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1 **Vascular plant densities estimate the age of undated lava flows in semi-arid environment**
2 **on Fogo Island (Cape Verde, Atlantic Ocean).**

3

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11

12 Abstract: The age of some lava flows on the east-north-east coast of Fogo Island (Cape
13 Verde) remains debated or unknown due to the inapplicability of the conventional dating
14 methods, while this information is important for a retrospective approach of volcanic hazard
15 evaluation and prevention. Historical lavas represent an opportunity to study plant succession
16 within a well-constrained chronological framework, and lava flow age was used usually as
17 variable to explain plant densities and species composition. Here, vascular plant densities
18 were also assigned as variables to explain lava ages. We surveyed 44 plots on eleven semi-
19 arid lavas representing a chronosequence of 60- c. 350-yr-old lavas, including two undated
20 lavas. We used Spearman's correlation to test the relationships between plant densities and
21 lava ages. Stepwise regression model was then used to identify which species were more
22 closely related to the age of lavas, and model equation was employed to predict the age of
23 undated lavas. Finally, we confront regression model age-predictions with principal
24 component analysis (PCA) result. Among 27 vascular plants, nine species were significantly
25 linked with lava ages. Regression model showed that *Sarcostemma daltonii* and *Lantana*

1 *camara* densities explained significantly lava ages (adjusted $R^2 = 0.733$, $P < 0.0001$). PCA
2 demonstrated similar plant species densities on lavas were related to similar year-old lavas.
3 Model age-predictions were congruent with PCA result supporting that vascular plant species
4 densities may provide useful information about the relative age of undated lava flows in arid
5 environment.

6

7 Keywords: Fogo Island, semi-arid lava flows, vascular plants, chronosequence, Cape Verde,
8 island biogeography.

9

10 **Introduction**

11 Fresh mineral material deposited at the surface of the Earth offer the opportunity to study the
12 pattern and the timing of colonization of volcanic substrate by vascular plant species.

13 Volcanic lava flows are especially unique as they are sterile material recovering a preexisting
14 landscape where volcanic eruption acts as a reset factor for plant colonization (e.g. Whittaker
15 1984, Thornton et al. 1992). Hence, plant colonization on lava flows is mainly limited by the
16 suitable conditions for establishment and it is well known that such conditions evolve mainly
17 with time and climatic conditions (e.g. Whittaker et al. 1984, Fenner 1987, Drake 1992, Drake
18 and Dombois 1993, Aplet et al. 1998, Cutler et al. 2008).

19 Primary plant succession in island volcanic environment has been studied by many workers
20 and the increase of plant diversity with the age of lava flow seems quite expected (e.g.
21 Whittaker et al. 1992, Partomihardjo et al. 1992, and Thornton et al. 1992, on Anak Krakatau
22 Island; Aplet et al. 1998 on Hawaii Island; Cutler et al. 2008 on Iceland; Magnússon et al.
23 2014 on Surtsey Island), although the exact shape of the age-diversity might differ (Cutler
24 2010). Furthermore, in volcanic environments where historic effusive products create new
25 sterile land surfaces, lava flows can be used as chronosequences to study plant population

1 development (Drake and Dombois 1993, Cutler et al. 2008, 2010). Indeed, plant succession
2 has been investigated by comparing sites that differ in age but were geologically and
3 climatically similar (e.g. Drury and Nisbet 1973, Miles 1979, Drake and Dombois 1993).
4 Usually, historical lavas represent an opportunity to study plant succession within a well-
5 constrained chronological framework, and lava flow ages were used as variable to explain
6 plant densities and species composition (e.g. Aplet 1998). Conversely, plant densities and
7 composition on lava flows might provide useful information for the distinction of undated
8 lavas. Indeed, where land surface ages is unknown, geo-ecological successions have been
9 used formerly as relative-age dating of glacial foreland (Matthews 1992). Here, plant densities
10 in semi-arid conditions were assigned as variables to explain lava flow ages and such
11 approach is still very poorly documented.

12 On the east-north-east coast of Fogo Island (Cape Verde), the ages of some lava flows remain
13 unknown due notably to the lack of charcoal beneath these lava flows, preventing ^{14}C dating
14 to be applied (Ribeiro 1960, Machado 1965, Torres et al. 1997, Day et al. 1999, Foeken et al.
15 2009), while this information may be relevant for a retrospective analysis of volcanic hazard
16 evaluation and prevention for local authorities. We argue that vascular plant species densities
17 may be used as indicator to provide information on the relative age of volcanic eruptions, as
18 complementary methodology or in case of non-applicability of the conventional methods such
19 as ^{14}C . We hypothesized that similar plant species densities in comparable semi-arid
20 environment on lava flows might be related to similar year-old lavas.

21

22 **Materials & Methods**

23 *Study area*

24 The Cape Verde Archipelago includes ten ocean islands stretching in the eastern Atlantic
25 Ocean between $14^{\circ}51'13'' - 17^{\circ}03'29''\text{N}$ and $22^{\circ}41'38'' - 25^{\circ}10'31''\text{W}$ at c. 580 km from the

1 nearest African mainland and 1,300 km south of the Canary Islands. With a land surface of
2 476 km², Fogo Island is the fourth largest island of the Archipelago and the highest, reaching
3 2,829 m a.s.l. at *Pico do Fogo* volcano (Machado 1965). Fogo is one of the most active
4 volcano of the Atlantic Ocean and the only active volcano of the Cape Verde archipelago for
5 the last centuries (Machado 1965a-b, Torres et al. 1997, Dionis et al. 2015). The island is a
6 shield volcano truncated by an 8 km-wide horseshoe-shaped caldera opened to the east. The
7 caldera is related to a massive collapse of the eastern flank of the island (Day et al. 1999), the
8 latter being mostly covered by historical lava flows (Dionis et al. 2015, Paris et al. 2017).
9 The semi-arid climate of Fogo Island experiences two seasons: a cool dry season (November
10 to June) with very low rainfall and cool temperatures, and a warmer season with occasional
11 rainfalls (July to October) (Soares 1956, Amaral 1991). Fogo Island has a mean annual
12 temperature of 24.2°C and rainfall of 272 mm year⁻¹ at São Filipe, southwestern coast
13 (<https://en.climate-data.org/>). However, rainfall experience high variability due to elevation
14 range, influence of the continental Sahel zone, and exposure to the trade winds (Soares 1956,
15 Amaral 1991, Ribeiro 1997, Olehowski et al. 2008). Annual precipitation ranges from c. 150
16 mm at sea level to > 600 mm in higher elevation. Fogo Island has a leeward dry south-west
17 coast and a windward wetter north-east coast exposed to the dominant maritime trade winds
18 (Amaral 1991). Thus, rainfall ranges from 150-200 mm year⁻¹ at sea level on the leeward
19 coast to 200-250 mm year⁻¹ on the windward coast.

20 Since the 15th century, native vegetation cover of Fogo Island has changed widely due to
21 human colonization (Chevalier 1935). However, despite human settlements and activities
22 such as deforestation, agriculture and farmland, overgrazing, and the spread of many
23 naturalized species (Duarte & Moreira 2009, Siegmund et al. 2005), 41 endemics species still
24 observed among a total of 373 vascular plants on Fogo Island (Duarte et al. 2008, Romeiras et
25 al. 2015).

1

2 <Figure 1. near here>

3

4 *Lava flows sampled*

5 We selected 11 basaltic lava flows as a chronosequence located in semi-arid climate on the
6 eastern coast of Fogo Island (Fig.1). The year of eruption (AD) was documented by using
7 reports and geological maps for nine lava flows (Torres et al. 1997; revisited by Paris et al.
8 2017), while the date of one eruption was uncertain (proposed as “1664?” in Torres et al.
9 1997, here named Nd.10 (1664?)). The age of dated lava flows ranged from 67 to *c.* 350 yrs
10 old (defined as “historical” lavas). Two other lava flows locally covered by 1769 lava
11 remained undated (Nd.1 and Nd.9; Nd.1 being younger than Nd.9 as evidenced by the map of
12 Paris et al. 2017).

13 All of the 11 lava flows sampled shared similar field characteristics: they were identify as a’a
14 lavas, i.e. rough lavas with a chaotic surface made of blocks formed during the fragmentation
15 of the cooling crust during lava emplacement. These lavas were also similar in geology as all
16 of the historical eruptions on Fogo Island produced alkali basalts classified as basanites in
17 terms of major-element composition, with clinopyroxene and olivine as dominant phenocrysts
18 (Machado 1965; Gerlach 1988, Doucelance et al. 2003, Cornu 2017). According to field
19 observation, these rough lava flows were not cultivated.

20

21 *Plant count on lava flows*

22 When using a chronosequence, replicate sites of a given age are often unavailable, making
23 statistical analysis difficult (Drake and Dombois, 1993). Here, three replicate plots of 314 m²
24 (each) were delineated in the central part of the 11 lava flow sampled (i.e. not at the flow front
25 or lateral levees where environmental conditions and accessibility to successional plant

1 species might be different). The distance between the three replicate plots per lava flow
2 ranged between 5 and 15 m (not shown). A total of 33 314 m² plots were delineated.
3 In addition, one replicate of 140 m² per lava flow (n=11) was performed using vertical aerial
4 photographs at ~ 4 m above ground acquired with a DJI Phantom 2 drone (Plot 4, Table 1).
5 We then identified and counted plant species in laboratory. Note that this additional drone
6 replicate was done to improve the whole sample and save time during field survey.
7 All plots were selected in order to maximize homogeneity of environmental parameters such
8 as geology, elevation, terrain roughness, and climatic conditions. General plot characteristics
9 are given in Table 1. In these plots, vascular plant species including (i) natives (i.e.
10 indigenous and endemic species), and (ii) naturalized species (i.e. formerly introduced, since
11 naturally dispersed in environment) were investigated. We recorded species richness,
12 abundance (i.e. the total number of plants), and species abundance (i.e. the number of
13 individuals per species). Fieldwork was led at the rainy season (in September) in the exposure
14 rainfall zone of 200-300 mm year⁻¹ (Olehowski et al. 2008).
15 In order to homogenise plot area, we calculated the density of every species per 314 m² and
16 140 m² plots (i.e. the number of individuals per species divided by plot area; here after species
17 density per m²). Thus, we obtained (i) the density of every species per plot and (ii) the density
18 of every species per lava flow (by summing species, divided by total plot area 1-4).

19

20 *Statistical analysis*

21 First, we used the simple Sørensen Index to confirm similarity of the three replicate plots on
22 each lava flow sampled (Plots 1-3, Table 1). Note that Sørensen Index was not calculated for
23 the 1951 lava flow (lack of vascular species on this lava).

24 Second, linear regression was used to observe the relationships between plants abundance and
25 species richness versus age of lava flows, while Spearman's correlation was used to provide

1 an overall picture of the relationships between each species density and the age of lava flows.
2 Note that plots of Nd.1 and Nd.9 lavas were not included in the analysis (undated lavas). In
3 order to limit some effect of intercorrelation between species, all vascular species age-
4 correlated were assigned as variable to explain the age of lava flows in stepwise regression
5 model. We then used stepwise model equation to provide age-prediction of both undated lava
6 flows.
7 Finally, in order to test if similar species densities were related to similar years of eruption,
8 we ran Principal Component Analysis (PCA, multivariate analysis) by using the density of
9 each vascular plant species (species composition) in the 44 plots. This result was presented
10 per lava flow. We observed which lava flows were significantly correlated with undated lavas
11 (Nd.1, Nd.9) and compared PCA result with model age-predictions.

12

13 <Table 1. near here>

14

15 **Results**

16 *Similarity of plot replicates*

17 Sørensen Index ranged between 0.5 to 1 supporting relative similarities of the three plot
18 replicates (Table 1). The mean value of Sørensen Index for the three plot replicates ranged
19 between 0.666 and 0.904 (Table 1).

20

21 *Plant species composition on lava flows*

22 In the 44 plots, we found a total of 27 vascular plant species representing an abundance of
23 3,092 individual plants. Abundance per lava flow ranged from 1 to 663 individuals while
24 species richness ranged from 1 to 19 species. Species richness per plot ranged from 0 to 16
25 while abundance ranged from 0 to 135 (Table 2). We encountered 15 shrubs, 5 trees, 2

1 succulents, 2 herbs, 2 ferns, and 1 vine. We observed more commonly *Sarcostemma daltonii*,
2 *Dryopteris* sp., *Polypodium* sp., *Euphorbia tuckeyana*, *Lavandula rotundifolia*, and
3 *Paronychia illecebroides* (Fig. 2). As expected, old a'a supported more species and
4 abundance than young a'a.

5 Almost 60% of the vascular plants observed in the plots were reported as native while the
6 others were naturalized, including invasive species (Table 2). These latter were mostly found
7 on the oldest and undated lava flows (Fig. 3).

8

9 <Table 2. near here>

10 <Figure 2. near here>

11 <Figure 3. near here>

12

13 *Relationships between plant species and age of lava flows*

14 Overall, total abundance and species richness in the 314 m² plots were significantly related to
15 the age of lava flows (Fig. 4a-b). Among the 27 plant species observed in the plots, nine
16 species were significantly linked with the age of lava flows: *Abrus precatorius*, *Asparagus*
17 sp., *Euphorbia tuckeyana*, *Jatropha curcas*, *Lantana camara*, *Lotus Jacobaeus*, *Lotus*
18 *purpureus*, *Polypodium* sp., and *Sarcostemma daltonii* (Table 3). Strongest relationships, with
19 R² ranging from 0.324 to 0.711, were observed with both native species *S. daltonii*, *E.*
20 *tuckeyana*, and the naturalized species *J. curcas*, *L. camara* (Table 3). No significant
21 relationship was found with the density of other species and the age of lava flows in the 44
22 plots (Spearman's correlation). Density of the pioneer endemic *S. daltonii* increased from 65
23 to c. 230-yr-old lava flows (Fig. 5). *Euphorbia tuckeyana* density increased from c. 220 to c.
24 250-yr-old lava flows and then decreased, while naturalized species *L. camara* and *J. curcas*
25 density strongly increased from c. 250 to c. 350-yr-old lava flows (Fig. 5).

1 Among the nine vascular plant species age-correlated, stepwise model showed a better fit of
2 species density versus age of lavas by using mostly *S. daltonii* with *L. camara* (Table 4).

3 According to stepwise model equation, Nd.1 and Nd.9 lavas would be ~ 249 and 256 ± 40 yr-
4 old, respectively.

5

6 <Figure 4a-b. near here>

7 <Table 3. near here>

8 <Figure 5. near here>

9 <Table 4. near here>

10

11 *Lava flows comparaison*

12 Significant relationships were found between species densities and similar years of volcanic
13 eruption (PCA, Fig. 6). Spearman's correlation values ranged from 0.497 to 0.778, $P \leq 0.01$
14 (Table 5). Lava flows were clearly distinguished with two groups: Nd.10 (1664?)-1785 and
15 1799-1857 (Fig. 6). Species densities of undated Nd.1 and Nd.9 lava flows were linked and
16 fitted with the 17th-18th century lava flows (Table 5 & Fig. 6). Nd.1 lava was linked with 1769
17 and 1785 lavas while Nd.9 lava was linked with Nd.10 (1664?) and 1769 lavas. The lava flow
18 Nd.10 (1664?) was significantly linked with 1785 lava (Table 5).

19 PCA axis F1 explained a large part of the total inertia of the dataset (44.63%, Fig. 6). This
20 axis was controlled mostly by *S. daltonii* (127.8%), *Dryopteris* sp. (11.1%), and *Polypodium*
21 sp. (2.5%) (Table 6). Axis F2 explained 18.5% of the total inertia; *Dryopteris* sp. (23.5%),
22 *Polypodium* sp. (9.2%), and *E. tuckeyana* (3.8%) were the most important explanatory
23 variables for this axis (Table 6).

24

25 <Table 5. near here>

1 <Figure 6. near here>

2 <Table 6. near here>

3

4 **Discussion**

5 *Trend in species and age of lava flows*

6 On Fogo Island, plant species richness and abundance are related to the age of lava flows.

7 Thus, colonization of the sampled lava flows by vascular plants is characterised by a temporal
8 evolution related to the age of lava flows with successive stages of vegetation development.

9 This result is congruent with many studies. For example, Drake and Dombois (1993)

10 demonstrated, on Hawaii Island, an increase in plants density on a chronosequence of six lava
11 flows aged between 47 and ~3,000-yr-old with changes in dominant species on the oldest

12 lavas. In Iceland, similar result was obtain from Cutler et al. (2008) whose defined, with a

13 850-yr chronosequence on seven lava flows, the stages of vegetation development as “Pioneer
14 colonization stage”, then “Pioneer expansion stage”, and “Higher plant colonization stage”

15 including additional species growing within the pioneer matrix.

16 On Fogo Island, the increase of plant species number with time appears to be very slow on the
17 semi-arid lava flows sampled. Indeed, we found only five and one species on the 1852 and

18 1951 lava flows, respectively. So, a period of at least 65 years is required for plant

19 colonization, namely by *S. daltonii*. This result is in agreement with Chevalier (1935) who

20 reported only one species (*S. daltonii*) on the 1852 lava flow, which was 83-yr-old in time of

21 observation. First, this time lapse before pioneer plants start to colonize lava may be explain

22 by changes of lava environment, here with a weak alteration of lava due to poor chemical

23 weathering of basic volcanic rock in such semi-arid conditions (Barros 1998, Karthe and

24 Siegmund 2004) leading to slow plant colonisation. For example, Anak Krakatau Island

25 (where vascular plants were extirpated due to major eruption in 1952) supports an extensive

1 forest along the wet eastern/north-eastern coastline, while the xeric island interior lavas
2 remain sparsely colonized by vascular plants (Partomihardjo et al. 1992). Second, plants
3 colonization on lava is controlled by the time required for random seeds dispersal from adult
4 plants. Indeed, it has long been demonstrated that during primary ecological succession on
5 lava flows, no seed bank exists in the sterile new substrate. Thus, all pioneer plants must be
6 recruited from the seed rain, involving wind dispersed taxa as well as mammal and bird-
7 dispersers availability (e.g. Drake 1992, Whittaker et al. 1992).

8 Our findings show that some vascular plant species led the relationships between species
9 density and the age of lava flows, among which *S. daltonii*, *E. tuckeyana*, *J. curcas*, and *L.*
10 *camara* are significant species. The endemic species *S. daltonii* is the most abundant species
11 observed on the lava flows sampled and the dominant pioneer on lavas of this area. It may
12 refer to early “Pioneer colonization stage” on lava flows < 160 yr-old. We then also observed
13 a significant increase density with time for species *E. tuckeyana*, supporting a “Pioneer
14 expansion stage” on 160-230 yr-old lava flows. Here, we also found naturalized species *J.*
15 *curcas*, and the well-known island invasive species *L. camara*. Moreover, stepwise model
16 confirms that density of *S. daltonii* associated with that of *L. camara* is the best indicator to
17 explain the age of lava flows sampled.

18 Overall, the presence of natives and naturalized species on the same lava might be viewed as a
19 bio-indicator of the oldest lava flows sampled and interpreted as “Higher plant colonization
20 stage” on > c. 230 yr-old lava flows. However, because a chronosequence assumes a
21 substitution of space for time, result provides only a partial assessment of succession (see
22 Drake and Dombois, 1993).

23

1 *Some references to invasive species*

2 On Fogo Island, the invasive species *L. camara* represents a potential threat for native species
3 established on the same lava flows, especially for the native *E. tuckeyana*, *L. jacobaeus* and *L.*
4 *purpureus*. Indeed, Chevalier (1935) reported that *E. tuckeyana*, *L. jacobaeus* and *L.*
5 *purpureus* were mostly found on the oldest lava flows on Fogo Island but *L. camara* was
6 never mentioned by the botanist among these natives. Here, *L. jacobaeus* and *L. purpureus*
7 were barely linked with the age of lava flows, while a strong significant relationship was
8 observed for the invasive *L. camara*. Similar result was found for the naturalized *J. curcas*.
9 Thus, our results suggest that *L. camara* and *J. curcas* seem to occupy habitat colonized by *L.*
10 *jacobaeus* and *L. purpureus* previously. We argue that *J. curcas* should be also viewed as an
11 invasive species on the northeast coast of Fogo Island.

12 Finally, we also observed some adults *A. precatorius*, only on the oldest sampled lava flows.
13 Formerly, this vine was reported as invasive species in numerous tropical islands, e.g. in the
14 Caribbean Islands (Holm et al. 1979), New Caledonia (MacKee 1994), Hawaiian Islands
15 (Wagner et al. 1999), and French Polynesia (Florence et al. 2007). Although not studied here,
16 it is possible that *A. precatorius* also become a dominant alien species on the oldest lava flows
17 of Fogo Island.

18

19 *Species densities fit period of eruption*

20 Plant species densities of the Nd.10 (1664?)-1785 lava flows group are clearly different from
21 the 1799-1857 lava flows group. This finding confirms the hypothesis that similar plant
22 species densities in comparable semi-arid environment on lava flows are related to similar
23 year-old lavas.

24 However, significantly-linked density group encompasses lavas with large age range (several
25 decades), e.g. Nd. 10 (1664?) linked with 1785, or 1799 linked with 1857. This confirms that

1 species composition and densities might remain similar during at least several decades on
2 Fogo Island. Thus, a range of several decades is necessary to detect a significant gap in plant
3 species densities and composition among semi-arid lava flows.

4 Species densities of the Nd.10 (1664?) lava flow are significantly correlated with those of
5 1785 lava flow. There is no doubt that Nd.10 (1664?) lava is older than 1785 lava, as
6 available maps of lava flows show that the Nd.10 lava is locally below the 1785 lava (Torres
7 et al. 1997; Paris et al. 2017). Torres et al. (1997) tentatively linked the Nd.10 lava flow to the
8 1664 eruption (Ribeiro 1997). Our results support that the Nd.10 (1664?) eruption occurred
9 lately in the 17th century or early in the 18th century. There are indeed several historical
10 accounts of eruptions during this period, including 1664, 1695, and 1721-25 (Ribeiro 1997).

11 Surprisingly, although species densities on the Nd.10 (1664?) and 1769 lavas were strongly
12 linked with 1785 lava, species densities of the Nd.10 (1664?) and 1769 lavas were not linked.
13 This might be explained by (i) the distance between Nd.10 (1664?) and 1769 lava (see Fig. 1)
14 leading to possible geographic disjunction in plants accessibility between sampled sites or (ii)
15 related to human disturbances. Indeed, while we assume that lava flows sampled were not
16 cultivated, Fogo Island is inhabited by more than 37,000 people with a mean density of 77
17 people per m²; hence the most part of the island is cultivated mainly by subsistence rainfed
18 farming (Barros 1998). Thus, human impacts such goats grazing, fire, or human picking
19 landscape plants on the lava flows sampled might disturb plant densities and colonization.

20 This may explain some lack of correlation as well as different levels of similarity (Sørensen)
21 observed among replicate plots, especially for *S. daltonii*, *Dryopteris* sp. *Polypodium* sp., and
22 *E. tuckeyana* which are the most important species to discriminate lavas on the east-north-east
23 coast of Fogo Island (PCA).

24

1 *Undated lavas*

2 Model age-prediction suggest that Nd.9 lava might be related to an eruption around 1761 ± 40
3 yr, and PCA shows that species densities of undated Nd.9 lava are linked with the former
4 1664-1769 lava flows. Accordingly, these findings lead us to classify Nd.9 lava as early 18th
5 century lava flow, possibly related to 1721-25 eruption. Similarly, model age-prediction
6 supports that Nd.1 lava might be related to an eruption around 1768 ± 40 yr. Species densities
7 of Nd.1 lava is linked with the 1769 lava, supporting a similar or slightly older period of
8 eruption in the 18th century.

9

10 **Conclusion**

11 Species densities are significantly related to the age of lava flows on Fogo Island. Moreover,
12 similar plant species densities in comparable semi-arid environment on lava flows were
13 related to similar year-old lavas. However, species densities may provide only an estimate of
14 year-old lavas with a gap of several decades on Fogo Island. Nevertheless, vascular plant
15 densities are helpful to detect the period of eruption. Consequently, when lava flow ages are
16 unknown because of non-applicability of the conventional dating methods, vascular plant
17 species densities may provide useful information on the relative age of volcanic eruptions.
18 Although not extended here, our results support that plant densities and composition might
19 represent another input for volcanic hazard evaluation, establishing a reliable chronological
20 framework of volcanic eruptions for the evaluation of volcanic hazard, especially for
21 probabilistic models.

22

23

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5

6

7 **References**

- 8 Amaral I. 1991. Cabo Verde: Introdução Geográfica. In: Albuquerque L, Santos MEM, eds.
9 *História geral de Cabo Verde* 1. Lisbon: Inst. Inv. Científica Tropical and Direcção-
10 Geral Património Cultural de Cabo Verde, 1–22.
- 11 Aplet GH, Hughes RF, Vitousek PM. 1998. Ecosystem development on Hawaiian lava flows:
12 biomass and species composition. *Journal of Vegetation Science* 9:17–26.
- 13 Barros de BG. 1998. *Landwirtschaftliche Praxis auf den Inseln Fogo und Brava (Kapverden)*
14 *und ihre Kompatibilität mit den offiziellen Beratungsempfehlungen*. Dissertation
15 Humboldt-Universität Berlin, Landwirtschaftlich-Gärtnerische Fakultät, Berlin.
- 16 Brochmann C, Rustan ØH, Lobin W, Kilian N. 1997. The endemic vascular plants of the
17 Cape Verde Islands, W Africa. *Sommerfeltia* 24:1–356.
- 18 Chevalier A. 1935. Les îles du Cap-Vert - Géographie, Biogéographie, Agriculture, Flore de
19 l'Archipel. *Revue de Botanique Appliquée* 15:733–1090.
- 20 Cornu MN. 2017. *Evolution magmatique d'un volcan bouclier océanique avant et après une*
21 *déstabilisation massive de ses flancs : Fogo, Cap Vert et Tenerife, Canaries*. PhD
22 Thesis, Université Clermont-Auvergne, 284 pp.
- 23 Cutler NA. 2010. Long-term primary succession: a comparison of non-spatial and spatially
24 explicit inferential techniques. *Plant Ecology* 208:123–136.

- 1 Cutler NA, Belyea LR, Dugmore AJ. 2008. The spatiotemporal dynamics of a primary
2 succession. *Journal of Ecology* 96:231–246.
- 3 Day SJ, Heleno da Silva SIN, Fonseca JFBD. 1999. A past giant lateral collapse and present-
4 day flank instability of Fogo, Cape Verde Islands. *Journal of Volcanology and*
5 *Geothermal Research* 99:191–218.
- 6 Day SJ, Carracedo JC, Guillou H, Pais FJ, Rodriguez Badiola E, Fonseca JFBD, Heleno SIN.
7 2000. Comparison and cross-checking of historical, archaeological and geological
8 evidence for the location and type of historical and sub-historical eruptions of multiple-
9 vent oceanic island volcanoes. In: McGuire WG, Griffiths DR, Hancock PL, Stewart IS,
10 eds. *The Archaeology of Geological Catastrophes*. London: Geological Society, Special
11 Publications, 171:281–306.
- 12 Deligne NI, Cashman KV, Roering JJ. 2013. After the lava flow: The importance of external
13 soil sources for plant colonization of recent lava flows in the central Oregon Cascades,
14 USA. *Geomorphology* 202:15–32.
- 15 Dionis SM, Pérez NM, Hernández PA, Melián G, Rodríguez F, Padrón E, Sumino H,
16 Barrancos J, D Padilla G, Fernandes P, Bandomo SS, M Pereira J, Semedo H, Cabral J.
17 2015. Diffuse CO² degassing and volcanic activity at Cape Verde islands, West Africa.
18 *Earth, Planets and Space* 67:48.
- 19 Doucelance R, Escrig S, Moreira M, Gariépy C, Kurz MD. 2003. Pb-Sr-He isotope and trace
20 element geochemistry of the Cape Verde Archipelago. *Geochimica et Cosmochimica*
21 *Acta* 67(19):3717–3733.
- 22 Drake DR. 1992. Seed dispersal of *Metrosideros polymorpha* (Myrtaceae): a Pioneer Tree of
23 Hawaiian Lava Flows. *American Journal of Botany* 79(11):1224–1228.
- 24 Drake DR, Dombois M. 1993. Population Development of Rain Forest Trees on a
25 Chronosequence of Hawaiian Lava Flows. *Ecology* 74(4):1012–1019.

- 1 Duarte MC, Romeiras MR. 2009. Cape Verde Islands. In: Gillespie R, Clague D, eds.
2 *Encyclopedia of Islands*. California: University of California Press, 143–148.
- 3 Duarte MC, Rego F, Romeiras MM, Moreira I. 2008. Plant species richness in the Cape
4 Verde Islands—eco-geographical determinants. *Biodiversity and Conservation* 17:453–
5 466.
- 6 FAO-UNESCO. 1997. Soil Map of the World, Revised Legend, with corrections and updates.
7 World Soil Resources Report 60. Rome. Reprinted with updates as Technical Paper 20.
8 Wageningen.
- 9 Faria de FX. 1974. Os Solos da Ilha do Fogo: Arquipélago de Cabo Verde. Serviço
10 Cartográfico do Exército Português, Lissabon.
- 11 Fenner M. 1987. Seed characteristics in relation to succession. In: Gray AJ, Crawley MJ,
12 Edwards PJ, eds. *Colonization, Succession and Stability*. Oxford: Blackwell Scientific
13 Publishers, 103–114.
- 14 Florence J, Chevillotte H, Ollier C, et al. (2007) *Base de données Nadeaud de l’Herbier de*
15 *Polynésie française (PAP) du Musée des Iles et de Tahiti*. Antenne IRD du MNHN,
16 Paris, Centre IRD de Tahiti, Délégation à la Recherche, Papeete. Available at:
17 <http://www.herbier-tahiti.pf>
- 18 Foeken JPT, Day SJ, Stuart FM. 2009. Cosmogenic ³He exposure dating of the Quaternary
19 basalts from Fogo, Cape Verdes: implications for rift-zone and magmatic
20 reorganisation. *Quaternary Geochronology* 4:37–49.
- 21 Gerlach DC, Cliff RA, Davies GR, Norry M, Hodgson N. 1988. Magma sources of the Cape
22 Verdes archipelago: Isotopic and trace element constraints. *Geochimica et*
23 *Cosmochimica Acta* 52(12):2979–2992.
- 24 Holm L, Pancho JV, Herberger JP, Plucknett DL. 1979. *A geographical Atlas of World*
25 *Weeds*. John Wiley & Sons, New York.

- 1 Karthe D, Siegmund A. 2004. Die Böden der Kapverden — Eine Bestandsaufnahme auf den
2 Inseln Fogo, Boavista und Santo Antão. *Geoökologie* 25:59–72.
- 3 Le Bas TP, Masson DG, Holtom RT, Grevemeyerm I. 2007. Slope failures on the flanks of
4 the southern Cape Verde Islands. In: Lykousis V, Sakellariou D, Locat J, eds. *Submarine*
5 *Mass Movements and their Consequences*, 337–345.
- 6 Marques R, Prudêncio MI, Waerenborgh JC, Rocha F, Dias MI, Ruiz F, Ferreira da Silva E,
7 Abad M, Muñoz AM. 2014. Origin of reddening in a paleosol buried by lava flows in
8 Fogo island (Cape Verde) *Journal of African Earth Sciences* 96:60–70.
- 9 Matthews JA. 1992. *The Ecology of Recently-deglaciated Terrain: A Geoecological*
10 *Approach to Glacier Forelands and Primary Succession*. Cambridge Studies in
11 Ecology, Cambridge University Press.
- 12 MacKee HS. 1994. Catalogue des plantes introduites et cultivées en Nouvelle-Calédonie.
13 Muséum National d'Histoire Naturelle, Paris, 164 p.
- 14 Olehowski C, Naumann S, Fischer D, Siegmund A. 2008 Geo-ecological spatial pattern
15 analysis of the island of Fogo (Cape Verde). *Global Planet Change* 64:188–197.
- 16 Paris R, Rodriguez-Gonzales A, Perez-Torrado F-J, Carracedo J-C, Collin A, Etienne S, and
17 Larrue S. 2017. *Volcanological map of Fogo Island (Cape Verde)*. Project PEPS CNRS-
18 UCA 2015-2016, Natural Park of Fogo.
- 19 Partomihardjo T, Mirmanto E, Whittaker RJ. 1992. Anak Krakatau's Vegetation and Flora
20 circa 1991, with Observations on a Decade of Development and Change. *GeoJournal*
21 28(2):233–248.
- 22 Ribeiro O. 1960. *A Ilha do Fogo e as suas erupcoes, 2nd Ed*. Memórias, serie geografica I.
23 Publ. Junto de Investigacoes do Ultramar, Lisboa, Portugal.
- 24 Scheffer, F., Schachtschabel, P., 2002. *Lehrbuch der Bodenkunde*. Heidelberg.

- 1 Siegmund A, Hohmann A, Meurer M, Wahl T. 2005. A satellite image based land-use
2 analysis for a geo-ecological differentiation of the natural landscape on the Cape Verde
3 Islands — the example of Fogo, Boavista and Santo Antão. In: Leyens T, ed. *Fauna and*
4 *Flora of the Atlantic Islands, Proceedings of the IV Symposium (Praia/ Cabo Verde, 9.–*
5 *13. Setembro 2002)*. Praia: Ministério do Ambiente, Agricultura e Pescas, 105–115.
- 6 Soares FA. 1956. O clima de Cabo Verde segundo algumas classificações. *Agros*
7 39(5/6):272–286; 347–379.
- 8 Torres PC, Madeira J, Silva LC, Brum da Silveira A, Serralheiro A, Mota Gomes A. 1997.
9 Carta geologica das erupcoes historicas da Ilha do Fogo: revisao e actualizacao. A
10 erupcao vulcanica de 1995 na Ilha do Fogo, Cabo Verde. Publ. IICT, Lisboa, 119-132.
- 11 Thornton IWB, Ward SA, Zann RA, New TR. 1992. Anak Krakatau - a Colonization Model
12 within a Colonization Model? *GeoJournal* 28 (2):271–286.
- 13 Wagner WL, Herbst DR, Sohmer S.H. 1999. Manual of the flowering plants of Hawaii.
14 Revised edition. Bernice P. Bishop Museum special publication. University of Hawai'i
15 Press/Bishop Museum Press, Honolulu.
- 16 Whittaker RJ, Bush MB, Partomihardjo T, Asquith NM, Richards K. 1992. Ecological
17 Aspects of Plant Colonisation of the Krakatau Islands. *GeoJournal* 28(2):201–211.
- 18 Whittaker RJ, Richards K, Wiriadinata H, Flenley J.R. 1984. Krakatau 1883 to 1983: a
19 biogeographical assessment. *Progress in Physical Geography* 8:60–81.
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Figure and caption

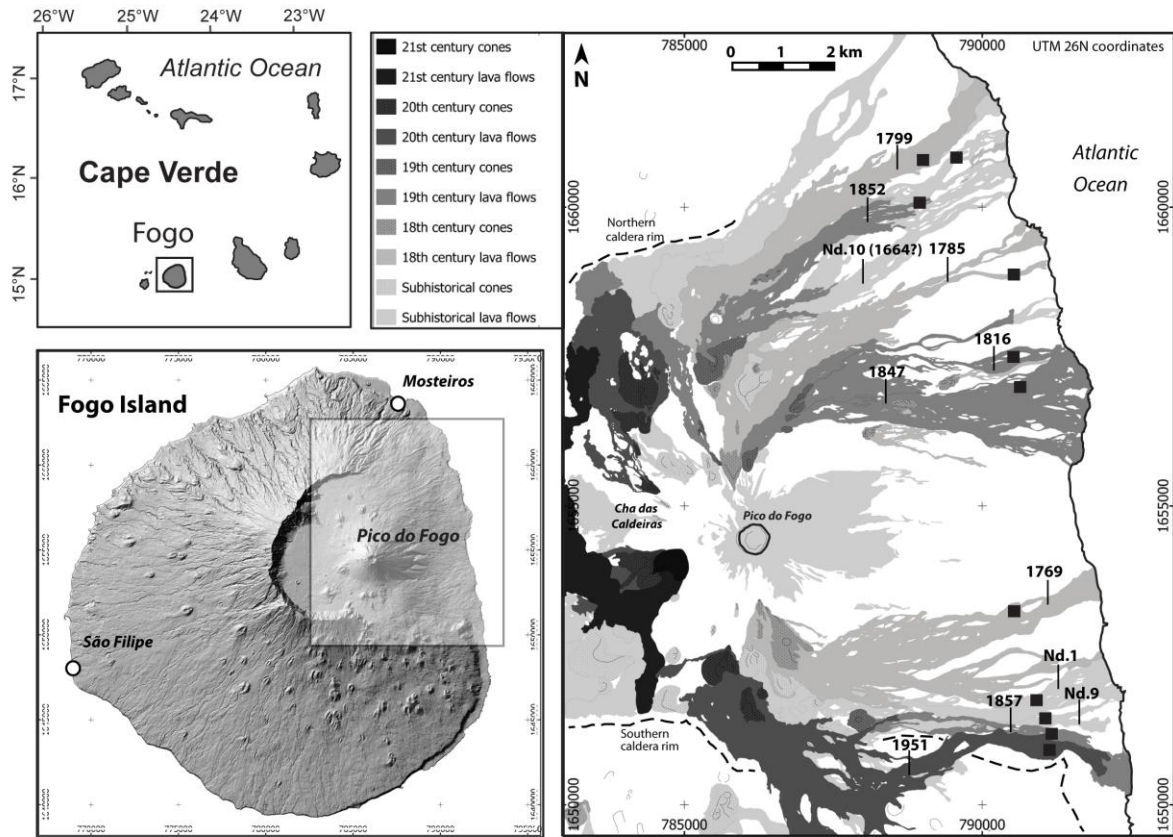
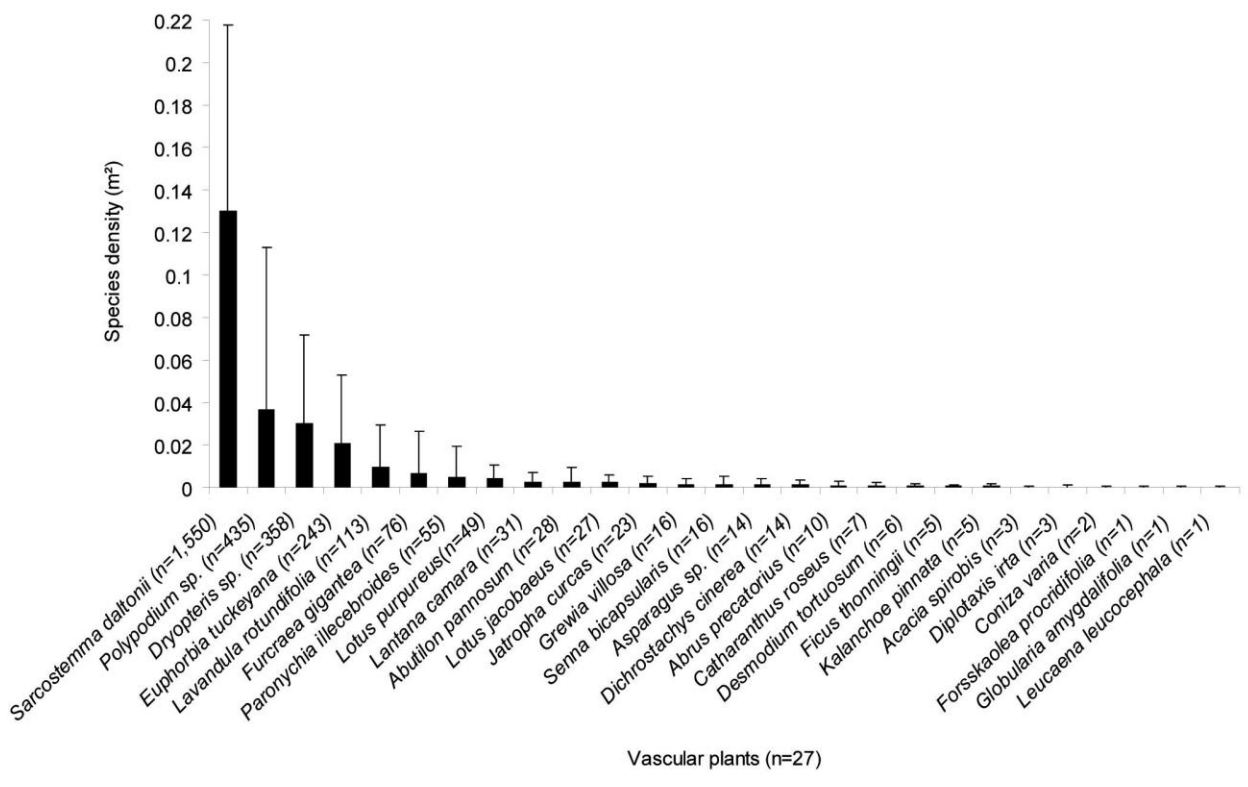


Figure 1. Study area with location of the sampling sites (black squares) on eleven lava flows of the east-north-east coast of Fogo (Cape Verde, Atlantic Ocean). Bold numbers on the surveyed lava flows refer to year of eruption (AD). The year of eruption of lava flows named “Nd.10 (1664?)” was uncertain, while “Nd.1” and “Nd.9” were not documented.

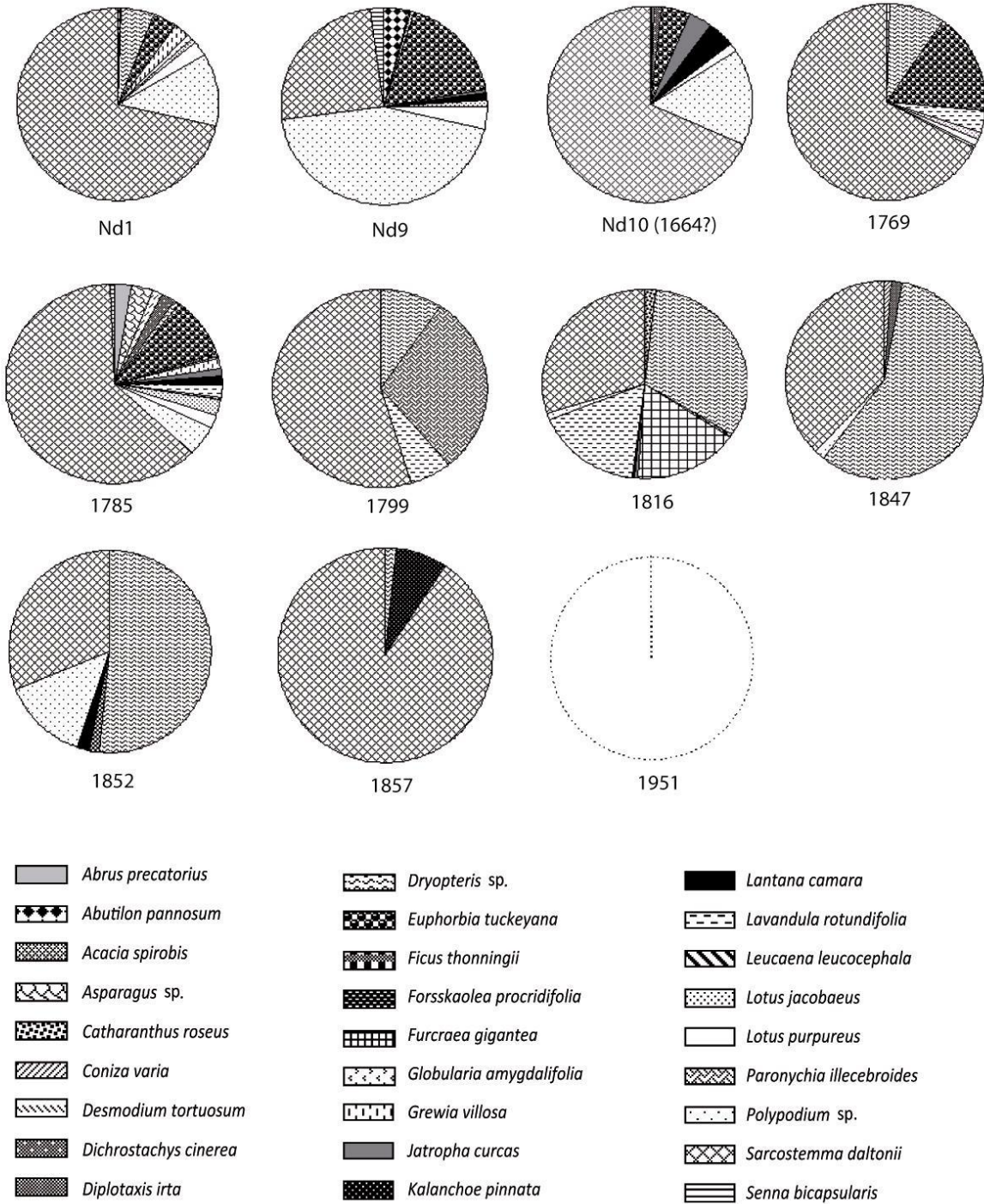
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Figure 2. Vascular plant species density observed on the overall 11 lava flows (Fogo Island, Cape Verde). Error bars refer to standard deviation.

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4 Figure 3. Vascular plant species composition (%) on the 11 lava flows (Fogo Island, Cape

5 Verde).

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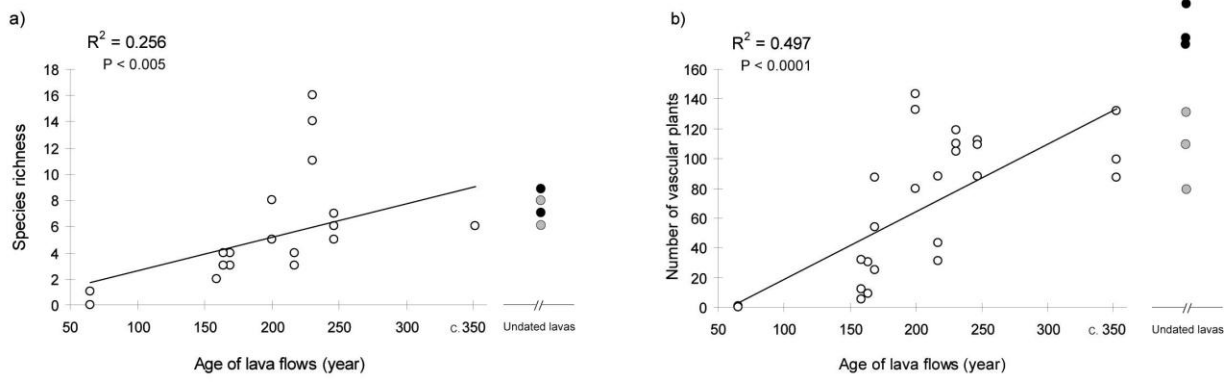
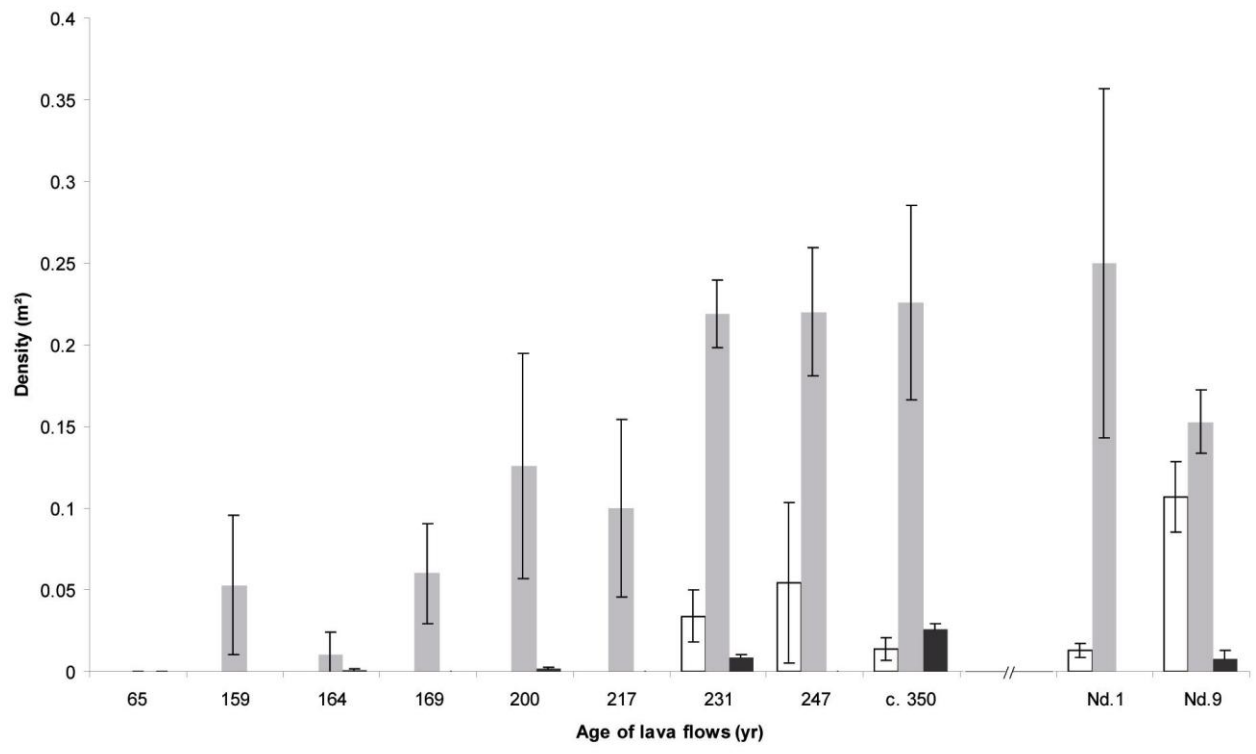


Figure 4a-b. Linear regression. Species richness and number of vascular plants in relation to the age of lava flows in 27 plots (314 m² each). Plots on undated lavas Nd.1 (grey circle) and Nd.9 (black circle) have been added as supplementary information.

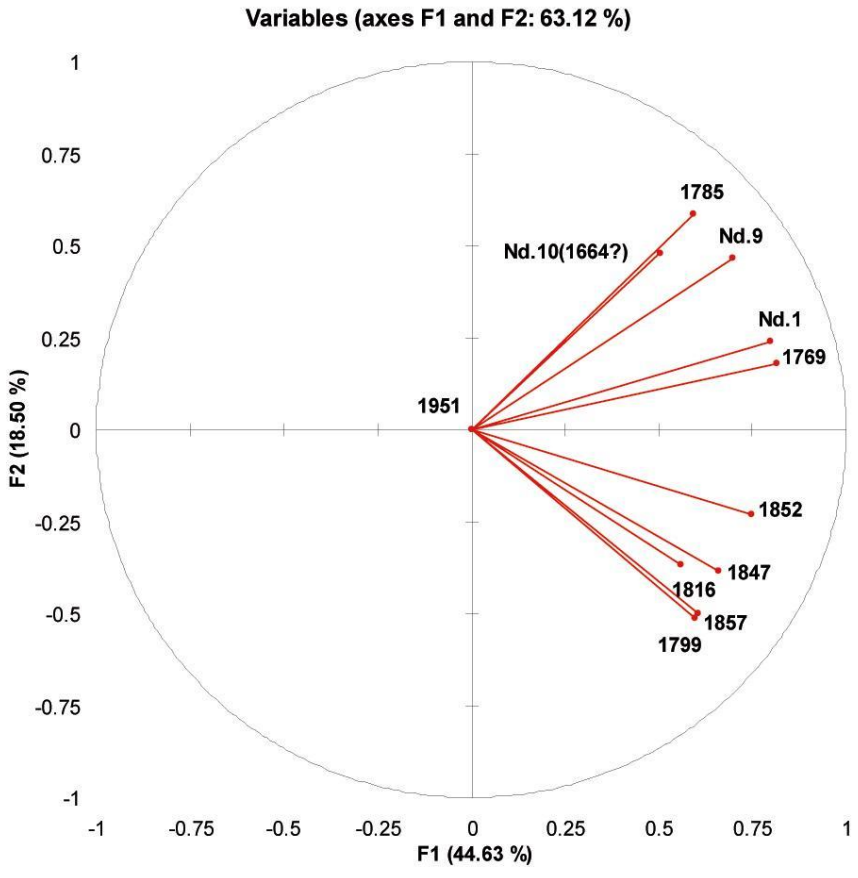
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Figure 5. Mean density of the native species *Sarcostemma daltonii* (grey bar), *Euphorbia tuckeyana* (colorless bar) and the naturalized species *Lantana camara* and *Jatropha curcas* (black bar) on the semi-arid surveyed lavas (Fogo Island, Cape Verde). The undated lavas Nd.1 and Nd.9 have been added as supplementary information. Error bars refer to standard deviation.

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Figure 6. Principal Component Analysis (PCA). Relationships between the 11 lava flows based on vascular plant species densities and composition in the 44 plots (Fogo, Cape Verde).

1 Table and caption

2 Table 1. Characteristics of the 44 plots surveyed on 11 lava flows of the east-north-east coast
 3 of Fogo Island (Cape Verde, Atlantic Ocean). Sørensen Index (plant similarity) is calculated
 4 for the three field plot replicates of 314 m² (plot numbers 1-3). Drone plot area: 140 m² (plot
 5 number 4). Numbers in brackets refer to mean value. px: pyroxene; ol: olivine.

| Lava flows | Plots & replicates | North (decimal degrees) | West | Elevation (m) | Exposure | Slope (°) | Geology* | Plant similarity (Sørensen) |
|---------------|--------------------|-------------------------|----------|---------------|----------|-----------|------------------------|-----------------------------|
| Nd.1 | 1 | 14.92231 | 24.29604 | 370 | ESE | 16 | alkali basalt, px | 0.750 |
| | 2 | 14.92268 | 24.29601 | 360 | ESE | 14 | | 0.714 |
| | 3 | 14.92251 | 24.29647 | 371 | ESE | 14 | | 0.714 |
| | 4 | 14.92227 | 24.29596 | 358 | ESE | 14 | | - |
| | | | | (364) | | (14.5) | | (0.726) |
| Nd.9 | 1 | 14.92128 | 24.29375 | 337 | ENE | 14 | alkali basalt, px | 0.875 |
| | 2 | 14.92137 | 24.29434 | 333 | ENE | 14 | | 0.750 |
| | 3 | 14.92175 | 24.29401 | 325 | ENE | 14 | | 0.777 |
| | 4 | 14.92167 | 24.29441 | 328 | ENE | 14 | | - |
| | | | | (330) | | (14) | | (0.800) |
| Nd.10 (1664?) | 1 | 15.00661 | 24.30733 | 200 | NE | 16 | alkali basalt, ol, px | 0.666 |
| | 2 | 15.00701 | 24.30742 | 205 | NE | 16 | | 0.833 |
| | 3 | 15.00621 | 24.30779 | 212 | NE | 16 | | 0.666 |
| | 4 | 15.00660 | 24.30732 | 212 | NE | 16 | | - |
| | | | | (208) | | (16) | | (0.721) |
| 1769 | 1 | 14.93913 | 24.29714 | 290 | ENE | 19 | alkali basalt, px (ol) | 0.545 |
| | 2 | 14.93911 | 24.29782 | 300 | ENE | 19 | | 0.923 |
| | 3 | 14.93936 | 24.29771 | 305 | ENE | 19 | | 0.666 |
| | 4 | 14.93912 | 24.29714 | 295 | ENE | 19 | | - |
| | | | | (297) | | (19) | | (0.711) |
| 1785 | 1 | 14.98868 | 24.29904 | 206 | ENE | 15 | alkali basalt, px (ol) | 0.866 |
| | 2 | 14.98887 | 24.29858 | 200 | NE | 19 | | 0.560 |
| | 3 | 14.98935 | 24.29865 | 204 | ENE | 16 | | 0.510 |
| | 4 | 14.99271 | 24.29783 | 205 | ENE | 16 | | - |
| | | | | (204) | | (16.5) | | (0.645) |
| 1799 | 1 | 15.00680 | 24.31145 | 325 | ENE | 26 | alkali basalt, px (ol) | 0.857 |
| | 2 | 15.00665 | 24.31179 | 333 | ENE | 26 | | 1 |
| | 3 | 15.00618 | 24.31178 | 332 | ENE | 26 | | 0.857 |
| | 4 | 15.00644 | 24.31174 | 326 | ENE | 26 | | - |
| | | | | (329) | | (26) | | (0.904) |
| 1816 | 1 | 14.97621 | 24.30168 | 372 | ENE | 20 | alkali basalt, px (ol) | 0.875 |
| | 2 | 14.97560 | 24.30101 | 365 | ENE | 24 | | 0.615 |
| | 3 | 14.97507 | 24.30047 | 360 | E | 24 | | 0.615 |
| | 4 | 14.97619 | 24.30165 | 361 | E | 24 | | - |
| | | | | (364) | | (23) | | (0.701) |
| 1847 | 1 | 14.97167 | 24.29803 | 313 | ENE | 17 | alkali basalt, px (ol) | 0.750 |
| | 2 | 14.97122 | 24.29827 | 317 | ENE | 17 | | 0.571 |
| | 3 | 14.97157 | 24.29841 | 320 | ENE | 17 | | 0.857 |
| | 4 | 14.97161 | 24.29809 | 318 | ENE | 17 | | - |
| | | | | (317) | | (17) | | (0.726) |
| 1852 | 1 | 15.00053 | 24.31219 | 429 | NE | 22 | alkali basalt, px | 0.857 |
| | 2 | 15.00033 | 24.31219 | 430 | NE | 23 | | 0.857 |
| | 3 | 15.00009 | 24.31228 | 433 | NE | 23 | | 0.750 |
| | 4 | 15.00022 | 24.31254 | 428 | NE | 23 | | - |
| | | | | (430) | | (22.75) | | (0.821) |
| 1857 | 1 | 14.91968 | 24.29332 | 327 | NE | 15 | alkali basalt, px | 1 |
| | 2 | 14.91964 | 24.29377 | 323 | NE | 15 | | 0.500 |
| | 3 | 14.92008 | 24.29409 | 320 | NE | 11 | | 0.500 |
| | 4 | 14.91951 | 24.29388 | 325 | NE | 11 | | - |
| | | | | (323) | | (13) | | (0.666) |
| 1951 | 1 | 14.91812 | 24.29366 | 334 | E | 10 | alkali basalt, px | - |
| | 2 | 14.91804 | 24.29338 | 332 | E | 10 | | - |
| | 3 | 14.91799 | 24.29305 | 331 | E | 10 | | - |
| | 4 | 14.91808 | 24.29345 | 330 | E | 10 | | - |
| | | | | (331) | | (10) | | |

6 * field observations

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Table 2. Vascular plant species observed in the 44 plots surveyed with species richness and total number of plants (Fogo Island, Cape Verde). Biogeographical status has been added with (I) indigenous (i.e. native but not endemic), (E) endemic, and (Ntz) naturalized species.

| Vascular plants (n=27) | Nd.1 | Nd.9 | Nd.10 (1664?) | 1769 | 1785 | 1799 | 1816 | 1847 | 1852 | 1857 | 1951 | Life-form | Biogeographic Status |
|--|-----------------|------------------|------------------|-----------------|------------------|----------------|-----------------|----------------|---------------|---------------|------------|------------|-------------------------|
| <i>Abrus precatorius</i> L. | | | x | | x | | | | | | | Vine | Ntz |
| <i>Abutilon pannosum</i> (G. Forst.) Schltld. | x | x | x | | | | | | | | | Shrub | I |
| <i>Acacia spirobis</i> Labill. | x | x | | | x | | | | | | | Tree | Ntz |
| <i>Asparagus</i> sp. | | | | x | x | | | | | | | Shrub/vine | Ntz |
| <i>Catharanthus roseus</i> (L.) G.Don | | | | | | | x | | | | | Herb | Ntz |
| <i>Coniza varia</i> (Webb) Willd | | | | | | | | x | | | | Shrub | E |
| <i>Desmodium tortuosum</i> (Sw.) DC.SG | | | | | x | | x | | | | | Shrub | Ntz |
| <i>Dichrostachys cinerea</i> (L.) Wight & Arn. | | | x | | x | | | | | | | Tree | I |
| <i>Diplotaxis irta</i> (A.Chev.) Rustan & L.Borgen | | | | | | | | x | | | | Herb | E |
| <i>Dryopteris</i> sp. | x | x | | x | x | x | x | x | x | x | | Fern | I? |
| <i>Euphorbia tuckeyana</i> Steud. ex Webb | x | x | x | x | x | | | | | | | Shrub | E |
| <i>Ficus thonningii</i> Blume | | | | | x | | x | | | | | Tree | I |
| <i>Farsskaalea procrudifolia</i> Webb | | | | | | | | | x | | | Shrub | E |
| <i>Furcraea gigantea</i> L. (Law) | | | | | | | x | | | | | Succulent | Ntz |
| <i>Globularia amygdalifolia</i> Webb | | | | | x | | | | | | | Shrub | E |
| <i>Grewia villosa</i> Willd | x | | | | x | | | | | | | Shrub | I |
| <i>Paronychia illecebroides</i> Webb | | | | | | x | | | | | | Shrub | E |
| <i>Jatropha curcas</i> L. | | x | x | | x | | x | | | | | Tree | Ntz |
| <i>Kalanchoe pinnata</i> (Lam.) Pers. | | | | | | | | | | x | | Succulent | Ntz |
| <i>Lantana camara</i> L. | | x | x | | x | | x | | x | | | Shrub/vine | Ntz |
| <i>Lavandula rotundifolia</i> Benth | x | | | x | x | x | x | | | | x | Shrub | E |
| <i>Leucaena leucocephala</i> (Lam.) de Wit | | | | | x | | | | | | | Tree | Ntz |
| <i>Lotus jacobaeus</i> L. | x | x | | x | x | | | | | | | Shrub | E |
| <i>Lotus pupureus</i> L. | x | x | x | x | x | | | | | | | Shrub | E |
| <i>Polypodium</i> sp. | x | x | x | x | x | | x | x | x | | | Fern | I? |
| <i>Sarcostemma daltonii</i> Decne. ex Webb | x | x | x | x | x | x | x | x | x | x | | Shrub/vine | E |
| <i>Senna bicapsularis</i> (L.) Roxb. | | x | | | x | | | | | | | Shrub | Ntz |
| Species richness per lava flow | 10 (6-8) | 11 (7-9) | 9 (6-6) | 8 (5-7) | 19 (11-15) | 4 (3-4) | 10 (5-8) | 5 (3-4) | 5 (3-4) | 3 (2-2) | 1 (0-1) | | |
| Number of plants per lava flow | 393 (77-130) | 663 (178-240) | 359 (87-132) | 356 (88-109) | 380 (105-119) | 188 (31-88) | 455 (80-133) | 175 (25-87) | 58 (10-30) | 64 (15-32) | 1 (0-1) | | |

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Table 3. Relationships between species density and age of lava flows in the plots (Spearman's coefficient correlation).

| Vascular species | Sample (n) | R ² | Intercorrelation |
|--------------------------------|------------|----------------|------------------|
| 1. <i>Abrus precatorius</i> | 10 | 0.114* | 2.3.4.5.6.7.8.9 |
| 2. <i>Asparagus</i> sp. | 14 | 0.136* | 1.3.4.8.9 |
| 3. <i>Lotus jacobaeus</i> | 15 | 0.160* | 1.2.4.6.8.9 |
| 4. <i>Lotus pupureus</i> | 16 | 0.265* | 1.2.3.6.7.8.9 |
| 5. <i>Polypodium</i> sp. | 94 | 0.161* | 1.6.7.8 |
| 6. <i>Lantana camara</i> | 24 | 0.334** | 1.3.4.5.7.8.9 |
| 7. <i>Jatropha curcas</i> | 20 | 0.323** | 1.4.5.6.8.9 |
| 8. <i>Euphorbia tuckeyana</i> | 112 | 0.485*** | 1.2.3.4.5.6.7.9 |
| 9. <i>Sarcostemma daltonii</i> | 1103 | 0.710*** | 1.2.3.4.6.7.8 |

P*** < 0.0001; 0.001** < P < 0.01; *P < 0.05

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Table 4. Plant species densities versus age of lava flows sampled (Stepwise regression model). Equation model is provided with the table.

| Rank of variable | Vascular plant species | Value | Standart deviation | t | Pr > t | Lower bound (95%) | Upper bound (95%) | Adjusted R ² |
|------------------|-----------------------------|---------|--------------------|-------|----------|-------------------|-------------------|-------------------------|
| 1 | <i>Sarcostemma daltonii</i> | 396.45 | 75.71 | 5.23 | < 0.0001 | 242.41 | 550.49 | |
| 2 | <i>Lantana camara</i> | 7337.75 | 1493.93 | 4.91 | < 0.0001 | 0.28 | 0.68 | |
| Model | Constant | 136.264 | 10.087 | 13.51 | < 0.0001 | 115.743 | 156.785 | 0.733 |

P-value to enter < 0.05; p-value to remove > 0.10

$$\text{Age of lava flows} = (136.263974515594 + 7337.7542282911 \times L. \text{ camara}) + (396.447385251673 \times S. \text{ daltonii})$$

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Table 5. Relationships between the 11 lava flows based on 27 vascular plant species densities (Spearman's correlation with PCA).

| Lava flows (n=11) | Nd.1 | Nd.9 | Nd.10 (1664?) | 1769 | 1785 | 1799 | 1816 | 1847 | 1852 | 1857 | 1951 |
|-------------------|--------------|--------------|------------------|--------------|-----------|--------------|--------------|--------------|--------------|-----------|------|
| Nd.1 | 1 | | | | | | | | | | |
| Nd.9 | 0.688 | 1 | | | | | | | | | |
| Nd.10 (1664?) | <i>ns</i> | 0.668 | 1 | | | | | | | | |
| 1769 | 0.778 | 0.558 | <i>ns</i> | 1 | | | | | | | |
| 1785 | 0.528 | <i>ns</i> | 0.589 | 0.676 | 1 | | | | | | |
| 1799 | <i>ns</i> | <i>ns</i> | <i>ns</i> | 0.492 | <i>ns</i> | 1 | | | | | |
| 1816 | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | 1 | | | | |
| 1847 | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | 1 | | | |
| 1852 | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | 0.497 | 0.617 | 1 | | |
| 1857 | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | 0.541 | <i>ns</i> | 0.500 | 0.500 | 1 | |
| 1951 | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | <i>ns</i> | 1 |

P ≤ 0.01; *ns* = not significant

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Table 6. Principal Component Analysis (PCA). Contribution of the species per axis (%) to the total inertia of the dataset.

| Vascular plants (n=27) | F1 | F2 | F3 | F4 | F5 | F6 | F7 | F8 | F9 | F10 |
|---------------------------------|--------|-------|-------|------|-------|-------|-------|-------|-------|-------|
| <i>Abrus precatorius</i> | 0.65 | 0.03 | 0.06 | 0.04 | 0.02 | 0.25 | 0.03 | 0.04 | 0.10 | 0.00 |
| <i>Abutilon pannosum</i> | 0.55 | 0.06 | 0.00 | 0.36 | 0.00 | 0.17 | 0.02 | 0.03 | 0.30 | 0.07 |
| <i>Acacia spirobis</i> | 0.73 | 0.00 | 0.03 | 0.13 | 0.00 | 0.03 | 0.02 | 0.04 | 0.08 | 0.26 |
| <i>Asparagus sp.</i> | 0.64 | 0.03 | 0.09 | 0.04 | 0.02 | 0.28 | 0.05 | 0.06 | 0.05 | 0.00 |
| <i>Catharanthus roseus</i> | 0.71 | 0.00 | 0.02 | 0.02 | 0.00 | 0.00 | 0.07 | 0.01 | 0.07 | 0.34 |
| <i>Coniza varia</i> | 0.72 | 0.00 | 0.01 | 0.18 | 0.00 | 0.08 | 0.01 | 0.00 | 0.06 | 0.29 |
| <i>Desmodium tortuosum</i> | 0.70 | 0.01 | 0.05 | 0.06 | 0.01 | 0.11 | 0.03 | 0.04 | 0.08 | 0.06 |
| <i>Dichrostachys cinerea</i> | 0.64 | 0.04 | 0.03 | 0.04 | 0.04 | 0.18 | 0.01 | 0.01 | 0.14 | 0.10 |
| <i>Diplotaxis irta</i> | 0.70 | 0.00 | 0.01 | 0.21 | 0.01 | 0.12 | 0.01 | 0.00 | 0.05 | 0.26 |
| <i>Dryopteris sp.</i> | 11.17 | 24.78 | 33.55 | 6.76 | 57.42 | 24.77 | 0.34 | 8.21 | 1.06 | 1.31 |
| <i>Euphorbia tuckeyana</i> | 0.23 | 3.37 | 0.27 | 1.11 | 0.09 | 2.00 | 0.46 | 0.02 | 24.82 | 2.33 |
| <i>Ficus thonningii</i> | 0.71 | 0.00 | 0.03 | 0.04 | 0.00 | 0.03 | 0.05 | 0.02 | 0.07 | 0.23 |
| <i>Forsskaolea procrifolia</i> | 0.69 | 0.00 | 0.00 | 0.13 | 0.00 | 0.05 | 0.01 | 0.26 | 0.08 | 0.46 |
| <i>Furcraea gigantea</i> | 0.23 | 0.44 | 0.10 | 5.42 | 1.47 | 1.42 | 3.42 | 0.97 | 0.12 | 0.12 |
| <i>Globularia amygdalifolia</i> | 0.75 | 0.00 | 0.03 | 0.12 | 0.00 | 0.04 | 0.02 | 0.03 | 0.07 | 0.30 |
| <i>Grewia villosa</i> | 0.61 | 0.02 | 0.10 | 0.14 | 0.00 | 0.05 | 0.05 | 0.06 | 0.68 | 0.08 |
| <i>Paronychia illecebroides</i> | 0.02 | 2.27 | 5.26 | 0.21 | 2.74 | 1.80 | 37.91 | 0.01 | 0.01 | 5.18 |
| <i>Jatropha curcas</i> | 0.56 | 0.08 | 0.01 | 0.02 | 0.12 | 0.04 | 0.01 | 0.04 | 0.24 | 0.85 |
| <i>Kalanchoe pinnata</i> | 0.61 | 0.02 | 0.03 | 0.32 | 0.40 | 0.02 | 0.45 | 0.00 | 0.11 | 0.25 |
| <i>Lantana camara</i> | 0.46 | 0.11 | 0.05 | 0.03 | 0.16 | 0.06 | 0.02 | 0.01 | 0.17 | 0.68 |
| <i>Lavandula rotundifolia</i> | 0.04 | 0.65 | 0.16 | 6.50 | 0.92 | 1.42 | 0.71 | 0.93 | 0.00 | 0.03 |
| <i>Leucaena leucocephala</i> | 0.75 | 0.00 | 0.03 | 0.12 | 0.00 | 0.04 | 0.02 | 0.03 | 0.07 | 0.30 |
| <i>Lotus jacobaeus</i> | 0.52 | 0.07 | 0.11 | 0.09 | 0.00 | 0.11 | 0.07 | 0.07 | 0.02 | 0.01 |
| <i>Lotus purpureus</i> | 0.37 | 0.18 | 0.01 | 0.29 | 0.00 | 0.07 | 0.03 | 0.01 | 0.01 | 0.02 |
| <i>Polypodium sp.</i> | 2.53 | 8.26 | 9.60 | 6.43 | 0.18 | 30.75 | 0.38 | 3.11 | 33.61 | 54.05 |
| <i>Sarcostemma daltonii</i> | 127.89 | 0.37 | 10.61 | 5.27 | 49.47 | 3.22 | 0.69 | 32.22 | 47.80 | 5.53 |
| <i>Senna bicapsularis</i> | 0.64 | 0.03 | 0.01 | 0.20 | 0.00 | 0.00 | 0.02 | 0.04 | 0.03 | 0.00 |

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