Seedling survival and growth of the invasive species *Prosopis juliflora* (Fabaceae) depend on habitat and seed dispersal mode in the Caatinga dry forest

Clóvis E de Souza Nascimento [1, 2] , **Carlos Alberto D da Silva** [3, 4] , **Inara R Leal** [5] , **Wagner de S Tavares** [Corresp., 6] , **José E Serrão** [7] , **José C Zanuncio** [8] , **Marcelo Tabarelli** [Corresp. 5]

1 Centro de Pesquisa Agropecuária do Trópico Semi-Árido, Empresa Brasileira de Pesquisa Agropecuária, Petrolina, Pernambuco, Brasil

2 Departamento de Ciências Humanas, Universidade do Estado da Bahia, Juazeiro, Bahia, Brasil

3 Centro Nacional de Pesquisa de Algodão, Empresa Brasileira de Pesquisa Agropecuária, Campina Grande, Paraíba, Brasil

4 Programa de Pós-Graduação em Ciências Agrárias, Universidade Estadual da Paraíba, Campina Grande, Paraíba, Brasil

5 Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Pernambuco, Brasil

6 Departamento de Fitotecnia/BIOAGRO, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brasil

7 Departamento de Biologia Geral, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brasil

8 Departamento de Entomologia/BIOAGRO, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brasil

Corresponding Authors: Wagner de S Tavares, Marcelo Tabarelli
Email address: wagner.tavares@ufv.br, mtrelli@ufpe.br

Abstract

Background. Biological invasion is one of the main threats to tropical biodiversity and ecosystem functioning. *Prosopis juliflora* (Sw) DC. (Fabales: Fabaceae: Caesalpinioideae) was introduced in the Caatinga dry forest at early 1940s as a food source for livestock and successfully spread across the region by invading and forming monospecific stands, particularly across former agricultural lands along river banks and flooding plains. As other invasive species, it may benefit from the soils and seed dispersal by livestock but the ultimate forces permitting successful invasion of Caatinga dry forest by this plant needs further studies. The objective was to understand how seed dispersal ecology and soil conditions collectively affect seedling performance and consequently the *P. juliflora* invasive potential.

Methods. Seed germination and seedling performance of *P. juliflora* in 10 plots and its associated soil attributes located across three habitats (floodplain, alluvial terrace and plateau) into a human-modified landscape of the Caatinga dry forest were examined. Seeds of this plant were exposed to four seed dispersal methods: deposition on the soil surface, burial in the soil, passed through cattle digestive tracts and encasing them in cattle manure and passed through mule digestive tracts and mixed with mule manure. The resulting seedlings were monitored through a year and their performance examined with expectancy tables.

Results. Soils differed among habitats, particularly its nutrient availability, texture and water with finely-textured and more fertile soils in the floodplain. Seedling survival rate of *P. juliflora* was highest in the first 30 days and declined between 30 to 60 days with stabilization at 70 days after germination in all seed treatments and habitats. Survival and life expectancy were higher in the floodplain at 75 days and lower in the plateau. *Prosopis juliflora* seedling survival and life expectancy were higher when its seeds were mixed with cattle manure.

Synthesis. *Prosopis juliflora* seedlings are sensitive to water stress and habitat desiccation. Therefore,

they benefit from the humid soils often present across human-disturbed floodplains. This plant also benefits from seed deposition/dispersal by domestic/exotic livestock in these landscapes, since animal manure represents a nutrient-rich and humid substrate for both seeds and seedlings. The quality of the seed dispersal service varies among livestock species, but this key mutualism between exotic species is due to the arillate, hard-coated and palatable seeds. *Prosopis juliflora* traits allow this species to take multiple benefits from human presence and thus operating as a human commensal.

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7 Clóvis Eduardo de Souza Nascimento[1,2], Carlos Alberto Domingues da Silva[3,4], Inara Roberta

8 Leal[5], Wagner de Souza Tavares[6], José Eduardo Serrão[7], José Cola Zanuncio[8], Marcelo

9 Tabarelli[5]

10

11 [1] Empresa Brasileira de Pesquisa Agropecuária, Centro de Pesquisa Agropecuária do Trópico

12 Semi-Árido, 56300-970, Petrolina, Pernambuco, Brasil

13 [2] Departamento de Ciências Humanas, Universidade do Estado da Bahia, 48900-000, Juazeiro,

14 Bahia, Brasil

15 [3] Empresa Brasileira de Pesquisa Agropecuária, Centro Nacional de Pesquisa de Algodão,

16 58428-095, Campina Grande, Paraíba, Brasil

17 [4] Programa de Pós-Graduação em Ciências Agrárias, Universidade Estadual da Paraíba, 58429-

18 570, Campina Grande, Paraíba, Brasil

19 [5] Departamento de Botânica, Universidade Federal de Pernambuco, 50670-901, Recife,

20 Pernambuco, Brasil

21 [6] Departamento de Fitotecnia/BIOAGRO, Universidade Federal de Viçosa, 36570-900, Viçosa,

22 Minas Gerais, Brasil

23 [7] Departamento de Biologia Geral, Universidade Federal de Viçosa, 36570-900, Viçosa, Minas

24 Gerais, Brasil

25 [8] Departamento de Entomologia/BIOAGRO, Universidade Federal de Viçosa, 36570-900,

26 Viçosa, Minas Gerais, Brasil

27

28 Corresponding Author:

29 Wagner de Souza Tavares

30 Departamento de Fitotecnia/BIOAGRO, Universidade Federal de Viçosa, 36570-900, Viçosa,

31 Minas Gerais, Brasil

32 E-mail address: wagnermaias@yahoo.com.br

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37 ecosystem functioning. *Prosopis juliflora* (Sw) DC. (Fabales: Fabaceae: Caesalpinioideae) was

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39 successfully spread across the region by invading and forming monospecific stands, particularly

40 across former agricultural lands along river banks and flooding plains. As other invasive species,

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42 successful invasion of Caatinga dry forest by this plant needs further studies. The objective was

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46 associated soil attributes located across three habitats (floodplain, alluvial terrace and plateau)

47 into a human-modified landscape of the Caatinga dry forest were examined. Seeds of this plant

48 were exposed to four seed dispersal methods: deposition on the soil surface, burial in the soil,

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50 mule digestive tracts and mixed with mule manure. The resulting seedlings were monitored

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52 **Results**. Soils differed among habitats, particularly its nutrient availability, texture and water

53 with finely-textured and more fertile soils in the floodplain. Seedling survival rate of *P. juliflora*

54 was highest in the first 30 days and declined between 30 to 60 days with stabilization at 70 days

55 after germination in all seed treatments and habitats. Survival and life expectancy were higher in

56 the floodplain at 75 days and lower in the plateau. *Prosopis juliflora* seedling survival and life

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61   landscapes, since animal manure represents a nutrient-rich and humid substrate for both seeds

62   and seedlings. The quality of the seed dispersal service varies among livestock species, but this

63   key mutualism between exotic species is due to the arillate, hard-coated and palatable seeds.

64   *Prosopis juliflora* traits allow this species to take multiple benefits from human presence and

65   thus operating as a human commensal.

66

68 **Introduction**

69   Biological invasion is an important threat to tropical biodiversity and ecosystem

70 functioning. Increased disturbance by ever-growing human populations will make terrestrial

71 tropical biotas more vulnerable to invasions (Simberloff et al., 2013; Roy et al., 2014; McGeoch

72 et al., 2016). This increased vulnerability is due to alien species benefiting from human

73 disturbances, such as land cleaning and soil degradation by agriculture and livestock. Humans

74 and their commensals, whether intentionally or not, favor alien species by creating altered or

75 novel habitats (Almeida et al., 2015; Jauni et al., 2015; Bellard et al., 2016; Malavasi et al.,

76 2016).

77   The mechanisms driving successful invasion by alien species and those restricting them

78 to particular habitats or conditions are key topics in invasion science (Blackburn et al., 2014;

79 Catford and Jansson, 2014; Hulme, 2015). The life-history strategy or trait package exhibited by

80 alien species affect their competitive performance or adaptability, while environmental

81 conditions, disturbance regimes, habitat degradation and the structure of native communities

82 (e.g. patterns of species richness and functional composition) are external forces controlling

83 invasion success (Gilioli et al., 2014; Goia et al., 2014; Banerjee and Dewanji, 2017). The

84 intrinsic and external factors collectively define the potential for successful invasion and delimit

85 its ecological context, the geographic coverage and potential damage to native biodiversity.

86 Successful invasions only occur when alien species can overcome external forces (Dalmazzone

87 and Giaccaria, 2014; Li et al., 2014; Svenning et al., 2014). These factors explain why a small

88 fraction of introduced alien species become invasive regardless of ecosystem type or habitat

89 integrity (Kalusová et al., 2014; van Wilgen and Richardson, 2014; Novoa et al., 2015).

90   Successful invasion of tropical plant species usually relies on the key life-history traits

91   across all life-cycle stages (Chapple et al., 2012; Malíková et al., 2012; Mullah et al., 2014), such

92   as vegetative reproduction, massive seed production, effective seed dispersal, high germination

93   success in a wide range of environmental conditions, fast growth and high phenotypic plasticity

94   (Moravcová et al., 2015; van Kleunen et al., 2015; Moran et al., 2017). The effective

95   colonization of human-degraded habitats usually requires dealing with physical stress,

96   particularly reduced soil nutrients and water availability (Boudiaf et al., 2013; Pérez et al., 2015;

97   Rathore et al., 2015). The naturalization and long-term establishment of invasive species depend

98   on integrating adaptive traits as functional strategies (Guo et al., 2018). However, the relative

99   contribution of each trait or strategy vary from case to case (Hulme and Barrett, 2013; Perkins

100   and Nowak, 2013; Rai, 2015).

101   The Caatinga of northeast Brazil is one of the largest blocks (nearly 1 million Km^2) and

102   the world most species-rich seasonally dry tropical forest (Silva et al., 2017). The regional

103   vascular flora reaches 3,000 species with one third endemic, including a myriad of Cactaceae

104   species—making this region the second diversity cactus species center globally (Silva and

105   Souza, 2018; Apgaua et al., 2018; Terra et al., 2018). The Caatinga was inhabited by hunter-

106   gather people for thousands of years (Leal et al., 2005; Mamede and de Araújo, 2008; Silva et

107   al., 2017). The Europeans arrived in the 16th century and the Caatinga dry forest has been

108   converted into human-modified landscapes by a combination of extensive cattle ranching, small-

109   scale subsistence farming and exploitation of forest products such as firewood, fodder, timber,

110   wood for charcoal, fruits and bushmeat (Silva et al., 2014; Leal et al., 2014; Ribeiro et al., 2015;

111   Silva et al., 2017). Nearly 10 million m^3 of firewood and charcoal are obtained per year from

112   native species, while goat (i.e. the exotic *Capra aegagrus* subspecies *hircus* L., 1758;

113   Artiodactyla: Bovidae) herds feeding on native vegetation exceed 16 million heads (Ribeiro et

114   al., 2015; Rito et al., 2017; Sfair et al., 2018). The Caatinga supports around 28 million people,

115   making it one of the most populated semiarid regions and one of the most degraded/vulnerable

116   Seasonally Dry Tropical Forests (SDTFs) globally (Oliveira et al., 2016; Moro et al., 2016; Rito

117   et al., 2016; Schulz et al., 2017; Silva et al., 2017).

118   The alien flora inhabiting the Caatinga includes 205 species of 135 genera and 48

119   families, including 61 Poaceae and 33 Fabaceae invasive species (Almeida et al., 2015). This

120   diverse alien flora includes the evergreen tree *Prosopsis juliflora* (Sw) DC. (Fabales: Fabaceae:

121   Caesalpinioideae), one of the world top 100 undesired species (Nascimento et al., 2014; Almeida

122   et al., 2015). This species is native to the Caribbean, Central America and South America, but

123   has been intentionally introduced worldwide for its economic value, utility to rural populations

124   and ecological rusticity due to its fast growth, ability to fix nitrogen and tolerance to arid

125   conditions and saline soils (Nascimento et al., 2014; Ilukor et al., 2016; Walkie et al., 2016).

126   *Prosopis juliflora* was introduced in the Caatinga at early 1940s as a food source for

127   livestock and successfully spread across the region by invading and forming monospecific

128   stands, particularly across former agricultural lands along river banks and flooding plains

129   (Almeida et al., 2015; Santos and Diodato, 2015; Oliveira et al., 2017). *Prosopis juliflora* forms

130   dense stands, apparently excluding or impelling the reestablishment of species-rich assemblages

131   of tree and shrub species, particularly on river banks degraded by shifting cultivation and

132   livestock overgrazing (Pegado et al., 2006; Andrade et al., 2009; Oliveira et al., 2012). Caatinga

133   dry forests along river banks are structurally complex due the presence of large tree species [e.g.,

134   *Libidibia ferrea* (Mart. ex Tul.) L.P. Queiroz, *Piptadenia stipulacea* (Benth.) Ducke (Fabales:

135   Fabaceae) and *Tabebuia aurea* (Silva Manso) Benth. & Hook.f. ex S. Moore (Lamiales:

136   Bignoniaceae)] and support a diverse flora, including endemic species such as the cactus *Cereus*

137   *jamacaru* DC. and *Pilosocereus gounellei* (F.A.C. Weber ex K. Schum.) Luetzelb.

138   (Caryophyllales: Cactaceae). *Prosopis juliflora*, as other invasive species, may benefit from the

139   soils and seed dispersal by livestock (Kebede and Coppock, 2015; Pasha et al., 2015; Alvarez et

140   al., 2017) but the ultimate forces permitting successful invasion of Caatinga dry forest by this

141   plant needs further studies (Shackleton et al., 2015; Abdulahi et al., 2017; Naudiyal et al., 2017).

142   The seed germination, seedling survival and life expectancy in *P. juliflora* across the

143   three main habitats covered by Caatinga dry forest were studied to understand how soil

144   conditions and seed dispersal ecology collectively affect seedling performance and consequently

145   the invasive potential of *P. juliflora*. Seeds exposed to four seed dispersal treatments were

146   deposited across a floodplain, alluvial terrace and plateau, with seed and seedling fate being

147   monitored for a year. The potential mechanisms behind differential seedling performance,

148   especially a positive synergism between human disturbance, key ecological services provided by

149   livestock and the life-history traits exhibited by *P. juliflora* was studied.

150

Material & Methods

152   **Study site.** The study was carried out in 10 sites across a 3.5-Km^2 human-modified Caatinga

153   landscape (9°00' S, 40°13' W; 377 m altitude) covering three habitats: floodplain, alluvial

154   terrace, and plateau (Supplementary materials 1 and 2). This landscape is typical of the Caatinga,

155   with farming households devoted to livestock production with animals raised extensively and

156   feeding on the Caatinga vegetation plus small patches devoted to subsistence agriculture and

157   remnant patches of Caatinga dry forest; i.e. the traditional Caatinga land use (Sampaio and

158   Costa, 2011). The landscape stretches over sedimentary basins, mountains, plateaus and ravines

159   covered by cambisols, eutrophic podzols, lithosols, non-calcic brown soils and planosols along

160   the São Francisco River valley (Razanamandranto et al., 2004). The river terrace has alluvial

161   deposits from the valley slopes with sedimentary clay, sandy or silty material in stratified silt

162   layers (Miranda et al., 2014). The floodplain, with slopes between 0 and 2° (Miranda et al.,

163   2011), consists of recent sediments from terraces (Babawi et al., 2016). The alluvial terrace, also

164   called the slope, consists of flat areas or benches, usually situated above the river level, with

165   gravel or thick sediment forming ancient terraces (Mukherjee et al., 2017). The plateau is a flat

166   terrain covered by a sedimentary clay mantle, which spreads following the river terraces (Silva et

167   al., 2008; Ferraz et al., 2013). The regional climate is hot semi-arid, with mean annual

168   temperature of 26.3 °C and relative humidity of 61.7%. The 570 mm annual rainfall is

169   concentrated between January and April (Ramos et al., 2011). The focal landscape was

170   completely covered by Caatinga dry forest prior to European settlement (Silva et al., 2008).

171   Regionally, Cactaceae, Euphorbiaceae and Fabaceae are the most species-rich plant families

172   (Leal et al., 2005; Silva et al., 2008).

173   **Soil attributes.** Soil attributes were estimated based on 10 soil samples per habitat type

174   (floodplain, alluvial terrace and plateau). Soil moisture was determined twice a week at 20 cm

175   depth from March 2014 to February 2015 (Francesca et al., 2010). The soil samples were

176   weighed to determine the wet mass (mw, g), dried in an oven at 105 °C for 24 hours and weighed

177   again to determine their dry mass (md, g). Soil moisture was determined by H (g.g^{-1})= (md −

178   mh) ÷ md or H (%)= (md − mh) ÷ md × 100. Physical (field capacity, sand, silt and clay content)

179   and chemical soil attributes [soil organic matter, phosphorus, potassium, calcium, magnesium,

180   sodium, aluminum and cation exchange capacity (CEC)] were also obtained via samples at 10 soil

181   samples per habitat type, with samples at 0-20 cm depth (Lopes et al., 2013). Soil analyses were

182   performed in the Laboratory for Soil, Water and Plant Tissue Analysis at EMBRAPA Semi-Arid

183   according to standard international protocols (Marques et al., 2007; Galindo et al., 2008).

184   **Seed germination and seedling performance across habitats.** *Prosopis juliflora* seeds were

185   exposed to four seed dispersal treatments as follows: seeds with artificially broken dormancy

186   deposited on the soil surface (T1); seeds with artificially broken dormancy buried in the soil to a

187   depth of 1.0 cm (T2); seeds that passed through the digestive tract of cattle (*Bos taurus*

188   subspecies *indicus* L., 1758; Artiodactyla: Bovidae) and mixed with cattle manure (hereafter

189   cattle-dispersed seeds) (T3) and seeds that passed through the digestive tract of mules (mare,

190   *Equus ferus* subspecies *caballus* L., 1758 × donkey, *Equus africanus* subspecies *asinus* L., 1758;

191   Perissodactyla: Equidae) and mixed with mule manure (hereafter mule-dispersed seeds) (T4).

192   These four seed dispersal treatments resemble natural seed dispersal modes and fates in the

193   Caatinga, as ripe fruits can be (1) consumed by livestock and deposited on the soil surface

194   immersed in manure; (2) remain intact on the ground and as the pod rots, seeds are deposited on

195   the soil surface and (3) carried by runoff and deposited in soil sediments (dos Santos et al.,

196   2006). These fates need further studies, although ripe pods are consumed by livestock including

197   cattle, goats, horses and mules (Nascimento et al., 2014). Seeds were manually collected from

198   mature fruits from several trees collected on the ground throughout 2013. Seeds were used to

199   feed livestock first and their manure collected.

200   *Prosopis juliflora* seeds were randomly sown on 120 1.4 m^2-field plots across the three

201   habitats (40 plots per habitat, Supplementary material 1). One hundred seeds were sown per

202   treatment and habitat, totaling 12,000 seeds (four treatments × three habitats × 40 replicates= 25

203   seeds per replicate). Seed dispersal treatments were set up in mid-March (i.e. rainy season) of

204   2014. Seeds were collected from several trees and animal dungs in the year preceding sowing

205   experiments. Seed dormancy was broken artificially by making a small incision with blunt

206   scissors on the opposite side of the micropylar region, while those that had passed through the

207   animal digestive tract were extracted from dried dung (Nascimento et al., 2014). Seeds obtained

208   from trees were sown at 10×10 cm spacing and those from the manure separated, counted,

209   mixed with 500 mL of the respective animal dung and sown at 10×10 cm spacing. Seed

210   germination and seedling survival were evaluated for each of the three habitats every five days

211   during the first 30 days and every 15 days thereafter for one year. *Prosopis juliflora* germination

212   is epigeal (Dube et al., 2010) and sprouted seeds (with cotyledons) were marked with toothpicks

213   and protected with wire netting to prevent animal damage. Seeds with their first cotyledon open

214   were classified as seedlings.

215   **Life expectancy and survival tables.** Life expectancy and survival tables of *P. juliflora* were

216   calculated (Bogino and Jobbágy, 2011) for each dispersal treatment and habitat considering age

217   classes of 15 days ($x = 15$). The number of *P. juliflora* survivors at the beginning of each age

218   class (Lx) and at the germination and seedling phenological stages were estimated based on

219   survival (lx) in these stages (Caswell, 1996) as follow: (a) number of dead individuals during the

220   age class x (dx): $d_x = L_x - L_{x+1}$; (b) mortality ratio for the age class x (qx): $q_x = d_x \div L_x$; (c) survival

221   rate during age x (sx): $s_x = 1 - q_x$; (d) age structure (Ex) as the number of alive plants from each

222   age class: $E_x = (L_x + L_{x+2}) \div 2$; (e) cumulative number of living individuals (Tx) by: $T_x = \sum_{j \geq x}^{y} E_x$

223   where j represents any age greater than or equal to that of class x; and (f) life expectancy for

224   individuals of age class x (ex): $e_x = T_x \div L_x$.

225   **Data analysis.** Differences in soil attributes were examined via analysis of variance and Tukey's

226   Honest Significant tests ($p < 0.05$) (Tukey, 1949). Non-normal (non-parametric) data obtained

227   from the three habitats were compared using the Kruskal-Wallis test statistic ($p < 0.05$) (Wallis,

228   1952) using the BioEstat 5.0 program (Ayres et al., 2007).

229

230   **Results**

231   **Soil physical attributes.** Caatinga habitats differed greatly in terms of soil physical attributes.

232   Field capacity was higher in the floodplain (F= 8.5454, df= 2, p= 0.0016; Fig. 1A), with the site

233   and the terrace supporting higher soil moisture (H= 12.5507, df= 2, p= 0.0019) than the plateau

234   (Fig. 1B). Soil clay content was higher in the floodplain followed by the plateau and the alluvial

235   terrace (H= 9.0142, df= 2, p= 0.011). The silt score was highest in the floodplain than in the

236   alluvial terrace and plateau (F= 6.6178, df= 2, p= 0.0048). The plateau and alluvial terrace had

237   the highest sand fraction (F= 8.2452, df= 2, p= 0.0019; Fig. 2A).

238   **Soil chemical attributes.** Chemical soil attributes differed across habitats with only the sodium

239   content being similar between them (H= 5.6227, df= 2, p= 0.0601). The phosphorus, calcium,

240   magnesium, aluminum, potassium and CEC concentrations were similar in the foodplain and

241   alluvial terrace and differed from those in the plateau ($p < 0.05$). The organic matter content in

242   the floodplain and plateau was similar but lower than that in the alluvial terrace (H= 17.8655, df=

243   2, p= 0.0001; Fig. 2B). Moreover, the soil organic matter content in the plateau was extremely

244   variable.

245   **Seedling survival and life expectancy.** *Prosopis juliflora* seedling survival was higher in the

246   first 30 days after germination, declined steeply from 30 to 60 days and tended to stabilize 70

247   days after germination for all seed dispersal treatments and habitats (Figs. 3–5). This plant

248   survival peaks in the floodplain were higher among seedlings from cattle-dispersed seeds,

249   followed by mule-dispersed and those deposited in the soil surface. Life expectancy was highest

250   approximately 75 days after germination in all seed treatments. The life expectancy in this

251   habitat reached 165 days among seeds deposited on the soil surface and cattle-dispersed ones,

252   but with 210 days among those buried in the soil and those dispersed by mules. Moreover,

253   seedling life expectancy exhibited peaks at 180, 195, 210 and 255 days with buried seeds, cattle-

254   dispersed, seeds on the soil surface and mule-dispersed seeds, respectively. Life expectancy of *P.*

255   *juliflora* reached 345 days across all treatments (Fig. 3; Supplementary material 3).

256   The *P. juliflora* survival peak in the terrace was higher among seedlings from cattle-

257   dispersed seeds, followed by those dispersed by mules and with lowest peak by those from seeds

258   buried in the soil. The longest life expectancy occurred within the first 15 days after sowing,

259   without increase from this period onwards. The life expectancy in the alluvial terrace reached

260   150 days for all seed treatments, except for those buried in the soil surface, which reached 165

261   days (Fig. 4; Supplementary material 4).

262   The survival peak for *P. juliflora* seedlings in the plateau was highest for those that were

263   cattle-dispersed followed by the mule-dispersed ones. Seedlings from soil surface seeds or buried

264   ones exhibited no survival peaks. The life expectancy peak among seedlings from soil surface or

265   buried was up to 15-day old, while this was up to 30- and 60-day among seedlings from mule-

266   and cattle-dispersed seeds, respectively. *Prosopis juliflora* seedling life expectancy reached 45

267   days among those deposited on the soil surface and dispersed by mules. However, it reached 120

268   and 165 days among seeds buried and cattle-dispersed, respectively (Fig. 5; Supplementary

269   material 5).

270

271   **Discussion**

272   The main habitats covered by the Caatinga dry forest differ in soil attributes or conditions.

273   Overall soils along floodplains and terraces have finer texture and are more humid and fertile

274   than those on the plateau, which are sandy and xeric. The way *P. juliflora* seeds are dispersed

275   and deposited (i.e. seed dispersal treatments) appears to respond to soil conditions and greatly

276   influences seedling performance across the main Caatinga habitats. The chances of seedling

277   survival when coated in manure and across floodplains are higher, while those deposited on the

278   soil surface on the plateau have a lower survival probability. The seedling life span was longer

279   from those originated with seeds immersed into cattle manure. Moreover, the benefit for seedling

280   dispersal depends on animal species (cattle *vs.* mule) and the habitat. Interactions between soil

281   attributes and seed dispersal by exotic species apparently define the *P. juliflora* potential as an

282   invasive species across human-modified Caatinga landscapes. The dominant species *Stipa*

283   *breviflora* Griseb. (Poales: Poaceae) expansion potential depends on climate changes in Chinese

284   temperate grasslands (Lv and Zhou, 2018). Extreme climatic change in Mediterranean rivers is

285   suggested to promote the disappearance of the pioneer and young succession stages of riparian

286   woodlands (Rivaes et al., 2013), particularly evident in Europe (Rivaes et al., 2014).

287   Soil differs across habitats, through which *P. juliflora* has been documented to exhibit

288   extreme variations in establishment and stand density in the Caatinga dry forest (Bailis and

289   McCarthy, 2011). *Prosopis juliflora* stands have been reported with densities as high as 140.39

290   stems per ha across floodplains and alluvial deposits at the Keoladeo National Park in Rajasthan,

291   India (Mukherjee et al., 2017) and in Tamil Nadu, India (Gandhi and Pandian, 2014). Such dense

292   monospecific stands suggest soil conditions and seedling ecology as potential key drivers for this

293   invasive species as previously documented for other regions in which *Prosopsis* species are

294   invasive (Ansley et al., 2018). *Prosopis* species largely benefit from seed dispersal by domestic

295   animals via dung pellets, improving seed germination and seedling performance and leading to

296   higher life expectancy (Miranda et al., 2011, 214; Razanamandranto et al., 2014). Seeds

297   deposited on the soil surface without manure had the worse seedling performance and survival in

298   our focal landscape; similar to that documented across a variety of habitats and biotas (Babawi et

299   al., 2016; Mukherjee et al., 2017).

300   *Prosopis juliflora* as an invasive plant species benefiting from dispersal services offered

301   by exotic animals is far from novel, with a number of examples for species of this genus (Abbas

302   et al., 2018). Ingestion and deposition by livestock is not required for *Prosopsis* seeds to

303   germinate, but it improved seedling performance and long-distance seed dispersal of this plant as

304   it has a patchy distribution and no native vertebrate species have been found to disperse *P.*

305   *juliflora* seeds in the Caatinga region. Seed dispersal by native ungulates [(i.e. dears, *Mazama*

306   *americana* Erxleben, 1777 and *Mazama gouazoubira* Fischer, 1814 (Artiodactyla: Cervidae)] is

307   theoretically possible but large vertebrates have been intensively extirpated in the Caatinga

308   region (Bragagnolo et al., 2019; de Oliveira et al., 2019). Caatinga supports nearly 30 million

309   cattle, goats and mules (Sampaio and Costa, 2011; Santos et al., 2017) as a large number of

310   active seed dispersers which spread through diverse habitat types, from old-growth forest stands

311   to degraded areas (Sampaio and Costa, 2011). Livestock frequently access humid habitats such

312   as river banks on their daily search for fresh water and native forage (Dias et al., 2019; Lopes et

313   al., 2019). Moreover, fodder availability is seasonal and scarce (Costa et al., 2016), while *P.*

314   *juliflora* fruits and foliage represent a permanent and appreciable food source for livestock, likely

315   stimulating its fruit consumption.

316   *Prosopis* has relatively hard pods and its sweet-arillate seeds probably evolved as a

317   response to consumption by native ungulates [e.g. cattle, goats, horses, mules and sheep *Ovis*

318   *aries* L., 1758 (Artiodactyla: Bovidae)], as an adaptation for contemporary consumption and

319   seed dispersal by domestic livestock (Nascimento et al., 2014; Almeida et al., 2015). Although a

320   substantial seed portion may be damaged or digested when consumed by livestock, the benefits

321   from dispersal outweigh this drawback. This may be particularly true in the Caatinga as the

322   native flora (mostly abiotically-dispersed) does not benefit from the dispersal services offered by

323   livestock.

324   Higher nutrient and water content in both floodplain soils and livestock manure may

325   enhance seedling performance of *Prosopsis* species. This was suggested for *Prosopis africana*

326   (Guill. & Perr.) Taub. seeds in sheep and zebu manure in the Sudanian savanna

327   (Razanamandranto et al., 2014) and *P. juliflora* in animal manure in the Caatinga in northeast

328   Brazil (Miranda et al., 2011, 2014). Causal mechanisms responsible for differential seedling

329   performance of that plant across seed dispersal modes and habitats were not explicitly examined

330   in our focal landscape. Seeds deposited on the soil surface rarely germinate due to dehydration as

331   observed for *Prosopis ferox* Griseback and *Prosopis flexuosa* DC. across semiarid regions of

332   Argentina and Sudan (Campos et al., 2011; Morandini et al., 2013; Yoda et al., 2015). High

333   *Prosopis caldenia* Burkart seed mortality has also been related to soil water availability

334   reduction across semiarid rangelands of Central Argentina (de Villalobos et al., 2005; de

335   Villalobos and Peláez, 2015; Risio et al., 2016).

336   Fine-textured soils with greater silt and clay quantities, as observed in the floodplain, are

337   expected to increase water retention and storage capacity, and thus may increase plant survival.

338   A similar phenomenon was observed for *P. caldenia* and *P. glandulosa* since allometric growth

339   and survival was directly proportional to the water availability along a topographic gradient in

340   the Chihuahuan Desert, Mexico, in the semiarid rangelands of Central Argentina and in the arid

341   and semiarid ecosystems of the United States of America (USA), respectively (Martínez and

342   López-Portillo, 2003; de Villalobos et al., 2005; Maestre and Reynolds, 2006). Water storage

343   capacity (Arcone et al., 2008) and organic matter, phosphorus and calcium accumulation are

344   usually higher in fine-textured soils with greater silt and clay quantities, found mainly in gallery

345   forests (Jiménez et al., 2008), which gives these soils a greater CEC (Shiferaw et al., 2004; Silva

346   et al., 2008). In synthesis, *P. juliflora* seeds and seedlings are sensitive to water stress and habitat

347   desiccation.

348   The higher nutrient availability in the floodplain and terrace, along with the low

349   aluminum content in the floodplain, may also be important because excess of this element in the

350   soil can impair the calcium, magnesium, phosphorous and potassium absorption by *Prosopis*

351   plants, as reported for *P. juliflora* in the Caatinga (Jiménez et al., 2008; Oliveira et al., 2017).

352   However, calcium and magnesium counteract this detrimental effect as observed for *Prosopis*

353   *alba* Griseb., *Prosopis pubescens* Benth. and *Prosopis ruscifolia* G. in the central and western

354   Gran Chaco phytogeographical region, Argentina, and in El Paso, Texas, USA, respectively

355   (Velarde et al., 2005; Meloni et al., 2012; Zapala et al. 2014). The soil nutrient availability

356   improved plant vigor, making them less vulnerable to drought stress in our focal landscape is

357   similar to that reported for *Prosopis cineraria* (L.) Druce (Ghaff) in United Arab Emirates (Gil

358   and Al-Shankiti, 2015; Song et al., 2017). Nutrient-rich soils increase the *P. juliflora* seedling

359   establishment, allowing its embryos to grow quickly (Nasr et al., 2012; Patil and Karadge, 2012;

360   El-Keblawy and Abdelfatah, 2014).

361   The high nutrient and water availability in animal manure also apparently creates suitable

362   microhabitats for seeds and seedlings. This substrate is favorable during the critical germination

363   and emergence periods, especially considering the spatially erratic rainfall in the Caatinga even

364   in the rainy season (Sampaio and Costa, 2011). Such services provided by livestock manure

365   benefit the *Prosopis* seeds of different species from South America to the Middle East and Africa

366   (Majd et al., 2013; Westphal et al., 2015; Araujo et al., 2017). On the other hand, the rapid

367   dehydration and hardening of animal manure reduced seed germination of *P. glandulosa* in the

368   arid and semiarid regions of northeastern Mexico and in the drylands of Japan (Garza et al.,

369   2013; Abdalla et al., 2017). The lower soil moisture in the plateau of the Caatinga accelerated the

370   drying and hardening process of cattle and mule manure (CE de SN, personal observation). This

371   adversely affected the *P. juliflora* germination and emergence and contributed to its lower

372   survival and life expectancy compared to the floodplain and terrace habitats.

373   The higher survival rate and life expectancy of *P. juliflora* seedlings germinated from

374   seeds mixed with cattle manure compared to those mixed with mule manure in the plateau can be

375   attributed to differences in the composition of these animal dungs (Campos et al., 2008;

376   Nascimento et al., 2014). Mule manure has a lower water content and higher fibrous sheath

377   content encasing seeds (Gonçalves et al., 2013). The fibrous sheath covering the seeds probably

378   reduces seed imbibition due to the fact that these animals are not ruminants like cattle

379   (Gonçalves et al., 2013). Both exotic and native ungulates can favor invasive plant species by (1)

380   creating disturbed habitats via feeding, trampling and movement, (2) controlling or eliminating

381   palatable native species and (3) dispersing seeds via endozoochory and epizoochory (Vavra et

382   al., 2007). The colonization and direct seed dispersal services provided by domestic ungulate

383   livestock was confirmed, and evidences for improved germination and seedling performance

384   associated with fruit consumption and the seed dispersal, coated in protective manure, to suitable

385   habitats was also confirmed.

386   Caatinga dry forest has been converted to small-scale farming for the agriculture and

387   livestock subsistence, as found in other dry forests and savannas globally (Miccolis et al., 2017;

388   Pérez-Marin et al., 2017). Farming has a continuous demand for the intentional introduction of

389   useful alien species such as cattle, goats and the multiple-use shrub *P. juliflora*, which has now

390   established throughout the Caatinga (Nascimento et al., 2014; Almeida et al., 2015; Ilukor et al.,

391   2016; Walkie et al., 2016). Seed and seedling sensitivity to water stress and desiccation limits the

392   *P. juliflora* proliferation and restricts its establishment to humid/more fertile soils even when its

393   seeds are coated in livestock manure. *Prosopis juliflora* has spread throughout the Caatinga

394   region establishing monospecific stands across floodplains, river banks and sedimentary deposits

395   despite such a life-history limitation. This invasion relies on a close mutualism between human

396   populations and their commensals as agriculture provided degraded habitats, affect soil

397   conditions across river banks via deposition of fine material, while livestock provide seed

398   dispersal services due to the presence of arillated and hard-coated seeds; i.e. a high-quality seed

399   dispersal service that is not available for the native flora in the Caatinga, thereby conferring an

400   adaptive advantage to *Prosopsis* species. *Prosopis juliflora* is expected to spread in the Caatinga

401   with dense populations locally because the rural populations continue to convert Caatinga dry

402   forest into degraded habitats (Sfair et al., 2018). The mutualism with human populations favors

403   *P. juliflora*, as found for other invasive *Prosopis* species across semiarid rangelands globally

404   (Busso et al., 2013). A general perspective on how some *P. juliflora* life-history traits confer

405   invasive capacity has been defined, but other traits (e.g. resprouting capacity, seedling tolerance

406   to herbivory and trampling, allelopathic abilities) enabling *P. juliflora* to become a human

407   commensal deserves further investigation.

408

Conclusions

The *Prosopis juliflora* invasion capacity promoted by its seedling survival and growth depend on habitat and seed dispersal mode in the Caatinga dry forest as this species benefits from human-disturbed, humid soils and manure-involved seeds provided by livestock. This perspective highlights plant-animal interactions among exotic species as potential driver for successful invasion, proliferation and habitat distribution of invasive plants in human-modified landscapes or rangelands.

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Figure 1

Field capacity (A) and soil moisture (B) in floodplain, alluvial terrace and plateau habitats, at 0-20 cm depth. Petrolina, Pernambuco State, Brazil.

Tukey's Honest Significant (field capacity) and Kruskal-Wallis (soil moisture) tests. Columns followed by the same letter are similar ($p < 0.05$). Error bars indicate standard deviation.
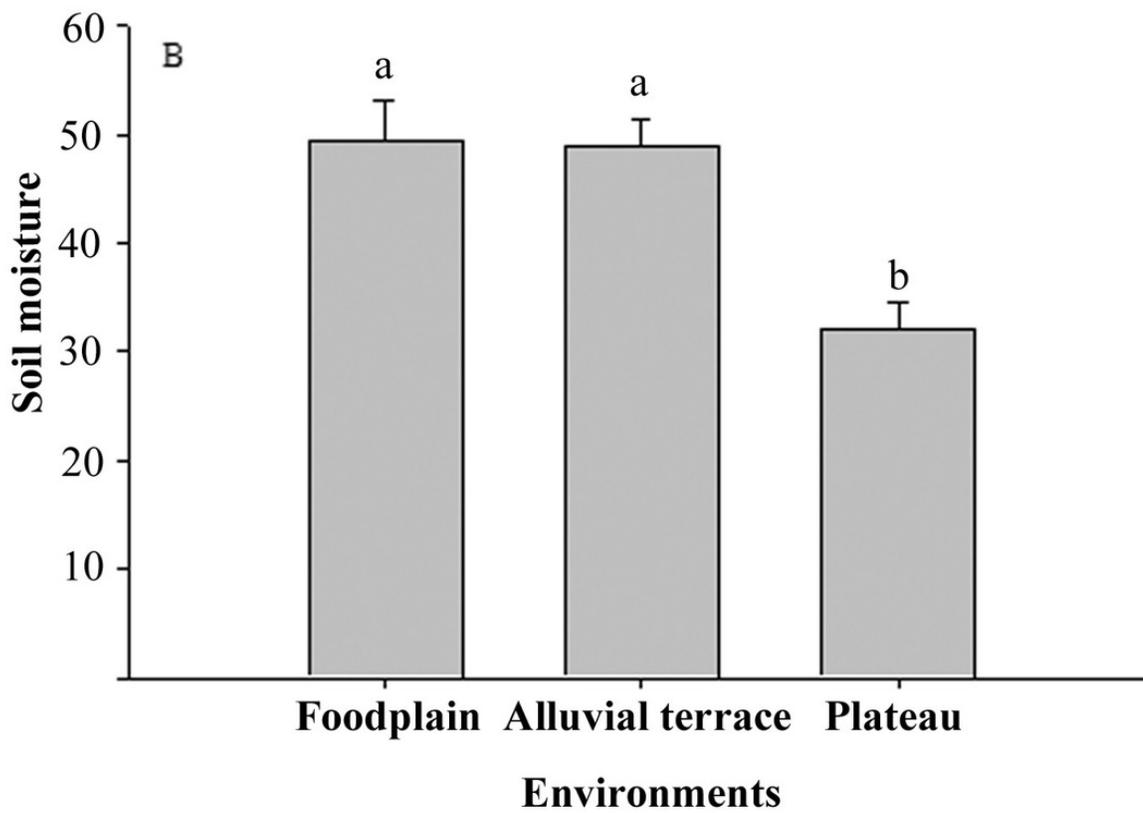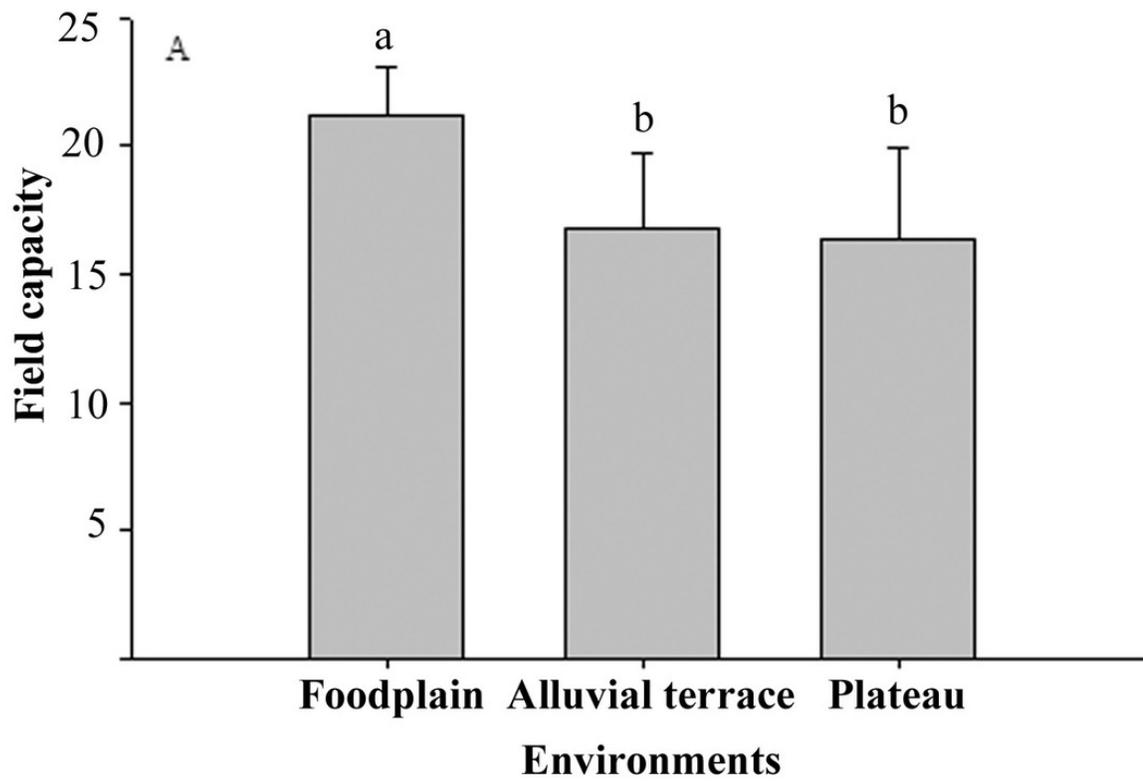
Figure 2

Particle size (A) and organic matter (OM) (g.Kg^{-1}), phosphorus (P) (mg.dm^{-3}), potassium (K) (cmolc.dm^{-3}), calcium (Ca) (cmolc.dm^{-3}), magnesium (Mg) (cmolc.dm^{-3}), aluminum (Al) (cmolc.dm^{-3}) and ca

Tukey's Honest Significant (sand and silt) and Kruskal-Wallis (clay, OM, P, K, Ca, Mg, Al and CEC) tests. Columns followed by same letter are similar ($p= 0.05$). Error bars indicate standard deviation.
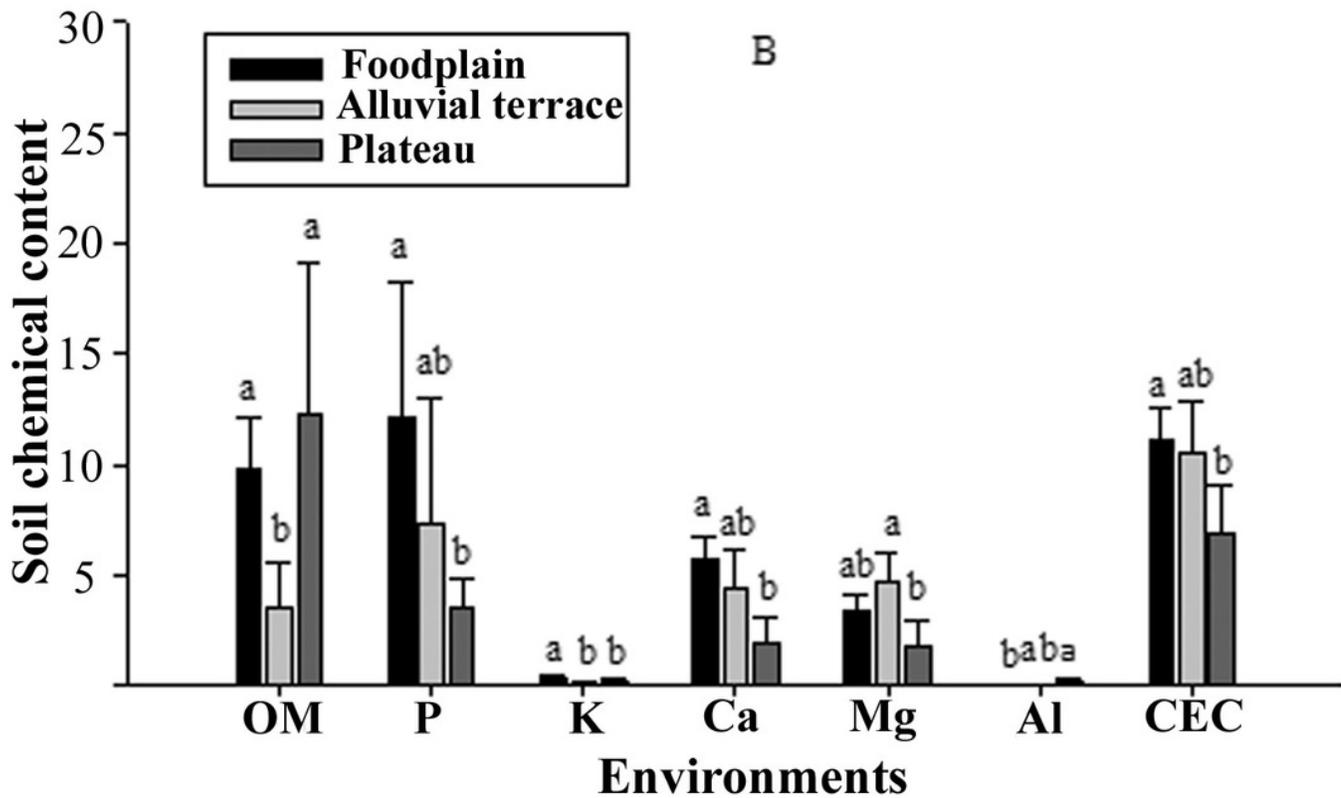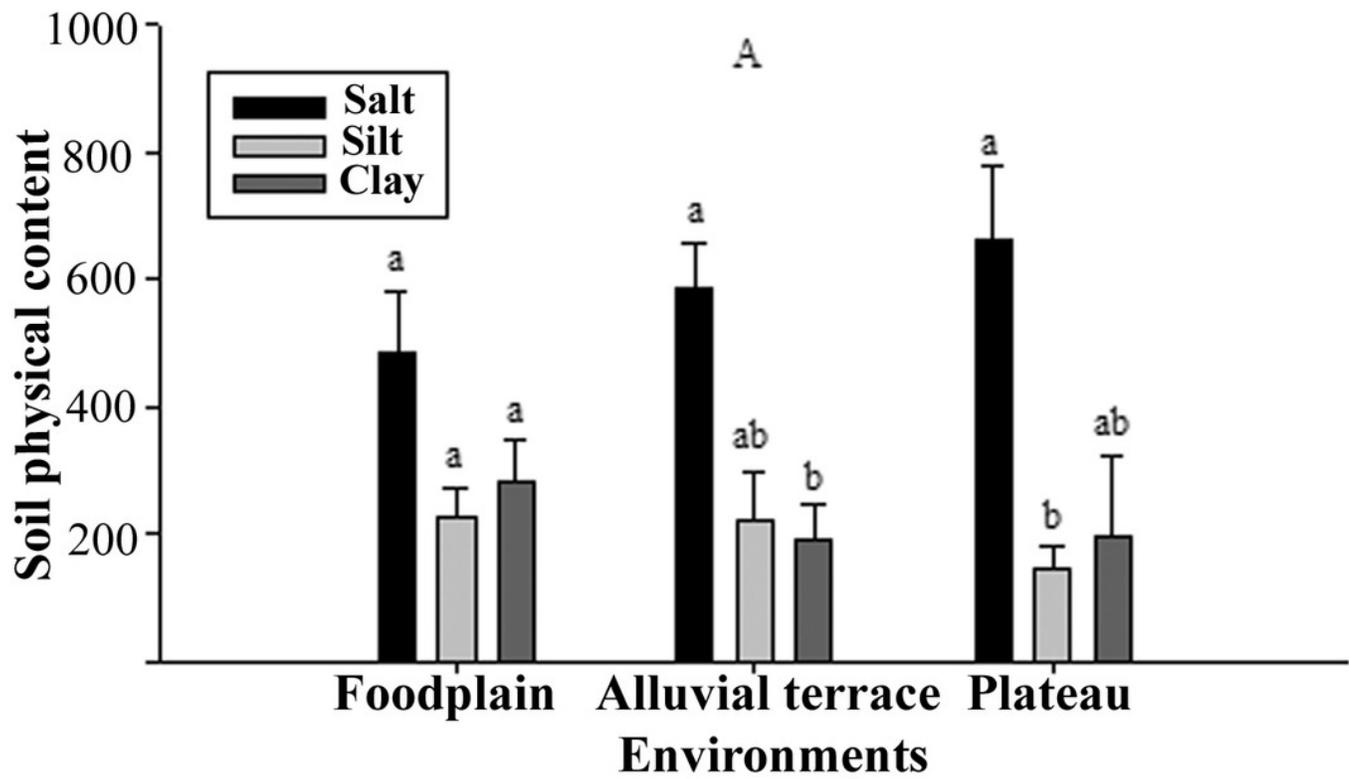
Figure 3

Survival (l_x) and life expectancy (e_x) of *Prosopis juliflora* sown on the soil surface (A), buried (B) or mixed with cattle (C) or mule (D) manure in the floodplain habitat up to 345 days. Petrolina, Pernambuco State,
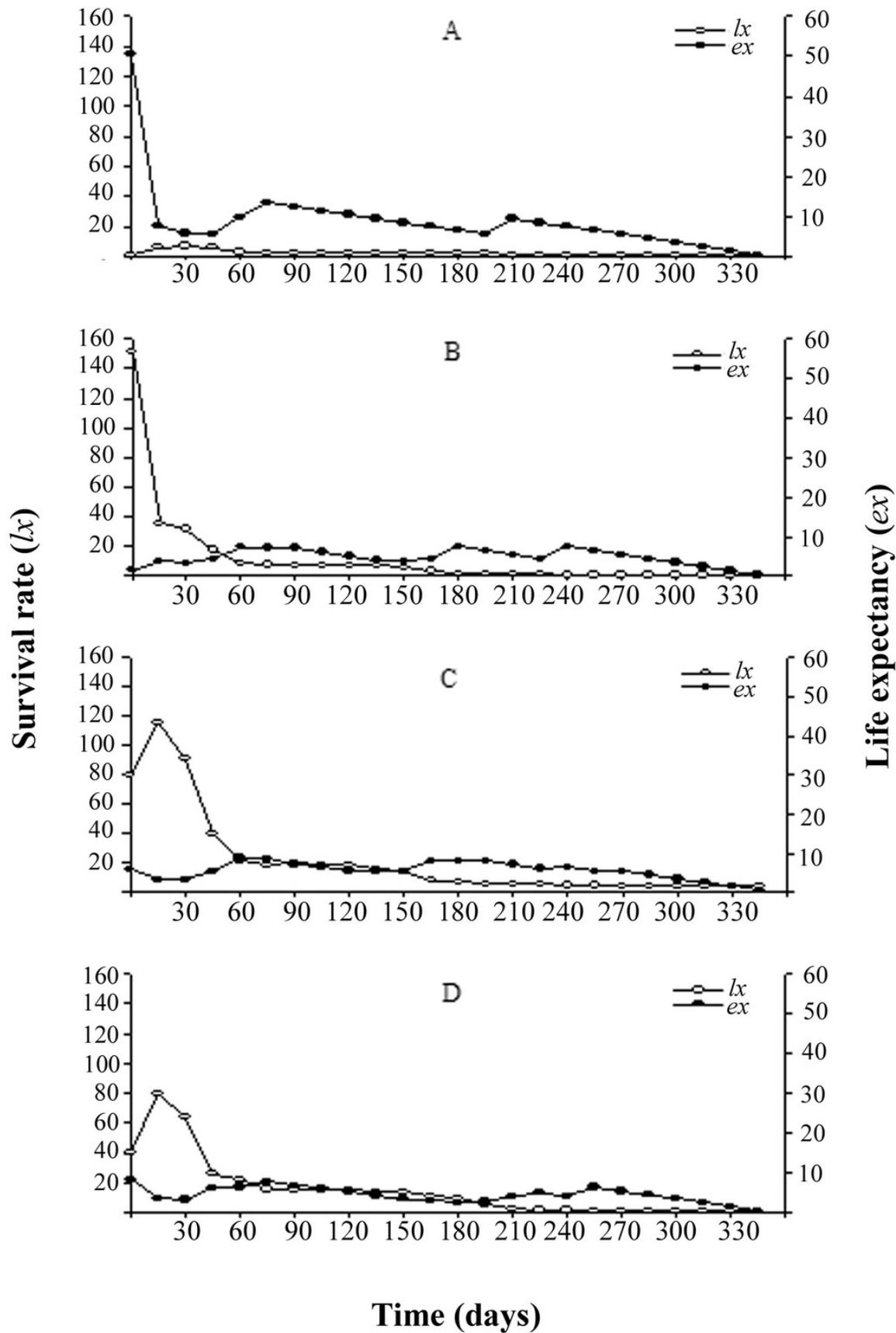
Figure 4

Survival (l_x) and life expectancy (e_x) of *Prosopis juliflora* sown on the soil surface (A), buried (B) or mixed with cattle (C) or mule (D) manure in the alluvial terrace habitat up to 165 days. Petrolina, Pernambuco S
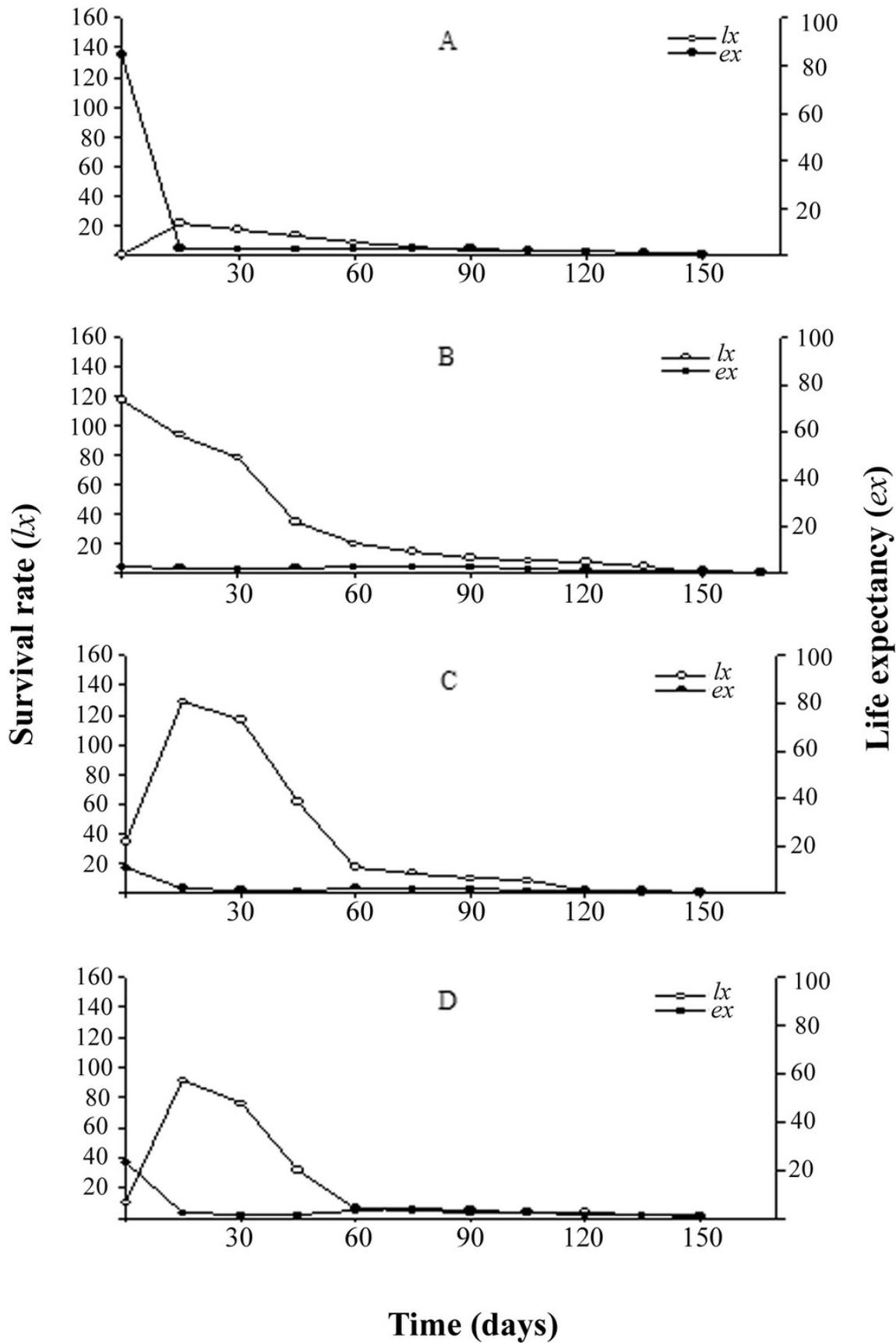
Figure 5

Survival (l_x) and life expectancy (e_x) of *Prosopis juliflora* sown on the soil surface (A), buried (B) or mixed with cattle (C) or mule (D) manure in the plateau habitat up to 165 days. Petrolina, Pernambuco State, Bra