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What drives performance potential of *Lantana camara* L. (*sensu lato*) in the invaded range?

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Abstract: *Lantana camara* L. (*sensu lato*), one of the world's worst invaders has disseminated rapidly and continues to expand in its invaded range. Invasiveness of a species can broadly be gauged by determining trait values, considered as manifestation of performance ability. In spite of vast range expansion, performance of *Lantana* in its different invaded ranges is under-studied. We measured vegetative and reproductive traits of *Lantana* in two of its invaded ranges with differential residence timeframes *viz.* India and South Africa. Comparative field observations revealed that the Indian populations were more vigorous than those in South Africa in terms of key traits. NMS ordination revealed that traits of *Lantana* in both ranges were significantly related to climatic variables. Substantially different mean annual temperature and/or residence timeframe in the two invaded ranges might have driven contrasting performance ability of *Lantana*. Results highlight that plant invaders may experience disproportionate success in varied invaded ranges owing to distinction in time elapsed since initial introduction in tandem with environmental factors, which may have crucial implications for their management. However, the study calls for further disentangling the factor(s) which contribute to species' invasive success in the invaded range.

Key words: Climate, invaded range, residence time, species complex, trait.

Introduction

A variety of factors have been suggested to influence invasiveness; these factors govern the extent to which a species introduced outside its native range may overcome various biotic and abiotic barriers to establish in a new environment (Wilson *et al.* 2007). A species may perform variably in contrasting introduced ranges. Notably, trait values in different invaded ranges may be considered as manifestations of species' performance as key functional traits possessed by plant invaders play a crucial role in their establishment, spread and better performance in the invaded range (Grotkopp *et al.* 2002; Matzek 2012; Parker *et al.* 2013). Introduced species' ability to modulate the range of traits increases its likelihood of successful establishment in heterogeneous environments (Goyal *et al.* 2014; Mincheva *et al.* 2016; Novak & Mack 2005). However, the importance of these traits in explaining success of plant invaders depends on the spatial scale and environmental context (Funk 2013; Kueffer *et al.* 2014; van Kleunen *et al.* 2015). Many empirical studies have explored invasion-linked traits from a biogeographical perspective by comparing invader's performance in native and invaded ranges (see Hinz & Schwarzlaender 2004; Hirsch *et al.* 2012; Seipel *et al.* 2015), but examining species' performance across different invaded ranges has been typically overlooked. We address this premise by examining key vegetative and reproductive traits of the world's worst invader, *Lantana camara* L. (*sensu lato*) (*Lantana*, hereafter) in two of its profusely invaded ranges, India and South Africa.

Lantana is a markedly ubiquitous invader with

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Table 1. History of *Lantana* introduction in India and South Africa.

	India	South Africa
Approximate time of introduction	1804[a,b,c,d]	1858[e]
Place of introduction	Royal Botanical Garden, Kolkata[a,c]	Cape Town Botanical Gardens[e,f]
Introduced from	Sri Lanka (earlier Ceylon)[b,g]	Unknown origin[e,f]
Approximate time since introduction (in years) [Residence time]	~213 years	~159 years

Thakur *et al.* 1992[a]; Hakimuddin 1929[b]; Pereira 1919[c]; Sharma *et al.* 2005[d]; Vardien *et al.* 2012[e]; McGibbon 1858[f]; Cronk & Fuller 1995[g]

a wide scale of distribution, and is invasive throughout tropical, subtropical and warm temperate areas (Sharma *et al.* 2005; Swarbrick *et al.* 1995). It currently occupies millions of hectares in India (13 million ha) and South Africa (2 million ha) and, continues to expand partly due to climatic suitability of the habitats and therefore has a high invasibility potential across the two ranges (Bhagwat *et al.* 2012; Goncalves *et al.* 2014; Vardien *et al.* 2012). Aggressive measures developed to eradicate *Lantana* in India and South Africa over the last two centuries have been largely unsuccessful (Bhagwat *et al.* 2012). Realizing the potential for species' expansion in the invaded range, there is a need to unravel the suite of factors that facilitate its performance and whether performance varies across the invaded ranges. Interestingly, time of introduction of *Lantana* in the two ranges differs substantially *viz.* ~213 years in India and ~159 years in South Africa; this provides the potential prospects to study the invader's performance in the two invaded ranges with different residential timeframes (see Table 1). The probability of species' invasive success increases with an increase in residence time *i.e.* time since introduction to a novel range (Rejmánek *et al.* 2005; Richardson & Pyšek 2006).

Success of an invasive species in its invaded range is attributed to intrinsic factors (*plant traits*) that make species, a better invader, extrinsic factors (release from natural enemies, hybridization or other novel ecological and evolutionary interactions), and/or biogeographical factors (residence time and climate) (Colautti *et al.* 2014). Although all these factors have been reported to contribute significantly to species' performance in the invaded range, longer residence time can substantially lead to a concomitant increase in species' invasive success (Rejmánek *et al.* 2005; Richardson & Pyšek 2006; Williamson *et al.* 2009). Residence time is thus a critical consideration for studies evaluating species' invasiveness in contrasting invaded ranges (Richardson & Pyšek 2006). Longer residence time of a species in a particular invaded range is suggestive of its higher propagule pressure and hence, greater probability of founding new populations and having a wider range of distribution (Pyšek & Jarošík 2005; Rejmánek *et al.* 2005; Williamson *et al.* 2009; Wilson *et al.* 2007). Estimating 'invasiveness' of *Lantana* through functional traits that better predict plant performance *viz.* growth and reproduction may provide insights on the role of residence time in driving its performance potential in the invaded range.

With the background understanding of different facets of *Lantana* invasion, we asked the following questions: (a) Does population density of *Lantana* differ in India and South Africa? (b) Are *Lantana* populations different in terms of their vegetative and reproductive traits in the two invaded ranges? (c) Do residence timeframe and climatic factors affect performance of *Lantana* across the two ranges? Essentially, species' invasive success can be evaluated by estimation of plant performance through key plant traits. To address these questions, variability in trait values of *Lantana* was used as a measure for species' performance in the two invaded ranges (see Matzek 2012). Results of the study will yield useful insights on the role played by residence time, plant traits and climatic factors in complementarity, in conferring fitness and/or competitive advantage to *Lantana* in the two invaded ranges. This will further allow us to determine factor(s) that best explain performance differences of *Lantana* in the invaded range. We anticipate that insights gained will improve our ability to manage *Lantana* in the two invaded ranges, otherwise considered to be the *battle lost* (Bhagwat *et al.* 2012).

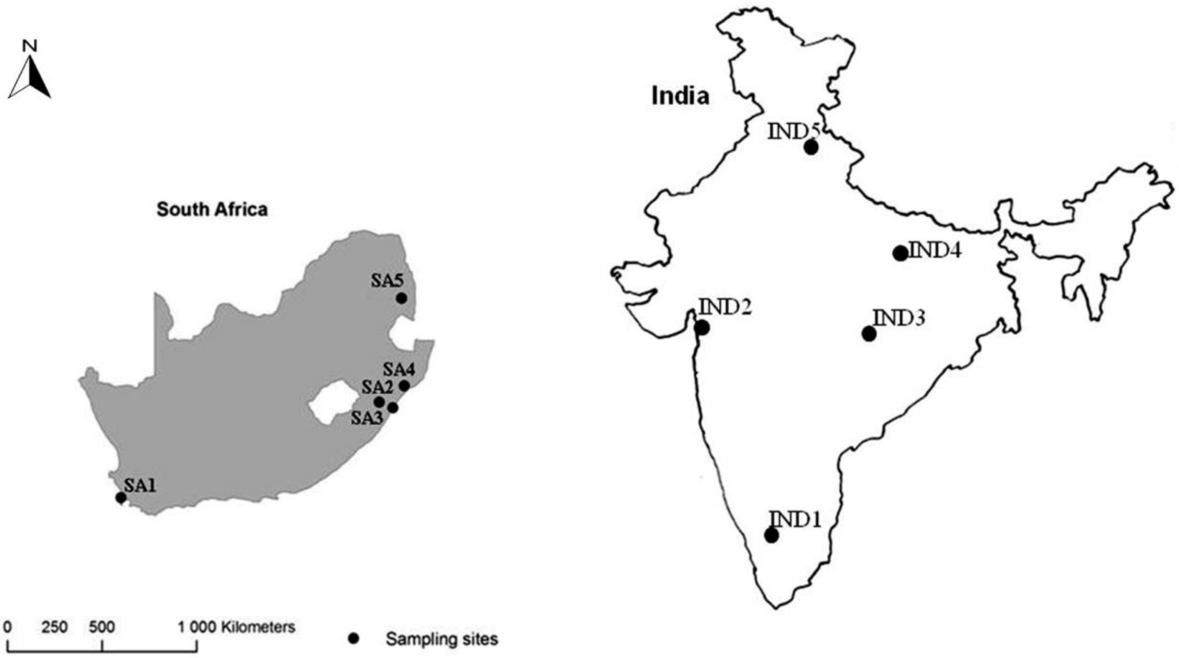

Fig. 1. Sampling sites in India (IND) and South Africa (SA). IND1: Chamarajanagar, IND2: Surat, IND3: Raipur, IND4: Renukoot, IND5: Devaprayag; SA1: Cape Town, SA2: Pietermaritzburg, SA3: Durban, SA4: Richard Bay, SA5: Kruger National Park.

Materials and methods

Study species

Lantana (Verbenaceae), a multi-stemmed bushy shrub is considered a native of South America or Mexico (Howard 1969; Spies & du Plessis 1987), while a few studies suggest West Indies to be the native range (Moldenke 1973; Palmer & Pullen 1995). Valued as an ornamental species, it was imported from America to Europe wherein extensive breeding and selection led to the present-day highly variable species complex, *Lantana camara* L. (*sensu lato*) (Goyal & Sharma 2015). Different suites of hybrids along with a few parental species were introduced into different European colonies (Day *et al.* 2003; Sanders 2006; Scott *et al.* 1997; Stirton 1977), where frugivorous birds spread them from gardens into the countryside (Johnson 2007; Mokotjomela *et al.* 2013a, b). The generic term *Lantana* has been used to address invasive *Lantana camara* L. (*sensu lato*) owing to extreme uncertainty existing in the composition of *Lantana* species complex (Goyal & Sharma 2015).

Sampling details

Five sites each in India and South Africa were sampled during the peak growth season of *Lantana* in 2008 and 2009 (Fig. 1; see Table 1, 2 for information on selected invaded ranges, coordinates and climatic variables of each sampling site). Mean annual temperature and mean annual precipitation values are long-term means from the public domain climate model (Hijmans *et al.* 2005) [Retrieved from: http://www.worldclim.org] (Table 2).

At each site, three locations were considered (each at a distance of at least 65 km to avoid spatial clumping of populations) wherein, three 10 m × 10 m plots (each at a distance of at least 2 km) were considered for estimation of population density (individuals per 100 m^2). Altogether, at each site, twenty individuals inhabiting well-lit habitats were randomly chosen for measurement of plant traits. Each individual was sampled for plant height, basal circumference of the stem clumps, primary branches per plant, and length of five randomly selected primary branches to estimate primary branch length. On five randomly selected primary branches, vegetative traits *viz.* branchlets per plant, leaves per plant, thorns (per 10 cm on the lower green portion of each branchlet), and thorn size were estimated. Reproductive traits such as inflorescences per branchlet, flowers per inflorescence, seeds per plant, fruit size and mass per ten fruits, seed size and mass per ten seeds were also determined for each individual. Reproductive

Table 2. *Lantana* populations in India (IND) and South Africa (SA). IND1: Chamarajanagar, IND2: Surat, IND3: Raipur, IND4: Renukoot, IND5: Devaprayag, SA1: Cape Town, SA2: Pietermaritzburg, SA3: Durban, SA4: Richard Bay, SA5: Kruger National Park.

Site	Geographical coordinates		Altitude (m.a.s.l.)*	Mean annual temperature (ºC)#	Mean annual precipitation (mm)§
	Latitude	Longitude			
India					
IND1	11º 55′ 49″ N	76º 59′ 51″ E	695	24	570
IND2	21º 11′ 39″ N	72º 45′ 74″ E	6	27	960
IND3	21º 14′ 11″ N	81º 42′ 59″ E	294	26	1040
IND4	25º 06′ 57″ N	82º 59′ 49″ E	149	26	830
IND5	30º 08′ 43″ N	78º 35′ 45″ E	583	21	1290
South Africa					
SA1	33º 59′ 40″ S	18º 26′ 07″ E	30	16	920
SA2	29º 36′ 25″ S	30º 21′ 57″ E	698	18	770
SA3	29º 51′ 51″ S	31º 00′ 20″ E	115	17	790
SA4	28º 52′ 32″ S	31º 31′ 16″ E	85	17	1200
SA5	25º 02′ 38″ S	31º 23′ 10″ E	424	21	575

index (Ri) was further estimated as the ratio of the total number of seeds to the plant height (Aronson *et al.*1993; Regehr & Bazzaz 1979).

Statistical analyses

The effect of invaded range (each representative of distinct residence timeframe; Table 1) on vegetative and reproductive traits of *Lantana* was analyzed by ANOVA. Linear regression analysis was used wherever necessary. Statistical analyses were performed using SPSS 16.0 (SPSS Inc. 2007). NMS ordination techniques are useful for summarizing population trait data and highlighting patterns in traits related to climatic conditions (Miller *et al.* 2011). Hence, *Lantana* trait values (16 vegetative and reproductive traits) were ordinated by Non-metric Multidimensional Scaling (NMS) performed with PC-ORD 5 (McCune & Mefford 1995) using population mean values to delineate unique traits that differentiate *Lantana* populations in India and South Africa. The relationships of NMS axis with altitude, mean annual temperature and precipitation were determined. Differences in mean values of altitude, mean annual temperature and mean annual precipitation of sampling sites in India and South Africa were analyzed through *t*-test.

Results

Lantana *populations inhabiting India and South Africa*

Lantana populations inhabiting the two invaded ranges did not exhibit substantial differences in population density; however key vegetative and reproductive traits showed significant differences. ANOVA indicated significant differences in plant height, primary branches per plant, branchlets per plant, leaves per plant, and thorns among the vegetative traits (Table 3). Significant differences were also observed in the reproductive traits *viz.* inflorescences per branchlet, seeds per plant, seed size and mass, and reproductive index (Table 3). Although flowers per inflorescence were not significantly different between the two ranges, Indian population showed higher mean values than those in South Africa. Higher trait values of *Lantana* in India might be indicative of species' better performance and higher invasion potential.

Relation between vegetative and reproductive traits

A few vegetative and reproductive traits of *Lantana* were significantly correlated. Correlation

Table 3. Vegetative and reproductive traits of *Lantana* in India and South Africa. Values are mean±SE.

Traits	Mean values		$F_{1,8}$	*P*
	India	South Africa		
Vegetative traits				
Plant height (cm)	696±81.42	535±59.1	2.56	**0.015**
Density (individuals per 100 m^2)$	18.6±3.9	20.8±3.3	0.17	0.683
Basal circumference (cm)	85.4±12.8	64.6±7.9	1.90	0.205
Primary branches per plant	25.4±1.5	17.4±1.1	17.68	**0.003**
Primary branch length (cm)	247±33.3	200±29.8	1.10	0.324
Branchlets per plant	27.8±2.7	18.4±2.4	6.74	**0.032**
Leaves per plant	17156±115	5101.5±21	10.32	**0.018**
Thorns (per 10 cm)	34.2±2.9	24.4±2.8	6.04	**0.039**
Thorn size (mm)	2.74±0.1	2.38±0.2	2.81	0.132
Reproductive traits				
Inflorescences per branchlet	17.2±0.97	12.2±1.6	7.39	**0.026**
Flowers per inflorescence	14.2±2.2	11.8±2.5	0.51	0.493
Fruit size (mm)	4.38±0.3	4.98±0.4	1.68	0.231
Fruit mass (g)	1.5±0.1	1.62±0.2	0.31	0.593
Seeds per plant	10857±2862	5937±700	11.37	**0.017**
Seed size (mm)	2.82±0.1	2.32±0.1	10.50	**0.012**
Seeds mass (g)	0.352±0.01	0.27±0.01	10.95	**0.011**
Reproductive index (*Ri*)	16.36±2.0	11.22±1.0	5.27	**0.042**

Population characteristic$; Values in bold are significantly different from each other at P<0.05.

matrices between vegetative and reproductive traits of *Lantana* populations inhabiting India and South Africa are presented in Table 4 and 5 respectively. A significant relationship between plant height and thorn size was observed for Indian *Lantana* population (r^2 = 0.84, P<0.05) while not for the South African *Lantana* population (r^2 = 0.16, P>0.05). Seed size and mass showed a highly significant negative correlation with Ri for the Indian *Lantana* population (r^2 = 0.86, P = 0.05; r^2 = 0.88, P = 0.04, respectively), while a positive correlation was observed for the South African population (r^2 = 0.24, P = 0.69; r^2 = 0.02, P = 0.96 respectively) (Fig. 2a, b).

Performance of Lantana *in relation to climatic variables*

Mean annual temperature (t_{value} = 5.105, P = 0.001) was significantly different for sampling sites in India as compared to South Africa. However, no such differences were observed in mean values of altitude (t_{value} = 0.413, P = 0.70) and mean annual precipitation (t_{value} = 0.55, P = 0.60) for India and South Africa. NMS ordination of *Lantana* population traits in India (NMS axis 1 and 2 explained 75% and 65% variability) and South Africa (NMS axis 1 and 2 explained 72% and 58% variability) revealed that Indian *Lantana* traits were significantly correlated with mean annual temperature and precipitation (Table 6); similarly, NMS axis 2 showed significant but relatively weak correlation with the climatic variables (Table 6). A similar trend was observed for South African *Lantana* population with traits significantly correlated to mean annual temperature and precipitation. However, altitude did not show a significant correlation with the traits for both Indian and South African *Lantana* populations (Table 6). Superimposed NMS ordination of 16 traits of *Lantana* populations sampled from India and South Africa indicates that *Lantana* populations inhabiting the two ranges can be differentiated on the basis of eight traits, namely, three vegetative traits *viz.* plant height, primary branch length, thorn size, and five reproductive traits *viz.* seeds per plant, fruit size and mass, and, seed size and mass (Fig. 3).

Discussion

Wide distribution of highly invasive *Lantana*, its rapid spread over diverse biogeographic regions

Table 4. Correlation among the vegetative and reproductive traits of *Lantana* in India.

Traits	PH	D	PB	BC	PBL	B	T	TS	I	F	FS	FM	SS	SM	Ri
D	0.67	1													
PB	0.85	0.49	1												
BC	**0.88**	0.87	0.82	1											
PBL	**0.96**	0.65	0.78	**0.87**	1										
B	**0.95**	0.62	**0.91**	**0.91**	**0.96**	1									
T	**0.95**	0.67	**0.89**	**0.93**	**0.97**	**0.99**	1								
TS	**0.84**	0.73	0.74	**0.93**	**0.93**	**0.93**	**0.95**	1							
I	−0.25	−0.84	−0.24	−0.61	−0.19	−0.24	−0.29	−0.39	1						
F	0.05	−0.69	0.20	−0.30	0.05	0.10	0.03	−0.14	**0.88**	1					
FS	−0.10	−0.77	0.16	−0.38	−0.12	−0.02	−0.09	−0.26	0.82	**0.96**	1				
FM	0.09	−0.64	0.29	−0.25	0.04	0.13	0.06	−0.15	0.80	**0.98**	**0.97**	1			
SS	0.79	**0.90**	0.54	0.80	0.69	0.64	0.67	0.61	−0.65	−0.48	−0.60	−0.41	1		
SM	0.77	**0.97**	0.54	0.86	0.72	0.67	0.71	0.71	−0.73	−0.57	−0.68	−0.52	**0.97**	1	
Ri	−0.67	**−0.97**	-0.40	−0.80	−0.64	−0.57	−0.61	−0.66	0.77	0.68	0.79	0.64	**−0.95**	**−0.98**	1
S	0.01	−0.72	0.13	−0.35	0.02	0.05	−0.12	−0.18	**0.91**	**0.99**	**0.95**	**0.96**	−0.50	−0.60	0.70

PH, Plant height (cm); D, Density (individuals per 100 m); PB, Primary branches per plant; BC, Basal circumference (cm); PBL, Primary branch length (cm); B, Branchlets per plant; T, Thorns (per 10 cm); TS, Thorn size (mm); I, Inflorescences per branchlet; F, Flowers per inflorescence; FS, Fruit size (mm); FM, Fruit mass (g); SS, Seed size (mm); SM, Seed mass (g); Ri, Reproductive index; S, Seeds per plant (values in bold are significantly related at $P<0.05$).

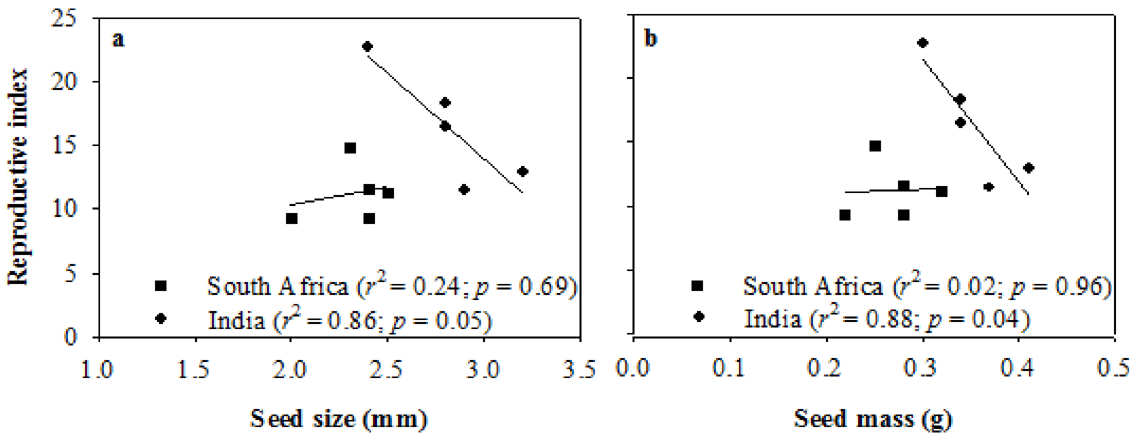

Fig. 2. Relationship between reproductive index (Ri) and, **a.** seed size (mm); **b.** seed mass (g) for *Lantana* populations in India and South Africa.

and high invasive success has been attributed to its wide ecological tolerance and adaptability to different environments (Broughton 2000; Day *et al.* 2003). In the present investigation, a comparative account of the performance of *Lantana* in two of its invaded ranges with differential residence timeframes reveals that *Lantana* populations in India are significantly more vigorous in terms of vegetative and reproductive traits than those in South Africa. Contrasting trait values of *Lantana* may be owed to significant differences in the species' residence timeframe in the two ranges. Residence time not only explains the range and frequency of current distribution but also invasion status of a species (Richardson & Pyšek 2006). Residence time represents a dimension of species' performance potential; the longer the species is present in a region, higher is the probability of its better performance (Richardson & Pyšek 2006). Studies suggest that invasive plants are known to co-adapt and undergo adaptive trait modulations to novel environmental conditions (Goyal *et al.* 2014; Maron *et al.* 2004; Prentis *et al.* 2008; Rogers & Siemann 2004). Higher adaptability of a species to climatic conditions in the novel range is related to the time since it first arrived *i.e.* residence time

Table 5. Correlation among the vegetative and reproductive traits of *Lantana* in South Africa.

Traits	PH	D	PB	BC	PBL	B	T	TS	I	F	FS	FM	SS	SM	Ri
D	−0.31	1													
PB	−0.64	−0.32	1												
BC	−0.50	0.41	0.51	1											
PBL	**0.98**	−0.19	−0.67	−0.36	1										
B	**0.88**	−0.02	**−0.91**	−0.62	**0.88**	1									
T	**0.99**	−0.36	−0.60	−0.55	**0.96**	0.86	1								
TS	0.16	−0.41	−0.17	−0.16	0.17	0.24	0.12	1							
I	0.59	0.12	−0.32	0.37	0.71	0.44	0.53	0.13	1						
F	0.46	−0.03	−0.11	0.47	0.58	0.26	0.39	0.31	**0.95**	1					
FS	−0.81	−0.22	0.84	0.18	**−0.89**	**−0.88**	−0.75	−0.19	−0.77	−0.60	1				
FM	−0.79	−0.00	0.75	0.18	−0.86	-0.84	−0.72	−0.49	−0.77	−0.69	**0.94**	1			
SS	0.18	−0.20	−0.28	−0.86	0.03	0.30	0.26	−0.27	−0.64	−0.78	0.12	0.24	1		
SM	0.48	−0.40	−0.39	**−0.96**	0.34	0.53	0.55	−0.09	−0.40	−0.53	−0.10	−0.03	**0.93**	1	
Ri	−0.06	0.21	0.35	**0.88**	0.07	−0.30	−0.10	−0.14	0.70	0.77	−0.13	−0.12	−0.87	−0.82	1
S	0.64	-0.08	−0.17	0.32	0.73	0.38	0.60	0.08	**0.96**	**0.94**	−0.66	−0.69	−0.57	−0.30	0.71

PH, Plant height (cm); D, Density (individuals per 100 m); PB, Primary branches per plant; BC, Basal circumference (cm); PBL, Primary branch length (cm); B, Branchlets per plant; T, Thorns (per 10 cm); TS, Thorn size (mm); I, Inflorescences per branchlet; F, Flowers per inflorescence; FS, Fruit size (mm); FM, Fruit mass (g); SS, Seed size (mm); SM, Seed mass (g); Ri, Reproductive index; S, Seeds per plant (values in bold are significantly related at $P<0.05$).

Table 6. Correlation of NMS axes with climatic variables for India and South Africa.

	Climatic variables	India	South Africa
NMS Axis 1	Altitude	0.11	0.38
	Mean annual temperature	−0.71**	0.79**
	Mean annual precipitation	0.86**	−0.77**
NMS Axis 2	Altitude	0.41	0.29
	Mean annual temperature	0.55*	−0.68*
	Mean annual precipitation	−0.63*	−0.56*

*$P<0.05$; **$P<0.01$.

(Foxcroft *et al.* 2011; Levin 1998). Species with longer residence timeframes have been suggested to be better adapted to existing climatic conditions in the invaded range (Dainese & Poldini 2012). *Lantana* has been present on the Indian sub-continent for ~54 years longer than in South Africa. Longer residence time in India potentially provided a greater opportunity for *Lantana* to undergo extensive hybridization events and/or adaptive trait modulations that might have facilitated better performance in conditions outside its tolerance range (see Mukherjee *et al.* 2011).

If climate of the novel habitat is matched closely to the region of origin, there is greater likelihood of establishment success (Coetzee *et al.* 2009). Putative parental species in genus *Lantana* are well-adapted to the tropical and subtropical climatic conditions in the native range *viz.* West Indies and South America. Rigorous selection and hybridization within the genus on introduction to Europe led to creation of innumerable cultivars for the horticultural industry (Howard 1969; Sanders 2006). These cultivars formed the source of introductions to climatically suitable ranges, India and South Africa in 19th century (Howard 1969; Morton 1994; Stirton 1977; Swarbrick 1985). Owing to climatic suitability, *Lantana* underwent rapid expansion in the two ranges. Marked differences in genetic stock introduced to India and South Africa might have also resulted in contrasting trait values of *Lantana* inhabiting the two ranges. Trait variability in the invaded ranges might be attributed to presence of different weedy and/or invasive genets of *Lantana* in India and South Africa (see Goyal & Sharma 2015). Mean annual temperature also differs significantly over the two ranges; possibly contributing to contrasting trait values. In spite of similar popu-

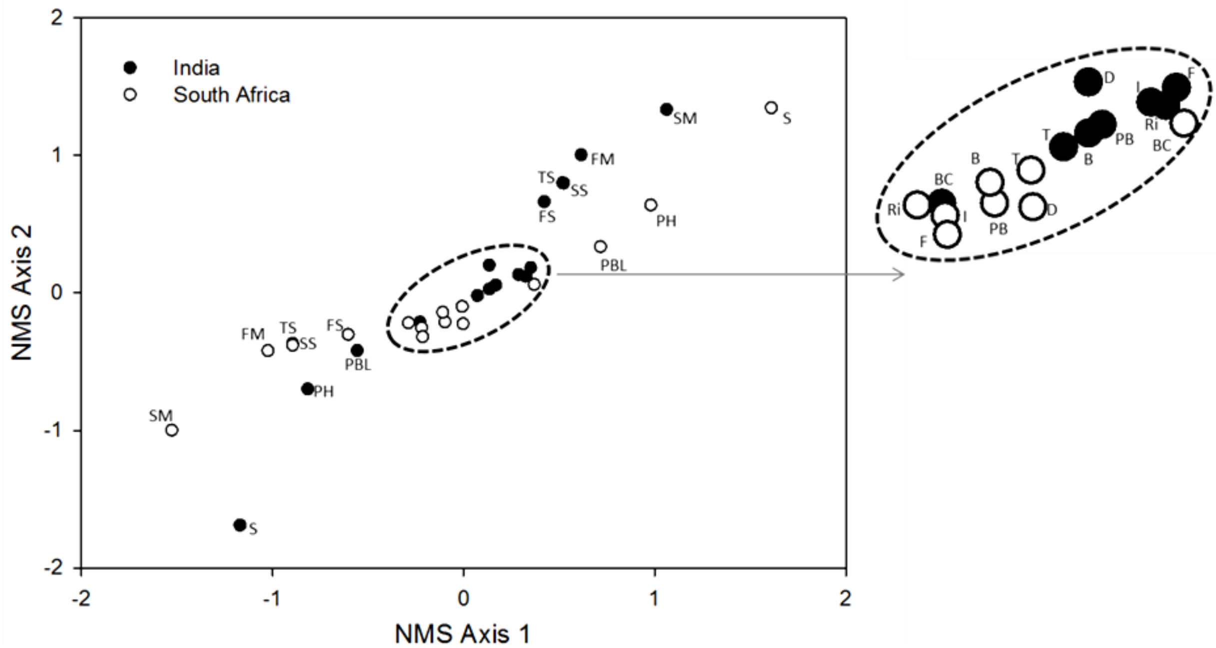

Fig. 3. NMS ordination of 16 vegetative and reproductive traits of *Lantana* populations in India and South Africa. *Lantana* populations inhabiting India and South Africa can be differentiated on the basis of 8 traits lying outside the central inset (central part of the figure is enlarged). PH, Plant height (cm); D, Density (individuals per 100 m^2); PB, Primary branches per plant; BC, Basal circumference (cm); PBL, Primary branch length (cm); B, Branchlets per plant; T, Thorns (per 10 cm); TS, Thorn size (mm); I, Inflorescences per branchlet; F, Flowers per inflorescence; FS, Fruit size (mm); FM, Fruit mass (g); SS, Seed size (mm); SM, Seed mass (g); Ri, Reproductive index; S, Seeds per plant.

lation densities in two invaded regions, higher mean annual temperature in India, thus better climate suitability might well explain the better performance of *Lantana* as revealed by vigorous vegetative and reproductive traits. This is corroborated by Zhang *et al.* (2014) that suggested that elevated temperature facilitates the invasiveness of *Lantana*. Differences between *Lantana* populations in the two invaded ranges might have also stemmed from intrinsic adaptive ability of *Lantana* to perform in heterogeneous environments.

Higher trait values leading to enhanced performance in India might explain rapid range expansion and greater impact of *Lantana* in the Indian sub-continent. *Lantana* extends over 13 million ha in India whereas in South Africa, it occupies less than 5 million ha (Bhagwat *et al.* 2012). Goncalves *et al.* (2014) highlighted that initial introductions into India occurred in highly climatically suitable habitats, while in Africa the species was introduced to less suitable habitats. Hence, late introduction of *Lantana* to less climatically suitable habitats may explain slower establishment and lower invasive success of *Lantana* in South Africa than in India. An additional consideration is that only three bio-control agents have been released for *Lantana* in India as compared to 20 in South Africa (Day *et al.* 2003; Julien & Griffith 1998). Greater number of bio-control agents may have reduced fitness and competitiveness of *Lantana* populations inhabiting South Africa. A further consideration is that three introduction events into South Africa have been reported while *Lantana* was introduced multiple times in India, suggesting potentially higher genetic diversity in India (Ray & Quader 2014; Vardien *et al.* 2012). Such accounts likely provided greater opportunity for hybridization and polyploidization events in India (Goyal & Sharma 2015; Kannan *et al.* 2013; Ray & Ray 2014). Importantly, Goncalves *et al.* (2014) demonstrated that while *Lantana* occupies subsets of its original native niche in Africa, its niche has shifted significantly in India towards warmer climates. In light of the above, we surmise that a range of traits possessed by *Lantana* complex may equip it to adapt to selective pressures and invade heterogeneous environments with variable vigor. Greater vigor of *Lantana* in India might be owed to its trait responses to higher temperature, facilitating species' niche shift over a longer residence time.

Implications of contrasting trait values for Lantana *invasiveness in India and South Africa*

Higher vegetative and reproductive trait values of *Lantana* in India than South Africa, in spite of similar population densities in the two ranges indicate its higher performance ability in India. Key vegetative and reproductive traits of *Lantana*, considered in the study emerged as prominent traits that potentially benefit species' range expansion. Ebeling *et al.* (2008) suggested that larger plant size and higher fecundity confer rapid adaptation to the species in the introduced range. Larger plant size of *Lantana* in India might be advantageous in highly competitive communities. *Lantana* individuals in India displayed more aggressive traits; they are prolific seeders with straggly, thorny stems suggesting that they are well-defended against herbivory. In addition, significantly positive relationship among the plant height, number of thorns, and thorn size potentially implies that thorns play a role in the "smothering effect" of *Lantana* that in turn facilitates the individual to increase in expanse.

Interestingly, variability in seed size, seed mass, and Ri of *Lantana* was significantly higher in India than South Africa. A much wider range of variability in reproductive traits is suggestive of broader plasticity potential of *Lantana* inhabiting India. Higher trait modulation potential for vegetative as well as reproductive traits indicates differential colonization response and immense flexibility of the species to perform in heterogeneous environments. The disparity within seed size and seed mass, significantly related to Ri demonstrates plastic behavior of *Lantana* populations in India. This suggests rapid increase in fitness is the adaptive strategy of the species (see van Kleunen & Fischer 2007). Higher Ri further enhances competitive ability through higher reproductive output and this may potentially add to the ability of *Lantana* to invade new habitats (Serrano *et al.* 2005). Higher adaptive trait modulation potential of *Lantana* might well be the reason behind invasion of large tracts of land in India (Sahu & Singh 2008). However, to test such assumptions, more information on hard traits (e.g. specific leaf area, relative growth rate, etc.) is needed at the individual level (Beckmann *et al.* 2009).

Avenues for future research

Inability to precisely identify the underlying factor(s) and mechanism(s) facilitating vigorous performance of *Lantana* in India undoubtedly prompts research attention. However, results of the study have highlighted that analysing invaders' performance in different invaded ranges with differential residence timeframes beholds significance to better understand and predict species' invasiveness in the invaded range. Significant variation existing in trait values of *Lantana* in the two studied ranges might be a result of differential climatic suitability owed to species' pre-adaptation, environmentally-driven adaptive trait modulations, and adaptive potential due to enormous genetic diversity and/or residence time. A gamut of traits possessed by constituents in the *Lantana* species complex might provide wider niche breadth and ever-increasing adaptive potential to *Lantana*, thus enabling invasion of heterogeneous habitats in the invaded range (the present study has considered two invaded ranges viz. India and South Africa). Distinguishing traits revealed by NMS ordination in the present investigation may be applied to differentiate *Lantana* populations in India and South Africa; however, differentiation will be more reliable by complementing vegetative and reproductive trait attributes with the species' genetic and genomic attributes. Nonetheless, details of cultivars introduced intentionally and/or unintentionally to India and South Africa are unknown, and this makes it difficult to dissect the precise intrinsic, extrinsic, and/or biogeographic factor(s) contributing significantly to species' invasiveness. Unresolved genetic composition of genus *Lantana* further adds to the problem (Goyal & Sharma 2015). Therefore, it is extremely important to disentangle *Lantana* species complex in order to holistically understand the determinants of variation in invader's performance across the invaded range.

Interestingly, a search with key words "*Lantana camara* and *India*" and "*Lantana camara* and *South Africa*" in Scopus resulted in 196 and 75 hits respectively (http:// http://www.scopus.com; date of search 14 December 2017). Higher hits for India potentially indicate that intensity of *Lantana* invasion and associated impacts are more pronounced in India than in South Africa. Further, it is indicative of a more challenging management scenario in India than South Africa. Studies highlight a dearth of plant invasion research which focused on control and management aspects in

India (Goyal 2015; Pandey & Sharma 2013). Although the authors addressed a call for control and management efforts in India, no considerable progress has been made. However, a dedicated centre, Centre of Excellence for Invasion Biology, established in 2004 exists in South Africa that aims to reduce the rates and impacts of biological invasions by promoting scientific understanding, predictive capability, and development of research capacity. The wider extent of plant invaders including *Lantana* in India warrants increased scientific effort and funding towards research to address the challenges related to control, management and mitigation of the impacts posed by plant invasions.

Conclusion

Invasive plant species may experience disproportionate success in invaded ranges owing to distinction in time elapsed since initial introduction. Higher vigor of *Lantana* might be owed primarily to higher mean annual temperature and longer residence time of the invader in India. Recognizing remarkable spread and better performance of *Lantana* in warmer areas in India, the invader may increase its expanse noticeably in future climate change scenarios. However, we cannot dissect the exact determinant(s) facilitating higher invasiveness with the current understanding of different facets of *Lantana* invasion. We reiterate that our understanding on different aspects of *Lantana* invasion is constrained by the limited understanding of *Lantana* species complex. Genomic attributes complemented with key species-level traits can be well-utilized for the resolution of *Lantana* species complex. Examining the variability in species' performance potential within and between different invaded ranges will facilitate our understanding on its adaptive potential to heterogeneous environments in view of ecological and evolutionary drivers of plant invasions.

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