# Diversity and distribution of extra-floral nectaries in the cerrado savanna vegetation of Brazil

**Aim** Throughout evolutionary history, plants and animals have evolved alongside one another. This is especially apparent when considering mutualistic relationships such as between plants with extra-floral nectaries (EFNs, glands on leaves or stems that secrete nectar) and the ants that visit them. Ants are attracted by the nectar and then protect the plant against destructive herbivores. The distribution of these plants is of particular interest, because it can provide insights into the evolutionary history of this unique trait and the plants that possess it. In this study, we investigated factors driving the distribution of woody plants with EFNs in the cerrado vegetation of Brazil. **Location** Brazil **Methods** We used a database detailing the incidence of 849 plant species at 367 cerrado sites throughout Brazil. We determined which species possessed EFNs and mapped their distributions. We tested for correlations between the proportion of EFN species at each site and (i) three environmental variables (mean annual temperature, mean annual precipitation, and the precipitation in the driest quarter of the year), (ii) a broad soil classification, and (iii) the total species diversity of each site. **Results** We found a wide range in the proportion of EFN species at any one site (0 – 57%). However, whilst low diversity sites had wide variation in the number of EFN species, high diversity sites all had few EFN species. The proportion of EFN species was positively correlated with absolute latitude and negatively correlated with longitude. When accounting for total species diversity, the proportion of EFN species per site was negatively correlated with precipitation in the driest quarter of the year and positively correlated with temperature range. **Main conclusions** These results suggest either that herbivore pressure may be lower in drier sites, or that ants are not as dominant in these locations, or that plant lineages at these sites were unable to evolve EFNs.

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# Introduction

The large-scale distribution patterns of many plant traits, as well as the factors that drive these distributions, are still poorly understood in many ecosystems. In particular, plants from the tropics were long believed to have more traits associated with defence against herbivores than plants in temperate latitudes (Schemske et al., 2009). The idea that plants in the tropics experience greater herbivore pressure, thus driving selection for improved defence or resistance traits, is key to our understanding of the factors influencing latitudinal gradients in plant traits and patterns of plant diversity.

The geographic implications of the distribution of plant herbivore defenses is complex, in part because there are many variables associated with geographic distribution. Various studies have demonstrated a general trend of increasing anti-herbivore defences in plants moving toward the equator (Coley & Barone, 1996; Fiala & Linsenmair, 1995; Oliveira & Oliveira-Filho, 1991; Pemberton, 1998; Schemske et al., 2009). This trend is generally believed to correlate with the intensity of current herbivory in the region, or the intensity of herbivory with which the flora's ancestors had to contend. For example, the presence of cyanide as a defensive compound has been demonstrated to vary in this way with latitude as an effect of temperature gradients (Jones, Keymer & Ellis, 1978). Further, the mutualistic relationship between ants (and less commonly, certain wasps and flies) and plants, involving extra-floral nectaries has been demonstrated to increase in abundance with decreasing latitude (Pemberton, 1998). Nevertheless, the results of both a recent meta-analysis and a global observational study contradict these findings, suggesting that plants at higher (temperate) latitudes possess greater herbivory resistance traits

than plants at lower (tropical) latitudes (Moles et al., 2011a and b).

Extra-floral nectaries (EFNs) are nectar-producing glands that occur on plant leaves or stems, and are therefore usually not involved in pollination (Fiala & Linsenmair, 1995). They are integral components in a particularly interesting mutualistic relationship between plants and insects, most often ants. These glands produce a sugary nectar that attracts ants, which either become resident or frequent visitors of the plant. The presence of ants has been demonstrated to result in lower levels of herbivory for the plant (Oliveira, 2004). This benefit is likely the result of the tendency of ant colonies to defend their homes and food sources from possible threats. However, the factors that drive variation in the incidence and abundance of EFN within and among communities remain unknown.

Several studies have determined that EFNs become more prevalent with decreasing latitude (Fiala & Linsenmair, 1995; Keeler, 1980; Oliveira & Leito-Filho 1987; Oliveira & Oliveira-Filho, 1991; Pemberton, 1998), but this information alone is not enough to deduce the cause, because the many potential explanatory variables confound each other in any given ecosystem and they are not always consistent along latitudinal gradients. Further, many such studies compare widely different ecosystems with contrasting evolutionary histories and distantly-related species. For example, the only previous large-scale study to date of EFN prevalence (Pemberton, 1998) was conducted in eastern Asia across a number of different biomes, so it is likely that many confounding factors were missed. A more rigorous approach would compare the same life forms and related species in the same ecosystem across a wide range of latitudes and varying environmental conditions. The Brazilian cerrado is a good candidate for this kind of study. The cerrado is a sa-

vanna biome that previously covered 2 million km$^2$ (about 22%) of Brazil, with a high

level of biodiversity (Oliveira & Marquis, 2002) and a relatively high abundance of plants

species with EFN compared to other parts of the world (Oliveira & Freitas, 2004). The

cerrado biome covers a wide latitudinal range from 23°S to a few sites close to the equator

(Oliveira and Marquis 2002), and is therefore a good place to study latitudinal variation

whilst controlling for as many biogeographic and ecological variables as possible.

For this study, we investigated the environmental factors influencing the distribution

of EFN. Specifically we ask (i) how the abundance of EFN varied with latitude, precip-

itation, temperature, soil type, and the species richness?, and (ii) do these relationships

support previous established relationships between plant defences and latitude? Based

on the current literature we predicted that EFN incidence increased with decreasing lati-

tude (i.e., closer to the equator), and that factors implicated in higher herbivore pressure

such as aseasonality would correlate with high EFN incidence.

## Materials and Methods

We restricted our analyses to woody plants. To consistently document woody plant

incidence across a wide range of latitude and environmental variation, we used the re-

vised dataset collected by Ratter et al. (2003) documenting the incidence of 849 tree or

large shrub species at 367 cerrado and Amazonian savanna sites throughout Brazil. This

dataset currently covers about 75% of the cerrado domain. Other woody communities

of the biome such as gallery and mesophytic forests were not included. Species richness

varied from Amazonian savannas containing only a single woody species to >100 in

the cerrado core area and its southern outliers. All taxa were identified to species-level,

making this dataset extremely valuable and virtually unique in large-scale plant datasets

(Figure 1).

Data on which of these species have extra-floral nectaries was obtained from Neotropical floras (Oliveira & Marquis, 2002; Pennington & Ratter, 2006), an online database (Keeler, 2008), and several journal articles (Oliviera & Leito-Filho, 1987; Oliviera & Oliviera-Filho, 1991; Diaz-Castelazo, et al., 2004, 2005; Oliviera & Fraitas, 2004; Marazzi et al., 2006; Machado et al., 2008; Goita & Klaus, 2009; Schoereder et al., 2010, see Supplementary Table 1). Currently, 1-2% of plant species have been confirmed to possess EFN and it is estimated that a further 1-2 % of species remain to be discovered with EFN (Weber & Keeler 2012). Thus, our estimates of EFN incidence in the cerrado biome are likely to be conservative, despite the above average knowledge of the species present in the system.

Bioclimatic data were derived from a 30″ gridded dataset consisting of interpolated 50-year normals from New World weather stations (Hijmans et al., 2005). Soil data were derived from a digitised version of the 0.0083 (nominally 1-km) resolution Mapa de Solos do Brasil (EMBRAPA, 1981), downloaded from the University of New Hampshire, EOS-WEBSTER Earth Science Information Partner (http://eos-webster.sr.unh.edu/home.jsp).

We examined correlates of EFN richness using a generalized linear modelling approach. We modelled the proportion of EFN species at each site as a function of annual mean temperature, temperature range, and temperature seasonality (SD of temperature), annual mean precipitation, precipitation in the driest quarter, and precipitation seasonality (coefficient of variation in precipitation), a broad soil classification, and total species

98  richness. Because we expressed proportion EFN as the number of species with EFNs out

99  of the total species richness per site, we used a binomial error structure. All explana-

100 tory variables were rescaled by subtracting the mean value and dividing by the standard

101 deviation to permit comparisons among them.

102    Finally we tested whether cerrado species with EFN were more widespread than

103 species without EFN (a measure of the ecological success of the species). We modelled

104 the number of occupied sites as a function of EFN incidence, using a generalised linear

105 model with a Poisson error distribution.

## 106 **Results**

107 A total of 98 tree and shrub species of the cerrado and Amazonian savannas were

108 documented to have EFN, out of a total of 849 species (Figure 1). These were dis-

109 tributed among 51 genera and 30 families (Figure 2). The families with the most species

110 with EFN were the Fabaceae, with 31 species, followed by the Bignoniaceae (8 species),

111 Simaroubaceae (6), Malpighiaceae (6), and Chrysobalanaceae (6) each.

112    Total species richness per site varied from 1 to 212 (mean = 57, sd = 33), and the

113 proportion of species with EFN at each site ranged from 0-58% (mean = 22%, sd = 9%,

114 Figure 3B). There were 39 sites without any species with EFN, and 153 sites with at least

115 25% of species with EFN. There was a greater proportion of species with EFN in the

116 south and east of Brazil (Figure 3A, C and D).

117    In the full generalised linear model containing all bioclimatic variables, four variables

118 had a statistically significant effect on EFN proportion (Figure 4, $P < 0.05$). Total species

119  richness, precipitation seasonality, and precipitation in the driest quarter all had negative

120  effects on EFN proportion; temperature range had a small positive effect on EFN pro-

121  portion (Figures 3 and 5).  These results indicate that cerrado sites with fewer species,

122  lower rainfall in the driest quarter of the year and low seasonality of precipitation all

123  had a higher proportion of species with EFNs. Sites with a greater range of temperature

124  had a slightly greater EFN proportion. There were no statistically significant effect of soil

125  category on EFN proportion.

126      Of all species in the dataset, 235 species (about 28%) occurred in only one site, 556

127  species (66%) occurred in <10, and 778 species (92%) occurred in <100 sites. Species with

128  EFN were on average slightly more widespread than species without EFN, occupying a

129  mean of four sites as opposed to three (Figure 6).

130  **Discussion**

131  We found high variability in the incidence of species with EFN species among sites,

132  ranging from 0 to 58%. Furthermore, we found evidence of a latitudinal gradient in EFN

133  proportion, converse to our prediction.  Sites further from the equator tended to have

134  slightly more species with EFN than those close to the equator (Figure 3C), implying

135  more defences at higher latitudes. However, we found a significant longitudinal gradient

136  as well (Figure 3D), so the situation is more complex than it might appear. What factors

137  cause such variation to occur across a reasonably consistent biome?

138      Sites with low species richness tended to have a higher proportion of species with

139  EFN. Whilst low richness sites may have inflated proportions EFN because each species

140 contributes more to the overall percentage (i.e., one out of four species is obviously a

141 larger percentage than one out of 20), it is likely that we can consider these results to have

142 some causal implications given the potential advantage of possessing EFN especially in

143 low diversity sites. This is because herbivores are present in any site with vegetation,

144 so the selective pressure for effective herbivore defences like EFNs is always present as

145 well. Further, in low diversity sites, rare species are not 'hidden' by common species,

146 and species-specific herbivores can more easily encounter their particular food source.

147 Unfortunately, no data on the abundance of species at each site are available, so we

148 cannot test whether species with EFN are more abundant than those without.

149 The trends in the geographic distribution of EFNs show a greater proportion of EFNs

150 as one moves south from the equator and east toward the Atlantic coast. This latitudinal

151 gradient is consistent with the recent findings of Moles et al. (2011), and contrary to the

152 idea that herbivory intensity increases toward the equator. Paleoecological evidence sug-

153 gests that lower latitudes have historically displayed greater herbivore diversity; however,

154 herbivory is not necessarily more intense along this same gradient (Moles et al., 2011). A

155 comprehensive understanding of the latitudinal distribution of herbivore defences would

156 require further inquiry into the latitudinal distribution of herbivory and we cannot nec-

157 essarily infer implications of the longitudinal gradient from this study. It is possible

158 that the climatic differences of coastal regions may play a role. However, that is not

159 exactly consistent with longitude. There are coastal sites around 55°W and non-coastal

160 sites around 45°W. Further study would need to be devoted to the climatic differences

161 between coastal regions and inland regions.

162 Climate was significantly correlated with EFN proportion. Clear negative relation-

163 ships existed between EFN proportion and both precipitation in the driest quarter of the

164 year and precipitation seasonality, but no significant trend was found with total annual

165 precipitation. This suggests that while precipitation is important, it is likely that ex-

166 tremes in precipitation are what drive EFN (or, more likely, ant abundance), rather than

167 total rainfall. This could have something to do with the effects of periods of drought on

168 the intensity of herbivory. One possible explanation, that would need to be investigated

169 further, is that in dry areas, herbivores get a significant portion of their hydration from

170 the vegetation on which they feed.

171 Sites with a greater annual temperature range had a higher proportion of EFN than

172 sites with a smaller range. Similar to the precipitation results, this implies that it could be

173 the extremes that have the greatest impact on variation. Data on the relationship between

174 the intensity of herbivory and temperature range would be required to fully understand

175 these results.

176 Finally, in order to fully investigate the relationship between plant defences and her-

177 bivore pressure, both sides of the equation must be determined. To date, measuring

178 plant defences has been the more logistically possible. However, effort must be made to

179 estimate herbivory in a consistent manner across ecosystems and biomes in order to fully

180 elucidate the patterns and drivers of variation in plant traits. In terms of traits such as

181 EFN, however, the relationship with insects is also of importance. No data is available on

182 ant abundance across the cerrado, and traits such as EFN may depend more on the avail-

183 ability of the plant's mutualist ants rather than herbivore pressure. Thus, plants in areas

184 of low ant presence or diversity may have evolved rather different defence mechanisms.

185 In conclusion, we have confirmed Moles et al. (2011a,b) suggestion that the latitudinal

gradient in plant defence traits is more complex than originally thought. At least for one specific defence mechanism (EFN) in the cerrado biome, more species of plants are defended at higher latitudes.

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## References

Blthgen, N. & Reifenrath, K. (2003) extra-floral nectaries in an Australian rainforest: structure and distribution. Australian Journal of Botany, 51, 515-527.

Bridgewater, S., Ratter, J.A. & Ribeiro, J.F. (2004) Biographic patterns, -diversity and dominance in the cerrado biome of Brazil. Biodiversity and Conservation, 13, 2295-2318.

Coley, P.D. & Barone, J.A. (1996) Herbivory and plant defences in tropical forests. Annual Review of Ecology and Systematics, 27, 305-335.

Díaz-Castelazo, C., Rico-Gray, V., Ortegaq, F. & Angeles, G. (2005) Morphological and secretory characterization of extrafloral nectaries in plants of coastal Veracruz, Mexico. Annals of Botany, 96, 1175-1189.

Díaz-Castelazo, C., Rico-Gray, V., Oliveira, P.S. & Cuautle, M. (2004) Extra-floral

205 nectar-mediated ant-plant interactions in the coastal vegetation of Veracruz, Mexico:

206 Richness, occurrence, seasonality, and ant foraging patterns. Ecoscience, 4, 472-481.

207 EMBRAPA (1981) Ministrio da Agricultura, Instituto Brasileiro de Desenvolvimento

208 Florestal, Secretria de Planejamento e Coordenao da Presidńcia da Republica, Fundao

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212 Pessoa, J.A.M. do Amaral. URL: http://eos-webster.sr.unh.edu/home.jsp, accessed: 5-

213 MAR-2012.

214 Fiala, B. & Linsenmair, K.E. (1995) Distribution and abundance of plants with extra-

215 floral nectaries in the woody flora of a lowland primary forest in Malaysia. Biodiversity

216 and Conservation, 4, 165-182.

217 Goita, W. & Klaus, J. (2009) Ant-plant association in different forests in Venezuela.

218 Neotropical Entomology, 38, 7-31.

219 Keeler, K.H. (1980) Distribution of plants with extra-floral nectaries in temperate com-

220 munities. American Midland Naturalist, 104, 274-280.

221 Keeler, K.H. (2008) World list of plants with extra-floral nectaries. URL: http://bsweb.unl.edu/Emer

222 floral/Cover.htm, accessed: Feb-2012.

223 Machado, S.R., Morellato, L.P.C., Sajo, M.G. & Oliveira, P.S. (2008) Morphological

224 patterns of extra-floral nectaries in woody plant species of the Brazilian cerrado. Plant

225 Biology, 10, 660-673.

226 Marazzi, B., Endress, P.K., Paganucci de Queiroz, L. & COnti, E. (2006) Phylogenetic

227 relationships within Senna (Leguminosae, Cassiinae) based on three chloroplast DNA

228 regions: patterns in the evolution of floral symmetry and extrafloral nectaries. American

229 Journal of Botany, 93, 288-303.

230 Moles, A.T., Bonser, S.P., Poore, A.G.B., Wallis, I.R. & Foley, W.J. (2011a) Assessing the

231 evidence for latitudinal gradients in plant defence and herbivory. Functional Ecology, 25,

232 380-388.

233 Moles, A.T., Wallis, I.R., Foley, W.J. et al. (2011b) Putting plant resistance traits on

234 the map: a test of the idea that plants are better defended at lower latitudes. New

235 Phytologist, 191, 777-788.

236 Oliviera, P.S. & Fraitas, A.V.L. (2004) Ant-plant-herbivore interactions in the neotrop-

237 ical cerrado savanna. Naturwissenschaften, 91, 557-570.

238 Oliviera, P.S. & Leito-Filho, H.F. (1987) Extra-floral nectaries: Their taxanomic dis-

239 tribution and abundance in the woody flora of cerrado vegetation in southeast Brazil.

240 Biotropica, 19, 140-148.

241 Oliveira, P.S. & Marquis, R.J. (eds). (2002) The Cerrados of Brazil. Columbia Univer-

242 sity Press.

243 Oliviera, P.S. & Oliveira-Filho, A.T. (1991) Plant-Animal Interactions: Evolutionary

244 Ecology in Tropical and Temperate Regions. John Wiley and Sons Inc. 163-175.

245 Pemberton, R.W. (1998) The occurrence and abundance of plants with extra-floral

246 nectaries, the basis for herbivore defensive mutualisms, along a latitudinal gradient in

247 east Asia. Journal of Biogeography, 25, 661-668.

248 Pennington, R.T. & Ratter, J.A. (eds). (2006) Neotropical Savannas and Seasonally Dry

249 Forests: Plant Diversity, Biogeography, and Conservation. CRC Press.

250 Pennington, T.D., Reynel, C. & Daza, A. (2004) Illustrated guide to the trees of Peru.

<sup>251</sup> Sherborne, Dorset: David Hunt.

<sup>252</sup> Ratter, J.A., Bridgewater, S., Ribeiro, J.F., Fonseca-Filho, J., Rodrigues da Silva, M.,
<sup>253</sup> Milliken, W., Pullan, M., Pott, A., Oliveira-Filho, A.T., Durigan, G. & Pennington, R.T.
<sup>254</sup> Analysis of the floristic composition of the Brazilian cerrado vegetation IV: Presentation
<sup>255</sup> of a Revised Data-Base of 367 Areas. URL: http://www.cerrado.rbge.org.uk, accessed:
<sup>256</sup> 20-FEB-2012.

<sup>257</sup> Schemske, D.W., Mittelbach, G.G., & Cornell, H.V. (2009) Is there a latitudinal gradient
<sup>258</sup> in the importance of biotic interactions? Annual Review of Ecology, Evolution, and
<sup>259</sup> Systematics, 40, 245.

<sup>260</sup> Schoereder, J.H., Sobrinho, T.G., Madureira, M.S., Ribas, C.R. & Oliveira, P.S. (2010)
<sup>261</sup> The arboreal ant community visiting extra-floral nectaries in the Neotropical cerrado
<sup>262</sup> savanna. Terrestrial Arthropod Reviews 3, 3-27.

<sup>263</sup> Vasquez M., R. (1997) Flórula de las reserves biológicas de Iquitos, Perú. Monographs
<sup>264</sup> in Systematic Botany from the Missouri Botanical Garden. MOBOT, St. Louis, MO, USA.

<sup>265</sup> Weber, M.G. & Keeler, K.H. (2013) The phylogenetic distribution of extrafloral nec-
<sup>266</sup> taries in plants. Annals of Botany, 111, 1251-1261.

<sup>267</sup> **Figure Legends**

<sup>268</sup> **Figure 1** Woody plant species with extra-floral nectaries from the cerrados of Brazil. A)
<sup>269</sup> *Inga vera*, Fabaceae; B) *Qualea grandiflora*, Vochysiaceae; C) *Tabebuia aurea*, Bignoniaceae,
<sup>270</sup> D) *Ouratea hexaperma*, Ochnaceae; E) *Qualea grandiflora*, Vochysiaceae; F) *Tabebuia aurea*,
<sup>271</sup> Bignoniaceae. Credits: Robin Foster, The Field Museum, Chicago, USA (A, C, F); Julio

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274 Biology/Unicamp, Campinas, SP, Brazil (B, E).

275 **Figure 2** The number of species, genera and families with (white) and without (grey)

276 extra-floral nectaries in the cerrado of Brazil from a sample of 849 species found in 367

277 sites.

278 **Figure 3** Variation in the proportion of species with extra-floral nectaries (EFN) in the

279 cerrado and Amazonian savannas of Brazil. A) Location of sample sites. Size of circle is

280 proportional to the proportion of species with nectaries. B) Proportion of species with

281 EFN as a function of total species richness. C) Proportion of species with EFN as a

282 function of latitude. D) Proportion of species with EFN as a function of longitude.

283 **Figure 4** Coefficient estimates from a binomial generalized linear model of the proportion

284 of species with extra-floral nectaries as a function of standardised bioclimatic variables,

285 soil type and total species richness in 367 sites in the cerrado and Amazonian savanna

286 vegetation of Brazil. Each point indicates the estimate, with thick and thin error bars

287 indicating one and two standard deviations, respectively.

288 **Figure 5** The proportion of species with extra-floral nectaries in 367 cerrado sites in Brazil

289 as a function of six bioclimatic variables.

290 **Figure 6** Range size of cerrado species with and without EFN. Range size was defined as

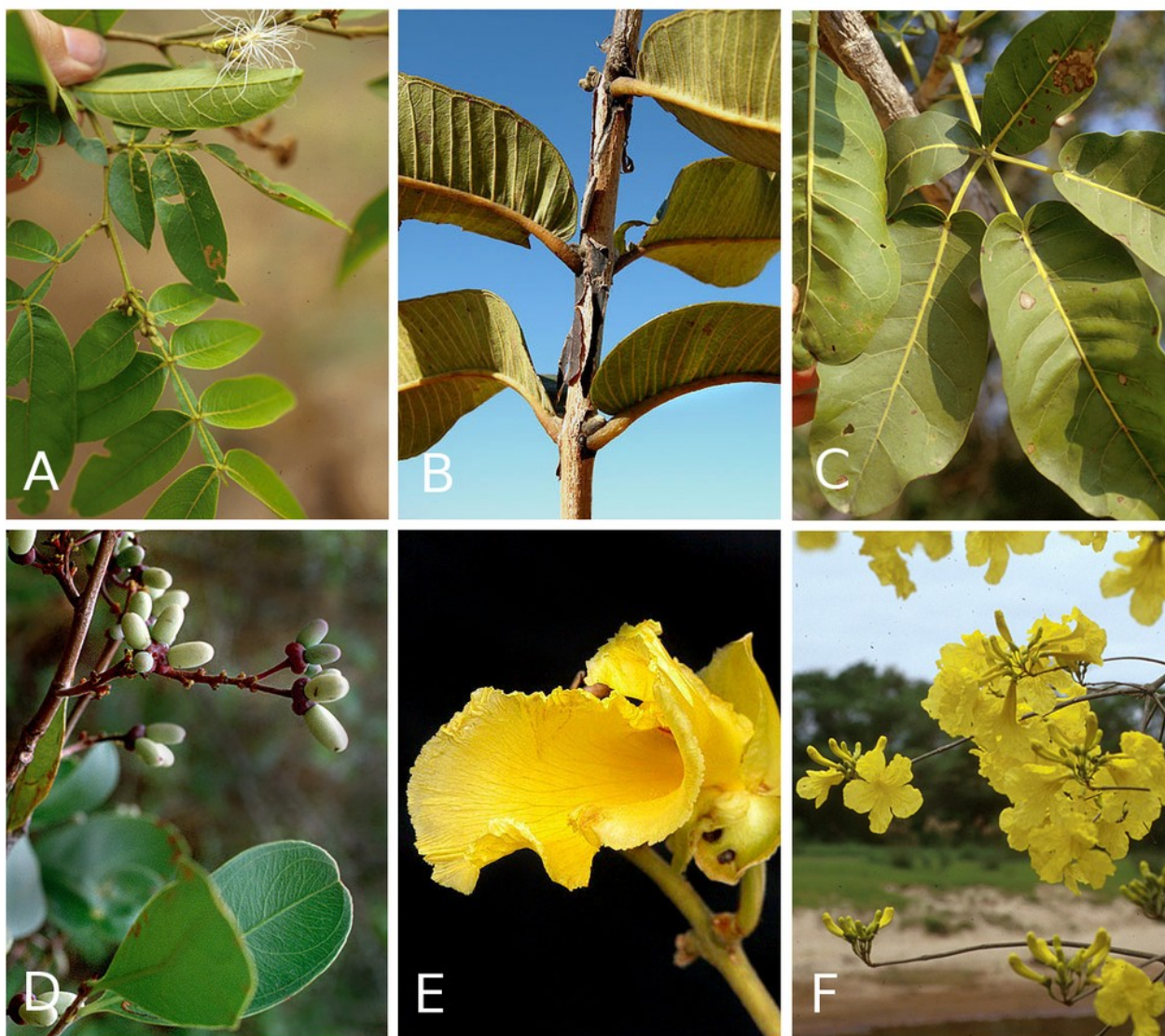
291 the number of occupied sites.

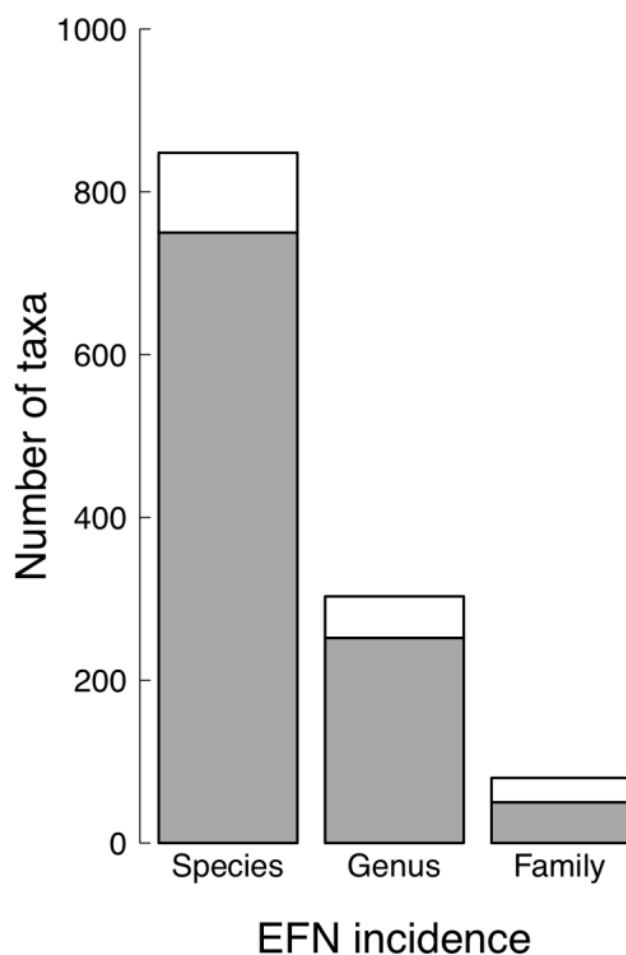
# Supplementary information

**Supplementary Table 1** Woody tree and shrub species with extra-floral nectaries of the cerrado region. TAB-delimited text file. Column names: Family = family, Genus = genus, Spp = specific epithet, Name = full latin binomial with authority, EFN = EFN present? (1 = yes), Site = location of EFN on the plant, Ref = reference source for information (Diaz = Diaz-Castelazo, C et al. (2004), Gottia = Goitia & Klaus (2009), Keeler = Keeler (2008), Machado = Machado et al. (2008), Marazzi = Marazzi et al. (2006), Oliviera = Oliviera & Leito-Filho (1987), Pennington = Pennington et al. (2004), Schoereder = Schoererder et al. (2010), Vasquez = Vasquez (Vasquez 1997))

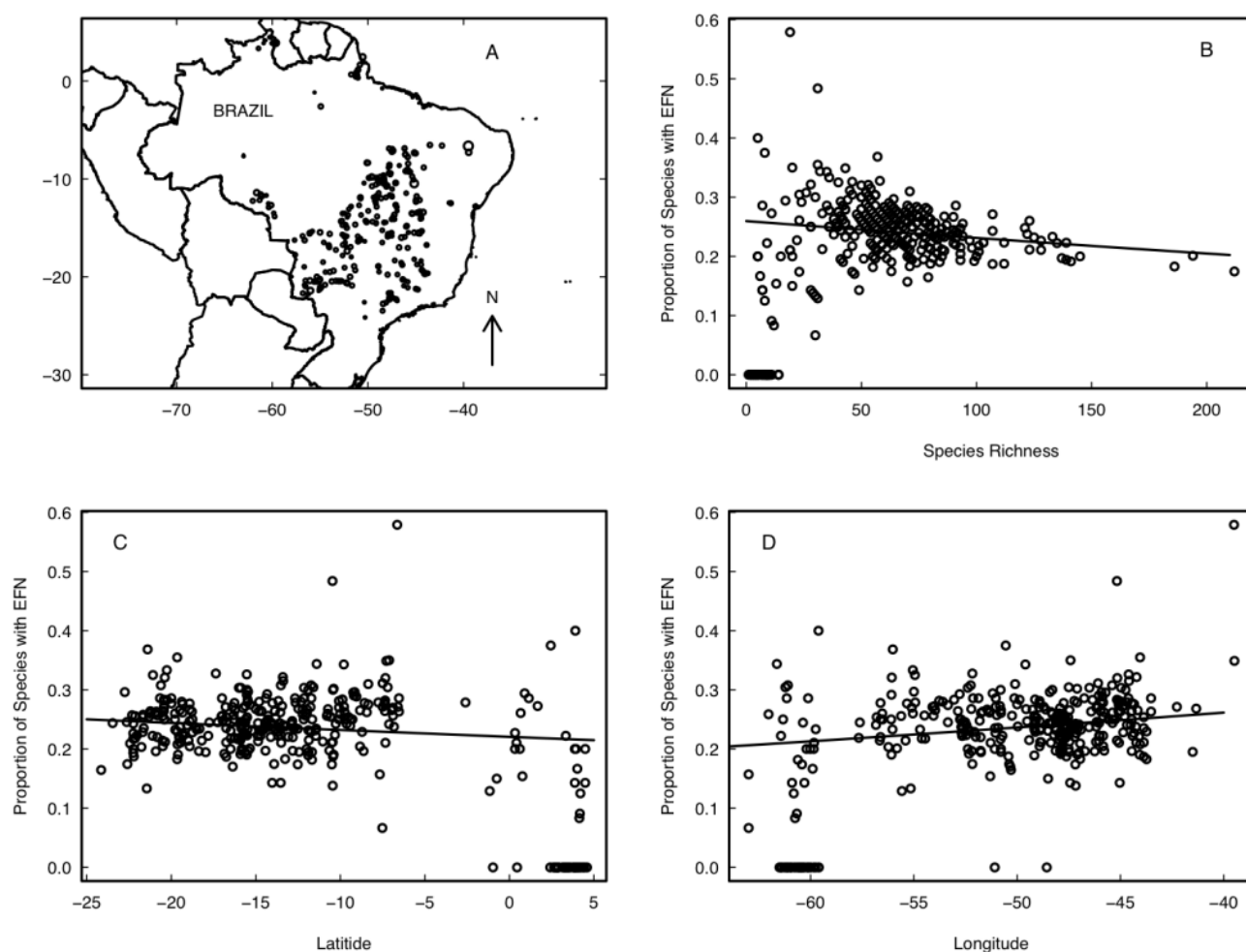
# Figure 1

Woody plant species with extra-floral nectaries from the cerrados of Brazil.

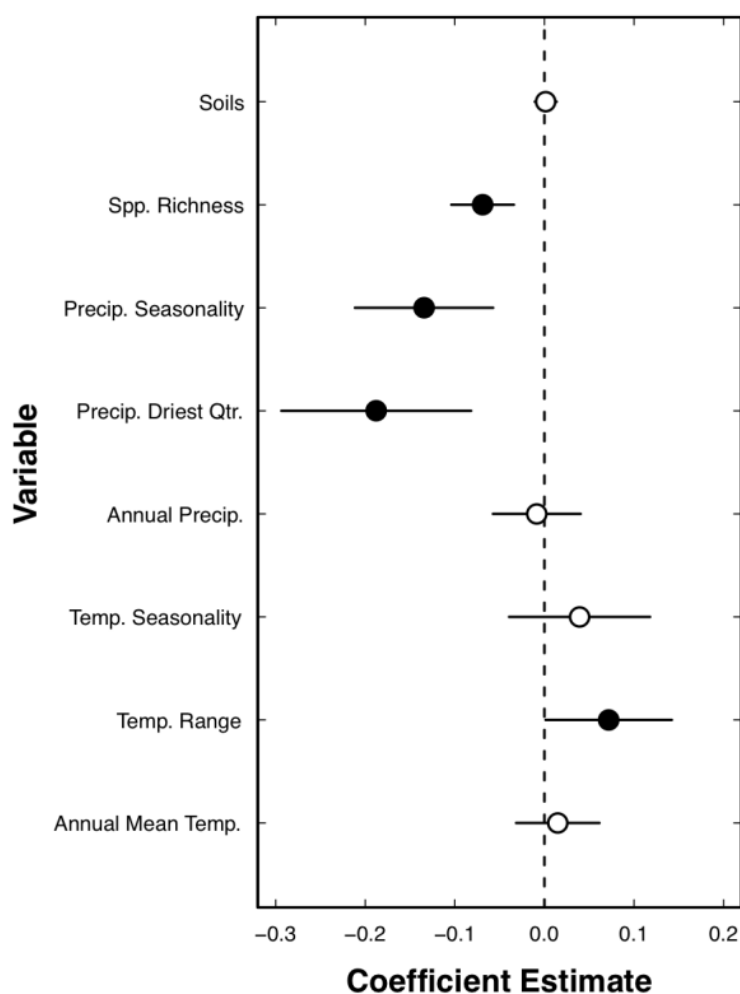
A) Inga vera, Fabaceae; B) Qualea grandiflora, Vochysiaceae; C) Tabebuia aurea, Bignoniaceae, D) Ouratea hexaperma, Ochnaceae; E) Qualea grandiflora, Vochysiaceae; F) Tabebuia aurea, Bignoniaceae. Credits: Robin Foster, The Field Museum, Chicago, USA (A, C, F); Julio Lombardi, Departamento de Botânica, Instituto de Biociências de Rio Claro, Universidade Estadual Paulista, SP, Brazil (D); Gustavo Schimizu, Dept. Plant Biology, Institute of Biology/Unicamp, Campinas, SP, Brazil (B, E).

# Figure 2

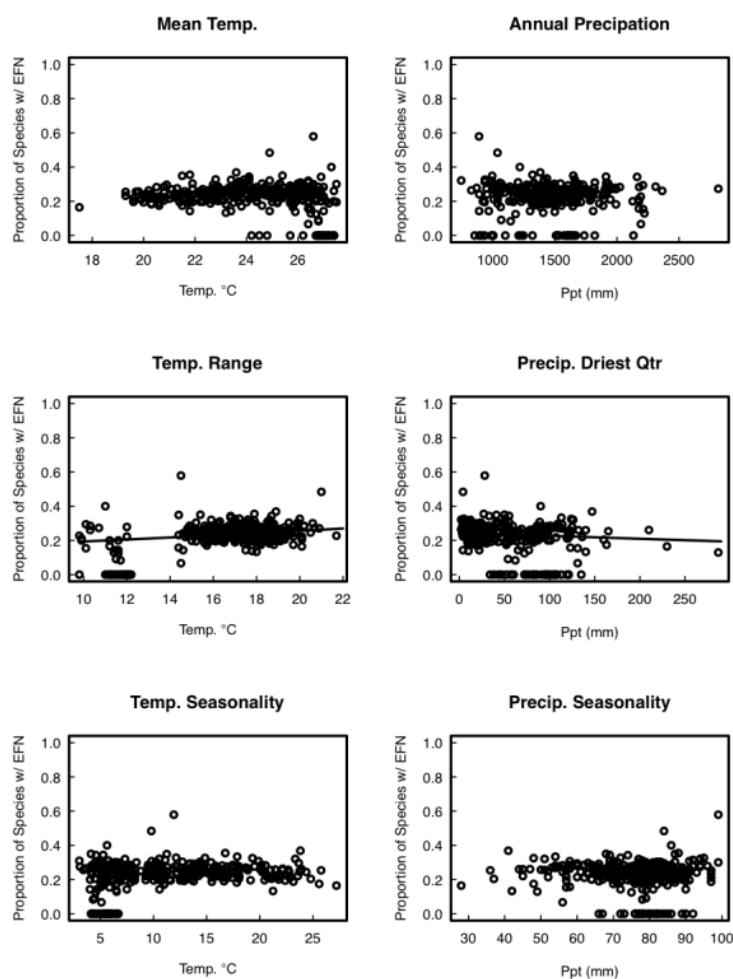
The number of species, genera and families with (white) and without (grey) extra-floral nectaries in the cerrado of Brazil from a sample of 849 species found in 367 sites

# Figure 3

Variation in the proportion of species with extra-floral nectaries (EFN) in the cerrado and Amazonian savannas of Brazil.

A) Location of sample sites. Size of circle is proportional to the proportion of species with nectaries. B) Proportion of species with EFN as a function of total species richness. C) Proportion of species with EFN as a function of latitude. D) Proportion of species with EFN as a function of longitude.

# Figure 4

Coefficient estimates from a binomial generalized linear model of the proportion of species with extra-floral nectaries as a function of standardised bioclimatic variables.

The model also included soil type and total species richness in 367 sites in the cerrado and savanna vegetation of Brazil. Each point indicates the estimate, with thick and thin error bars indicating one and two standard deviations, respectively.

# Figure 5

The proportion of species with extra-floral nectaries in 367 cerrado sites in Brazil as a function of six bioclimatic variables.

# Figure 6

Range size of woody cerrado species with and without extra-floral nectaries.

Range size was defined as the number of occupied sites out of 367 sites throughout the cerrado and Amazonian savannas of Brazil.