

# Naturalized alien flora of the Indian states: biogeographic patterns, taxonomic structure and drivers of species richness

Inderjit  · Jan Pergl · Mark van Kleunen  · Martin Hejda · Cherukuri Raghavendra Babu · Sudipto Majumdar · Paramjit Singh · Surendra Pratap Singh · Sugali Salamma · Boyina Ravi Prasad Rao · Petr Pyšek 

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**Abstract** Despite an existing India-wide inventory of alien plant species, an inventory documenting the occurrence of naturalized alien plant species in each of the Indian states (including union territories) was not available yet. We compiled from the literature a list of naturalized alien vascular plant species with data on their occurrence in 33 Indian states, and related the richness of naturalized species per state to climate, socioeconomic parameters and human influence. In total, we report 471 naturalized species in India, which

represents 2.6% of the total flora of this country, and for 449 of them we provide the distribution in the states. The highest and lowest numbers of naturalized species are reported from Tamil Nadu (332) and the island Lakshadweep (17), respectively. The families richest in naturalized species are Compositae (75), Leguminosae (60) and Poaceae (36). The highest numbers of naturalized aliens occurs in states located at lower latitudes in the tropics, and in more northerly located states that even in the dry period still have relatively high amounts of precipitation. Naturalized species richness of a state is furthermore positively related to socioeconomic factors represented by the percentage of the population living in urban areas, and

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Inderjit (✉) · S. Majumdar  
Department of Environmental Studies, Centre for  
Environmental Management of Degraded Ecosystems  
(CEMDE), University of Delhi, Delhi, India  
e-mail: [inderjitdu@gmail.com](mailto:inderjitdu@gmail.com)

J. Pergl · M. Hejda · P. Pyšek  
Department of Invasion Ecology, Institute of Botany, The  
Czech Academy of Sciences, 252 43 Průhonice, Czech  
Republic

M. van Kleunen  
Department of Biology, University of Konstanz,  
Universitätsstrasse 10, 78457 Constance, Germany

M. van Kleunen  
Zhejiang Provincial Key Laboratory of Plant Evolutionary  
Ecology and Conservation, Taizhou University,  
Taizhou 318000, China

C. R. Babu  
Centre for Environmental Management of Degraded  
Ecosystems (CEMDE), University of Delhi, Delhi, India

P. Singh  
Botanical Survey of India, CGO Complex, Salt Lake City,  
Kolkata 700 064, India

S. P. Singh  
Central Himalaya Environment Association (CHEA), 06  
Waldorf Compound, Nainital, Uttarakhand 263001, India

S. Salamma · B. R. P. Rao  
Department of Botany, Sri Krishnadevaraya University,  
Anantapuramu 515003, India

P. Pyšek  
Department of Ecology, Faculty of Science, Charles  
University, Viničná 7, 128 44 Prague, Czech Republic

human population density. The state-wise inventory of naturalized alien species improves our knowledge on threats associated with plant invasions in India, and can be used to provide arguments for promoting programs on conservation of native biodiversity in the country as well as in particular states.

**Keywords** Exotic plants · Plant invasion · Naturalization · India · Species richness · Climate · Socioeconomic factors

## Introduction

Invasion by alien plants (i.e. plant species introduced by humans to regions outside their native distribution; Richardson et al. 2000; Pyšek et al. 2004; Blackburn et al. 2011) is an important aspect of the Anthropocene (van Kleunen et al. 2015; Dawson et al. 2017; Pyšek et al. 2017). The situation is alarming because already more than 13,000 plant species (4% of the extant global vascular flora) have become naturalized somewhere on the globe as a result of human activity (van Kleunen et al. 2015; Pyšek et al. 2017), and many of them represent a threat to biodiversity (Hulme 2009; Hulme et al. 2009; McGeoch et al. 2010; Early et al. 2016). Alien plants have invaded virtually all parts of the world but the numbers vary a lot among regions all around the globe (van Kleunen et al. 2015; Dawson et al. 2017; Pyšek et al. 2017). The greatest numbers of naturalized plant species are recorded for North America (~ 6000), and Europe (~ 4000), whereas the lowest numbers (after Antarctica; ~ 160) are recorded for temperate Asia (~ 2200) and tropical Asia (~ 2000 species) (van Kleunen et al. 2015). In Asia, however, there are many emerging economies where the numbers of alien naturalized species are predicted to increase considerably in the future (Seebens et al. 2015). Therefore, more detailed alien species inventories of these regions are needed.

Due to the widely documented impacts of invasive alien species on native biodiversity, ecosystem functioning and economy, as well as human health (Vilà et al. 2010, 2015; Pyšek et al. 2012b; Kumschick et al. 2015; Rumlerová et al. 2016), invasive alien species have long been recognized as a key component of global environmental change (Millennium Ecosystem Assessment 2005; Kettunen et al. 2009). However,

only a small proportion of species introduced by humans establish and maintain populations without direct human aid (naturalized species *sensu* Richardson et al. 2000; Blackburn et al. 2011). Although only a subset naturalized species spread rapidly (i.e. become invasive), and even fewer have strong negative ecological and economic impacts (Blackburn et al. 2014), documenting which alien species have become naturalized is a prerequisite for better understanding the causes of plant invasions. Detailed lists of naturalized alien plants using a standardized classification started to appear in the 2000s and over the last decade became available for many countries, with most research concentrated in Europe (e.g. Essl and Rabitsch 2002; Pyšek et al. 2002, 2012a; Medvecká et al. 2012; see Lambdon et al. 2008 for overview of national checklists). A major improvement in this field occurred recently, with the compilation of such lists in the Global Naturalized Alien Flora (GloNAF) database (van Kleunen et al. 2015; Pyšek et al. 2017). While lists of naturalized species are available for some Asian countries such as China (Liu et al. 2006; Wu et al. 2010; Jiang et al. 2011), Singapore (Corlett 1992), Hong Kong (Corlett 1992), Sri Lanka (Iqbal et al. 2014), Nepal (Shrestha 2016) and Taiwan (Wu et al. 2003, 2004a, b; Wu and Wang 2005), large parts of Asia are still data-deficient (van Kleunen et al. 2015; Pyšek et al. 2017).

Prior to the compilation of the GloNAF database, one of the large Asian countries without a state-wise inventory of naturalized alien plants was India. There is, however, information available on the invasive alien species of India (Reddy et al. 2008; Bhatt et al. 2012), and Khuroo et al. (2012) published an account of 1599 alien plant species of India with data on their invasion status, native ranges, and families to which alien species belong. This India-wide inventory categorized the alien species according to whether they were cultivated, casual, naturalized or invasive, with separate categories ‘casual or naturalized’ and ‘naturalized or invasive’, where the status could not be assigned with certainty. Furthermore, although recently Adhikari et al. (2015) used ecological niche modelling to identify hotspots of invasive alien species, an empirical overview of where in India the alien species actually occur is lacking. There are, however, numerous reports on the presence of alien plant species in different states of India (see Electronic Supplementary Material 1) that could be used to make

an inventory of naturalized species for each state and union territory.

The Republic of India has an area of 3.288 million km<sup>2</sup> in an environmentally heterogeneous part of tropical Asia, and has 1.33 billion inhabitants (382 inhabitants per km<sup>2</sup>). India is likely to be prone to plant invasions due to several historical and geographical factors (IndianStat 2017). Many natural and human-created migration routes opened possibilities for invasion by alien species, and long-lasting human influence, which diversified the already naturally heterogeneous landscape mosaic, created suitable habitats for alien species (Bogaert et al. 2014; Paschou et al. 2014). In India, there are 29 states and seven union territories, which vary widely in climate, size, human population density and socioeconomic aspects. These features, together with a high biodiversity and in-depth knowledge of plant communities make the country suitable for studying regional patterns of plant invasions.

Here, we provide, the first inventories of naturalized plant species of the Republic of India for each of its states. We explore the basic taxonomic composition and ecological characteristics of the naturalized alien flora, and analyze the main climatic, geographic and socioeconomic drivers of the regional richness of naturalized species.

## Methods

### State-wise inventory of naturalized species

To prepare an inventory of naturalized alien vascular plant species (following the definition of Richardson et al. 2000; Blackburn et al. 2011) for each of India's states and union territories (hereafter collectively referred to as states) with information about the origin, distribution and life form of the species, we consulted national and regional floras, e-floras, and research articles published in scientific journals (Electronic Supplementary Material 1). We chose different states and union territories of India (administrative units) rather than biogeographic units because most of the original data sources on naturalized species use administrative units. In addition, data on some of the potential drivers, such as gross domestic product (GDP) and human population density, are only available for administrative units. Alien species that

are only cultivated and not naturalized in the wild were not included in the inventories.

We considered the current states of Andhra Pradesh and Telangana jointly as one region termed “Andhra Pradesh”, because the two states separated only in 2014, and as a consequence most floristic and socioeconomic data do not distinguish between them. Furthermore, naturalized species of the union territories Dadra Nagar and Haveli, and Daman and Diu were combined with the state of Goa (Rao 1985). Therefore, our inventory has 33 instead of 36 states (i.e. 29 true states and 7 union territories), but covers the entire Republic of India.

As the different sources often use different names for one and the same species, we provide in this paper also a standardized taxonomy of the naturalized Indian flora according to “The Plant List” (<http://www.theplantlist.org>). Taxonomic standardization was done with the help of the Taxonstand package (Cayuela et al. 2017) in R (R Core Team 2016). Taxonomic standardization also facilitated finding data on native ranges and life forms. In the Electronic Supplementary Material 2, we also provide the original names used in particular data sources.

### Data on life-form and origin of species

Plant species identified as naturalized were assigned to the following life-form categories: annual/biennial herb, perennial herb, shrub, tree, aquatic plant, climber. Species were further classified according to their region of origin (native range); each was assigned to one or more of the major biogeographically defined areas (continents) of the Taxonomic Databases Working Group (TDWG; currently named Biodiversity Information Standards; Brummitt 2001). Species whose native range is unknown, as they are only known from cultivation, and species that originated through recent hybridization are listed as a separate category. Origin data were taken from the working database GloNAF (van Kleunen et al. 2015), and then validated by using local floras and online sources.

### Environmental and socioeconomic data on Indian states

Data on climate (climate scores defined by Dupin et al. 2011), rural versus urban population size (IndianStat

2017), total area (km<sup>2</sup>), population density of Indian states (inhabitants/km<sup>2</sup>), and GDP per capita (US\$; NITI Aayog 2015) was collected from various sources (Electronic Supplementary Material 1). The urban and rural population sizes were calculated from the percentages of the population living in cities (urban) and villages (rural). States were assigned to zono-biomes (see Pyšek et al. 2017 for details), and geographical coordinates (latitude and longitude) taken as those of the centroid of the state.

To describe and quantify the climate of the individual states, we used the 19 bioclimatic variables available through the WorldClim database (see <http://www.worldclim.org>; Hijmans et al. 2005) to create three principal component axes (PCAs) that together explain nearly 85% of the variation present in the original 19 variables (following Dupin et al. 2011). The resulting PCAs represent three uncorrelated linear combinations of the original climate data, with the first one (PCA1) mainly representing mean annual temperature, the second one (PCA2) mainly representing precipitation during wet or warm periods, and the third one (PCA3) mainly representing precipitation during the driest period (Dupin et al. 2011).

### Statistical analysis

To test whether there are differences in the numbers of naturalized species among the Indian states in terms of representation of species with different life histories and of different origins, their counts were analysed by row  $\times$  column contingency tables, using generalized linear models with the log-link function and a Poisson error distribution (e.g. Crawley 1993). The adjusted standardized residuals of G-tests were compared with critical values of the normal distribution to assess which life-history category or region of origin is represented more or less than would be expected by chance (Řehák and Řeháková 1986). As preliminary inspection of the data revealed that there is a large group of very widespread species (occurring in more than 31 of the 33 states) and another group of species that are less widespread, we tested whether these two groups differ with regard to the predominant continent of origin and life forms.

To test the effects of geographic and socioeconomic variables (zonobiome, climate scores, population density, percentage of population living in urban areas, longitude, latitude, GDP per capita) on the

naturalized species richness of individual states, regression trees were applied (Breiman et al. 1984; De'ath and Fabricius 2000). To account for differences in size of the state, area was used as a weighting factor. Regression trees were constructed using binary recursive partitioning, with the default Gini-index impurity measure used as the splitting index, in CART v. 7.0 (Breiman et al. 1984; Steinberg and Colla 1995). To find an optimal tree, a sequence of nested trees of decreasing size, each being the best of all trees of its size, was produced, and their re-substitution relative errors, corresponding to residual sums of squares, were estimated. Ten-fold cross-validation was used to obtain estimates of relative errors for these trees. Following De'ath and Fabricius (2000), the most likely (modal) single minimum cost tree was chosen for description from a series of 50 cross-validation runs.

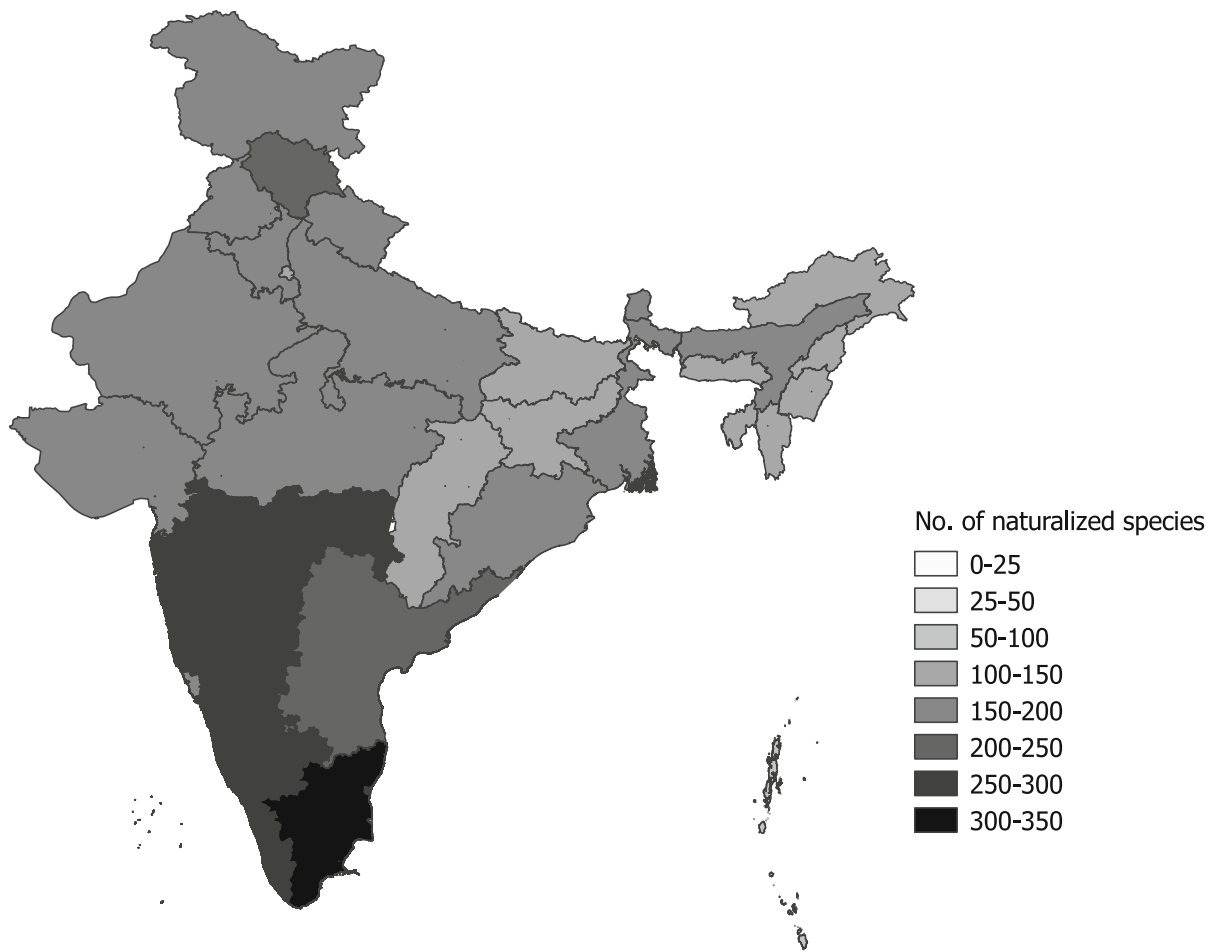
## Results

### Patterns of naturalized species richness across states and underlying factors

The naturalized alien vascular flora of India consists of 471 species; for 22 of them, the distribution in Indian states is unknown (Electronic Supplementary Material 3). In addition, there are 12 cryptogenic species with uncertain alien/native status in India (Electronic Supplementary Material 4). The analyses below are based on the 449 naturalized alien species with known distributions across the 33 states (given in Electronic Supplementary Material 2).

The number of naturalized alien species was highest in Tamil Nadu (332) and lowest in Lakshadweep (17) (Fig. 1; Table 1). The average number of naturalized species in a state is  $168.8 \pm 61.4$  (mean  $\pm$  SD). The average number of states per species was 12.4, and there are 110 species that occur in 31 or more of the states.

The regression tree with the socioeconomic (human population density, population size, percentage of population living in urban areas, per capita GDP), geographic (latitude, longitude) and climate (climatic PCA axes) explanatory variables shows that the highest numbers of naturalized alien species, after accounting for differences in area, are in tropical states located below 20° latitude. These tropical



**Fig. 1** Choropleth map of naturalized plant species richness in the Indian states

states harbour on average 270 naturalized alien species. In states located further to the north, those that during the driest season still have relatively high amounts of precipitation harbour more naturalized species than states with less precipitation (Fig. 2). In states with a seasonally dry climate, the number of naturalized species is fine-tuned by human population density, with a general trend towards increased naturalized species richness with increasing population density. The percentage of the population that live in urban areas and mean annual temperature (i.e. PCA axis 1) appear to be the most important surrogates at the first split, which is correlated with latitude (Fig. 2).

#### Composition of the naturalized flora of India: taxonomic composition, origins and life forms

The 449 species that compose the naturalized flora of Indian regions with known distribution belong to 271 genera, of which 80 genera have their representatives among the subset of 110 widespread species (i.e. the ones occurring in 31 or more states). The corresponding figures for families are 77 and 34, respectively. The number of naturalized species was highest in Compositae (75), followed by Leguminosae (60) and Poaceae (36) (Table 2). If the number of presences in states summed up over all naturalized species in a family is taken as a measure of naturalization success, the Compositae (880) and Leguminosae (727) are also the most widespread families. Some families rank higher based on the summed number of presences than

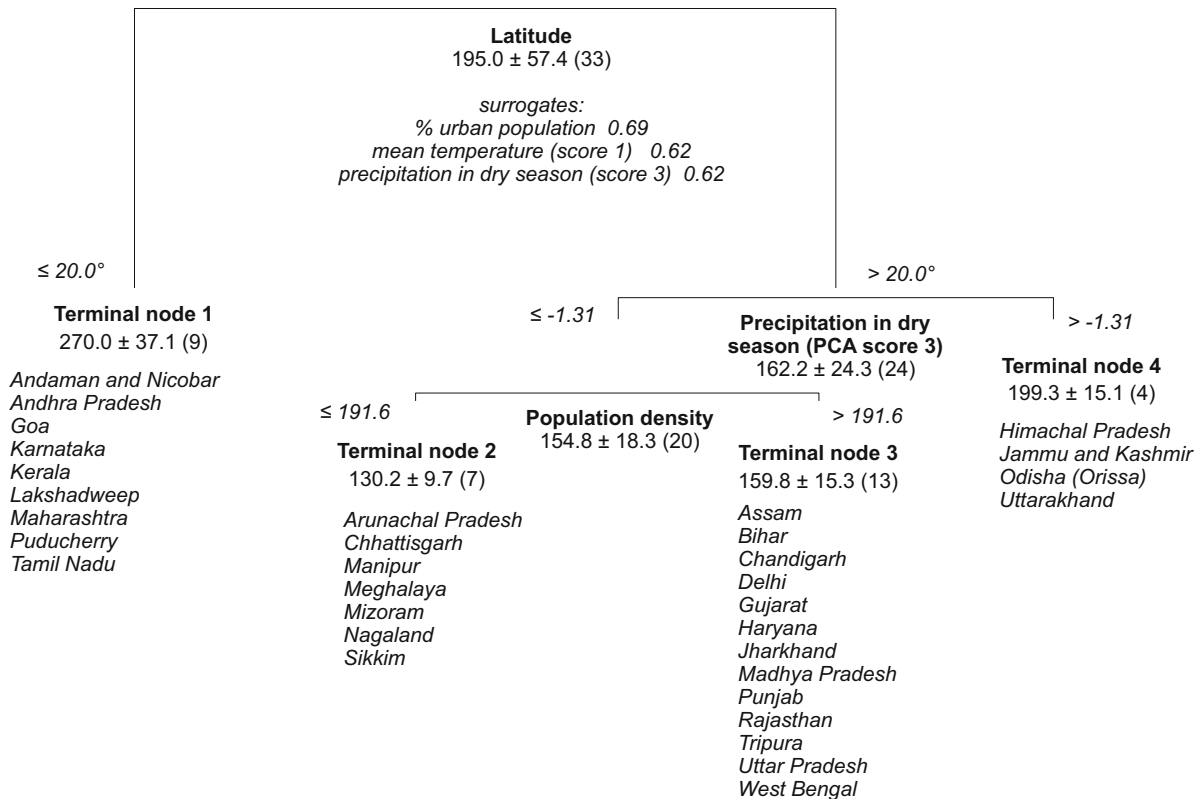
**Table 1** The numbers of naturalized species and geographic and socioeconomic characteristics of the 33 Indian states (mainly corresponding to true states and union territories (UT); see “Methods” section) used in this study\*

States/UT	Area (km <sup>2</sup> )	Population#	Population density# (per sq km)	Urban population (%)#	GDP (per capita, USD) (2013-14)	No. of species
Andaman & Nicobar <sup>1</sup>	7219	379,944	46	32.6	2395	96
Andhra Pradesh <sup>2</sup>	275,156	49,506,799	308	29.6	1555	228
Arunachal Pradesh	81,998	1,382,611	17	20.8	1519	137
Assam	79,091	31,169,272	397	12.9	738	152
Bihar	97,526	103,804,637	1102	10.5	482	144
Chandigarh	135	1,05,686	9252	89.8	40,687	127
Chhattisgarh	139,989	25,540,196	189	20.1	1057	121
Delhi	1274	11,007,835	11,297	93.2	5996	142
Goa <sup>3</sup>	4187	1,457,723	394	62.2	4939	181
Gujarat	185,028	60,383,628	308	37.4	1822	161
Haryana	44,083	25,353,081	573	28.9	2248	152
Himachal Pradesh	55,173	6,856,509	123	9.8	1750	232
Jammu & Kashmir	106,214	12,548,926	124	24.8	1036	192
Jharkhand	75,640	32,966,238	414	22.2	758	117
Karnataka	189,305	61,130,704	319	34	1636	272
Kerala	38,569	33,387,677	859	26	1737	290
Lakshadweep <sup>1</sup>	38	64,429	2013	44.5	931	17
Maharashtra	31,3051	112,372,972	365	42.4	2225	283
Manipur	21,738	2,721,756	122	25.1	772	134
Madhya Pradesh	305,278	72,597,565	236	26.5	1033	151
Meghalaya	22,509	2,964,007	132	19.6	1080	149
Mizoram	20,869	1,091,014	52	49.6	1375	129
Nagaland	16,649	1,980,602	119	17.2	1313	134
Odisha	148,981	41,947,358	269	15	954	199
Puducherry	558	1,244,464	2598	66.6	2491	134
Punjab	50,989	27,704,236	550	33.9	1696	160
Rajasthan	341,999	68,621,012	201	23.4	1224	169
Sikkim	7260	607,688	86	11.1	2962	157
Tamil Nadu	130,124	72,138,958	480	44	1941	332
Tripura	10,446	3,671,032	350	17.1	1090	127
Uttarakhand	53,243	10,116,752	189	25.7	1779	181
Uttar Pradesh	241,863	199,581,477	828	20.8	701	171
West Bengal	85,284	91,347,736	1029	28	1314	192

\*Data taken from various sources (see Supplementary material 1); #Data year 2011

<sup>1</sup>Island states<sup>2</sup>The state of Andhra Pradesh was recently divided into Andhra Pradesh and Telangana in 2014. Both new states are considered under Andhra Pradesh<sup>3</sup>Species from the State of Goa and Union territories (i) Daman and Diu and (ii) Dadra Nagar and Haveli were considered under Goa (see Rao 1985)





**Fig. 2** Regression tree showing factors that drive the number of naturalized species in a state, weighed by its area (see Jarošík 2011). Length of the nodes represents the improvement value. The explanatory variables included are population size, human population density, percentage of urban population, latitude, longitude, per capita GDP and climatic scores derived as linear

combinations of bioclimatic variables that explain 83.5% of the variance of the bioclimatic data (see Dupin et al. 2011): temperature (PCA score1), precipitation in the wet and warm season (PCA score 2), and precipitation in the driest season (PCA score 3). The surrogates for the splits are shown in italics with their association values

by the species number alone: Malvaceae, Verbenaceae, Passifloraceae and Cactaceae (Table 2). On the other hand, some families that are amongst the richest in naturalized species are not represented among the widespread species (e.g. Acanthaceae, Alismataceae, Casuarinaceae, Nyctaginaceae).

Three genera are represented by 10 or more naturalized species (*Solanum*, *Ipomoea* and *Euphorbia*) (Table 2). The genus with the highest number of naturalized species (15) is *Solanum*, but the genus with the highest number in terms of the sum of presences across states is *Euphorbia* (235). Other genera that despite of being represented by fewer species rank quite high by the sum of presences in states are *Opuntia* and *Alternanthera* (Table 2).

To find out whether there is any pattern with regard to the continents of origin of the naturalized species and their occurrence in the Indian states, we produced

choropleth maps for the numbers of alien species per state for each of the continents of origin (Fig. 3). Overall, the patterns are similar for most continents of origin, and show an under-representation of species of European origin (Fig. 3).

As there is a large group of species ( $n = 110$ ) that are recorded in 31 or more states (out of 33 states) and thus are widespread across the entire territory of India (Fig. 4, Table 2), we compared this group with species occurring in fewer states ( $n = 339$  species, on average in 6.2 states) to see if the two groups differ in terms of their origin and life history.

The widespread and less widespread species did not differ in terms of their life-form composition ( $\chi^2 = 1.38$ ,  $df = 5$ ,  $p = 0.927$ ). The naturalized flora of India consists of 47.0% perennial herbs (211 taxa), 45.7% annual and biennial herbs (205), 29.2% shrubs (131), 13.4% trees (60), 11.4% climbers (51) and 2.4%

**Table 2** The most represented families and genera in the naturalized flora of India, with at least three species

Families	Number of species	Number of state presences	Genera	Number of species	Number of state presences
Compositae	75	880	<i>Solanum</i>	15	207
Leguminosae	60	727	<i>Ipomoea</i>	13	171
Poaceae	36	324	<i>Euphorbia</i>	12	235
Solanaceae	28	405	<i>Senna</i>	9	176
Euphorbiaceae	21	380	<i>Trifolium</i>	7	35
Amaranthaceae	19	247	<i>Acacia</i>	6	60
Convolvulaceae	19	237	<i>Alternanthera</i>	6	127
Brassicaceae	11	110	<i>Opuntia</i>	6	135
Lamiaceae	11	122	<i>Oxalis</i>	6	35
Malvaceae	10	161	<i>Erigeron</i>	5	40
Verbenaceae	9	124	<i>Gnaphalium</i>	5	70
Caryophyllaceae	8	78	<i>Oenothera</i>	5	38
Onagraceae	8	85	<i>Passiflora</i>	5	75
Apocynaceae	7	112	<i>Physalis</i>	5	74
Passifloraceae	7	138	<i>Amaranthus</i>	4	39
Rubiaceae	7	43	<i>Datura</i>	4	76
Cactaceae	6	135	<i>Lepidium</i>	4	30
Oxalidaceae	6	35	<i>Merremia</i>	4	23
Papaveraceae	6	84	<i>Stachytarpheta</i>	4	72
Polygonaceae	6	50	<i>Acmella</i>	3	45
Asparagaceae	4	55	<i>Agave</i>	3	47
Boraginaceae	4	89	<i>Ageratina</i>	3	16
Alismataceae	3	10	<i>Argemone</i>	3	64
Cleomaceae	3	66	<i>Bidens</i>	3	28
Iridaceae	3	18	<i>Brachiaria</i>	3	10
Myrtaceae	3	24	<i>Cleome</i>	3	66
Plantaginaceae	3	65	<i>Cytisus</i>	3	12
Rhamnaceae	3	23	<i>Dysphania</i>	3	14
Salviniaceae	3	39	<i>Heliotropium</i>	3	80

An additional measure used is the sum of recorded presences of the family or genus across all its representatives

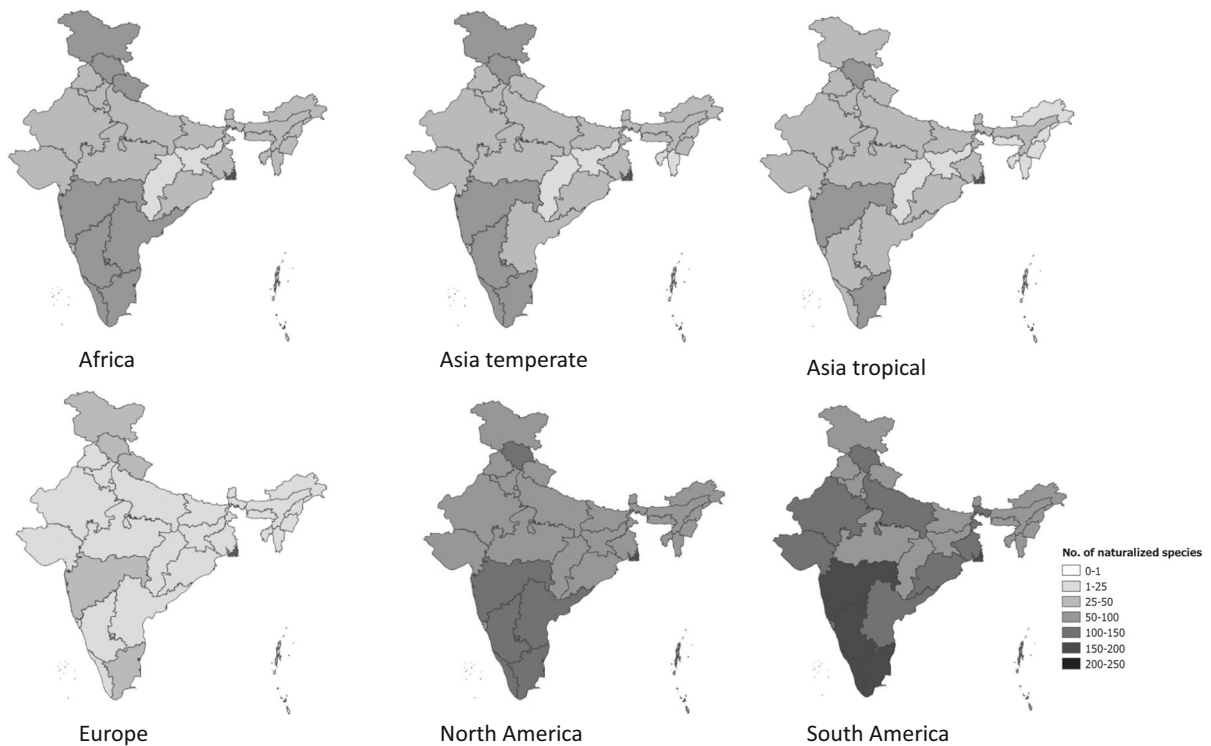
aquatic species (11). Note that the sum of the species numbers exceeds 100%, because some species belong to multiple life-form categories.

The widespread and less widespread species differed in the predominant TDWG continents of origin ( $F$  test = 8.54,  $df = 7$ ,  $p < 0.001$ ). The widespread ones were represented more than expected by chance if they come from South America (69.1%) or North America (52.7%), and less than expected if they come from temperate Asia, tropical Asia or Europe. The less widespread species were under-represented if they come from South America, and over-represented if they come from Europe (Fig. 5).

## Discussion

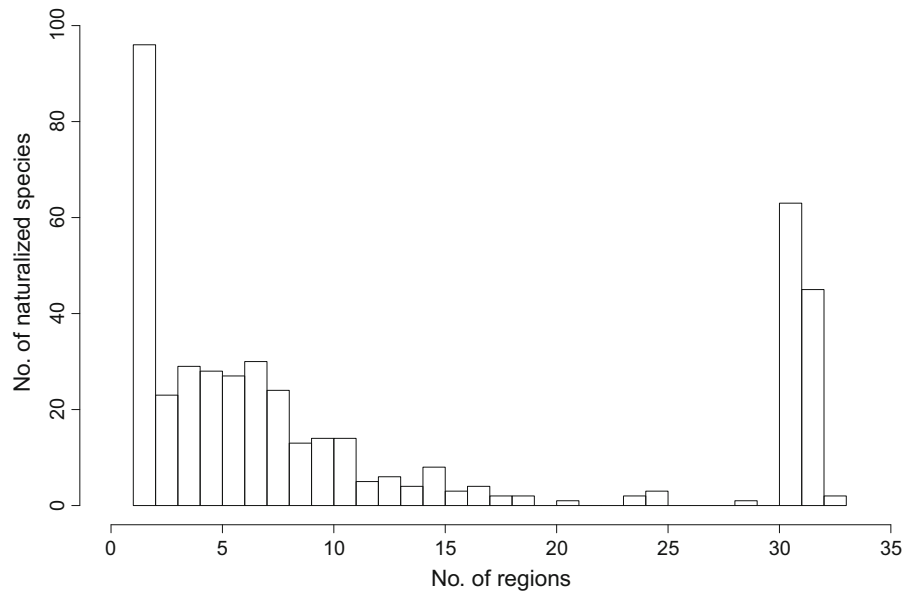
The naturalized alien vascular flora of India consists of 471 species, which represent 2.6% of the total plant richness of this country (18,259 species). For 22 naturalized species, there was no data on their distribution within India, and therefore the dataset analysed quantitatively in this paper was restricted to the 449 remaining species. Unlike previous studies on plant invasions in India, we present an inventory from each of 33 states (including true states and union territories), and focus on alien species that have become naturalized.





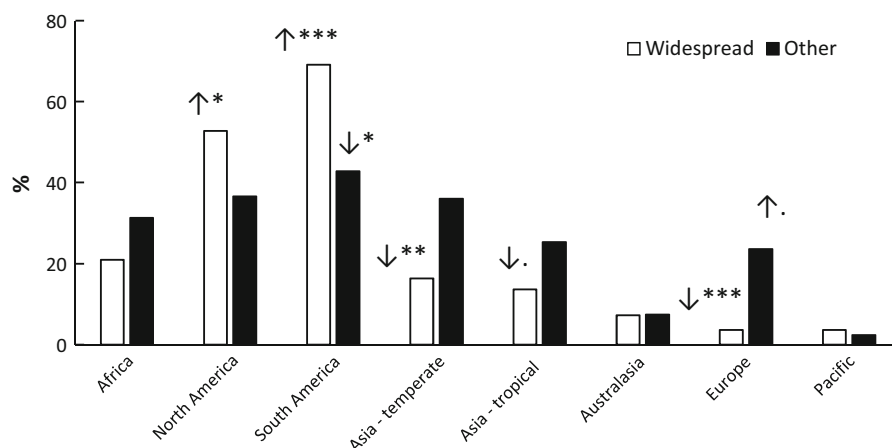
**Fig. 3** Choropleth maps showing the richness of naturalized species of different origin in the 33 Indian states

**Fig. 4** Histogram showing the numbers of naturalized species according to the number of Indian states ( $n = 33$ ) in which they occur



In a study on alien plants in India, Khuroo et al. (2012), report a total of 1599 alien species, but do not provide data on their distribution across the different states. Khuroo et al. (2012) classified the alien species

as cultivated (812), casual (57), casual/naturalized (114), naturalized (256), naturalized/invasive (134) and invasive (225). So, after excluding the cultivated and casual species, the total number of naturalized



**Fig. 5** Frequency distribution of the regions of origin shown separately for the group of most widespread species occurring in 31 or more Indian states (white bars), and the species occurring in fewer states (black bars). Regions that significantly differ

between the two groups ( $G$  test;  $p < 0.1$ ,  $* < 0.05$ ,  $** < 0.01$ ,  $*** < 0.001$ ) are indicated by an arrow. The direction of arrows indicate over- or under-representation within the group

species previously reported for India ranges from 615 to 729 species. The number of 471 naturalized taxa in our inventory is thus considerably lower. We believe that this discrepancy is caused by the fact that for many species in India, there is contradicting evidence on their biogeographic status in earlier works. Therefore, when preparing the inventory of naturalized alien species of India, we adopted a conservative approach, and only included species for which there is good evidence that they are naturalized aliens. In the Electronic Supplementary Material 3, we provide a list of species that in some previous works have been considered naturalized but do not qualify as naturalized according to our criteria. We consider these species either as native or cultivated based on the references given in the Electronic Supplementary Material 3.

We found that the largest number of naturalized species in India belong to the Compositae (75) followed by the Leguminosae (60) (Table 2). This accords with the recent figures for invasive species in India reported by Adhikari et al. (2015). These authors found that out of 155 invasive alien plant species in India, the largest number belong to Compositae (23) followed by Leguminosae (15). Khuroo et al. (2012), on the other hand, report that the Leguminosae (178) rather than Compositae (134) had the largest number of naturalized alien species. This small discrepancy might be caused by the stricter criteria that we used for classifying a species as alien or native. Our study thus

confirms that, as in alien floras of other countries, the Compositae family has high numbers of naturalized and invasive species (Pyšek 1997, 1998; Daehler 1998; Lambdon et al. 2008). Most likely this reflects that the Compositae is the largest dicotyledon plant family, and consequently, it is more likely that it includes many naturalized and invasive species. Pyšek et al. (2017) actually show for the global naturalized flora that although the Compositae have the largest number of naturalized species, this number is not higher than one would expect by chance, given the large total number of species in the family. Nevertheless, many of the most widely naturalized species also appear to be Compositae, with an average of  $\sim 10$  Indian states per species. One reason for the naturalization success could be that many Compositae species produce a large seed crop, e.g. *Ageratina adenophora*, *Chromolaena odorata*, *Mikania micrantha* and *Solidago gigantea* (Witkowski and Wilson 2001; Tiwari et al. 2005; Mandal and Joshi 2014; Horvitz et al. 2014; Kalwij et al. 2014; Day et al. 2016).

Our data showed that the naturalized flora of India mainly consists of annual/biennial (45.7%) and perennial herbs (47.0%), with only few woody species (13.4%). Herbs have short generation times, and are therefore more likely to establish and spread rapidly. Indeed some herbaceous species, such as *Chromolaena odorata* and *Ageratina adenophora*, form large populations and dominate communities in the Peechi

area in Kerala, and the Mussoorie hills in Uttarakhand, respectively (Mangla et al. 2008; Inderjit et al. 2011). Nevertheless, there are also some woody species, such as *Prosopis juliflora*, that are widespread and dominate plant communities (Kaur et al. 2012).

The highest numbers of naturalized alien species were found in states that even during the driest season receive relatively high amounts of precipitation. This is in line with findings of Lambdon et al. (2008), who identified precipitation as one of the key climatic factor shaping the richness of regional alien floras in Europe. Harsh environments with low moisture or soil fertility may be less invasible because few species are adapted to such harsh environments (Zafferan et al. 2015). Ashbacher and Cleland (2015) found that increased rainfall has more positive impacts on herbaceous alien species than on native species. These authors reported that the response to the shift in rainfall pattern depends upon the relative growth of alien versus native species. Alien annual grasses suppressed native species under experimentally maintained high soil moisture (Goldstein and Suding 2014). However, differences between native and alien species in the response to water availability are not always consistent (Funk and Zachary 2010; Liu et al. 2017).

Globally, most alien plant species have naturalized in only few regions, and only few species are very widespread (Pyšek et al. 2017). In line with this, we found that most of the naturalized species occur in only few regions in India (Fig. 4). However, we also found that a remarkably large number of species are very widespread and occur in almost all states. Most of these species occurred in all 31 mainland states, but not necessarily in the island state, Lakshadweep. This indicates that these species after their introduction to the Indian subcontinent managed to spread all over the mainland. This could be because these species have a wide environmental tolerance. Interestingly, these widespread species did not differ from less widespread species with regard to life form. However, they differed to some extent with regard to their native distribution ranges; while species from South America were more frequent than expected among the widespread species, the opposite was true for species of European origin. Possibly, this reflects that the climates in India are much more similar to the ones found in South America than to the ones found in Europe.

In this paper, we provide the first state-wise inventory of naturalized alien species of India, and analyse its composition and distribution of species across the different states. Together with other such regional inventories and analyses (e.g. Arianoutsou et al. 2009; Kull et al. 2012; Khuroo et al. 2012), this contributes to a better understanding of plant naturalizations around the world (van Kleunen et al. 2015; Pyšek et al. 2017). Moreover, this inventory and analysis improve our knowledge on threats associated with plant invasions in India, and can be used to provide arguments for promoting programs on conservation of native biodiversity in the country as well as in particular states.

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**Authors contribution** PP, JP and MvK initiated the idea and outlined the paper; Inderjit, CRB, PS, SM, SPS, SS and BRPR collected data on species taxonomy and distributions; MH verified data on origin; JP analysed the data; CRB, SM and Inderjit prepared the list of species reported as alien in many previous Indian checklists that do not qualify as naturalized species; PP, MvK and Inderjit wrote the paper and all authors commented on the final draft.

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