

Bromeliad species of the Atlantic forest of north-east Brazil: losses of critical populations of endemic species

José A. Siqueira Filho and Marcelo Tabarelli

Abstract In this paper we examine the number of known populations of 86 bromeliad species recorded in the Atlantic forest of north-east Brazil, to test the following predictions: (1) the current number of populations of most bromeliad species inhabiting the Atlantic forest of north-east Brazil is critically low, (2) the number of extant populations of a particular species is associated with the ecological attributes of the species, and (3) habitat loss determines, at least in part, the current distribution and number of populations of each species. At present there are at least 535 bromeliad populations in this forest but 61.6% of species have < 6 populations and 24.4% have only one known population. The mean number of populations per species was significantly lower among species endemic to this part of the Atlantic forest, species recorded in only one vegetation type, forest and inselberg species, and obligatory epiphytic and terrestrial species. We were unable to relocate 41

populations recorded between 1920 and 1996, and populations of 20 species have become locally extinct. For these bromeliads geographic range, habitat specificity and life form appear to determine which species are more vulnerable to extinction. The species that have < 6 extant populations include 27 species that are endemic to this forest. These species need to be evaluated for inclusion on both the IUCN and Brazilian Red Lists. Some of these species will only survive if the fragments containing the last populations are declared as protected areas.

Keywords Brazilian Atlantic forest, Bromeliaceae, ecological attributes, habitat loss, plant endemism, species extinction.

This paper contains supplementary material that can only be found online at <http://journals.cambridge.org>

Introduction

Three questions still challenge conservation planners: how many species, which species, and by what processes will species be extirpated by habitat loss and fragmentation in tropical forests (Turner, 1996). Answers to these questions are essential for managing landscapes to avoid large-scale impoverishment of biota (Bierregaard *et al.*, 2001). In the case of tropical forests, threatened groups of plant species have been identified based on ecological attributes such as geographical distribution (Andersen *et al.*, 1997), abundance (Laurance *et al.*, 1997), dependency on vertebrate seed dispersers (Silva & Tabarelli, 2000) and sensitivity to edge-effects (Laurance, 2001).

Bromeliaceae is one of the most speciose plant families in the neotropics, with > 2,930 species in 56 genera (Luther, 2002). Bromeliads include terrestrial xerophytes

and both facultative and obligatory epiphytes, and occur in a wide range of habitats. However, it is in tropical rainforests that bromeliads attain their highest species richness at any spatial scale (Benzing, 2000). High levels of species richness in these forests are associated in particular with the presence of epiphytes, which grow on trunks and branches, especially on canopy and emergent trees, and make bromeliad species a conspicuous element of neotropical rainforests (Benzing, 2000).

With > 500 species and varieties the Brazilian Atlantic forest is considered an evolutionary centre of the Bromeliaceae (Martinelli, 1994). Although many species occur in the montane and cloud Atlantic rainforests of south-east Brazil (Lima & Guedes-Bruni, 1997) a large number have also been recorded in the forest of north-east Brazil, a biogeographic subregion of the Brazilian Atlantic forest (Silva & Casteleti, 2003). Before 1970 only 36 species had been recorded in this forest (Andrade-Lima, 1966), but 50 further species were subsequently discovered (Siqueira Filho, 2003) of which six were previously undescribed (Siqueira Filho & Leme, 2000, 2002; Leme & Siqueira Filho, 2001).

Because of forest conversion to sugar cane fields < 6% of the Atlantic forest of north-east Brazil remains. In addition to habitat loss, the remaining forest is now reduced to archipelagos of small fragments, and

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protected areas are few and small (Silva & Tabarelli, 2000). There are at least four reasons to believe that habitat loss and fragmentation will reduce the abundance of bromeliad species in this region. Firstly, several species occupy narrow geographic ranges (Smith & Downs, 1974, 1977, 1979). Secondly, forest fragmentation causes local and regional extirpation of emergent trees (Laurance *et al.*, 2000), which constitute a key habitat for epiphytic bromeliad species (Benzing, 2000; Dimmit, 2000) and vertebrate seed dispersers (Chapman *et al.*, 2003). Thirdly, forest fragmentation leads to habitat dissection and invasion of ruderal plants, and makes fragments prone to forest fires (Tabarelli *et al.*, 2004). Fourthly, forest fragmentation usually facilitates plant collecting by local human populations (Clark *et al.*, 1995).

We therefore expect that (1) the current number of populations of most bromeliad species inhabiting the Atlantic forest of north-east Brazil is critically low, (2) the number of extant populations of a particular species is associated with the ecological attributes of the species, and (3) habitat loss determines, at least in part, the current distribution and number of populations of each species. Here we quantify the current number of populations of the 86 bromeliad species (of which *c.* 50% are endemic; Siqueira Filho, 2003) recorded in this part of the Atlantic forest; analyse their ecological attributes with respect to geographical range, habitat specificity, life form, pollination and seed dispersal mode, and check 334 historical plant records to test these predictions.

Study area

The Atlantic forest of north-east Brazil is an 80-km wide strip of forest that once covered 56,400 km² to the north of the São Francisco river (Fig. 1) but now covers only 5.6% of the original forest extent (IBGE, 1985). The extant forest comprises five vegetation types determined by an annual rainfall gradient (900–2,400 mm) from the coast inland (Table 1). Despite its relatively small area this forest is one of the most distinctive centres of endemism in South America (Prance, 1987; Brown Jr & Freitas, 2000; Silva *et al.*, 2004). The most recent review of the biogeography of the whole Atlantic forest region, based on the distribution of plants, butterflies, reptiles, birds and primates, confirmed that north-east Brazil is one of five areas of endemism in the Atlantic forest (Silva & Casteleti, 2003). The total remaining areas of natural vegetation is now reduced to 3,198 km² (Table 1).

Methods

Number of populations

We consider a population to be any group of individuals recorded in any forest fragment surrounded by a

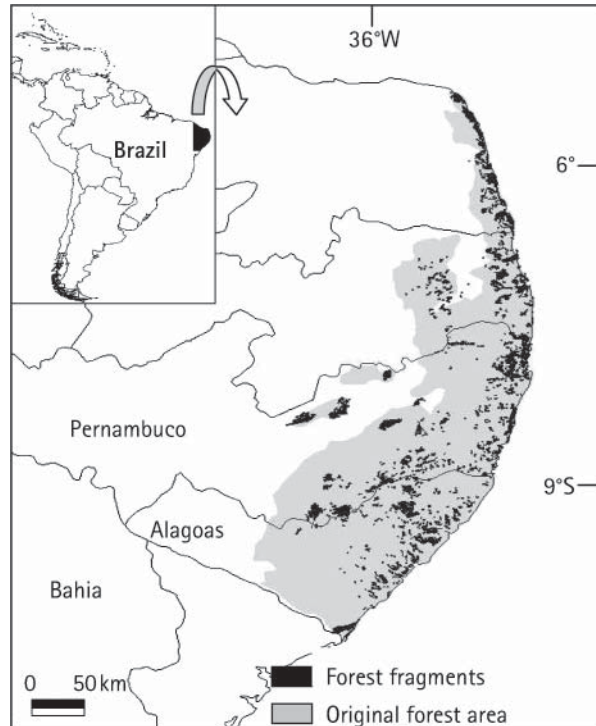


Fig. 1 The original extent of the Atlantic forest of north-east Brazil, and the extant fragments.

Table 1 The five vegetation types of the Atlantic forest of north-east Brazil, with original coverage and area remaining (from Conservation International *et al.*, 1994).

Vegetation type	Original area(km ²)	Remaining area, km ² (%)
Ecotonal forest	19,715.1	665.8 (3.3)
Semi-deciduous forest	16,045.1	803.7 (5.0)
Open forest	11,576.7	832.9 (7.1)
Evergreen forest	6,141.1	280.3 (4.5)
Restingas	2,922.8	614.7 (21.1)
<i>Total</i>	56,400.8	3,197.6 (5.6)

non-forest matrix or any patch of inselberg vegetation (*sensu* Barthlott & Porembski, 2000). This is a simple, operational and replicable concept that implies that the number of populations is correlated with the total number of forest fragments and inselbergs inhabited by each species. To estimate the number of populations of these 86 bromeliad species we used three sources of information: (1) the analysis of 657 plant records and their voucher specimens in eight regional herbaria: UFP, IPA, PEUFR, ALCB (Holmgren *et al.*, 1990), EAN, MAC, MUFAL and HST (Barbosa & Barbosa, 1996), (2) monographs and checklists (Smith & Downs, 1974, 1977, 1979; Siqueira Filho, 2002, 2004), and (3) data obtained from bromeliad surveys at 239 localities in the Atlantic forest

of north-east Brazil. We have conducted surveys since 1996, resulting in 288 new bromeliad records (Siqueira Filho, 2002, 2004). Specimens from surveys by JASF are available at the herbaria of UFP, HB and WU (Holmgren *et al.*, 1990).

Ecological attributes

The 86 species were categorized into 21 ecological groups with respect to five attributes: (1) geographical range, (2) habitat specificity, (3) life form, (4) pollination mode, and (5) seed dispersal mode. This categorization was based on our personal knowledge of species' life histories, accounts of life history traits (Smith & Downs, 1974, 1977, 1979), herbarium specimens, and collection of living plants by JASF.

Geographical range categories are: endemic to the Atlantic forest of north-east Brazil, endemic to the Brazilian Atlantic forest, and widely distributed (i.e. also recorded in other ecosystems). Habitat specificity is categorized at three levels. Macrohabitat refers to the number of vegetation types (Table 1) in which each species occurs. Mesohabitat refers to particular habitat preferences, *viz.*: forest, inselberg, and indifferent (species inhabiting both mesohabitats). Microhabitat refers to particular habitats within forest vegetation: understorey, canopy (both canopy and emergent trees), and indifferent (species inhabiting both microhabitats).

Three life forms were recognized: obligatory epiphytes, terrestrial, and facultative, i.e. species with both terrestrial and epiphytic individuals. There are two types of pollinator: vertebrates (bats and hummingbirds), and invertebrates (insects, according to floral syndromes described by Faegri & Pijl, 1979). Seed dispersal is by two types of agent: vertebrates for species that produce diaspores attached to a fleshy pulp, or other features typically associated with vertebrate dispersal agents (endozoochorous species *sensu* Roosmalen, 1985), and abiotically, i.e. those with winged seeds or plumes. After assigning bromeliad species and populations to these ecological groups we calculated the mean number of populations per species in each of the 21 ecological groups.

Habitat loss

To examine the role played by habitat loss in the current patterns of abundance of bromeliad species we selected 334 historical population records (1920–1996) for 72 species with available herbarium specimens. For each of these records we identified where specimens were collected and we tried to relocate from these populations in 239 surveys during 1996–2002. Populations were categorized as still present in forest fragments or locally

extinct. In this way we identified the total number of populations that have apparently gone locally extinct since 1920 and what has happened to their habitat.

Statistical analysis

Differences in the proportion of bromeliad species within categories were analysed with G tests (Sokal & Rohlf, 1995). Differences in average number of populations between the 21 ecological groups and among ecological groups within categories of geographical range were analysed using Kruskal-Wallis tests, a nonparametric ANOVA (Sokal & Rohlf, 1995).

Results

Of the 86 bromeliad species recorded in the Atlantic forest of north-east Brazil 48 belong to the Subfamily Bromelioideae (55.8%), 33 to Tillandsioideae (38.3%), and five to Pticarnioideae (5.8%). The number of located populations and the five ecological attributes of each of the 86 species are given in the Appendix, and the number of species and populations and mean number of populations per species in each of the 21 ecological groups in Table 2. We located 535 bromeliad populations, with 1–26 populations of each species. However, 61.6% of species had < 6 populations and 24.4% had only one population ($G = 35.7$, $df = 4$, $P < 0.0001$). Nearly half of the species (48.8%) are endemic to this forest, most (72%) occur in only one or two vegetation types, are forest species (63.8%), and are understorey or forest canopy/emergent species (84.2%). Obligatory epiphytic species, pollinated and dispersed by vertebrates, were the most common.

The mean number of populations per species was significantly lower among species endemic to this part of the Atlantic forest, species recorded in only one vegetation type, forest and inselberg species, and obligatory epiphytic and terrestrial species. Comparing the categories that represent the two geographical extremes, amongst the widely distributed species ($n = 26$) but not amongst the species endemic to the north-east forest ($n = 42$), mean number of populations of forest and inselberg species was significantly lower than that of indifferent species (Fig. 2a; $H = 10.9$, $df = 2$, $P = 0.0041$). The mean number of populations of understorey, canopy and indifferent species did not differ significantly amongst either the species endemic to the north-east forest or the widely distributed species (Fig. 2b). The mean number of populations of obligatory epiphyte and terrestrial species was less than half of that of facultative species amongst species endemic to the north-east forest (Fig. 2c; $H = 11.6$, $df = 2$, $P = 0.0028$), but there were no significant differences amongst the widely distributed species.

Table 2 Ecological groups (see text for details) of the 86 bromeliad species of the Atlantic forest of north-east Brazil, with the number of species and populations categorized in each group, and mean number of populations per species in each group.

Ecological groups	No. of species (% of total) ¹	No. of populations	Mean no. of populations per species (\pm SE) ²
Geographical range			
Endemic to Atlantic forest of north-east Brazil	42 (48.8)	212	5.1 \pm 0.94 a
Endemic to Brazilian Atlantic forest	18 (20.9)	103	5.7 \pm 0.97 ab
Widely distributed	26 (30.2)	220	8.4 \pm 1.3 b
Macrohabitat			
One type	41 (47.6)	91	2.2 \pm 0.26 a
Two types	21 (24.4)	118	5.6 \pm 0.67 b
Three types	10 (11.6)	109	10.9 \pm 2.3 b
Four types	10 (11.6)	152	15.2 \pm 1.7 c
Five types	4 (4.6)	65	16.2 \pm 1.9 c
Mesohabitat			
Forest	53 (63.8)	284	5.3 \pm 0.69 a
Inselberg	13 (15.6)	53	4.1 \pm 1.1 a
Indifferent species	17 (20.4)	194	11.4 \pm 1.9 b
Microhabitat			
Forest understorey	25 (35.7)	131	5.2 \pm 1.1
Forest canopy/emergent	34 (48.5)	278	8.1 \pm 1.2
Indifferent species	11 (15.7)	71	6.4 \pm 1.7
Life form			
Obligatory epiphyte	32 (37.2)	171	5.3 \pm 0.84 a
Terrestrial	25 (34.8)	130	4.3 \pm 0.83 a
Facultative	24 (27.9)	234	9.7 \pm 1.6 b
Pollination mode			
Vertebrate-pollinated	56 (65.8)	340	6.1 \pm 0.83
Invertebrate-pollinated	29 (34.1)	194	6.6 \pm 1.1
Seed dispersal			
Vertebrate-dispersed	48 (55.8)	340	7.8 \pm 0.99
Abiotically-dispersed	38 (44.1)	195	5.1 \pm 0.78

¹We were not able to categorize a few of the 86 species, especially those currently being described, according to all attributes, and therefore not all of the seven groups sum to a total of 86.

²Numbers followed by different letters are significantly different (Kruskal-Wallis test $P \leq 0.05$).

We were unable to relocate 41 populations recorded between 1920 and 1996 (12.3% of all records) and populations of 20 of the species (27.7%) have become locally extinct. These extinctions included 29 records, comprising seven species, in which the whole forest fragment containing the populations had disappeared. Local extinction was significantly more frequent among those populations recorded between 1920 and 1970 (79.4% of all local extinctions; $G = 8.28$, $df = 1$, $P = 0.003$), but even some of the populations only discovered in the early 1990s are now extinct.

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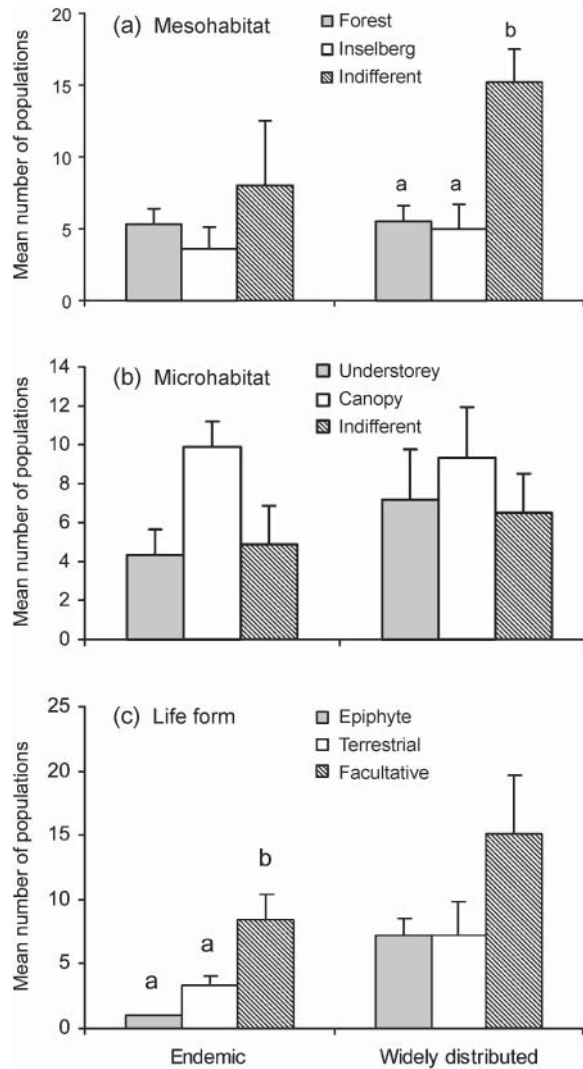


Fig. 2 Mean number of populations (\pm SE) of bromeliad species within categories of geographical range (see Table 2), and of mesohabitat (a), microhabitat (b), and life form (c) in the Brazilian Atlantic forest of north-east Brazil ($n = 86$ species, $n = 432$). Categories with different letters are significantly different (Kruskal-Wallis test, $P < 0.05$).

Discussion

Our results indicate that the number of populations of most bromeliad species in the Atlantic forest of north-east Brazil is critically low. Two thirds of the bromeliad species have < 6 known populations, and a lower number of populations per species is associated with a narrow distribution range, a high level of habitat specificity at different spatial scales, and life forms that are more specialized (i.e. obligatory epiphyte and terrestrial species).

Patterns of abundance, including the number of populations, result from both historical and ecological processes such as evolutionary history, genetic structure, habitat availability and human disturbance (Cody, 1986; Major, 1988). In the case of the bromeliads of this part of the Atlantic forest, species occurring in only one vegetation type and forest and inselberg species have a particularly low mean number of populations. Bromeliad species occurring in only one vegetation type (41 of 86 species, 47.6%) will have been restricted, before forest fragmentation, to areas of 2,922–19,715 km² (Table 1). Similarly, inselberg species occur in a habitat that makes up, overall, an almost undetectable portion of the whole region. Thus it is reasonable to conclude that the lower number of populations of these ecological groups is a pattern that has emerged from the combination of a high level of habitat specificity and a low level of habitat availability at a regional scale.

The loss of a total of 29 populations from seven species since 1920 indicates the severity of the effects of habitat loss. These losses included the only known populations of *Vriesea rectifolia* in this part of the Atlantic forest, and all known populations of *Tillandsia* sp.. In addition *Guzmania monostachia*, *Tillandsia kegeliana* and *Hohenbergia ridleyi* have lost c. 25% of their known populations since 1920. Despite an increase in official protection for the Atlantic forest region, a recent survey (Tabarelli *et al.*, 2005) revealed that the north-east Atlantic forest has lost 10% of its remaining forest cover since 1989. In this period 5.6% of fragments examined were totally cleared and 11.4% of them became 35.7% smaller.

In addition to habitat loss, historical and current illegal collecting of ornamental species may be contributing to reductions in bromeliad populations, although the evidence is anecdotal. Fifty-six percent of the local extinctions recorded in this study were of nine species that are valued as ornamentals, e.g. *Portea leptantha* (26 populations, two local extinctions), *Aechmea mulfordii* (11, 4), and *Aechmea lingulata* (25, 3). The same has happened to other species in this region. The ornamental species *Neoregelia pernambucana*, *Vriesea psittacina* and *Guzmania lingulata* have been intensively collected and almost eliminated from forest fragments close to human settlements (Siqueira Filho & Leme, 2000; Siqueira Filho, 2002, 2004). Local extinction due to illegal collection also includes populations within protected areas. *Billbergia morelii* and *Cryptanthus zonatus* were last recorded in Dois Irmãos State Park by D.A. Lima in 1954 and G. Mariz in 1972, respectively (voucher specimens UFP 3763 and IPA 7444).

Habitat loss is also the main threat to bromeliad species in other parts of the Brazilian Atlantic forest because several species are endemic to small tracts of forest and restricted to particular habitats. For example,

Aechmea kertesziae and *Billbergia brasiliensis* are endemic to the Atlantic forest in Santa Catarina State and their habitat has been drastically reduced within the last few decades (Klein, 1990). In 1997 24% (480) of all bromeliad species were considered threatened with global extinction (Walter & Gillett, 1998), and 8–12 species are expected to disappear per year because of habitat loss (Dimmit, 2000).

Number of populations and rate of population decline determine the vulnerability of a species to extinction (Goerck, 1997; IUCN, 2004). Our results suggest that, for bromeliads in the Atlantic forest of north-east Brazil, geographic range, habitat specificity and life form appear to determine which species are more vulnerable to extinction. The species that have < 6 extant populations (61.6% of the species in the region) are on the brink of regional extinction. This also includes 27 species that are endemic to the Atlantic forest of north-east Brazil and therefore facing possible global extinction. These species need to be evaluated for inclusion on both the IUCN and Brazilian Red Lists. Some of these species will only survive if the fragments containing the last populations are recognized as irreplaceable (*sensu* Rodrigues *et al.*, 2004) key areas for biodiversity, and declared as protected areas by the Brazilian government.

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Appendix

The Appendix for this article is available online at <http://journals.cambridge.org>

Biographical sketches

José Alves de Siqueira Filho has carried out research on the systematics, reproductive ecology and conservation of bromeliad species in north-east Brazil since 1995. He has also helped in the creation of protected areas for bromeliad species.

Marcelo Tabarelli is a member of the advisory bureau of Conservação Internacional do Brasil. Since 1998 his main research has concerned plant ecology and conservation, and in particular the impacts of habitat fragmentation on vascular plants in neotropical forests.