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**Walkiria R. Almeida, Ariadna V. Lopes,
Marcelo Tabarelli & Inara R. Leal**

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The alien flora of Brazilian Caatinga: deliberate introductions expand the contingent of potential invaders

Walkiria R. Almeida · Ariadna V. Lopes ·
Marcelo Tabarelli · Inara R. Leal

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Abstract Alien floras have been examined at regional and continental scales, but the connections between the cause of introduction and the nature and invasiveness of alien floras remain poorly explored. This is despite the fact that initial introduction determines the alien species pool from which the invasion proceeds. Here we examine the profile of the alien flora of the Brazilian Caatinga, a semi-arid tropical vegetation, in order to define the major connections between economic activities, introduction pressure and nature of the alien flora in terms of taxonomy, native ranges and economic use. Alien plant species introduced in the Caatinga ecosystem were compiled from the literature as well as from herbaria surveys. A total of 205 alien plants species were recorded, distributed across 135 genera and 48 families. The alien flora of the Caatinga ecosystem is clearly explained in terms of taxonomy, native ranges

and use by human populations. The highest numbers of alien species belong to the families Poaceae (61 spp.) and Fabaceae (33). Nearly one-third of the alien flora is represented by tropical forage plants, particularly grasses from Africa and America, which were introduced deliberately, particularly as forage for grazing livestock. Finally, 20 alien species were considered invasive, nine of them deliberately introduced, such as those species serving as forage for livestock. The Caatinga “case” calls attention to the socio-ecological drivers of alien floras and to which extent particular regions or biotas are susceptible to experiencing further biological invasion due to deliberate introductions.

Keywords Biological invasion · Cause of introduction · Plant introductions · Seasonally dry tropical forest · Unintentional introductions

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W. R. Almeida
Programa de Pós-Graduação em Biologia Vegetal,
Universidade Federal de Pernambuco, Av. Prof. Moraes
Rego s/no, Recife, PE 50670-901, Brazil

A. V. Lopes · M. Tabarelli · I. R. Leal (✉)
Departamento de Botânica, Universidade Federal de
Pernambuco, Av. Prof. Moraes Rego s/no, Recife,
PE 50670-901, Brazil
e-mail: irleal@ufpe.br

Introduction

Human activities have supported the movement of individuals and/or propagules from thousands of plant species to regions outside their natural range, facilitating biological invasions (e.g., Richardson 2011) with disastrous impacts on native biotas (e.g., Simberloff et al. 2010). Such biological invasions represent a major threat to biodiversity and ecosystem integrity globally, representing the second-most

important cause of species extinction (Vitousek et al. 1997). In addition to species extinction and biotic homogenization at multiple spatial scales, synergies between human-mediated habitat disturbance and biological invasions may threaten ecosystem integrity, for example by providing biomass for intense fires (e.g., Brooks et al. 2004; Simberloff et al. 2010).

Successful invasion relies on three dependent steps: an alien species must be introduced, develop viable populations without direct human help (i.e., a naturalized species) and spread from the introduction area over new habitats and regions (Richardson et al. 2000; Chapple et al. 2012). Although just a small fraction of the alien species pool becomes invasive, the forces promoting species introduction determines the size and nature of the alien species pool and, consequently, the chance of successful events of invasion (Richardson et al. 2000; Chapple et al. 2012). In the case of plants, while deliberate introductions are primarily determined by socio-economic and ecological conditions and favor species heavily dependent on human interventions, unintentional introductions rely on the intrinsic dispersal ability of species (Pyšek 1998; Chapple et al. 2012). As a result, deliberate and unintentional introductions will produce alien floras with different identities (Pyšek 1998), from dispersal ability to ecological requirements, and invasive potential (Chapple et al. 2012).

In the last decades, alien floras have been examined at regional and continental scales (particularly countries and continents; e.g., Harris et al. 2007; Lambdon et al. 2008; Weber et al. 2008; Khuroo et al. 2012) but the connections between the introduction mode (deliberate and unintentional), the nature and invasiveness of alien floras remain poorly explored. This is despite the fact that in many regions initial introduction determines the alien species pool from which the invasion proceeds (Richardson et al. 2000; Chapple et al. 2012).

The Caatinga vegetation represents a singular biogeographic region and one of the largest seasonally dry tropical forests of the American continent (Bullock et al. 1995; Pennington et al. 2009). With thousands of native plant species, including a myriad of endemics, Caatinga biota has faced intensive habitat degradation, ranging from soil exhaustion to deliberate introductions of exotic plants for supporting farming-based activities (Leal et al. 2005; Cavalcante and Major 2006). Some of these exotics are now

invasive and threats native biodiversity (Nascimento et al. 2014). Here we examine the profile of the alien flora of the Brazilian Caatinga in order to define the major connections between economic activities, introduction pressure and nature of the alien flora in terms of taxonomy, native ranges and economic use. We highlight the connections between socio-ecological forces as drivers of the nature of alien floras, and briefly examine the extent to which the Caatinga ecosystem is susceptible to invasion and is threatened by deliberate introductions. This socio-ecological approach helps identify the drivers promoting invasion of the Caatinga ecosystem.

Materials and methods

The Caatinga ecosystem

The Caatinga vegetation is a mosaic of scrub vegetation and patches of dry forest (Bullock et al. 1995), considered as a seasonally dry tropical forest (SDTF) in northeast Brazil (Pennington et al. 2009). Extending for about 800,000 km², the Caatinga ecosystem experiences a rainfall between 240 and 900 mm/year and a 7–11 month dry season (see Leal et al. 2003). The native Caatinga flora consists of 4,478 species (Siqueira Filho et al. 2012), including those occurring exclusively in relictual patches of humid forest and savannas. Fabaceae, Euphorbiaceae, Cactaceae and Bromeliaceae account for the majority of native shrub and tree species, and nearly 20 % of the Caatinga flora is endemic (see Giulietti et al. 2004).

Approximately 28 million people live in the Caatinga ecosystem (Santos et al. 2011). Slash-and-burn agriculture, cattle-raising and forestry have converted Caatinga vegetation into mosaics of regenerating forest stands with different ages immersed in open-habitat matrices (Leal et al. 2005). Such human-modified landscapes have historically been exposed to both deliberate and unintentional introductions of alien plant species in an attempt to improve production and make farming-based activities viable (Giulietti et al. 2004; Leal et al. 2005).

The profile of the Caatinga alien flora

Alien plant species (sensu Richardson et al. 2000) introduced in the Caatinga ecosystem were identified

by reviewing: (1) literature/databases of alien plant species from Brazil and worldwide (see Appendix 1 in Supplementary Material), and (2) herbarium collections provided by the Reference Center on Environmental Information (CRIA, see Appendix 2 Supplementary Material for a list of the collections consulted) to verify the occurrence of alien plant species in the Caatinga ecosystem. All alien plant species recorded in the Caatinga ecosystem were included in our survey. Alien species occurring in humid, montane forest (i.e., *brejos de altitude* a sort of relictual montane forest recognized as an Atlantic forest center of endemism) and savanna areas (i.e., *cerrado*) located within the Caatinga ecosystem were not considered here. Among the alien flora we identified invasive species (sensu Richardson et al. 2000) using the above mentioned sources of information.

The cause of introduction (i.e., deliberate or unintentional; Carlton and Ruiz 2005) was determined from scientific literature and the I3 N Brazil invasive species (Instituto Hórus 2012). The cause of introduction of species lacking historical records was determined on the basis of their current uses (Harris et al. 2007; Weber et al. 2008). Ornamental plants were considered as deliberately introduced, although it is not always associated with trade. The scientific nomenclature of alien plant species was updated using Plantminer (Carvalho et al. 2010), which classifies species according to the Angiosperm Phylogeny Group (Stevens 2001 onwards), and crosschecks the user list for synonyms, replacing them with the currently accepted name. To gather taxonomic information on the plant species, Plantminer submits queries to taxonomic databases including the World Checklist of Selected Plant Families (WCSP), Tropicos, and The International Plant Names Index (IPNI).

Native ranges were obtained from all available sources, including the specialized Internet web pages and published similar studies (see Appendix 3 in Supplementary Material). Information on native ranges of alien plants differs according to the source, and was recorded using the standardized geographical regions of the Taxonomic Database Working Group (Brummitt 2001). Alien plant species were assigned to mutually exclusive categories; as follows: (1) Temperate: North America, Europe, and Temperate Asia; (2) Tropical: Tropical Africa, Mesoamerica (incl. Mexico), South America, Tropical Asia, and

Australasia; and (3) Widespread: those naturally occurring across tropical and temperate regions (Wu et al. 2004).

Statistical analysis

We used Chi square goodness of fit tests to compare observed and expected numbers of alien plant species in Caatinga with each of the following (1) cause of introduction for each family and (2) cause of introduction for native range. We considered only families with more than five species to conform to the assumptions of the test.

Results

A total of 205 alien plants species were recorded for the Caatinga ecosystem. From the 57 (27.8) species presenting historical information, 54 (26.34 %) were deliberately introduced and three (1.46 %) were unintentionally introduced (see Appendix 4 in Supplementary Material). 69 species (33.66 %) exhibited economic use, suggesting deliberate introductions, while 79 (38.54 %) alien species have not any economic use; i.e., unintentional introductions (Appendix 4). Plant introductions for human food (28 species), ornamental (15), textile (5) and forestry (4) purposes have also been documented (Appendix 4). Thus, deliberate introductions accounted for 60 % the introductions experienced by the Caatinga ecosystem, particularly forage grasses (63 forage species, Appendix 4).

The alien plant species were distributed in 135 genera and 48 families. Highest numbers of species were in families Poaceae (61 spp.) and Fabaceae (33). An additional ten families comprised 27.8 % of all species listed, while 36 families (26.3 %) were represented by three or fewer species (Appendix 4). Most of the Poaceae (88.5 %; $\chi^2 = 34.6$, $df = 1$, $p < 0.0001$) and Fabaceae species (72.7 %; $\chi^2 = 5.9$, $df = 1$, $p = 0.0148$) were deliberately introduced, particularly as sources of forage. In contrast, most species in Amaranthaceae, Asteraceae, Apocynaceae, Solanaceae and Convolvulaceae were unintentionally introduced. Twenty-four (27.32 %) genera were represented by two or three species, while 104 (50.73 %) genera were represented by only one species. *Bracharia* (Poaceae; 12 spp.), *Amaranthus* (Amaranthaceae;

7), *Digitaria* (Poaceae; 7), *Prosopis* (Fabaceae; 7), *Acacia* (Fabaceae; 7), *Eragrostis* (Poaceae; 4), and *Panicum* (Poaceae; 4) accounted for 21.95 % of the total alien flora.

Approximately 57 % (102 spp.) of alien plant species in the Caatinga originated in tropical regions: 39 (28.7 %) species from Africa, 32 (23.5 %) from South America, 28 (20.6 %) from Mesoamerica, and 21 (15.4 %) from Tropical Asia. Around 43 % (77 spp.) of the native ranges of alien plants included tropical and temperate areas. No species was classified as exclusively temperate. However, approximately 60 % of the deliberately introduced species were tropical, while approximately 30 % belonged to tropical and temperate native climates ($\chi^2 = 10.414$, $df = 1$, $p = 0.0013$). Only 20 of all the species were considered invasive, of which 13 (75 %) were deliberately introduced.

Discussion

Our results suggest that alien plant species represent an important portion of the Caatinga biota. The alien flora has clearly benefited from both deliberate and unintentional introductions. It is clearly biased in terms of taxonomy, native ranges and use by human populations. While Poaceae and Fabaceae accounted for almost 50 % of the total alien species, a substantial part of the alien flora consists of families and genera represented by few species introduced unintentionally. In fact, nearly 1/3 of the alien species is currently represented by tropical forage plants, particularly deliberately introduced grasses from Africa and America. A quarter of the invasive alien species registered for the Caatinga are comprised of forage grasses.

The review of alien floras at large spatial scales has frequently been carried out based on political divisions such as countries or regions, rather than biogeographical units such as the Caatinga ecosystem. This makes cross-flora comparisons and even socio-ecological analyses of the invasion process more difficult. As a working hypothesis we propose that SDTF and semi-arid regions devoted to agriculture and/or cattle-raising tend to support a large number of alien plant species consisting of aggressive and resistant forage species, particularly grasses. However, our findings support the trend that (1) alien floras mainly result

from the deliberate introductions, and (2) large and cosmopolitan plant families (emphasizing certain families or orders) represent a substantial portion of alien floras at the regional biota/spatial scale (Pyšek 1998). This is the case for the large plant families Poaceae and Fabaceae, which have been dominant in alien floras of many countries in the world (e.g., Pyšek 1998; Lambdon et al. 2008; Weber et al. 2008; Fonseca et al. 2013; Zenni 2013). In general, Brassicaceae, Rosaceae, Amaranthaceae and Solanaceae are among the largest contributors to alien species in many European countries (Pyšek 1998), while Amaranthaceae, Convolvulaceae, Euphorbiaceae, Lamiaceae and Solanaceae are common families among to alien floras in Asia (e.g., Wu et al. 2004; Khuroo et al. 2012).

The size of a plant family is not, however, a reason for prevalence in alien floras. Although family size has been considered a predictor of the number of alien plants in alien floras (e.g., Pyšek 1998; Khuroo et al. 2012), the dominance of Poaceae and Fabaceae in the Caatinga is likely to result from another source of pressure. Tropical species of *Brachiaria*, *Digitaria*, *Panicum*, *Prosopis*, *Melinis* and *Pennisetum*, among others, have been introduced in the Caatinga ecosystem as forage species (Giulietti et al. 2004), a process facilitated by similar environmental conditions between the Caatinga and some areas of Africa and Asia which confer drought resistance to these taxa (Williams and Baruch 2000). Tree species of *Prosopis* have been intentionally introduced in the Caatinga ecosystem and *Prosopis juliflora* takes advantage of degraded lands along river banks (Nascimento et al. 2014). This species continues to spread and proliferate throughout the region, creating monospecific stands in areas previously degraded by intensive agriculture or grazing (Fabricante and Siqueira Filho 2012; Nascimento et al. 2014).

Despite commercial connections among America, Europe and Africa, the dominance of forage grass species in the Caatinga ecosystem does not agree with hypothesis of introductions taken place due to historical trade pathways (Jiménez et al. 2008; Khuroo et al. 2012). Note that trade routes offer opportunities and propensity for species transportation, thus creating propagule pressure (Chapple et al. 2012). Most alien plant species in central Chile and California originated in Europe, specifically in the Mediterranean basin, the historical source of modern human immigration associated with Spanish colonization (Jiménez et al.

2008). More recently, it has been proposed that most of the alien plant species in India originate from Tropical America (especially Brazil and Mexico) as a consequence of propagule pressure via historical trade routes (Khuroo et al. 2012). Although Brazil has experienced a long period of European colonization, this pathway seems to have had little influence on both deliberate and unintentional introductions in the Caatinga ecosystem so far.

As many STDF, cattle raising is expected to persist as a major economic activity in the Caatinga ecosystem. It promotes deforestation, habitat fragmentation, degradation and the introduction of alien plant species for the improvement of productivity or even for adaptation in face of future climatic changes. Rather than imposed by trade (e.g., Pyšek 1998; Jiménez et al. 2008; Khuroo et al. 2012), deliberate introductions of forage species will continue to provide opportunities for invasion as they will benefit from degraded areas as *Prosopis* species have (Nascimento et al. 2014). As annual rainfall faces considerable reduction as part of global climate change (Dore 2005), it is likely that farmers will demand more aggressive and drought-resistant forage species to support over 50 million grazing animals (IBGE 2012). The Caatinga “case” calls attention to the socio-ecological drivers of alien floras and the extent to which particular regions or biotas are susceptible to further biological invasion via deliberate introductions.

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