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1 **Why are woody plants fleshy-fruited at low elevations? Evidence from a**
2 **high-elevation oceanic island**

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15 **Abstract**

16 **Question**

17 The composition of fruit types, fleshy vs dry fruits, greatly influences the functioning of
18 plant communities. Literature documenting spatial patterns of fruit types at fine scale is
19 abundant. However, studies at larger geographical scale remain scarce, especially on
20 high-elevation oceanic islands that provide a great environmental heterogeneity. Here, we
21 investigated how abiotic factors explained the proportion of fleshy-fruited species (pFF) on

1 Réunion. We asked (i) which abiotic factors were most related to pFF, (ii) if fleshy-fruited
2 canopy species were more sensitive than fleshy-fruited shrubs to harsh climatic conditions
3 and (iii) what are the relationships between pFF, endemism and phylogenetic relatedness.

4 **Location**

5 Réunion (3070 m a.s.l), Mascarene archipelago, South-West Indian Ocean.

6 **Methods**

7 We used a dataset of 429 vegetation plots and assigned fruit types, growth forms and
8 geographical distribution to 213 native woody species. Phylogenetic trees were
9 constructed for each plot. We used GLMs to measure the relationship between pFF and
10 abiotic factors, controlling for spatial autocorrelation. We then assessed the relationship
11 between pFF, the standardized net relatedness index and the proportion of endemic
12 species.

13 **Results**

14 The top model explained 78% of the variation in pFF. Elevation was by far the best
15 predictor, with pFF decreasing from 81% at 50 m a.s.l to 0% at 3000 m a.s.l. At low
16 elevations, pFF was higher on the wet windward (81%) than on the leeward (70%) where
17 phylogenetic clustering was evident. Almost half (48%) of woody plants was fleshy-fruited
18 trees at low elevations. The proportion of fleshy-fruited trees declined sharply with
19 elevation and was significantly related to precipitation of the driest month contrary to the
20 proportion of fleshy-fruited shrubs that showed a hump shaped pattern along elevational
21 gradient and no correlation with precipitation of the driest month. At high elevations, most
22 plant assemblages were phylogenetically clustered and strongly dominated by single-
23 island endemic dry-fruited plants.

1 **Conclusions**

2 The striking relationship between pFF and elevation, the shift among fleshy-fruited growth
3 forms along climatic gradients and the phylogenetic clustering of assemblages subjected
4 to harsh climatic conditions, suggested that climatic factors were the main drivers of the
5 distribution of fruit types on Réunion. To explain the absence of fleshy-fruited species at
6 high elevations, we hypothesized that native fleshy-fruited lineages lacked the evolutionary
7 potential to adapt and fleshy-fruited cold-adapted lineages had major difficulties reaching
8 Réunion.

9 **Keywords**

10 Community ecology; ecophylogenetics; elevational gradient; endemism; island
11 biogeography; niche conservatism; seed dispersal strategy

12 **Abbreviations:** DF=dry-fruited; FF=fleshy-fruited; NRI=standardized net relatedness
13 index; pFF=proportion of fleshy-fruited plants; pFFtree=proportion of fleshy-fruited trees;
14 pFFshrub=proportion of fleshy-fruited shrub; pMS=proportion of Mascarene-shared
15 species; pSIE=proportion of single-island endemic species

16 **Main text**

17 **Introduction**

18 Plant fruit type, i.e. fleshy versus dry, greatly influences seed dispersal strategy (Howe &
19 Smallwood 1982). Fleshy-fruited (FF) plants typically depend on vertebrates for their
20 dispersal, e.g. endozoochory. On the contrary, dry-fruited (DF) plants are dispersed by
21 diverse vectors, among which the wind. Because wind dispersal produces not directed and
22 scattered distribution, Turner (2001) considers it as poorly effective in tropical rain forest.
23 Investing in structures that attract and reward frugivorous animals implies a great cost for
24 plants. This is evidenced by the fact that FF plants are overwhelmingly woody because

1 they can allocate sufficient resources (Yu et al. 2017), Willson et al. (1989) reported for
2 example that more than 90% of FF plants were woody at four Queensland sites. As a
3 consequence, abiotic factors that strongly influence resource availability may play an
4 important role in shaping the distribution of fruit types. Several studies have investigated
5 climatic and geographical factors underlying broad-scale patterns in fruit type on tropical
6 mainland (see Almeida-Neto et al. 2008; Correa et al. 2015; Chen et al. 2016), but none
7 have on oceanic islands. High-elevation islands are relevant study systems because
8 (i) they present strong ecological gradients and provide a suitable environmental
9 heterogeneity to understand the composition of fruit type across assemblages (Irl et al.
10 2016); (ii) they possess impoverished and well-studied floras, e.g. taxonomy, phylogeny
11 and geographical distribution of species. Hence, oceanic islands, with their small
12 manageable areas for research in comparison to mainland provide a good opportunity to
13 investigate the mechanisms underlying the distribution of fruit types (Santos et al. 2016).

14 **Relationship between abiotic factors and the distribution of fruit types**

15 On high-elevation oceanic islands, one may expect the proportion of FF species (pFF) in
16 woody plant assemblages to decrease with elevation. In lowland island habitats, several
17 fine-scale studies suggest that pFF is high, i.e. between 54% and 83% (Strasberg 1996;
18 Meehan et al. 2002; Arévalo et al. 2007; Pau et al. 2009), potentially reaching similar
19 levels to that observed in continental tropical forests, i.e. between 46% and 89% (Jordano
20 1992). Recent studies have shown that pFF decreases significantly with elevation on
21 continents and have emphasized the role of climate and especially temperature as a
22 primary driver of fruit type distribution (Buitrón-Jurado & Ramírez 2014; Yu et al. 2017). On
23 oceanic islands, the low mass elevation effect strongly influences climatic conditions (Irl et
24 al. 2016). The rapid decline of soil fertility with decreasing temperature and increasing
25 cloudiness (Tanner et al. 1998; Carbutt et al. 2013), and the presence of a trade wind

1 inversion layer inducing lower water availability (Leuschner & Schulte 1991), result in
2 trade-offs in plant functional traits along elevational gradients. Anemochorous dry-fruited
3 (DF) plants better adapted to high-elevation conditions (Buitrón-Jurado & Ramírez 2014)
4 may thus dominate high-elevation assemblages. However, in addition to environmental
5 factors, biogeographic constraints may influence pFF with increasing elevation. Thus, the
6 dominance of anemochorous species in tropical montane forests of Pacific islands may be
7 a consequence of the great isolation of these oceanic islands (Chapman et al. 2016).

8 Because fleshy fruits are usually water-rich fruits, FF species may be more common
9 where water availability is high (Yu et al. 2017). The latter is primarily related to the
10 amount of precipitation. The positive influence of precipitation on richness and proportion
11 of fleshy fruitedness has thus been shown at both regional (Almeida-Neto et al. 2008;
12 Correa et al. 2015) and continental scales (Chen et al. 2016). On tropical high-elevation
13 oceanic islands, trade winds generate a climatic divide, with a windward side wetter than
14 leeward side. Consequently, FF species are expected to be more common on the former
15 than on the latter. Furthermore, water availability may be related to topographic factors
16 (Oddershede et al. 2015). Topographic factors might thus influence the distribution of fruit
17 types, e.g. by saturating soils in water on flat lands or increasing drought on steep slopes.

18 On high-elevation islands, FF species are expected to be less common among tree
19 canopy species when climatic conditions become harsher, e.g. in areas subjected to
20 drought and/or to low temperatures. Trees may be more limited in the amount of water
21 they can invest into fleshy fruits because they are more exposed to evapotranspiration
22 than shrubs that grow in the understory and are buffered by the canopy, (Yu et al. 2017).
23 Thus, in the wet and fertile lowlands of oceanic islands, a large majority of species bearing
24 fleshy-fruits is expected to be trees as observed on mainland (Chen et al. 2016). On the

1 contrary, FF species that occur at higher elevations may mainly be shrubs benefiting from
2 a DF plant canopy.

3 **Relationship between phylogeny, endemism and the distribution of fruit types**

4 Ecophylogenetics states that harsh environments should produce phylogenetically
5 aggregated assemblages when key ecological traits are conserved (Webb et al. 2002),
6 which is the case for fruit types on oceanic islands (García-Verdugo et al. 2014). Hence,
7 investigating phylogenetic relatedness of woody species may help in better understanding
8 the role of abiotic forces in constraining the distribution of fruit types (Santos et al. 2016).

9 On high-elevation oceanic islands, one may expect different spatial patterns of
10 phylogenetic relatedness. Indeed, these islands show high levels of endemism at high
11 elevations (Steinbauer et al. 2016), which may be a result of *in situ* radiations among DF
12 lineages (García-Verdugo et al. 2014). Radiations of some lineages into a wide range of
13 habitats may lead to phylogenetic overdispersion (Mouquet et al. 2012). At the same time,
14 radiations may lead to phylogenetic clustering if species coexist at fine scale. In the latter
15 case, a strong association between abiotic gradients and the degree of clustering within
16 assemblages would help demonstrate the role of environment in shaping communities
17 (Cadotte & Tucker 2017).

18 In this paper, our primary goals were to investigate (i) which abiotic factors were
19 most related to pFF, (ii) if fleshy-fruited canopy species were more sensitive than fleshy-
20 fruited shrubs to harsh climatic conditions and (iii) the relationship between pFF, endemism
21 and phylogenetic relatedness to unravel how abiotic factors shape the distribution of fruit
22 types. We chose Réunion as a study system, which is host to the longest bioclimatic
23 gradient in the South-West Indian Ocean and protection of its rich and unique biota is
24 considered crucial (Mittermeier et al. 2004).

1 **Material and methods**

2 **Study area**

3 Réunion, at 2512 km² is the largest and youngest (2-3 million years) volcanic island in the
4 Mascarene archipelago, located in the Indian Ocean 750 kms east of Madagascar
5 (Fig.1a). Its steep relief reaches 3070 m a.s.l. in the oldest part of the island at the Piton
6 des Neiges and 2630 m a.s.l. in the southeast at the Piton de la Fournaise (Fig.1b&1c).
7 Réunion experiences a tropical oceanic climate with the south-eastern trade winds
8 generating orographic precipitation on the windward side of the island (Fig.1d). On the
9 coast, annual precipitation ranges from 500-1500 mm on the leeward side, to 5000 mm on
10 the windward, reaching up to 12 000 mm between 1300 and 1800 m a.s.l. (Jumeaux et al.
11 2011). Annual mean temperature ranges from 26 °C at sea level to 11°C on the summits. A
12 thermal inversion layer is usually encountered between 2000 and 2380 m a.s.l, with the
13 driest conditions and frequent frost in winter (up to 100 days of frost per year on the top of
14 the island) (Ah-Peng, unpubl.). Consequently, high elevations are defined above 2000 m
15 a.s.l on Réunion.

16 The vegetation zonation along the elevational gradient is strongly associated with
17 climatic conditions (Cadet 1977). These zones range from tropical rain forest (windward)
18 and semi-dry forest (leeward) at sea level, through to tropical mountain cloud forest then
19 subalpine shrubland above 2000 m (Strasberg et al. 2005). According to Baider et al.
20 (2010), Réunion hosts 550 native angiosperm species, of which 45% are woody. Native
21 species are mainly found in well-preserved native habitats, which still cover one third of the
22 island (Fig.1e). While native mountain habitats are well preserved, lowland habitats have
23 been almost completely transformed. Two corridors of native forest remain relatively intact
24 from sea level to the subalpine vegetation, one on the leeward side and one on the
25 windward side on the active volcano, the Piton de la Fournaise (Strasberg et al. 2005).

1 These corridors are crucial to understanding past vegetation assemblages at low
2 elevations.

3 **Sampling**

4 We used an historical dataset comprising more than 850 vegetation plots (quadrats)
5 sampled in the 1970s, mostly in native habitats (Cadet 1977). The sampling area ranged
6 from 25 m² in high-elevation shrubland to 2500 m² in lowland tropical forests. In each plot,
7 Cadet recorded the number and cover of vegetation strata. For each stratum, Cadet
8 recorded the list of tracheophyta at species level and growth forms with the Braun-
9 Blanquet semi-quantitative method.

10 We removed all plots occurring in secondary vegetation where native species were
11 no-longer present, in highly disturbed forests where invasive species dominated or on lava
12 flows of less than 300 years old to avoid successional biases. In the 429 selected plots
13 (Appendix S2 described in Appendix S1), alien species were rare or assumed to have
14 negligible effect on assemblage structure. A GIS points layer was created on the basis of
15 geographical information provided by Cadet, e.g. elevation, topographic description,
16 orientation, steepness, track proximity, and field knowledge of the authors (Fig.1e). The
17 distribution of plots was not random, however, it encompassed most broad habitat units
18 and environmental gradients, e.g. elevation (Appendix S3, Fig.S1), precipitation,
19 topographic complexity.

20 We focused on woody plant species, i.e. woody angiosperms (208 species) and
21 arborescent ferns (5 species), for the following reasons: (i) Most woody species were
22 taxonomically named in the 1970s (Rivals 1952; Bosser et al. 1976 - ongoing) compared
23 to herbaceous species, which were often only determined to genus. (ii) FF species usually

1 are woody plants that contribute significantly to the structure of tropical plant communities
2 (Willson et al. 1989; Yu et al. 2017)..

3 *Relationship between the distribution of fruit types and abiotic factors*

4 We categorized the fruit of each woody species as either fleshy or dry according to the
5 description in the *Flore des Mascareignes* (Bossier et al. 1976 - ongoing). Fruits were
6 classified as fleshy if they possessed noticeable fleshy pericarps, e.g. drupes, berries, or
7 fleshy appendages when mature, e.g. aril, receptacle. Tree ferns, which produce spores,
8 were assigned to dry fruits. For each plot, we calculated the FF and DF species richness
9 (respectively **nFF** and **nDF**), and the proportion of FF species (**pFF** = nFF / woody species
10 richness).

11 We categorized the growth form of each species as tree, shrub or climber according
12 to the description in the *Flore des Mascareignes*. To assess the contribution of FF growth
13 forms to pFF, we calculated the proportion of FF shrub species (**pFFshr** = FF shrub
14 species richness / woody species richness) and the proportion of FF tree species (**pFFtree**
15 = FF tree species richness / woody species richness). Climbers, i.e. creepers and lianas,
16 were excluded from our analyses because only 20 species were found in Cadet's survey.

17 We extracted 19 bioclimatic variables (see <http://www.worldclim.org/bioclim>) from
18 Météo France (Jumeaux et al. 2011). All climatic data spanned the years 1980-2010 and
19 were computed using monthly means. Topographic data were derived from a digital
20 elevation model provided by the IGN (<http://professionnels.ign.fr/bdalti>). The resolution of
21 the digital elevation model was resampled to a raster resolution of 150 x 150 m and
22 topographic variables extracted with the software SAGA version 5.0.0.

1 *Fruit types, phylogenetic relatedness and geographical distribution of species*

2 We constructed phylogenetic trees for vegetation plots based on the phylogeny from
3 Zanne et al. (2013) (R package 'brranching'). We assumed that the resolution of deep
4 nodes was sufficient to assess the phylogenetic relatedness in our analyses.

5 Finally, we assigned a geographical distribution to woody species following Boulet
6 et al. (2012). We calculated the proportion of single-island endemic species from Réunion
7 (**pSIE** = endemic species richness / woody species richness) and the proportion of
8 Mascarene-shared species (**pMS** = Mascarene-shared species richness / woody species
9 richness), i.e. archipelago endemic species shared by Réunion and Mauritius and/or
10 Rodrigues.

11 **Statistical analyses**

12 *Relationship between the distribution of fruit types and abiotic factors*

13 All statistical analyses were conducted in R ver. 3.4.3 (R Core Team). For data exploration,
14 we used the framework proposed by Zuur et al. (2010). To minimize the effect of
15 collinearity, we retained six environmental variables with variance inflation factors < 3
16 (Tab.1).

17 The relationship between binomial data responses (species proportion) and
18 environmental variables were analyzed using generalized linear models (GLM) with
19 binomial distribution (Guisan et al. 1999). We did not include interaction terms in
20 regressions because of the limited increase in the models' explanatory power and the
21 difficulties of assessing interactions between continuous variables (Aiken et al. 2003). To
22 avoid inflation of type I & II errors in models, we accounted for the possible effects of
23 spatial autocorrelation on parameter estimates. Firstly, we constructed models with
24 environmental predictors only (E-GLM). The residuals of each model were tested for

1 spatial autocorrelation using Moran's I (Dormann et al. 2007). A significant spatial
2 autocorrelation was detected in the residuals of all E-GLMs. We then constructed
3 environmental-spatial models (ES-GLM) using the Moran eigenvector filtering function (R
4 package 'spdep') to remove spatial autocorrelation from the residuals (Griffith & Peres-
5 Neto 2006). For all E-GLMs and ES-GLMs, we assessed the best fitting GLM using Akaike
6 information criteria (R package 'dredge'). Finally, we constructed spatial models without
7 environmental predictors (S-GLM) to assess the contribution of Moran eigenvectors to the
8 explained deviance of models. Pseudo-R² of models were calculated by the relationship "1
9 – residual deviance/ null deviance".

10 By interpolation, we predicted pFF on a spatial grid over Réunion constituted by
11 111 460 cells of 150 x 150 m using a partial regression, i.e. excluding Moran eigenvectors,
12 on environmental variables (Le Rest et al. 2013). Due to the large transformation of native
13 lowland habitats, spatial interpolation is a relevant method to understand what the former
14 distribution of fruit types on Réunion may have been.

15 *Fruit types, phylogenetic relatedness and geographical distribution of species*

16 For each vegetation plot, we calculated the standardized net relatedness index
17 (NRI) (R package 'Picante'), to estimate the influence of phylogenetic relatedness on the
18 species pool (Webb et al. 2002). To infer phylogenetic structure, the observed NRI of
19 assemblages was compared to a null expectation obtained by randomly sampling the
20 species pool 1000 times while keeping species richness constant. Positive and negative
21 NRI values respectively superior or inferior to the 5th or 95th quantiles of the simulated
22 distribution were considered as significant and thus indicated phylogenetic clustering or
23 over-dispersion.

1 To visualise the relationships between phylogenetic relatedness, geographical
2 distribution and fruit type composition, a principal component analysis was conducted
3 using NRI, pSIE, pMS and pFF.

4 **Results**

5 **Relationship between the distribution of fruit types and abiotic factors**

6 A total of 213 woody species were identified, belonging to 65 families of tracheophyta (62
7 angiosperms and 3 ferns). 124 woody species were FF (58%) (Appendix S4, Tab.S1).
8 Across vegetation plots, pFF ranged from 0 to 89% (42 FF species in 47 woody species),
9 pFFtree from 0 to 67% (20 FF tree species in 30 woody species) and pFFshr from 0 to
10 40% (6 FF shrub species in 15 woody species).

11 The goodness of fit of ES-GLMs was substantial and not a consequence of
12 including spatial filtering as a fixed effect (Appendix S4, Tab.S2). ES-GLMs no longer
13 showed a significant spatial autocorrelation. In ES-GLMs, elevation was always the best
14 predictor (Tab.2). pFF and pFFtree were highly influenced by precipitation of the driest
15 month, whereas pFFshrub was not. Topographic wetness and protection had a negative
16 influence on pFF, but this influence remained weak in comparison with climatic variables.
17 Neither mean diurnal range, nor insolation had any significant effect (Tab.2).

18 pFF was very high at low elevations and decreased sharply with elevation (5% each
19 100 m loss in montane forest, maximum negative slope at 1500 m a.s.l.) (Fig.2). FF plants
20 were rare above 2000 m a.s.l (only 5 FF species in 39 woody species sampled in 43
21 vegetation plots) and absent above 2400 m a.s.l. Almost half (48%) of all woody species
22 were FF trees at low elevations. pFFtree declined sharply with elevation whereas
23 pFFshrub showed a hump-shaped pattern with a peak around 750 m a.s.l. At low
24 elevations, pFF was higher in the wettest areas due to the strong presence of FF trees.

1 Spatial interpolation suggested that most native habitats may have been strongly
2 dominated by FF plants prior to human transformation (Fig.3). In addition, lowland habitats
3 were probably FF species-rich (Appendix S4, Fig.S1).

4 **Fruit types, phylogenetic relatedness and geographical distribution of species**

5 No shift in fruit type occurred on Réunion among woody species radiations (Appendix S4,
6 Fig.S2). The widest radiations belonged to DF lineages. Most of DF species (54%) were
7 endemic, whereas FF species showed equal proportions (40%) between endemic and
8 Mascarene-shared species. pSIE and pMS ranged respectively from 4% to 100% and from
9 0% to 59%. NRI ranged from -2.9 to 4.1, 51 and 44 woody species assemblages were
10 respectively phylogenetically overdispersed and aggregated in a significant manner.

11 On the first PCA axis accounting for 72% of the total variance, pFF and pMS were
12 strongly related, and both were negatively related to pSIE and NRI (Fig.4). Woody
13 species-rich assemblages were sorted along the first axis depending on their elevation. On
14 the second PCA axis accounting for 18% of the total variance, pSIE and NRI were
15 negatively related. FF species-rich assemblages were sorted along the second axis
16 depending on precipitation of driest month. In other words, at low elevations, FF species-
17 rich assemblages were dominated by Mascarene-shared species. These assemblages
18 were phylogenetically random or overdispersed in wet areas all across the year and more
19 clustered in drier areas. At middle elevations where pFF decreased strongly, pSIE showed
20 a strong increase and assemblages were phylogenetically random or overdispersed. At
21 high elevations where FF species were absent, assemblages were dominated by endemic
22 closely related species.

23 **Discussion**

1 **A striking elevational gradient in pFF**

2 An overwhelming majority of woody species bear fleshy fruits at low elevations, while FF
3 species are absent at high elevations (above 2400 m a.s.l.) on Réunion. Although several
4 works showed a significant decrease of pFF with elevation (Buitrón-Jurado & Ramírez
5 2014; Chapman et al. 2016; Yu et al. 2017), to our knowledge this is the first time that
6 such a striking change is highlighted (0% - 81%). The magnitude of this gradient at
7 landscape scale on Réunion is greater than the one shown at continental scale by Chen et
8 al. (2016). The sharp decrease of pFF with elevation on Réunion shows how important the
9 last remaining vegetation corridors along environmental gradients are in understanding
10 biodiversity patterns. In particular, our analyses show the singularity of lowland remnants
11 where canopies are dominated by FF tree species. Moreover, we show that the distribution
12 of fruit types is related to rather different patterns of endemism and phylogenetic structure
13 depending on the climatic variables. These observations demonstrate the relevance of
14 high-elevation oceanic islands as study systems of ecological trait distribution (Warren et
15 al. 2015; Irl et al. 2015; Santos et al. 2016).

16 **Abiotic factors as the main drivers of the fruit type distribution**

17 The striking relationship between elevation and pFF suggests a strong bottom-up control
18 of communities, i.e. the availability of resources controls the fruit type composition. FF
19 plants strongly dominate assemblages at low elevations where the productivity is highest
20 (Cleveland et al. 2011) and where the availability of nutrients is high, both crucial for fruit
21 production (Kramer & Kozlowski 1979). With increasing elevation, temperature declines,
22 soil conditions deteriorate (particularly where the relief is steep) and cloudiness becomes
23 more persistent, leading to lower nutrient availability (Bruijnzeel & Veneklaas 1998; Tanner
24 et al. 1998; Carbutt et al. 2013; Dalling et al. 2016) to make fleshy fruits.

1 The elevation at which frost appears may be a major threshold for tropical species
2 adapted to warm conditions (Sarmiento 1986) and for FF species where freezing of
3 succulent cells is known to cause irreparable damage to the diaspore (Burke et al. 1976).
4 Areas above 1500 m a.s.l experience several days of frost a year on Réunion and frost is
5 frequent in winter at high elevations in subalpine shrubland. In the latter, low temperatures
6 combined with aridity are probably the main components of the strong environmental
7 stresses that determine assemblages and promote the coexistence of anemochorous
8 species belonging to radiations within Asteraceae and Ericaceae (Monasterio & Sarmiento
9 1991; Pelser et al. 2007; Strijk et al. 2012; Schwery et al. 2015). FF species that occur in
10 subalpine shrubland on Réunion are usually shared with Mauritius and have a wide
11 elevational range (Appendix S4, Fig.S3). Extinction of endemic FF species with a narrow
12 niche might have occurred, e.g. during the last explosive events of the Piton des Neiges
13 some 230000-12000 years ago, but this explanation seems unlikely because the high
14 levels of habitat diversity has allowed to maintain high richness of endemic DF plants with
15 a narrow niche (Strijk et al 2012). The absence of endemic FF plants at high elevations
16 may rather reflect the inability of FF lineages to adapt to high elevation conditions. FF
17 lineages that radiated on Réunion, e.g. six species within *Badula* (Primulaceae) despite
18 the young age of Réunion (Bone et al. 2012), are well represented below 2000 m a.s.l and
19 may be limited by their *tropicality* along strong climatic gradients (Kerkhoff et al. 2014;
20 Vetaas et al. 2018). In Hawaii archipelago, 76 FF radiated species appeared in less than
21 1,5 million years within the genus *Cyanea* (Campanulaceae) and are all encountered
22 below 2000 m a.s.l. (Givnish et al. 2009), which is also the lower bound of subalpine
23 shrubland. Thus, niche conservatism may be a major driver of diversification pattern on
24 oceanic islands (Ibanez et al. 2018) and may explain why so many FF species cannot
25 adapt to high elevation conditions.

1 In the lowlands, woody plants are more likely to bear fleshy fruits on the windward
2 side where there is no dry season. The positive, linear influence of precipitation on pFF
3 has already been shown for mainland worldwide (Almeida-Neto et al. 2008; Correa et al.
4 2015; Chen et al. 2016) and Madagascar (Bollen et al. 2005). Lower pFF on the leeward
5 may be the consequence of higher water requirements for making fleshy diaspores.
6 However, pFF remains high in the semi-dry forest, i.e. 70% at sea level (only about 10%
7 lower than the windward side), which is probably because the dry season is moderate on
8 Réunion in comparison with tropical dry deciduous forests (Cadet 1977). The fact that
9 phylogenetic clustering and randomness are respectively observed on the leeward and the
10 windward shows that high levels of pFF in the semi-dry forest are reached among
11 particular lineages on Réunion. This phylogenetic structure supports the idea that the
12 ability to tolerate drought and fire shapes woody species distribution patterns at large scale
13 (Slik et al. 2018).

14 The relationship between pFF and precipitation is more hump-shaped than linear on
15 Réunion. At mid elevations particularly, massive precipitation and strong topographic
16 wetness lead to lower pFF. Cadet (1977) raised the possibility that high precipitation, in
17 areas where the edaphic drainage is weak, could have an inhibitory effect on forest
18 dynamics. Pioneer DF plants that are less nitrogen demanding than FF plants may be less
19 impacted by the difficulties with the uptake of nitrogen due to the reduced microbial
20 metabolism in cool and very wet soils (Grubb 1977). Topographic factors, however, have
21 an overall weak influence on the distribution of fruit types in our analyses. The pattern of
22 residuals of ES-GLM shows that pFF is systematically overestimated in a common mid-
23 elevation habitat, *Erica* thicket, which often occurs on narrow ridges. This suggests that the
24 resolution of topographic rasters, i.e. 150 x 150 m, is probably too low to correctly describe
25 the effect of topographic factors on the distribution of fruit types (Oddershede et al. 2015).

1 **Fleshy-fruited trees more sensitive to stressful conditions than fleshy-fruited**
2 **shrubs**

3 We find a shift within assemblages when we assess the contribution of FF growth forms to
4 pFF, and show that spatial pattern of FF woody species is mostly driven by FF trees. As
5 hypothesized, FF trees are probably more sensitive to the more stressful canopy
6 conditions than FF shrubs (Qian et al. 2017). In our study, two main phenomena
7 distinguish FF trees from FF shrubs: (i) pFFtree declines sharply with elevation whereas
8 pFFshrub shows a hump shaped pattern. At low elevations, FF trees strongly dominate
9 canopies (Strasberg 1996) and the latter is increasingly enriched with DF trees in montane
10 forest (Appendix S4, Fig.S4). At high elevations, FF trees disappear above 2000 m a.s.l.,
11 whereas FF shrubs are encountered until 2400 m a.s.l., possibly benefiting from the
12 protection of the DF species canopy (Larcher 2003). (ii) pFFtree is related to precipitation
13 of the driest month whereas pFFshrub is not. In the lowlands, FF trees are thus more
14 dominant within assemblages on the windward where precipitation is ample all year long.
15 The fact that pFFshrub is not related to precipitation shows that shrubs growing in the
16 understory probably experience far less evapotranspiration than canopy trees allowing
17 them to invest more water in fleshy fruits (Yu et al. 2017).

18 **Phylogenetic structure, fruit types and climatic conditions**

19 We highlight phylogenetic clustering and a significant decrease of pFF in areas where
20 climatic conditions are harsh, i.e. drought on the leeward at low elevations and drought
21 combined to low temperature at high elevations. This relationship between compositional
22 data, traits and climatic conditions demonstrates a strong influence of the environment in
23 community structure (Cadotte & Tucker 2017). Our analyses also show that there is a
24 greater number of phylogenetically overdispersed assemblages (51 *versus* 44) that occur
25 between low elevations and upper montane forest, in areas without any dry season.

1 However, we lack elements to further discuss the potential mechanisms underlying this
2 pattern. We note that many overdispersed assemblages display high levels of endemism
3 in montane forest, while clustered assemblages are widely dominated by endemic dry-
4 fruited species at high elevations. Thus, this observation demonstrates that high
5 endemism at fine scale is not necessarily related to a certain phylogenetic pattern.

6 **The role of dispersal limitation at landscape and regional scales**

7 According to the traditional view of filters shaping communities, the dispersal filter is the
8 first to act (Cadotte & Tucker 2017). An oceanic island like Réunion allows one to explore
9 the potential role of dispersal limitation at two geographical scales by asking the following
10 questions: is the distribution of fruit types shaped by the ability of FF or DF species (i) to
11 reach neighboring habitat patches at landscape scale or (ii) to reach Réunion at regional
12 scale?

13 At landscape scale, we have several reasons to think that dispersal limitation may
14 play a minor role in shaping the distribution of fruit types. Our results show that seed
15 dispersal strategies are fundamentally different between assemblages at low and high
16 elevations. In the lowlands, the rich frugivorous vertebrate fauna, e.g. giant turtle, skinks,
17 fruit pigeons, flying foxes, described by the first settlers (Cheke & Hume 2008) and
18 attested by sub-fossil archives (Mourer-Chauvire et al. 1999), corroborates the large
19 dominance of FF plants. Yet, even if this rich frugivorous fauna once occurred throughout
20 the lowlands of Réunion, we show that FF species-rich assemblages are phylogenetically
21 more clustered on the leeward where there is a dry season. In montane forest, frugivorous
22 vertebrates were abundant until the late 19th century (Cheke & Hume 2008), but pFF
23 decreases sharply with elevation. Moreover, FF species are absent at high elevations,
24 although opportunistic frugivorous birds probably disperse small-seeded FF plants above
25 2500 m a.s.l. (Cheke 1987). Hence, most FF plants do (or did) not seem to have any
18

1 dispersal limitation but are (or were) probably not able to grow because of harsh
2 environmental conditions in these habitats. Long distance-dispersal limitation may
3 differentially influence the distribution of fruit types depending on elevation. At low
4 elevations, FF assemblages are species-rich, phylogenetically diverse and mainly
5 composed of Mascarene-shared or widespread species. This supports the idea that FF
6 species have a high potential for inter-island colonization (García-Verdugo et al. 2014;
7 Carvajal-Endara et al. 2017), despite the relative isolation of Réunion (Strijk et al. 2012). At
8 higher elevations, biogeographic constraints may enforce the decrease of pFF. FF
9 lineages preadapted to high elevation conditions, e.g. holarctic, austral antarctic taxa that
10 maintain high levels in pFF in the Andes (Buitrón-Jurado & Ramírez 2014), are almost
11 absent on Réunion, except one single species of *Rubus* (Rosaceae). The closest source
12 of subalpine FF preadapted lineages is at minimum 850 km away in Madagascar where
13 subalpine shrubland covers small and disjunct areas (Crowley 2004). Consequently,
14 subalpine shrublands are very isolated habitats at regional scales and cold-adapted plant
15 lineages may have major difficulties crossing unfavorable habitats (Slik et al. 2018).
16 Moreover, subalpine shrublands show a striking resemblance on Réunion, Comoros,
17 Madagascar and East Africa, and are all dominated by closely related species within the
18 genus *Erica* (McGuire & Kron 2005). This suggests that, at regional scale, (i) similar abiotic
19 conditions probably drive vegetation patterns at high elevations (Irl et al. 2016) and (ii)
20 species pool might be impoverished in FF preadapted lineages, resulting in a strong
21 regional forcing of pFF on Réunion (Ibanez et al. 2018). A larger scale study is required to
22 better understand the role of biogeographic constraints in shaping spatial patterns of fruit
23 types within oceanic islands.

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5 **Author contributions**

6 Sébastien Albert, Olivier Flores and Dominique Strasberg conceived the ideas and
7 collected the data; Sébastien Albert, Olivier Flores, Mathieu Rouget and Dominique
8 Strasberg analysed the data; and Sébastien Albert wrote the paper with assistance from all
9 coauthors.

10

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1 **Supporting Information**

2 Additional Supporting Information may be found in the online version of this article:

3 Appendix S1. This appendix includes a Table S1 that describes the Table in
4 Appendix S2.

5 Appendix S2. This appendix includes a Table S1 that presents summarized data for
6 the 429 vegetation plots (species richness, pFF, NRI, endemism, abiotic factors, UTM
7 coordinates).

8 Appendix S3. This appendix includes a Figure S1 that presents the distribution of
9 plot elevation.

1 Appendix S4. This appendix includes additional Figures (S1, S2, S3, S4) and Tables
2 (S1, S2) to further demonstrate the role of abiotic factors in shaping the distribution of fruit
3 types on Réunion.

1 **Tables****Tab.1.** List of environmental variables and their abbreviations used as explanatory variables in GLMs. The minimum and maximum values are extracted from the 429 historical plots.

Variables	Description	Unit	Min	Max
Elevation	Elevation above sea level	m a.s.l.	50	3000
Insolation	Annual direct insolation	kWh m ⁻²	488,90	2930,40
Mean diurnal range	Mean of the monthly temperature ranges (monthly maximum minus monthly minimum)	° C	5,77	11,13
Precipitation of the driest month	Total precipitation during the driest month	mm	6,62	495,49
Protection	Measure of the openness/protection calculated by analyzing the degree to which the surrounding relief protects the given cell	-	0,01	0,85
Topographic wetness	Index quantifying topographic control on hydrological processes	-	0,87	7

Tab.2. Scaled coefficients and standard errors of the best fitting ES-GLMs (GLM with environment predictors and spatial filtering). pFF is the fleshy-fruited species proportion, pFFtree the fleshy-fruited tree species proportion and pFFshr the fleshy-fruited shrub species proportion. “^2” quadratic term; “Log” napierian logarithm term. Moran eigenvectors included in models are not shown here.

	pFF		pFFtree		pFFshr	
	Pseudo-R ² = 0,78		Pseudo-R ² = 0,74		Pseudo-R ² = 0,50	
	Coef	se	Coef	se	Coef	se
Intercept	0,47***	0,031	-0,62***	0,034	-1,22***	0,031
Elevation	-0,98***	0,034	-0,78***	0,041	-0,50***	0,042
Elevation ²	-0,26***	0,034	-0,29***	0,039	-0,32***	0,040
Insolation	-	-	-	-	0,05 ^{NS}	0,026
Precipitation of the driest month	0,15***	0,036	0,16***	0,031	-	-
Precipitation of the driest month ²	-0,07***	0,014	-0,12***	0,016	-	-
Log(protection index)	-0,06**	0,022	-	-	-	-
Topographic wetness index	-0,07**	0,026	-	-	-0,05*	0,026

2