutations in below-ground nutrient cycling, as well as functioning and composition of microbial communities (Kourtev et al., 2003). Soil composition in our study plots showed an increase in chemical properties and macronutrient concentration with invasion by *P. hysterophorus*, but a decrease in Mg and Ca. This indicated that *P. hysterophorus*, due to its invasive capabilities, alters the soil chemistry in its rhizosphere. This may in turn result in the soil feedbacks influencing the other enzymatic activities and microbial interactions, thereby, exerting an indirect competition on the co-occurring floristic diversity (Sanon et al., 2012). Some previous studies have reported mixed effects of *P. hysterophorus* on soil structure with our study findings aligning with Timsina et al. (2011) but contradictory to Osunkoya et al. (2017). Enhanced soil chemical properties and nutrient composition could be attributed to the release of allelochemicals by *P. hysterophorus*, along with a higher amount of decomposing residues and faster decomposition rates (Pyšek and Pyšek, 1995; Timsina et al., 2011). Reduction in Mg and Ca could be due to high levels of competing elements or long-term imbalance in N, P and K (Guo et al., 2016). Despite the non-significant differences in soil composition between IP_A and IP_B, P_B had a larger impact on vegetation. This impact may be a result of direct interference through allelopathy, competition for the resources or the comparatively larger biomass production of this morphotype (Hejda et al., 2009; Gnanavel, 2013; Sharma et al., 2017).

4.3. Way forward and management implications

Inflection in the invasive attributes of alien plant species is common during ecological disturbances, and in certain cases, these responses can be powerful enough to facilitate the process of natural selection. Invasive plant species evolve local adaptations as frequently and as strongly as native plant species within their alien ranges (Oduor et al., 2016). Adjustments to varying degrees of climate and habitat ranges via complex interplay of rapid evolutionary changes, locally adapted ecotypes and phenotypic plasticity have also been documented in other aggressive invasive species such as *Bromus tectorum, Alliaria petiolata* etc. (Hufft and Zelikova, 2016; Blossey et al., 2017). *Spartina alterniflora*, a perennial grass found in salt marshes, has evolved ecotypes differing in flowering duration, and plant height via a combination of environmental and genetic factors in response to variable edaphic conditions (Anderson and Treshow, 1980). In the present study, these variations are observed only on the phenotypic scale and there is a possibility of these changes being inheritable and plastic. Since phenotypically plastic species are believed to be more favored during climate change (Chown et al., 2007), the adaptations observed in *P. hysterophorus* enhance probability of its survival and expansion during ecological disturbances. However, our study involved only the mature/flowering plants of *P. hysterophorus*, but similar studies at different developmental stages of the invasive plant may provide further insights into the genesis of such morpho-functional differences.

A constant check on the invasion patterns of the plant within its introduced range is therefore, considerably important. Conservation managers need to distinguish between the morphotypes as their impact on composition of associated flowering species differ largely. Individuals with shrub like woody characters, greater canopy structure, larger biomass and better reproductive output represent a severe threat to the local flora. Management plans for *P. hysterophorus* should take these adaptations into consideration and can prioritize the efforts accordingly. So far, mechanical, chemical, biological and integrated approaches have been undertaken for the control of invasive plant in the study area (Batish et al., 2004). Despite the efforts, it can be found growing unchecked in various habitats, which indicates lack of appropriate management strategies. Studies excavating the unexplored aspects related to the invasion biology of *P. hysterophorus* may contribute to the improvement of these strategies. Furthermore, long-term checks are required to eliminate the invasive plant along with constant monitoring of these behavioral changes, which may help in anticipating forthcoming predicaments for suitable preventive measures.

5. Conclusions

Based on the results of the study it can, therefore, be concluded that the changes in the morpho-functional behavior of *P. hysterophorus* may influence its competitive ability, performance and ecological impact. Conservation managers can exploit information provided in the study to understand invasion patterns of *P. hysterophorus*, to identify the morphotype with higher ecological impact and to reconsider/prioritize management efforts accordingly.

Moreover, further research focusing on the genetic aspects is required to validate if these adaptations are inheritable. It is pertinent to explore the plausible genesis of the phenotypic variations as these responses may be an outcome of the post-introduction rapid adaptive evolution thus, holding a substantial ecological significance. The role of morpho-physiological traits in promoting differential invasional meltdown effects by the two morphotypes of *P. hysterophorus* can also be explored during further studies.

Author's contribution

DRB, SK and RKK conceived the ideas; AK and DRB designed methodology; AK collected the data; AK, DRB and HPS analyzed the data; AK and HPS designed the draft of the manuscript; all authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

AK is thankful to University Grants Commission (India) for the research fellowship. Authors are grateful to Mr. Gurudev Mongia (Herbarium Incharge, Department of Botany, Panjab University, Chandigarh) for the help in identification of various plant species.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2019.03.129.

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