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# **Collapse of dispersal trait diversity across a long-term chronosequence reveals a strong negative impact of frugivore extinctions on forest resilience**

Sébastien Albert<sup>1</sup>, Olivier Flores<sup>1</sup>, Dominique Strasberg<sup>2</sup>

<sup>1</sup> Université de la Réunion, UMR PVBMT, F-97410 St Pierre, La Réunion, France; <sup>2</sup>

Université de la Réunion, UMR PVBMT, F-97400 St Denis, La Réunion, France

## **Abstract**

**1.** Understanding how seed dispersal disruption may alter plant community diversity and dynamics over a large temporal scale remains a challenge. Here, we use a long-term chronosequence to compare changes in the richness and composition of different dispersal trait assemblages in communities established before and after human colonisation in the Mascarene archipelago.

**2.** Our study was located on Réunion on the slopes of the Piton de la Fournaise, one of the most active volcanoes worldwide. We analysed 151 vegetation surveys on lava flows dated between 1401-AD and 1956-AD and in tropical rainforests established on older substrata. We defined five classes of substratum age, according to the well-known chronology of native frugivore defaunation: “old substrata” and [1401, 1665[ when frugivores were abundant and diverse before permanent human settlement; [1665, 1800[ when large-bodied frugivore populations were strongly reduced; [1800, 1900[ when large-bodied frugivores went extinct and small-bodied frugivores were still abundant; [1900, 1956] decline in the populations of small-bodied frugivores.

Based on dispersal traits, we categorised 146 native woody species as anemochorous, small fleshy-fruited or large fleshy-fruited, *i.e.* plant of which fruit could not theoretically be dispersed by extant frugivores.

**3.** Changes in dispersal trait diversity strongly correlated with the chronology of defaunation. Species-rich communities settled before human colonisation were strongly dominated by fleshy-fruited species. Large fleshy-fruited plants in the oldest communities settled after human colonisation declined markedly and almost disappeared after 1800. The richness of small fleshy-fruited plants decreased less rapidly across the chronosequence, with medium levels on [1665, 1800[ and [1800, 1900[ lava flows and low levels on [1900, 1956] lava flows. Conversely, the richness of anemochorous plants remained unchanged. Communities settled before human colonisation had a similar composition. Fleshy-fruited assemblages showed strong species loss across the chronosequence, while anemochorous assemblages showed strong species turnover, which was probably due to lower dispersal limitation.

**4. Synthesis.** Our results provide the first insights into the tremendous impact that frugivore extinction has on plant colonisation dynamics over 300 years. The dramatic loss of fleshy-fruited plant diversity on historical lava flows highlights the irreplaceable dispersal role played by frugivores, especially large-bodied species. The conservation of plant-animal mutualistic interactions is invaluable and refaunation efforts need to be undertaken in areas where frugivores have been extirpated.

## Résumé

**1.** Comprendre comment la rupture des interactions de frugivorie peut altérer la diversité et la dynamique des communautés végétales sur une grande échelle temporelle demeure un défi. Ici, nous utilisons une chronoséquence de plus de six siècles pour comparer les changements dans la richesse et la composition de différents assemblages basés sur les traits de dispersion au sein de communautés établies avant et après la colonisation humaine de l'archipel des Mascareignes.

**2.** Notre étude est située à La Réunion sur les pentes du Piton de la Fournaise, l'un des volcans les plus actifs au monde. Nous analysons 151 relevés de végétation sur des coulées de lave datées entre 1401-AD et 1956-AD, et en forêt tropicale humide sur des substrats plus anciens. Nous définissons cinq classes d'âge de substrat, selon la chronologie bien connue de la défaunation des frugivores indigènes : “vieux substrats” et [1401, 1665[ quand les frugivores étaient abondants et diversifiés avant la colonisation humaine permanente; [1665, 1800[ quand les populations des grands frugivores étaient fortement réduites; [1800, 1900[ quand les grands frugivores étaient éteints et les petits frugivores encore abondants; [1900, 1956] déclin des populations de petits frugivores. Nous caractérisons 146 espèces ligneuses indigènes selon leurs traits de dispersion : anémochores, à petits fruits charnus ou à gros fruits charnus, *i.e.* les fruits ne peuvent être théoriquement dispersés par les frugivores relictuels.

**3.** Les changements dans la diversité des traits de dispersion sont fortement corrélés à la chronologie de la défaunation. Les communautés avec une grande richesse spécifique établies avant la colonisation humaine sont largement dominées par les espèces à fruits charnus. Les plantes à gros fruits charnus dans les communautés éta-

blies peu après le début de la colonisation humaine déclinent très fortement et disparaissent quasiment après 1800. La richesse des plantes à petits fruits charnus diminue moins vite le long de la chronoséquence, avec des niveaux moyens sur les coulées de lave de [1665, 1800[ et [1800, 1900[, puis faibles sur les coulées de lave du 20<sup>ème</sup> siècle. En revanche, la richesse des plantes anémochores ne change pas de manière significative. Les communautés établies avant la colonisation humaine ont une composition comparable. Les assemblages de plantes à fruits charnus montrent une forte perte d'espèces le long de la chronoséquence tandis que les assemblages anémochores montrent un fort remplacement, probablement en raison d'une faible barrière à la dispersion.

**4. Synthèse.** Nos résultats montrent pour la première fois l'impact considérable de l'extinction des frugivores sur la dynamique de colonisation des plantes sur plus de 300 ans. L'effondrement de la diversité des plantes à fruits charnus sur les coulées de lave historiques souligne le rôle irremplaçable joué par les frugivores, en particulier les espèces de grande taille. La conservation des interactions mutualistes plantes-animaux est primordiale, et des efforts de refaunation doivent être entrepris dans les zones où les frugivores ont disparu.

## **Keywords**

Anemochory; biodiversity loss; defaunation; island biology; plant-animal mutualistic interactions; seed dispersal disruption; succession; zoochory

## **Abbreviations:**

AD: anno Domini; ADF: anemochorous dry-fruited; asl: above sea level; LFF: large fleshy-fruited; SFF: small fleshy-fruited;  $S_{st}$ : standardised richness

## 88    **Introduction**

89    The decline in large vertebrates is a global phenomenon (Blackburn, 2004; Dirzo et  
90    al., 2014; Hansen & Galetti, 2009; Steadman, 1995; Young, McCauley, Galetti, &  
91    Dirzo, 2016). For decades it has been raising serious concern with regard to the con-  
92    sequences for plant-animal mutualistic interactions (Bond, 1994; Emmons, 1989; Jan-  
93    zen, 1974). Notably, frugivore vertebrates (hereafter referred to as "frugivores") play a  
94    prominent role and their extirpation alters seed dispersal process (Babweteera &  
95    Brown, 2009; 2016; Jordano, Garcia, Godoy, & Garcia-Castano, 2007; McConkey &  
96    Drake, 2006; Meehan, McConkey, & Drake, 2002; Riera, Traveset, & Garcia, 2002;  
97    Wotton & Kelly, 2012; Young et al., 2016). Ecological and evolutionary consequences  
98    at plant population level include altered regeneration (Levi & Peres, 2013; Wotton &  
99    Kelly, 2011; Zeng, Swihart, Zhao, Si, & Ding, 2019), reduced connectivity (Pérez-Mén-  
100    dez, Jordano, & Valido, 2018), downsized dispersal traits (Galetti et al., 2013) and  
101    altered genetic diversity (Carvalho, Galetti, Colevatti, & Jordano, 2016). Recent stud-  
102    ies reported the transforming effects of frugivore loss on plant communities, by com-  
103    paring seedling recruitment between intact and defaunated sites (Effiom, Nunez-Iturri,  
104    Smith, Ottosson, & Olsson, 2013; Terborgh et al., 2008; Vanthomme, Bellé, & Forget,  
105    2010; Wandrag, Dunham, Duncan, & Rogers, 2017; Wright et al., 2007). However, to  
106    our knowledge, no study has yet examined how seed dispersal disruption may jeop-  
107    ardise whole tree communities over a period exceeding thirty years. Our research uses  
108    a long-term chronosequence of lava flows that spans a frugivore defaunation time  
109    range of 300 years on Réunion, an oceanic island that belongs to the Mascarenes. It  
110    has been one of the latest tropical archipelagos to be colonised by humans in the 17<sup>th</sup>  
111    century, which makes it a unique study system, particularly since: (1) the kinetics of  
112    frugivore extinction is well documented by subfossil records (Hume, 2013; Mourer-

Chauvire, Bour, Ribes, & Moutou, 1999) and historical archives (Cheke & Hume, 2008; Loughnon, 2005); and (2) high volcanic activity has produced numerous lava flows, which provide an ideal natural experiment to date and explain patterns of plant community changes (Fig. 1).

Seed dispersal is a key process for ecosystem recovery after disturbance, such as lava flows. Dispersal is the only possible pathway by which plant colonise disturbed areas where the living biomass, including soil seed banks, has been totally destroyed (Walker & Moral, 2003). In relation to seed dispersal strategies, fruit traits are important for understanding plant colonisation mechanisms: plants with large or small fleshy fruits mainly depend on frugivores for their dispersal, whereas most plants with dry fruits depend on abiotic dispersal vectors, *e.g.* wind (Howe & Smallwood, 1982; van der Pijl, 1982). In most tropical rainforests, frugivorous vertebrates are key components of forest succession, since they play a far greater role than wind in dispersing woody plants (González-Castro, Yang, & Carlo, 2019; Ingle, 2003; Whittaker, Bush, & Richards, 1989). Hence, past and present frugivore defaunation probably has severe consequences on ecosystem recovery and forest dynamics after disturbance. This is especially the case on tropical oceanic islands, where a mass extinction of frugivore vertebrates has frequently followed human colonisation (Blackburn, 2004; Heinen, van Loon, Hansen, & Kissling, 2017; Steadman, 1995). Therefore, we would expect drastic changes in the diversity and composition of fleshy-fruited plant assemblages on lava flows, before and after human colonisation, compared to anemochorous dry-fruited (ADF) plant assemblages, which remain unaffected.

The fruit of fleshy-fruited plants varies considerably in size, typically ranging from a few millimetres to over 50 cm (Guimarães, Galetti, & Jordano, 2008). This suggests that different sized frugivores are required for effective dispersal (Hansen &

Galetti, 2009; Naniwadekar, Chaplod, Datta, Rathore, & Sridhar, 2019). Critical fruit size thresholds exist among plant communities: for example, the early extinction of megafauna limited the dispersal of many large-seeded plants (Federman et al., 2016; Guimarães et al., 2008). Fruit size of ca 13 mm is documented as a critical threshold, both on the mainland (Dowsett-Lemaire, 1988; Galetti et al., 2013) and on oceanic islands (McConkey & Drake, 2015). As defaunation primarily extirpates large vertebrates (Dirzo et al., 2014), most oceanic islands are strongly depauperate in large-bodied frugivores (McConkey & Drake, 2015; Schleuning, Böhning-Gaese, Dehling, & Burns, 2014). In some places, including Réunion, they have been totally extirpated and therefore absent for several centuries (Heinen et al., 2017). In addition to the contrast between ADF vs fleshy-fruited species, we would also expect to see dramatic changes in diversity and composition within fleshy-fruited species given that large fleshy-fruited (LFF) plant assemblages are likely to have been impacted for a longer period (since human colonisation) than small fleshy-fruited (SFF) plant assemblages.

In this paper, we use a comparative approach to investigate whether dispersal failure caused by defaunation leads to severe diversity loss in plant communities studied across a long-term chronosequence of lava flows. We focus on changes in the richness and composition of ADF, SFF and LFF plant assemblages settled on substrata belonging to five age classes, which we consider as a proxy of dispersal agent availability (Fig. 1). We compare plant communities settled before permanent human settlement in 1665-AD, when frugivores were abundant and diverse, to more recent communities established after the extinction of large-bodied frugivores and the decline in the population of small-bodied frugivores began. First, we test whether changes in richness relate to the availability of frugivores. We expect the richness of LFF and SFF plant to be high on ancient lava flows that were colonised when frugivores were still



abundant. In theory, LFF plant richness should decrease faster across the chronosequence (from oldest to youngest lava flows) than SFF plant richness because large-bodied frugivores became extinct sooner than small frugivores. On the contrary, dispersal limitation for ADF plants is low, therefore, variation in ADF plant richness should be independent of the defaunation history. It may even increase across the chronosequence because early primary successional stages are often dominated by ADF species (Walker & Moral, 2003). Second, we analyse  $\beta$ -diversity and its two components, *i.e.* nestedness and turnover, which respectively result from the loss (or gain) of taxa and from the replacement of taxa (Baselga, 2010), to detect variation in plant community composition across the chronosequence. We expect strong dispersal limitation in fleshy-fruited species to lead to a significant increase of nestedness across the chronosequence, especially for LFF plants. On the contrary, if ADF species suffer no major dispersal limitation and can all reach lava flows, we should detect higher species replacement or species gain on recent lava flows (Wandrag et al., 2017).

## **Material and methods**

### **Study area**

Réunion (2512 km<sup>2</sup>) is the largest island in the Mascarene archipelago. It is located in the biodiversity hotspot that characterises the South-West Indian Ocean islands (Mittermeier et al., 2004) (Fig. 2). The study site is located in the South-East of Réunion on the slopes of the Piton de la Fournaise. This shield volcano is one of the most active in the world. More than 238 eruptions have been recorded since the second half of the 17th century (Morandi et al., 2016). For 5000 years, most lava flows have occurred in the most recent caldera of the Piton de la Fournaise. Eruptions have also occurred

outside the caldera along three rift zones (Morandi et al., 2016). The Piton de la Fournaise area has a humid tropical climate throughout the year below 750 m asl, *i.e.* annual mean temperature ranges from 19 to 25°C and precipitation in the driest month ranges from 75 to 350 mm, with large inter- and intra- annual variations (Jumeaux, Quetelard, & Roy, 2011). This area shelters almost all that remains of the tropical rainforest on Réunion and represents the last sanctuary of its kind in the Mascarene archipelago (Strasberg et al., 2005).

## **Data collecting**

### *Vegetation sampling and frugivore guild characterisation*

We used a historical dataset sampled in the 1970s by the French botanist Cadet (1977). It is invaluable because it includes forests that have since been destroyed (Appendix Fig. S1). We retained 151 vegetation plots sampled in pristine or relatively undisturbed habitats, where alien plants were rare or had little overall cover (Fig. 2). Twenty-eight plots were settled on well-developed soils as reported by Cadet (1977) in his technical notes. We did not have proper dating for these substrata, but based on the very likely slow pedogenesis, we assumed that they were at least 1000 years old (Meunier et al., 2010). One-hundred and twenty-three plots were located on 27 lava flows dated between 1401 AD and 1956 AD: (i) three lava flows were dated by <sup>14</sup>C (Morandi et al., 2016), (ii) sixteen lava flows were known from historical sources (Cadet, 1977; Stieltjes, 1986) and (iii) eight lava flows were dated using an indirect approach based on the size distribution of long-lived ADF pioneer trees found on lava flows (Strasberg, Michon, Daux, & Muro, 2012). Because <sup>14</sup>C dating could not be used

in several areas such as the caldera that, however, hosted isolated old remnant forests, the tree size method allowed to expand the chronosequence and to add some heterogeneity in the sampled ecological situations.

We assigned the 151 vegetation plots to five substrata age classes, defined according to the availability of dispersal agents, as documented by subfossils records (Hume, 2013; Mourer-Chauvire et al., 1999) and historical archives (Cheke & Hume, 2008) (Fig.1). Namely, the first class was “old substrata” on which plant communities assembled when frugivores were numerous and where pedological conditions were supposed to be more favorable. This class therefore included our reference control plots (n = 28 plots); the second class was [1401, 1665[, when frugivores were still numerous and diverse (n = 36 plots); the third class was [1665, 1800[, when large-bodied frugivore populations were severely reduced, while small-bodied frugivore populations were less impacted (n = 23 plots); the fourth class was [1800, 1900[, when large-bodied frugivores were extinct and small-bodied frugivores, especially the native bulbul (*Hypsipetes borbonicus*) and the hoopoe starling (*Fregilupus varius*), were still abundant (n = 37 plots); the fifth and most recent class was [1900, 1956], when populations of extant small-bodied frugivores further declined to extremely low densities (n = 27 plots) (Fig.1).

Spatial distribution of study plots was not random given the volcanic eruption pattern, as well as difficulties in accessing some remote locations (Fig. 2 & Appendix Fig. S2). All plots on “old substrata” were outside the caldera; plots on [1401, 1665[ lava flows were all located in the southern half of the Fournaise area, whereas those on [1665, 1800[ lava flows showed a wider distribution; plots located on [1800, 1900[ and [1900, 1956] lava flows were respectively located in south-central Fournaise area and in the caldera. In the latter area, old growth native forests were already rare

and very fragmented in 1975. Cadet (1977) also used different sampling areas ranging from 500 to 1000 m<sup>2</sup> on pre-defaunation lava flows and from 100 to 1000 m<sup>2</sup> on historical lava flows (Fig. 2).

For each plot, Cadet (1977) recorded the cover of tree, shrub and herbaceous *strata* and maximum canopy height. For each *stratum*, he recorded the list of tracheophyta at species level, including seedlings with the Braun-Blanquet semi-quantitative method. These data allowed us to quantify species richness, composition and vegetation structure. We focused on woody species, *i.e.* woody angiosperms and arborescent ferns because they were taxonomically well known in the 1970s, unlike herbaceous species. In addition, they contribute significantly to the structure of plant communities from the early stages of vegetation development on (Cadet, 1977).

#### *Dispersal traits of woody species*

Woody species were assigned to three functional groups based on dispersal traits. Fleshy-fruited plants that were originally dispersed by a rich native frugivore fauna (Fig. 1 & Appendix Tab. S1) were assigned to two dispersal trait groups based on fruit size (Izhaki, 2002; McConkey & Drake, 2015): small fleshy-fruited (SFF) and large fleshy-fruited (LFF) species. These two groups were defined according to the mean value for fruit (or arillate seed) diameter, *i.e.* above or below 13 mm, which is the maximum gape width of *Hypsipetes borbonicus*, the largest extant frugivore on Réunion (body mass = 55 g) (Cheke, 1987). Plants that use wind dispersal mechanisms and do not depend on animal dispersal were categorised as anemochorous dry-fruited (ADF). Dry-fruited plant species whose dispersal strategy remained unclear were included in the overall analysis of diversity, but not assigned to a specific dispersal trait group. These species are not common in lowland forests on Réunion.

## Statistical analyses

We constructed a presence-absence matrix for each plot and each dispersal trait group based on species presence at any growth stage, *i.e.* in any vegetation *stratum*. Species could thus be present at seedling or sapling stage only.

### *Plant species richness across the chronosequence*

We modeled plant species richness across the chronosequence using a multiple regression approach to take into account the relative influence of plot area, elevation, precipitation of driest month and isolation that substantially varied across study plots (Appendix Fig. S2). To assess plot isolation, we used a habitat map to construct a binary raster of native closed-canopy forests at 100 m resolution and calculated the proportion of native forests in the 100 hectares surrounding each plot. The five variables used for analyses showed moderate collinearity with maximum variance inflation factors < 4.

The relationship between count data responses (species richness of all woody plants, ADF, SFF, LFF and not-assigned plants) and explanatory variables including the five variables and four interaction terms, *i.e.* age of lava flow x (isolation + elevation + precipitation + area), were analysed using generalized linear models (GLMs) with a Poisson distribution (O'Hara & Kotze, 2010). Using a type-II analysis of deviance, we dropped the non-significant terms for each GLM. We used the Moran eigenvector filtering function (R package "spdep") to account for possible effects of spatial autocorrelation on parameter estimates (Bivand et al., 2015). Pseudo- $R^2$  of GLMs were calculated by the relationship "1 – residual deviance/null deviance". We finally estimated the standardised values of species richness ( $S_{st}$ ) across the chronosequence by fixing

the four other variables to their mean value (sampling area = 591 m<sup>2</sup>, elevation = 354 m asl, precipitation of driest month = 226 mm, isolation = 46 % of native forests).

### *Community composition across the chronosequence*

We performed pairwise dissimilarity analyses between vegetation plots and used the *beta.pair* function (R package *betapart*) to decompose total  $\beta$ -diversity (measured by Sorensen dissimilarity) into its two components, nestedness and turnover (measured by Simpson dissimilarity) (Baselga & Orme, 2012). We then constructed six distance matrices by calculating the absolute values of the difference between each pair of plots for age of lava flow, sampling area, elevation, precipitation of driest month and isolation. Because age of lava flow was an ordinal variable, we converted the five age classes to numerical values from 1 (old substrata) to 5 ([1900; 1956]). We also calculated the Euclidean geographical distance for each plot pair. To take into account the influence of sampling area, elevation, precipitation of driest month, isolation and Euclidean distance on dissimilarities across the chronosequence, we could not use a multiple regression as we did for species richness because of obvious violation of the assumption on independence (Anderson et al., 2011). Consequently, we performed partial Mantel tests with 1000 permutations (R package *ecodist*) to examine the influence of age of lava flow on each dissimilarity while controlling for other variables, and vice versa (Goslee & Urban, 2007).

## **Results**

### **Species richness across the chronosequence**

The age of lava flow was by far the best predictor of species richness for woody plants overall ( $n = 151$ ,  $p = 1.7e-27$ ; pseudo- $R^2 = 0,87$ ), small fleshy-fruited (SFF) plants ( $p =$

4.7e-27; pseudo- $R^2 = 0,84$ ) and large fleshy-fruited LFF plants ( $p = 6.2e-41$ ; pseudo- $R^2 = 0,87$ ) (Appendix Tab. S2 & Fig. S3). Conversely, elevation was the best predictor for anemochorous dry-fruited (ADF) plant richness ( $p = 3.7e-16$ ; pseudo- $R^2 = 0,70$ ). Isolation also had a strong influence on the richness of the four groups, but only on post-defaunation lava flows for all woody plants, SFF and LFF plants.

The estimated standardised species richness ( $S_{st}$ ) for woody plants overall decreased considerably across the chronosequence, *i.e.* with decreasing substrata age (Fig. 3):  $S_{st}$  was similar on pre-defaunation substrata, *i.e.* 32.9 and 35.4 in “old substrata” and [1401; 1665] respectively, then declined markedly to 17.6 in [1665; 1800[ and [1800; 1900[, and dropped down to 11.5 species in [1900; 1956]. This general downward trend across the chronosequence concealed very different changes that were evidenced when dispersal trait groups were considered separately (Fig.3).  $S_{st}$  for ADF plants ranged from 4.8 to 6.2 species and showed no significant trend across the chronosequence. Changes in species richness of fleshy-fruited plants drove the general trend of woody plant species.  $S_{st}$  for SFF plants was similar on pre-defaunation substrata, *i.e.* 20.9 and 22.5 in “old substrata” and [1401; 1665], respectively, then strongly decreased in [1665; 1800[ to 10.8 species. It was similar in [1800; 1900[ with 11.3 species and dropped down to 5.4 species in [1900; 1956].  $S_{st}$  for LFF plants followed a similar pattern to SFF plants, although their decline was more abrupt: LFF plant richness was similar on pre-defaunation substrata, *i.e.* 6.1 and 7.3 in “old substrata” and [1401; 1665], respectively. It showed a strong decrease to 1.1 species in [1665; 1800[, fell to 0.4 species in [1800; 1900[ and 0 in [1900; 1956]. The independently standardized estimated richness across dispersal trait groups overall summed to the overall richness of woody species with a low average relative difference of 0.5%, which suggested a good accuracy of the separate estimates (Appendix

Fig. S4). Lastly, we also performed statistical analyses without taking into account lava flows whose dating was based on pioneer trees development and obtained similar conclusions (Appendix Fig. S5).

### **Community composition across the chronosequence**

The total  $\beta$ -diversity measured by Sorensen dissimilarity with control plots as reference ("old substrata") showed a highly significant increase across the chronosequence for woody plants overall (from 0.35 to 0.90), as well as within each dispersal trait group (ADF, from 0.35 to 0.78; SFF, from 0.35 to 0.89; LFF, from 0.33 to 0.62) when other variables were controlled (partial Mantel test,  $p < 0.001$ ) (Fig. 4 & Appendix Fig. S6). For woody plants overall, turnover and nestedness increased significantly across the chronosequence (partial Mantel tests,  $p < 0.001$  &  $p < 0.001$ ). However, turnover was the main driver of composition changes, in relation with fleshy-fruited (both LFF and SFF) and ADF species dominating assemblages on old and recent lava flows, respectively (Fig. 3). Within dispersal trait groups, the general increase in Sorensen dissimilarity concealed very different situations evidenced when the two components of  $\beta$ -diversity were considered separately.

For ADF assemblages, the turnover strongly increased across the chronosequence from 0.26 to 0.64 (partial Mantel test,  $p < 0.001$ ), whereas nestedness was low and stable (partial Mantel test, NS) and mostly influenced by elevation and isolation (Fig. 4 & Appendix Fig. S6). For SFF assemblages, the turnover was mostly influenced by elevation and showed a weak increase from 0.26 to 0.32 across the chronosequence (partial Mantel test,  $p = 0.04$ ), whereas nestedness strongly increased from 0.09 to 0.57 (partial Mantel test,  $p < 0.001$ ). For LFF assemblages, dissimilarity analyses involve a shorter chronosequence, given that LFF plants are totally absent on



[1900; 1956] lava flows, and showed similar trends as SFF assemblages. The turnover was mostly influenced by elevation and remained stable between 0.19 and 0.29 (partial Mantel test, NS), whereas nestedness strongly increased from 0.12 to 0.37 (partial Mantel test,  $p < 0.001$ ). Overall, species replacement was the main phenomenon driving species composition of ADF assemblages across the chronosequence, while SFF and LFF plant assemblages that remained on recent lava flows constituted a subset of the communities found on “old substrata”.

## Discussion

### Frugivory disruption as a major cause of fleshy-fruited plant diversity loss

Plant dispersal trait diversity is strongly related to the availability of dispersal agents across a long-term chronosequence on the Piton de la Fournaise volcano. This suggests that the extinction of large-bodied frugivores has severely limited dispersal for many plant species since the early 18<sup>th</sup> century, *i.e.* less than a century after the first human settlements. It appears to be a major cause of the fleshy-fruited plant diversity loss on historical lava flows. The negative impact of frugivore defaunation on tree recruitment has already been shown at community level (Effiom et al., 2013; Terborgh et al., 2008; Vanthomme et al., 2010; Wright et al., 2007). Nevertheless, to our knowledge, our study is the first to reveal such a dramatic collapse of dispersal trait diversity of the temporal scale of several centuries. Our research was made possible because frugivore defaunation in the Mascarene archipelago has been well documented (Cheke & Hume, 2008; Loughon, 2005) and because the high volcanic activity on Réunion provides numerous lava flows that constitute a natural experiment acting as a “time machine”.

Forests on old substrata and lava flows that occurred before permanent human settlements are widely dominated by fleshy-fruited species (Albert, Flores, Rouget, Wilding, & Strasberg, 2018). They include LFF plants, that are usually big trees (Diaz et al., 2004; Thompson & Rabinowitz, 1989) with an important structural role in native forests (Appendix Fig. S7 & Fig. S8). LFF plants are far less present on lava flows that occurred while the large-bodied frugivores were strongly decreasing in number. Hence, it is likely that effective dispersal at ecosystem level was disrupted before the dispersers of most LFF species actually went extinct, as shown elsewhere (McConkey & O’Farrill, 2016). LFF plants, including seedlings, are very scarce on lava flows that occurred after the extinction of all large-bodied frugivores in 1800. This shows that the latter play an extremely important role because they can swallow large fruits and are more likely to deposit seeds away from the parent tree (Naniwadekar et al., 2019; Wotton & Kelly, 2012). This also suggests that potential dispersal alternatives are very unreliable, *e.g.* secondary dispersal by introduced vertebrates or cyclone-mediated seed dispersal (Babweteera & Brown, 2009; Federman et al., 2016). The richness of SFF plants also decreases on lava flows that occurred after 1665, despite the abundance of several important frugivores for this species group, the native bulbul and the hoopoe starling. Large-bodied frugivores do not just eat LFF plants and also play an important role in SFF plant dispersal (Bollen & Elsacker, 2002; Florens et al., 2017; Oleksy, Giuggioli, McKetterick, Racey, & Jones, 2017). In fact, their extinction has probably led to a decrease in the dispersal efficiency of most fleshy-fruited plants (Babweteera & Brown, 2009; Carvalho et al., 2016) and to the inability of many SFF plants to reach isolated post-defaunation lava flows (Jordano et al., 2007; Wotton & Kelly, 2012). We show that SFF richness eventually collapses on lava flows from the 20<sup>th</sup> century, as already suggested (Chevennement, 1990; Strasberg, 1994; Thébaud &

Strasberg, 1997). We also reveal that the few fleshy-fruited species that colonise these areas are usually present on older substrata. Conversely, ADF plant richness remains unchanged across the chronosequence, despite strong species replacement. This finding suggests that successional changes occur within ADF assemblages across the chronosequence, but only rarely in fleshy-fruited assemblages (Wandrag et al., 2017).

#### **Potential post-dispersal limitations**

The pattern that we detected could partly be explained by post-dispersal factors, such as environmental filtering, e.g. light requirements, depth soil, or biotic interactions, e.g. seed predation (Wang & Smith, 2002).

We have consistent evidence that the total absence of many fleshy-fruited plant species, even at early life stages, on lava flows dating from [1665; 1800[ and [1800; 1900[ is not a consequence of environmental filtering. Although shade tolerance or light requirements were not considered in our analyses, it is likely that some SFF understorey shrubs have difficulty germinating in open canopy vegetation, especially on the most recent lava flows. However, the proportions of LFF and SFF plants do not depend on canopy cover (Appendix Fig. S9). Many vegetation plots on historical lava flows show a well-developed canopy, but totally lack a LFF tree that is very common on pre-defaunation lava flows (*Labourdonnaisia calophylloides*, Sapotaceae, Appendix Fig. S10). Moreover, the presence of long-lived pioneer trees across the chronosequence provides relevant insights: a SFF pioneer tree (*Sideroxylon borbonicum*, Sapotaceae) is common on lava flows that occurred when small frugivores were abundant, but is much less prevalent on [1900; 1956] lava flows, despite favorable light conditions. On the contrary, an ADF pioneer tree (*Agarista salicifolia*, Ericaceae) is present across the entire chronosequence (Appendix Fig. S10). Finally, soil type is

another factor that might limit recruitment, but our analyses show a standardised richness as high on old substrata as on [1401, 1665[ lava flows and a low  $\beta$ -diversity between these categories. Hence, most big trees found on well-developed soils are able to establish and develop on [1401, 1665[ lava flows that usually display a very thin soil on continuous rock (Meunier et al., 2010) (Appendix Fig. S11).

Seed predation may also be an important mechanism that limits plant recruitment (Forget, 2005; Hubbell, 1980; Janzen, 1970). Rats are usually the main seed predators on oceanic islands (Shiels & Drake, 2015) and probably reached high densities in the late 17<sup>th</sup> century, after their introduction on Réunion (Cheke & Hume, 2008). Since then, rat populations may have remained at high levels. It is however unlikely that seed predation by rats could explain the temporal shift observed between LFF and SFF plants across the chronosequence. A few LFF plants are common at all growth stages in extant mature rainforest on pre-defaunation lava flows, despite the abundance of rats (Strasberg, 1996), whereas they are totally absent from post-1800 lava flows. Hence, seed predation may play a secondary role in limiting recruitment, as shown by Wotton & Kelly (2011) in New Zealand.

#### **Primary succession disruption and implications for conservation**

Our analyses show that, in less than five centuries, primary succession on lava flows has led to plant assemblages of woody plants similar in richness and composition to those found on old substrata. The fact that LFF plants probably lost their dispersal capacity after 1800 shows that they were already present on historical lava flows in 1800. Hence, well under 200 years might have been enough for the establishment of most shade-tolerant tree species. This temporal scale is consistent with Thornton

(1997), who documents the assembly of the Krakatau Islands ecosystem after its destruction in 1886, *i.e.* three years after the islands' sterilisation: despite the sea barrier (12 km from the closest source and 40 km from mainland Java and Sumatra), six zoochorous plants were recorded as soon as 1896, 23 in 1905, 35 in 1920, 68 in 1934 and 124 species in 1992. In the case of the Krakatau Islands, Whittaker & Jones (1994) emphasise the crucial role played by fruit pigeons able to transport large-seeded plants that became established in the decades following the initial disturbance.

The absence of many native species on historical lava flows has probably had severe consequences on succession processes. For instance, the absence of LFF tree species may have caused competition release (Hurtt & Pacala, 1995), possibly benefiting alien plants with low dispersal limitation. Recent surveys on post-1800 lava flows reveal the presence of the same native plant communities as those surveyed by Cadet (1977), as well as the generally low or absent regeneration of native species (Albert, Flores, Franc, & Strasberg, 2019), suggesting arrested succession (Cohen, Singhakumara, & Ashton, 1995). Together, these findings demonstrate that plant communities of different ages do not follow the same trajectory and that the vegetation stages originally described by Cadet (1977) do not represent successional seres (Walker, Wardle, Bardgett, & Clarkson, 2010). Therefore, it is unlikely that the structure and diversity of native plant communities on historical lava flows will ever be as rich as the tropical rainforests on pre-defaunation substrata.

The persistently high LFF plant richness on pre-defaunation lava flows supports the fact that, despite the loss of all large-bodied frugivores since 1800, plant communities can display a high level of resilience *in situ*, but a very low level of resilience by migration (Grubb, 1987). The plant communities on pre-defaunation lava flows are

among the most important and well-preserved testimony of Mascarenes' lowland ecosystems (Strasberg, 1996), and their protection is considered crucial (Mittermeier et al., 2004). Our results confirm that their loss would be particularly dramatic because these ecosystems have lost their resilience. Although most of the remaining lowland ecosystems are protected as part of the Réunion National Park, the high frequency of lava flows in this area of Réunion may lead to their gradual destruction. In 2007, for example, the last fragment of tropical rainforest at sea level was destroyed (Appendix Fig. S1). Moreover, the apparent maintenance of diversity on pre-defaunation lava flows is probably due to the fact that our study uses presence/absence data and does not take into account a potential failure of local recruitment for many species of the canopy. Several shade-tolerant long-lived trees hardly regenerate (Strasberg, 1996) and long-lived pioneer trees are often unable to reach gaps nearby, which makes them particularly sensitive to local extinction in the near future (Wandrag et al., 2017).

Today, frugivory disruption combined with alien plant invasion (see Potgieter, Wilson, Strasberg, & Richardson, 2014) leads to the development of novel ecosystems with extremely low taxonomic and functional diversity. Given the dramatic loss of native fleshy-fruited plant diversity on recent lava flows, conservation strategies should include the lack of native vegetation recovery as a matter of urgency. Restoring the seed dispersal function will be necessary in defaunated ecosystems (Correia, Timóteo, Rodríguez-Echeverría, Mazars-Simon, & Heleno, 2017), as has already been done on several islands in the Indo-Pacific region (Griffiths, Hansen, Jones, Zuël, & Harris, 2011; Pedrono et al., 2013). The fact that there will be no altitudinal escape for most fleshy-fruited plants in the context of climate change makes the situation even more urgent (McConkey et al., 2012).

## Conclusion

Defaunation can cause negative impacts on ecosystem functioning comparable with those from major drivers of global change (Young et al., 2016). However, its long term impact on dynamics of very long-lived trees is not sufficiently documented. Our study brings a first evidence of frugivore defaunation effect at community level over a temporal scale of 300 years. The studied chronosequence of lava flows acting as a “time machine” and harboring plant communities settled before and after human colonisation provides a natural experiment on one of the last tropical islands colonised by humans. To our knowledge, this is the first time that such a collapse of dispersal trait diversity has been shown. It strongly argues in favour of restoration programs targeting the re-establishment of seed dispersal interactions by promoting native frugivore populations and rewilding projects focusing on large vertebrates.

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519 **Authors' contributions**

520 Sébastien Albert, Olivier Flores and Dominique Strasberg developed the ideas for the  
521 research and collected data. Sébastien Albert and Olivier Flores analysed the data.  
522 All authors contributed critically to the drafts of the paper and have given their approval  
523 for publication.

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## 525 **Supporting information**

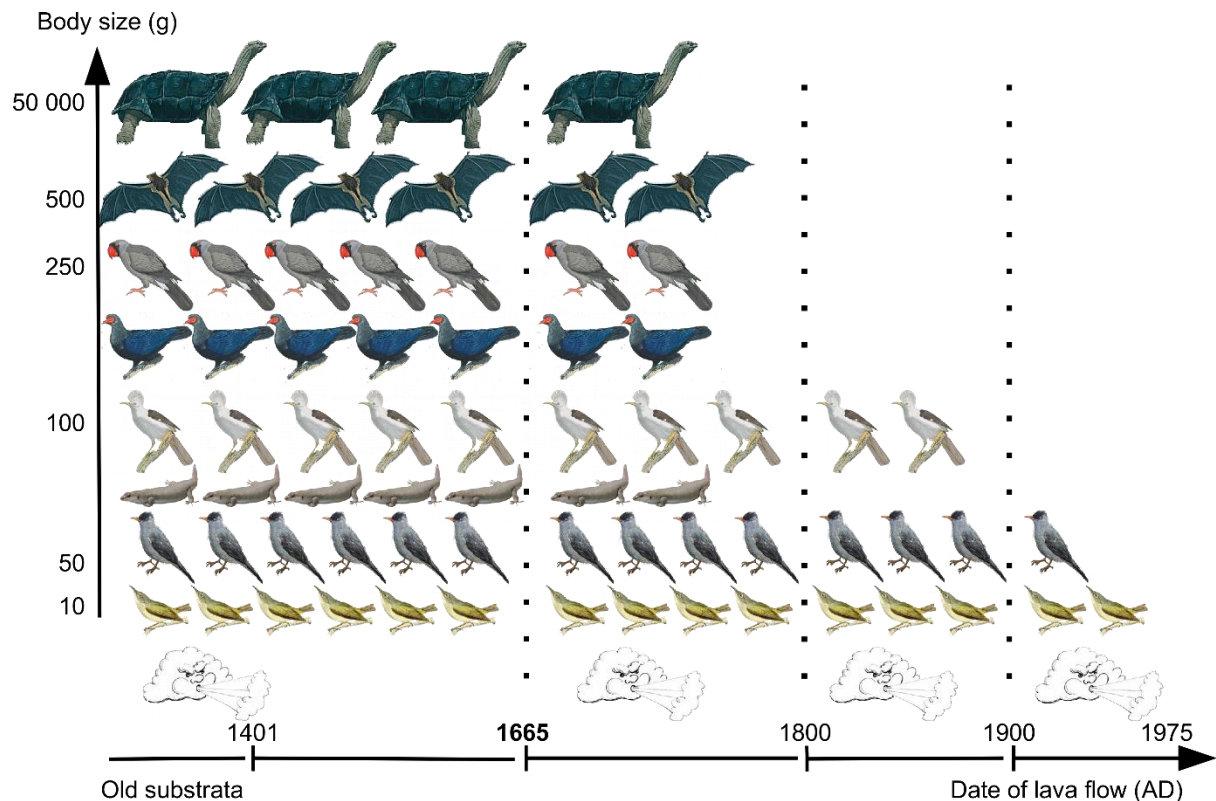
526 Appendix. This appendix includes Table (S1) and Figures (S1, S2), presenting additional  
527 information on methods, and Table (S2) and Figures (S3 to S11), presenting  
528 additional results related to species richness, species composition and vegetation  
529 structure across the chronosequence.

## 530 **Data accessibility**

531 Data available from the Dryad Digital Repository:  
532 <https://doi.org/10.5061/dryad.2v6wwpzhm> (Albert, Flores, & Strasberg, 2019)

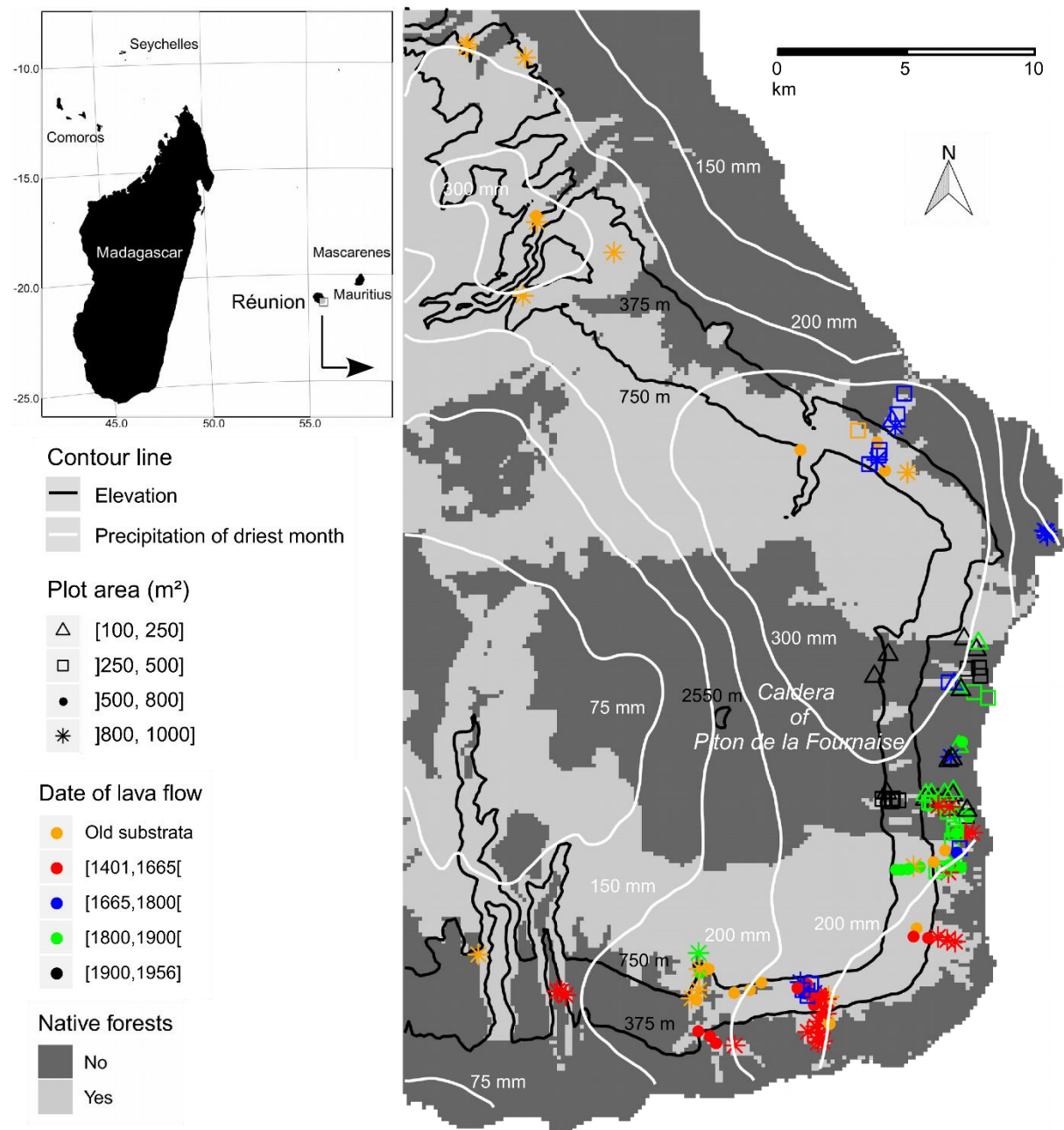
533

## Figures

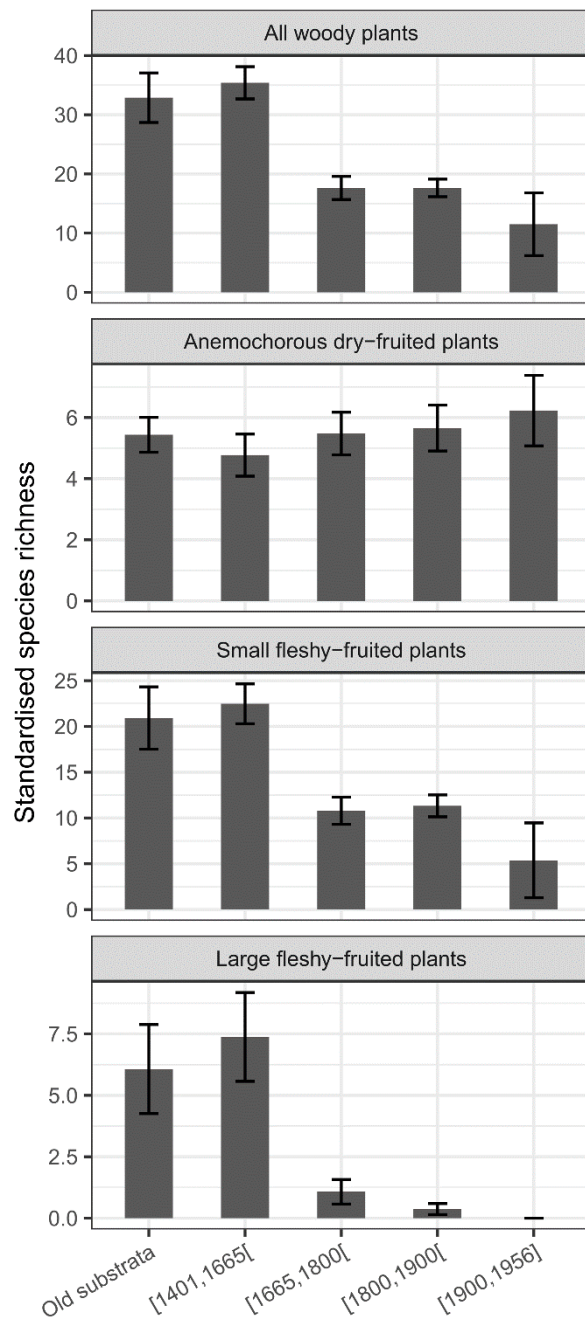


**Fig. 1.** Historical milestones in relation to availability of dispersal agents on Réunion across a long-term chronosequence of lava flows. Availability through time in native frugivores (from top to bottom: giant tortoises, flying foxes, parrots, fruit pigeons, starlings, skinks, bulbuls and white-eyes) is inferred from Cheke and Hume (2008) and Lounnon (2005). Native frugivore assemblages were diversified and oversized until the first human settlements were established in 1665 AD. After 135 years of human settlement throughout the lowlands, habitat destruction and overharvesting led to the extinction of large-bodied frugivores by 1800. The Réunion bulbul was abundant until the beginning of the 20<sup>th</sup> century, when populations declined sharply. They have remained at low levels throughout the 20<sup>th</sup> century until Cadet's sampling in 1975. Wind is assumed to be constantly present across the chronosequence. The giant tortoises, flying foxes, parrots, fruit pigeons and starlings were illustrated by Julian Hume, the white-eyes by John Gerrard Keulemans, the skinks by Josh Noseworthy and the bulbuls by Dominique Strasberg. For more details about frugivores, see Appendix Tab. S1.

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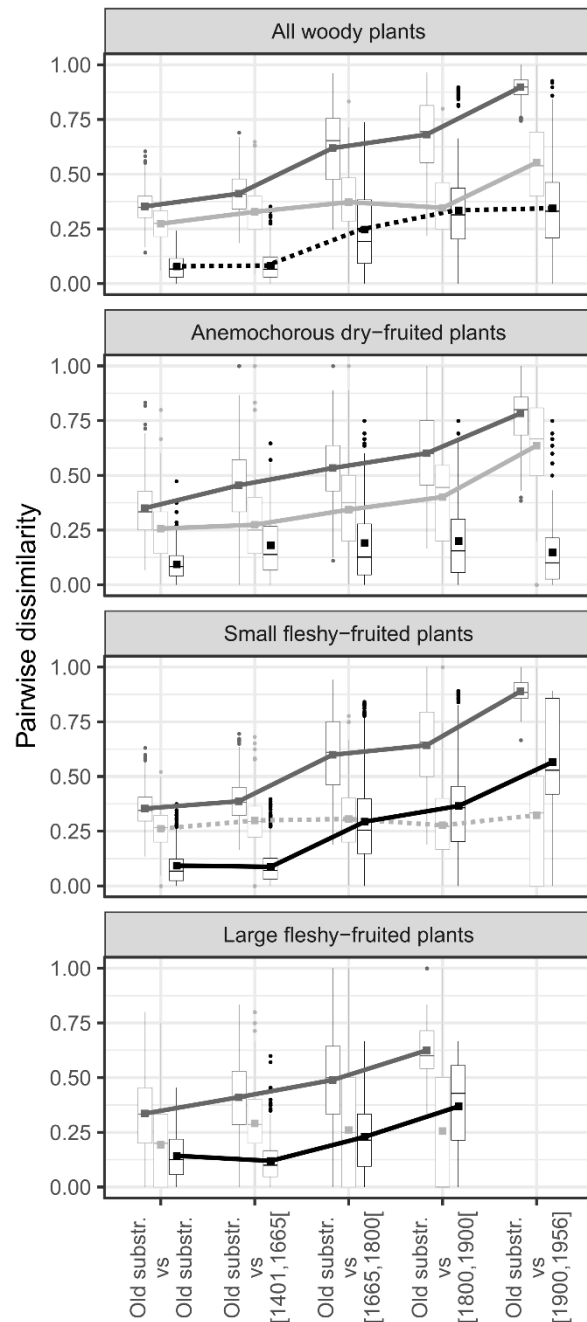


**Fig. 2.** The study site on Réunion in the Piton de la Fournaise area. Réunion is an oceanic island in the South-West Indian Ocean, situated between Madagascar and Mauritius in the Mascarenes. The massif of the Piton de la Fournaise extends across the South-Eastern third of the island (white rectangle). The 151 vegetation plots are located on the windward side below 750 m asl and shown according to lava flow dating: 123 plots in four classes are located on lava flows that occurred between 1401 and 1956; and 28 plots are found on old substrata, i.e. over 1000 years old.



**Fig. 3.** Estimated standardised richness of native woody plants at any growth stage across the chronosequence (sampling area fixed at 591 m<sup>2</sup>, elevation at 354 m asl, precipitation of driest month at 226 mm, isolation at 46% of native forests). Richness is independently assessed for woody plants overall and for three dispersal trait groups: anemochorous dry-fruited, small fleshy-fruited and large fleshy-fruited plants that respectively depend on wind, frugivores of various size and large-bodied frugivores. Confidence intervals at 95% on estimated standardised richness are given by error bars. Note that large fleshy-fruited plants are completely absent on the most recent lava flows.





**Fig. 4.** Pairwise Sorensen (dark grey), turnover (light grey) and nestedness (black) dissimilarities between native plant assemblages on old substrata (used as reference) and native plant assemblages in each lava flow age class. Pairwise dissimilarities are independently assessed for woody plants overall and for three dispersal trait groups: anemochorous dry-fruited, small fleshy-fruited and large fleshy-fruited plants that respectively depend on wind, frugivores of various size and large-bodied frugivores. Boxplots and squares respectively display raw and mean values for each age class. Solid lines are displayed when the age of lava flow is the most explanatory variable

*apart the effect of area, elevation, precipitation of driest month, isolation and geographical distance (Appendix Fig. S2). Dotted lines are displayed when the age of lava flow has a significant effect, but is not the most explanatory variable. Note that large fleshy-fruited plants are completely absent on the most recent lava flows.*