

How vertebrate extinctions threaten tropical forests

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Most tropical trees produce fleshy fruits that are eaten by vertebrates (known as frugivores) that disperse plant seeds. The regeneration of tropical forests therefore depends on frugivore populations, which are in sharp decline, or even extinct in many parts of the world. This is the case of the emblematic dodo that disappeared from Mauritius shortly after its colonization by humans, as well as most of the frugivorous vertebrates of the Mascarene Islands. These volcanic islands of the Indian Ocean constitute a unique model to study the consequences of vertebrate extinction on forest dynamics. Indeed, the history of vertebrate extinctions is very well documented, and the analysis of floristic compositions of lava flows of different ages allows to reconstitute the dynamics of their recolonization by plants, and to highlight the impact of extinctions of frugivorous vertebrates on the functioning of tropical forests.

1. Why study the consequences of extinctions in the Mascarene Islands?

1.1. The importance of frugivory in the functioning of forests

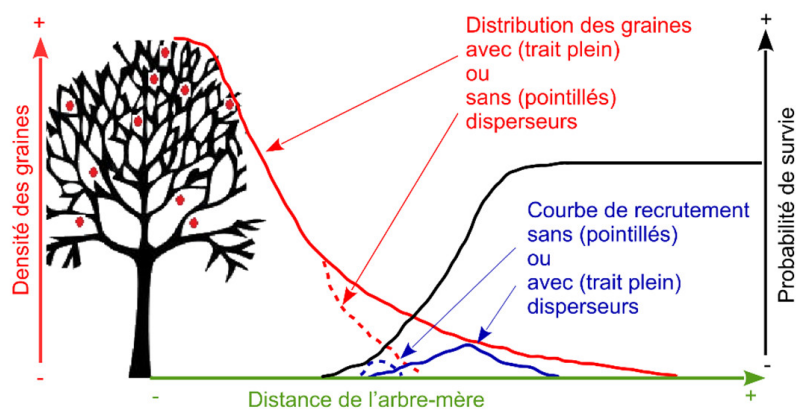


Figure 1. Solid line model of Janzen and Connell showing the importance of seed dispersal to escape various recruitment limitations near the mother tree. Loss of frugivores results in seed accumulation at the base of the mother tree and a drop in seedling recruitment. This pattern is verified in multiple tree species, especially in the tropics. [Source: Author's diagram adapted from various works cited in ref. [1]]

Frugivory (literally 'eating fruit') is a mutualistic interaction (see [Symbiosis & parasitism](#)) between an animal (usually vertebrate) and the fleshy fruits of a plant: the seed(s) in the fruit is (are) dispersed by the animal, which obtains in return a reward by consuming the flesh of the fruit.

Among **plant-animal interactions**, the interactions between frugivorous vertebrates and fleshy-fruited plants have long remained little studied, compared to herbivory or pollination. Indeed, it was not until the work of Janzen and Connell that the crucial influence of **dispersal** on plant population and community dynamics was recognized (Figure 1) [1].

Many **ecosystems** are largely **dominated** by **plants with fleshy fruits**. For example, they represent between 75% and 90% of woody plants in the tropical rainforests of Central Africa, Papua or Costa Rica [2] and between 54% and 90% of tropical island forests [3]. If we consider a broader definition of frugivory by including some dry-fruited plants, temperate forests themselves have between 25 and 55% of plants adapted to dispersal after ingestion by vertebrates [2]. Thus, **frugivory** plays a **central role** in the **functioning** of most **ecosystems at global scale**.

Until the 1990s, frugivory was mainly studied as a **co-evolutionary process** of interaction between two species. With the acceleration of **biodiversity loss** and generalized defaunation, the issue of **tropical forest conservation** has become central. Indeed, trying to preserve a forest dominated by fleshy-fruited trees could be totally ineffective in the absence of dispersing frugivores (Figure 1). Worse, **vertebrate collapse** could compromise the very ability of ecosystems to rebuild at a time when large-scale destruction of tropical ecosystems continues and global warming makes plant mobility crucial [4]. The global collapse of vertebrate populations that we are currently experiencing thus raises worrisome questions about the resilience of these ecosystems. This is especially true since large vertebrates, which are the most capable of efficiently dispersing a multitude of woody species, are disappearing first [5],[6].

1.2. The interest of the Mascarene Islands as a study system



Figure 2. The Mascarene Archipelago is located in the Indian Ocean east of Madagascar and comprises three main islands: Reunion, Mauritius and Rodrigues. [Source: Figure adapted from ref [7] and reproduced with permission of the editor]

The **Mascarene Islands** (Figure 2) [7] are, along with the Galapagos, the **last large tropical archipelago** to have been **permanently colonized by man**. The original vertebrate faunas of these archipelagos are thus relatively well known because they were described by European settlers and scientific explorers from the 17th century onwards. The numerous accounts that

follow in the 17th and 18th centuries converge as to the diversity and the relatively disharmonic and plethoric character of the original fauna of the archipelago [8]:

The Mascarenes are devoid of terrestrial mammals, but also of continental bird forms such as hornbills, which are often important frugivores in Old World tropical forests.

These absences provide vacant niches that are occupied by reptiles (giant land tortoises and skinks), bats (flying foxes), and especially diverse lineages of birds: bulbuls [9] (Figure 3), hoopoes, pigeons, parrots, rails, and white eyes.

Among the birds, the pigeon family plays a particularly important role in the Mascarenes and includes various species of founingos [10] and dodos. The latter birds, which have lost the ability to fly, probably never existed in Reunion Island because of the relative geological youth of the island.



*Figure 3. The endemic Reunion bulbul, *Hypsipetes borbonicus*, about to swallow a fruit of an endemic Rubiaceae shrub, *Gaertnera vaginata*. [Source: © Sébastien Albert]*

The size of the frugivore populations particularly impressed the first settlers in the Mascarene Islands. Pioneers described "clouds" of flying foxes in the sky, a plethora of founingos wandering into the kitchens of matrons, a multitude of bulbuls and parrots, huge colonies of giant tortoises stretching in a continuous gathering over hundreds, even thousands of meters [11].

Because there is a strong **correlation** between **frugivore** population **size** and **dispersal efficiency** [12], it is likely that the plant species that were consumed by this hyper-abundant fauna enjoyed highly efficient dispersal. The faunal **collapse** that **followed** the onset of **human colonization** in the 17th century probably had, and still has, **deleterious consequences** on the **regeneration** of many species of **fleshy-fruited plants**.



*Figure 4. View of the Piton de la Fournaise caldera at low altitude. In the foreground is an 18th century flow bearing 20 m high pioneer trees (*Sideroxylon borbonicum*). On the right are visible the lava flows of 2002 and 2004 whose beige color comes mainly from the lichen *Stereocaulon vulcanii*. [Source: © Hugo Santacreu, reproduced with permission]*

In the Mascarenes, it is unsettling to be able to visit relatively young ecosystems with trees over 350 years old that have established themselves in a world without humans. Reunion Island is home to *Piton de la Fournaise*, whose caldera and many recent flows have substrates that are not (or hardly [\[13\]](#)) cultivable (Figure 4). This terrestrial volcano, which is among the most active in the world, has thus largely contributed to the remnants of tropical rainforest, as almost all native forests on cultivable soils have been destroyed below 500 m of altitude. The set of native plant formations installed on substrates of different ages constitutes a chronosequence, classically used to study ecological succession. By **substituting space for time** [\[14\]](#), the **chronosequence** of the **lava flows** of Piton de la Fournaise allows us to **associate** the **availability of frugivores** at a given **date** with a large number of dated lava flows.

Finally, the Mascarene Islands present a remarkable plant diversity despite their relative distance from continental sources. The flora of the archipelago is now well known from the taxonomic and functional points of view in comparison with the large continental forests. These elements, combined with the good knowledge of the original fauna of the archipelago and its extinction kinetics, contribute to make it a remarkable system for studying the long-term consequences of the breakdown of frugivory interactions.

2. Rapid extinctions since human colonization

2.1. A terrible record in the Mascarenes, as in the oceanic islands

The **collapse of vertebrate populations** is now **global** [\[15\]](#), but the **islands have experienced** a **major faunal collapse** with **human colonization**. The largest documented wave of vertebrate extinctions in the last 20,000 years occurred in the birds of the Pacific, where an estimated 2,000 species became extinct due to human colonization [\[16\]](#). These were mainly land birds (rails, pigeons, parrots and passerines), among which were many frugivorous species. These island birds disappeared mainly for the following reasons:

Destruction and fragmentation of native habitats;

Hunting;

The **introduction of terrestrial vertebrates**, mainly mammals (rats, cats, dogs and pigs in the lead) which rapidly **decimated** these **species** deprived of escape or protection behavior from predators.



Figure 5. Parrot hunting in Mauritius during the expedition of Dutch admiral Jacob van Neck in 1598. The cassowary-like birds are misrepresentations of dodo. [Source: Engraving by J. T. De Bry in 1601, Rights Reserved]

If we consider frugivore extinctions more generally, the archipelagos of Hawai'i, Seychelles, Marianas, Tonga, and Mascarene Islands appear to be particularly affected [17]. Some islands have now lost all their native frugivores, such as Oahu and Lanai in Hawai'i or Guam in the Marianas. But the three Mascarene Islands are not left behind, with Mauritius being infamous for the extinction of the iconic dodo since the beginning of human colonization.

In the Mascarene Islands, the accounts of early explorers (Figure 5) and the subfossil record give us a relatively accurate history of the defaunation of frugivores [8, 11]. The world's largest skink probably became extinct in Mauritius before the 15th century, the dodo as early as the 17th century and the Rodrigues solitaire in the 18th century. The giant tortoises, the rougette, the hoopoes, the founingos and all the parrots except the Mascarene parakeet, whose populations were often very reduced at the end of the 18th century, are all extinct in the second half of the 19th century.

Today, only the Mauritian flying fox, the Mascarene parakeet and the Telfair skink (in Mauritius only), the Rodrigues flying fox, as well as the bulbuls and white eyes remain from the original frugivore fauna. The rapidity of the extinctions appears puzzling, particularly in Reunion Island where the populations of all the large frugivores had collapsed in 70 years after the settlement of humans and became extinct in less than two centuries of permanent human colonization. Bory de Saint Vincent who, during his visit in 1801, surveyed Reunion Island, noted that there were still majestic forests in the South-East of the island, but that the large fauna was totally absent.

2.2. Forests without frugivores and frugivores without forests: understanding the Reunion / Mauritius paradox

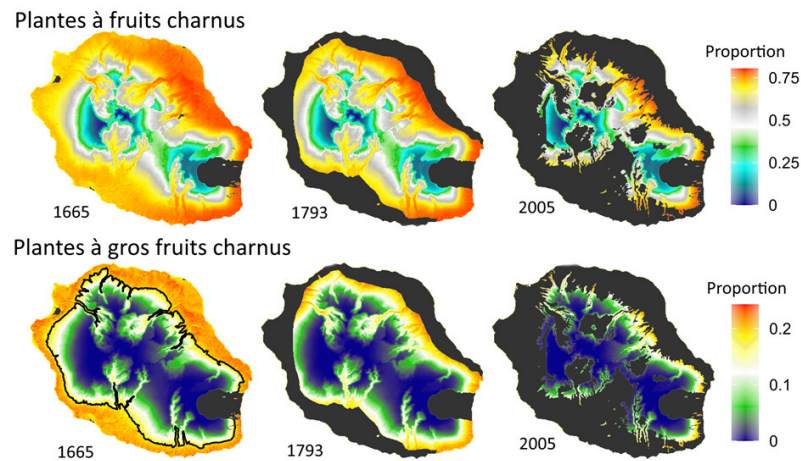


Figure 6. Modeling the proportions of plants with fleshy fruits and large fleshy fruits (> 12 mm diameter) in woody plant communities in Reunion. Areas rich and poor in native (large) fleshy-fruited plants are shown in warm and cold colors, respectively. Each model is repeated three times: at the beginning of permanent human settlement without transformed habitat in 1665; masking transformed native habitat in 1793; masking transformed habitat in 2005. [Source: Figure adapted from reference [18], license (CC BY)]

In the Mascarene Islands, extinctions show surprising disparities between islands and between the lineages of forest vertebrates shared by the two main islands of the archipelago: the extinction record is more severe in Reunion Island where more than a third of the native habitats remain compared to Mauritius where more than 95% of them have been transformed [8].

To understand this paradox, the chronology of extinctions and the main factors involved since the beginning of human colonization have been studied [18]:

The number of introductions of exotic vertebrates, especially predators known for their devastating impact on islands

Not only has Mauritius Island earlier introductions of predatory mammals (*Rattus*), but also in greater numbers with - for example - macaques and mongooses which have never been introduced to Reunion Island. These multiple introductions have nevertheless spared some islets in the North of Mauritius which have become important sanctuaries for various species of reptiles.

Overhunting, linked to changes in human demography.

The settlers of both islands were inveterate hunters, and although Reunion Island was overhunted earlier than Mauritius, the explosion of the human population in Mauritius from the end of the 18th century onwards did not lead to the total extinction of its large native fauna.

These two factors alone cannot explain the observed paradox.

Habitat transformation, considering the altitudinal characteristics of remnant habitats and the underlying functional implications.

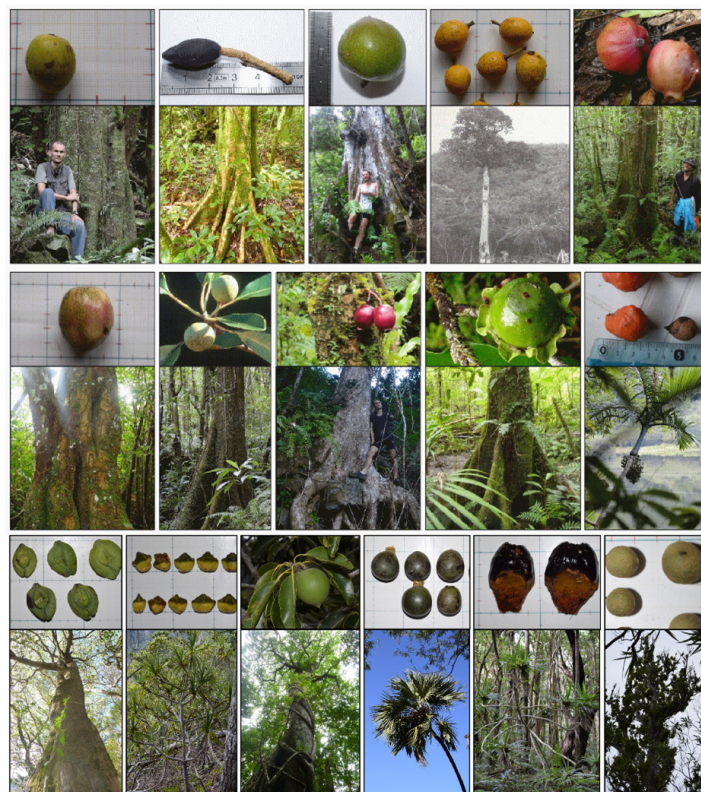


Figure 7. Examples of large-fruited trees that play an important role in the canopies of Reunion Island. In the first row at the top, from left to right, *Cassine orientalis* (Celastraceae), *Noronhia broomeana* (Oleaceae), *Sideroxylon majus* (Sapotaceae), *Drypetes caustica* (Putranjivaceae), *Hernandia mascarensis* (Hernandiaceae). In the middle row, from left to right, *Ochrosia borbonica* (Apocynaceae), *Labourdonnaisia calophylloides* (Sapotaceae), *Syzygium cymosum* (Myrtaceae), *Diospyros borbonica* (Ebenaceae), *Hyophorbe indica* (Arecaceae). At the bottom, from left to right, *Terminalia bentzoe* (Combretaceae), *Pandanus sylvestris* (Pandanaceae), *Mimosa balata* (Sapotaceae), *Latania lontaroides* (Arecaceae), *Pandanus purpurascens* (Pandanaceae), *Scolopia heterophylla* (Salicaceae). [Source: Photo montage by the author with photos © by Alexis Gorissen, Arnaud Rhumeur, Jean-Louis Rivière and Sébastien Albert, reproduced with permission of the authors]

In Reunion Island, the destruction before 1800 of the majority of the most favorable habitats and the inability of mountain habitats to serve as effective refuges for frugivores probably played a crucial role in the rapidity of extinctions (Figure 6). This is amply documented for frugivores that have rapidly lost most lowland habitats dominated by large-fruited plants (Figure 7). In contrast, Mauritius Island had highly favorable and relatively compact native habitats until the end of the 19th century, which probably and at least for a time allowed many native vertebrates to escape the multiple disturbances induced by humans.

Several vertebrate species came close to extinction in the second half of the 20th century, but ambitious conservation measures have allowed them to return to less worrisome population sizes. This is the case of the pink pigeon and the Mascarene parakeet in Mauritius, which may soon make a comeback in Reunion Island (see Focus: What can be done to restore dispersal?).

3. The consequences of the loss of frugivores on forest regeneration

3.1. Rich native forests unable to rebuild

Understanding how disruption of interactions between fleshy-fruited plants and frugivorous animals can alter the diversity and dynamics of plant communities over the long term remains a challenge. Because of the generally long life span of woody fleshy-fruited plants, such studies must indeed be conducted over a long time frame.

The chronosequence of more than six centuries of lava flows from the Piton de la Fournaise allows us to compare changes in the richness and composition of different plant guilds established before and after human colonization of Reunion in 1665 (Figure 8) [19]. In lowland tropical rainforests:

151 floristic surveys are analyzed on 28 lava flows dated between 1401 and 1956, and on older substrates (> 1000 years). These surveys are classified into 5 substrate age classes used as a proxy for native frugivore availability:

Surveys on "old substrates" (with soil) and on flows dated between 1401 and 1665 when frugivores are abundant and diverse prior to permanent human colonization;

Surveys on flows from 1665 to 1800, when populations of large frugivores were greatly reduced;

Surveys on flows from 1800 to 1900, when large frugivores got extinct and small frugivores were still abundant;

Surveys on flows from 1900 to 1956, when small frugivore populations also declined.

Dispersal syndromes of 146 native woody species are characterized: anemochorous plants, other dry-fruited plants, small fleshy-fruited plants, and large fleshy-fruited plants, with the fruits of the latter theoretically not dispersible by small frugivores.

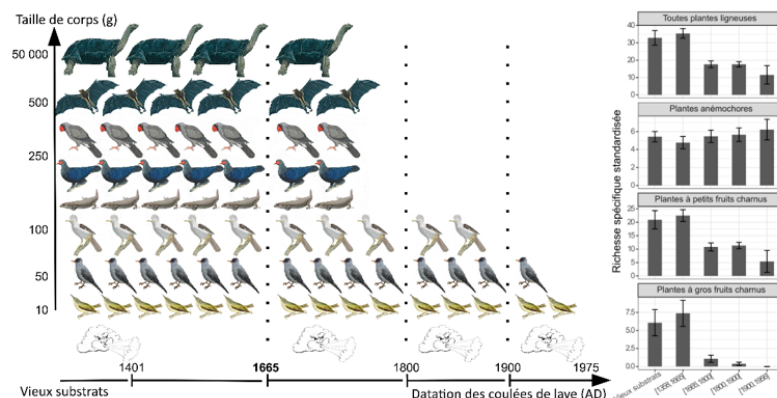


Figure 8. Left, Historical milestones in relation to the availability of dispersal agents in Reunion Island along a lava flow chronosequence. From top to bottom: giant tortoises, flying foxes, parrots, fruit pigeons, hoopoes, skinks, bulbuls and white eyes. In contrast, wind is consistently present over the entire study period. Right: Changes in species richness along the lava flow chronosequence for all woody plants and each guild studied (area standardized to 591 m²). [Source: Figures adapted from reference [19] and reproduced with permission]

Changes in dispersal trait diversity are strongly correlated with defaunation chronology (Figure 8).

The **communities** established **before** human **colonization** have a **high** species **richness** and a comparable composition. They are largely dominated by fleshy-fruited species and rich in large fleshy-fruited plants (see also Figure 7).

In the communities established shortly **after** the **beginning** of human **colonization**, **diversity declines very sharply**, especially in large fleshy-fruited plants. The latter almost disappear on the post-1800 flows despite often favorable conditions (Figure 9).

The richness of small fleshy-fruited plants decreases less rapidly than the richness of large fleshy-fruited plants, with medium levels in the 17th to 19th century flows, then low levels in the 20th century flows. In fact, the more fragmented by lava flows the forests are (Figure 4), the higher the negative impact on the richness of this guild (Figure 8). This effect is most visible on historical flows, showing that the loss of large frugivores has severely impaired the long-distance dispersal ability of small fleshy-fruited plants.

In contrast, the **richness** of **anemochorous plants** remains **stable** throughout the chronosequence due to a much lower barrier to dispersal.



Figure 9. Large-seeded tree seedlings (*Calophyllum tacamahaca*, *Syzygium cymosum*, *Diospyros borbonica*) from direct sowing in the center of the 1800 lava flow. Direct sowing in 40 experimental plots has shown that it is indeed the loss of dispersal that explains the total absence of these species on this lava flow. [Source: photo © Alexis Gorissen, reproduced with permission]

Thus, the **collapse of fleshy-fruited plant diversity** on historic lava flows underscores the **irreplaceable role** played by **frugivores**, especially large species.

Finally, an important lesson of this study concerns the reservations around the use of chronosequences to study ecological succession [14]. For what has long been interpreted as typical stages of forest development in Reunion Island is in fact only a signature of their capacity to reconstruct themselves at a given date. In two centuries 200-year-old forests nowadays will not resemble those that are 400 years old today, mainly because the most emblematic plants of old-growth forests cannot reach them. This is all the more worrying because other disruptions to forest dynamics are at work, with recent lava flows, for example, now largely invaded by alien plants that have no trouble dispersing.

3.2. Native plant diversity on borrowed time in old-growth forests

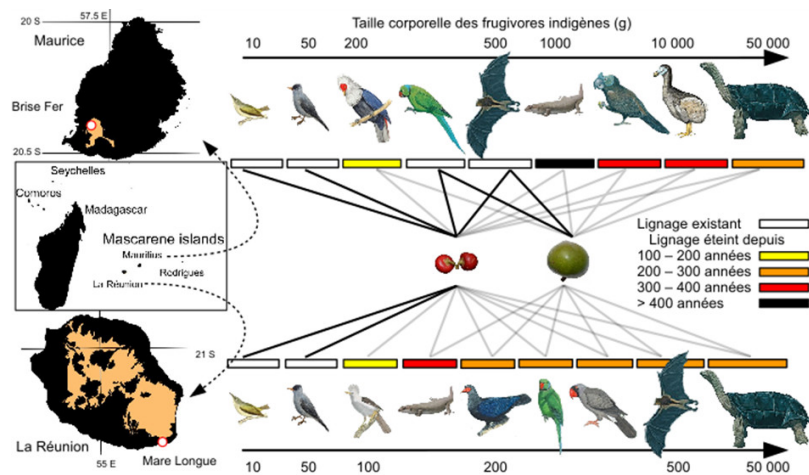


Figure 10. Key representatives of native frugivores at Brise Fer (Mauritius) and Mare Longue (Reunion Island). Past and present frugivory interactions are given by the gray and black lines, respectively. From right to left, in decreasing order of body size: giant tortoises, dodo (Mauritius only), Mauritian parrot (Mauritius), giant skink (Mauritius), flying fox, Mascarin parrot (Reunion Island), parakeets, founingoes, skinks, hoopoes (Reunion Island), bulbuls and white eyes. The periods of extinction of the vertebrate lineages is indicated by the colored rectangles. The red and green berries symbolize several hundred species of plants with small and large fleshy fruits, the latter not being dispersible by small frugivores. [Source: adapted from reference [22], reproduced with permission]

It has been known since the end of the 2000s that the accelerated loss of frugivores is profoundly modifying the regeneration of old-growth tropical forests in continental environments, even when they benefit from protected status [11],[20],[21]. While the Mascarene Archipelago has lost all of its largest frugivores since human colonization, Mauritius retains a large population of fruit bats (mean body mass = 450 g) and parrots, while Reunion Island has a native bulbul (55 g) as the main extant frugivore

(Figure 10) [22]. This intra-archipelago disparity thus provides an opportunity to compare the regeneration of the two best preserved lowland forests: *Mare Longue* in Reunion and *Brise Fer* in Mauritius (Figure 11).



Figure 12. The endemic Reunion white-eye *Zosterops borbonicus* pollinating the flowers of *Bakerella hoyifolia* (Loranthaceae), a mistletoe that had not been seen for over 50 years before its rediscovery in 2016 at Saint-Philippe. [Source: Photo © Jean-Louis Rivière, reproduced with permission]

The comparison of the two best preserved lowland forest sites in the Mascarene Islands shows a much better recruitment of fleshy-fruited plants at *Brise Fer* in Mauritius compared to *Mare Longue* in Reunion. This result is all the more striking as the species richness is half as high at *Mare Longue* (50 species) compared to *Brise Fer* (100 species). Nevertheless, fleshy-fruited plants with large seeds regenerate poorly at both sites. These results suggest that:

The Reunion bulbul, the largest frugivore still present on this island, does not effectively disperse most of the large canopy trees despite still playing an important role for various small-fruited plants.

Conversely, the large frugivorous vertebrates still present at *Brise Fer* allow massive recruitment of many plants, but do not seem to efficiently disperse the large-seeded plants they feed on for

There are other limitations to recruitment, such as seed predation by rats or browsing of seedlings and saplings by introduced mammals (Java deer, crab macaque), that require further study to unravel these results. But these limitations probably act secondarily to dispersal limitation.

In the long term the loss of diversity observed in the juvenile cohorts could lead to a significant depletion of the canopy at *Mare Longue* and to a strong shift in the canopy composition at *Brise Fer*.

Finally, these results show that at *Brise Fer*, where the guava (*Psidium cattleianum*) invasion was controlled in the 1990s, the forest retains a certain resilience thanks to the maintenance of the large frugivore fauna. Conversely, the uninvaded forest of *Mare Longue*, often considered one of the most beautiful testimonies of tropical rainforest in the archipelago, will continue to lose diversity inexorably if dispersal is not restored by direct sowing or reintroduction (see Focus on What to do to restore dispersal?).



Figure 12. The endemic Reunion white-eye *Zosterops borbonicus* pollinating the flowers of *Bakerella hoyifolia* (Loranthaceae), a mistletoe that had not been seen for over 50 years before its rediscovery in 2016 at Saint-Philippe. [Source: Photo © Jean-Louis Rivière, reproduced with permission]

In addition to large fleshy-fruited plants, strictly air plants (hemiparasitic or epiphytic) with fleshy fruits are particularly threatened by the loss of frugivores because the fruits that fall to the ground will never give a seedling. For example, *Bakerella hoyifolia* is a hemiparasitic plant that is now rare in Reunion (Figure 12). Our work shows that this plant is widely pollinated by the endemic passerine *Zosterops borbonicus*, but the numerous fruits produced are not consumed (or are too rarely consumed) [23]. These fruits thus fall to the ground without any possibility of development of a seedling.

4. Messages to remember

Fruit-eating vertebrates play a **crucial role** in tropical **forests** that are largely dominated by **fleshy-fruited** plants. The loss of vertebrates therefore raises worrying questions about the future of these ecosystems.

The **Mascarene** Archipelago is a **remarkable** study **system** because the history of vertebrate extinctions and its rich island flora are well known.

Reunion Island has lost all its large frugivores, while Mauritius still retains some despite the loss of 95% of its native habitats. It is the early loss of lowland habitats in Reunion that explains this paradox.

The **loss of frugivorous** vertebrates had resulted in the incapacity of the **rainforest** to **rebuild** for over 200 years on the lava flows of Piton de la Fournaise.

A comparison of the best preserved old-growth forests of the archipelago shows that the **regeneration is causing greater concern** in Reunion Island than in Mauritius Island where extant flying foxes play a key role.

It is possible to **restore** the recruitment of various tree species thanks to **direct sowing**.

Nevertheless, the **return of large frugivores** would ensure effective seed dispersal for multiple native plants.

Notes

Cover image. An artist's views of vertebrates in the Mascarene Islands before human colonization. **On the left**, frugivory interaction in a Mauritian understory between the fleshy fruits of an endemic threatened Sapotaceae (*Sideroxylon*) and: (i) in the background, the Mauritian parrot *Lophopsittacus mauritianus* (extinct in the 17th century) which was one of the largest

parrots in the world, and (ii) in the foreground, the green echo parrot *Psittacula eques echo* (vulnerable), the only native parrot species still present in the Mascarene Islands. **On the right**, birds perched in a wall in Reunion Island. In the foreground, three species of pigeons, including the blue founingo (*Alectroenas* sp., extinct in the 18th century); in the background, the Mascarene parakeet (*Psittacula eques eques*, extinct in the 18th century). Illustrations © Julian Hume reproduced with permission of the author.

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