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~~With or without frugivores? Flying foxes sustain woody plant regeneration~~Differing severity of frugivore loss contrasts the fate of native forests on the land of the Dodo (Mascarene archipelago)

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Differing severity of frugivore loss contrasts the fate of native forests on the land of the Dodo (Mascarene archipelago)

ABSTRACT

Frugivore loss has the potential to alter the regeneration of tropical hyperdiverse forests. However, no study has investigated tree diversity maintenance within old-growth protected forests on tropical oceanic islands where conservation stakes are considerable. In the Mascarenes, the largest frugivores including the Dodo went extinct after human colonization in the 17th century. Mauritius, today devoid of almost all its native habitats, retains an important population of flying foxes, while Réunion, largely covered by native habitats, has lost all but one of its native frugivores, a bulbul. Using census data of 130 woody species from 3-ha permanent plots from Mauritius (MAU-BF) and Réunion (REU-ML), we show that most fleshy-fruited species regenerate poorly at REU-ML, in contrast to MAU-BF, although large-seeded fleshy-fruited species regenerate poorly at both sites. The difference in recruitment is all the more striking because local woody plant diversity at MAU-BF is double that at REU-ML. Changes observed in the understory will probably lead to a strongly impoverished canopy at REU-ML, and to canopy shift composition at MAU-BF. Hence, the protected but highly fragmented forests on Mauritius are likely more resilient than those on Réunion usually considered best preserved within the ecoregion. Although processes other than seed dispersal might also be at work, flying foxes probably ensure effective dispersal of numerous native fleshy-fruited plants on Mauritius, contrary to only bulbuls on Réunion. To efficiently protect tropical rainforests on islands and continents alike, there is an urgent need to protect extant frugivores populations and reinstate seed dispersal function wherever necessary.

KEYWORDS

Frugivore extinction; island biology; Janzen-Connell effect; plant diversity loss; protected tropical forest; seed dispersal disruption

INTRODUCTION

Vertebrates play an important role as mutualistic pollinators or seed dispersers in most tropical forests worldwide (Dirzo et al., 2014; Turner, 2001). Recently, it has become clear that their loss has the potential to deeply alter tropical forest composition (Albert et al., 2020b; Dirzo et al., 2014; Effiom et al., 2013; Terborgh et al., 2008; Trolliet et al., 2019; Wandrag et al., 2017). Most conservation strategies have for decades involved integrating forest habitats into protected areas. However, preserving forests in which mutualistic vertebrates are absent or at low density might be ineffective when their functioning highly depends on plant-animals interactions (Laurance et al., 2012).

The various life-history strategies of trees complicate the assessment of the impact of frugivore extirpation, but studies at community level indicate an alteration of the recruitment for numerous fleshy-fruited plants in defaunated protected forests of the Neotropics (Terborgh et al., 2008), Central Africa (Effiom et al., 2013; Trolliet et al., 2019) and Borneo (Harrison et al., 2013). Changes in recruitment were detected just a few decades after frugivore decline or loss, being mainly the consequence of the negative distance- and/or density-dependent effects on germination or seedling survival close to maternal trees (Comita et al., 2014; Connell, 1971; Janzen, 1970). Other works have also shown how fruit consumption by frugivores may enhance the recruitment of fleshy-fruited plants by removing potential physical/chemical dormancy (Soltani et al., 2018; Traveset et al., 2008) or more simply, by cleaning the seed of flesh that could attract pathogens and seed predators causing propagule mortality (Levi and Peres, 2013). Hence, frugivores play a central role in closing the loop of dispersal in habitats largely dominated by fleshy-fruited plants (Wang and Smith, 2002).

In theory, the decline and extirpation of frugivores threaten tropical forests not only on continents, where they can be hyperdiverse (Terborgh et al., 2008), but also on oceanic islands

(Hansen et al., 2008). Despite their isolation and small areas, oceanic islands can indeed host substantial richness in fleshy-fruited species, e.g. one forest patch on Mauritius harbours more than 60 tree species per hectare of which 89% are fleshy-fruited (Florens et al., 2017a, 2012). This relative diversity is comparable to some African continental tropical rainforests (Turner, 2001). Hence, one may expect a higher negative impact of frugivore loss on diversity maintenance on tropical oceanic islands since numerous frugivores went extinct after human colonization (Hansen and Galetti, 2009; Heinen et al., 2017), and having no options of alternative seed dispersal systems (Guimarães et al., 2008).

Fleshy-fruited plant species vary in their vulnerability following the extinction of frugivores (Guimarães et al., 2008). Plants with large fruits and/or large seeds are particularly at risk because large vertebrates often constitute the first guild to be extirpated (Dirzo et al., 2014; Hansen and Galetti, 2009; Heinen et al., 2017). Several studies have shown that insular large-seeded tree species experience recruitment failure at plant population level due to disperser loss (Carpenter et al., 2018; Hansen et al., 2008; Wotton and Kelly, 2011). Although large-seeded species are reputedly well adapted to the strong competition encountered in tropical understory (Leishman et al., 2000), their seedlings/saplings can be strongly depleted at community level in defaunated sites (Effiom et al., 2013; Harrison et al., 2013; Terborgh et al., 2008; Trolliet et al., 2019). To our knowledge however, the relationship between recruitment patterns inferred from size-distributions and defaunation has never been carried out before on islands, where one may expect a strong negative impact of large-bodied frugivore extinction on large-seeded plant recruitment.

This study aims to assess the impact of frugivore extinction on forest regeneration by comparing diameter cohorts of native woody species within two islands sharing a close biogeographic history, but with different trajectories since human colonization (Fig.1). Mauritius and Réunion had lowland species-rich forests dominated by fleshy-fruited species (Albert et al., 2018; Florens et al., 2017a; Strasberg, 1996). On Réunion, the extirpation of large frugivores from Réunion dates back two centuries (Fig.1). Consequently, primary succession dynamics have been severely altered after frugivore extinctions and great uncertainty remains about the capacity of established forests to maintain their diversity in the near future (Albert et al., 2020b). On Mauritius by contrast, *Pteropus niger* still exists in large populations and is a keystone species which feeds fruits of at least 53% of woody plants (Florens et al., 2017a; Fig.1). With a mean body mass of 450 g, this flying-fox is about nine times larger than the bulbul *Hypsipetes borbonicus*, the largest extant frugivorous bird on Réunion (Cheke and Hume, 2008). This critical difference in the defaunation history between the islands provides a relevant opportunity to use these two main islands of the Mascarenes as pseudo-replicates, and to isolate the effects of seed dispersal from other factors on plant recruitment. Although this biogeographical setting is relevant to address the effects of defaunation on forest regeneration, we note that Mauritius cannot be considered as a strict control in terms of frugivory interaction. Indeed, Mauritius also lost its largest frugivore species that were able to swallow large fruits (Fig.1) and their extirpation has probably not been fully compensated for by the surviving fauna (Howe, 2016; Meehan et al., 2002; Trolliet et al., 2019).

Using census data from permanent plots at Brise Fer on Mauritius (MAU-BF) and Mare Longue on Réunion (REU-ML), we address three complementary hypotheses in response to differential alteration of seed dispersal networks. First, we assume that plant diversity is better maintained at MAU-BF than at REU-ML. In particular, at community level, we expect that the diversity among juveniles should be similar or greater than that of adults at MAU-BF, whereas it should be lower at REU-ML. Second, within species, we assume a higher number of juveniles relative to adults at MAU-BF than at REU-ML. Indeed, few juveniles in proportion at a given time may indicate a declining population (Condit et al., 1998). Third, we hypothesize seed size to have a strong influence on plant diversity and juveniles ratio. The extinction of all Mascarene frugivores able to swallow fruit >13 mm in diameter probably led to recruitment failure of large-seeded fleshy-fruited plants on both islands, although the extant flying foxes might have, to some extent, carried out the function of these extinct large frugivores on Mauritius.

However, some plants, especially small-seeded species, might also have difficulties in regenerating in the understory independently of their ability to be dispersed, because of adverse establishment conditions, including competition and shade (Howe and Smallwood, 1982; Leishman et al., 2000). This could be particularly true at REU-ML where the canopy is higher and the understory darker than at MAU-BF.

METHODS

Study sites

Réunion (2512 km², 2-3 million years) and Mauritius (1865 km², 7.8 million years), the two largest islands of the Mascarene archipelago in the tropical Indian Ocean, are respectively 750 and 900 km east of Madagascar (Fig.1). They are part of the biodiversity hotspot of South-West Indian Ocean islands (Mittermeier et al., 2004). The Mascarene islands share most of their animal and plant lineages, with a great number of endemic species given their relatively small terrestrial area (Kier et al., 2009). Mauritius and Réunion host 691 native flowering plant species (273 single island endemic and 150 Mascarene endemic) and 550 species (165 single-island endemic and 140 Mascarene endemic), respectively (Baider et al., 2010). Extinct and threatened species make 10.9% and 81.7% on Mauritius, while 1.2% and 50.9% on Réunion (Baider et al., 2010). Lower rates of plant extinction and threat on Réunion is attributed to its higher native cover (30%) than on Mauritius (4.4%), although lowland habitats have been almost completely transformed on Réunion (Florens et al., 2012; Strasberg et al., 2005). In that context, permanent plots at Brise Fer on Mauritius (MAU-BF) and Mare Longue on Réunion (REU-ML) are used for conservation purposes to monitor the remnants of evergreen wet tropical rainforest in the Mascarenes (Cadet, 1977; Florens et al., 2012; Safford, 1997; Strasberg et al., 2005).

Mare Longue (Réunion)

The three 1-ha plots at REU-ML (centred around 21°21'13'' S, 55°44'40'' E) were in reserve (68 hectares), now included in the National park of Réunion (Fig.1). This site is at the lower reaches of the last continuous corridor of vegetation in the Mascarenes running from 100 m asl to the volcano caldera at 2400 m. This forest corridor is surrounded by secondary vegetation and sugar cane fields at lower elevations. The studied plots are situated between 130 and 340 m asl and receive ca 4000 mm of mean annual rainfall (Réchou et al., 2019;Tab.1). The forest at REU-ML is classified as a lowland tropical rainforest with no deciduous species (Cadet, 1977) and is little invaded by alien plants . It is set on pahoehoe basaltic lava flow estimated at ca 430 years old (Albert et al., 2020a) and not yet significantly altered. Emergent trees can reach 25 m high and canopy is about 15-20 m, with an average of ca 900 stems >10 cm dbh per hectare and basal area over 70 $m^2.ha^{-1}$ (Tab.1).

Brise Fer (Mauritius)

The three 1-ha plots at MAU-BF (centred around 20°22'20'' S, 57°26'10'' E) are near the western edge of Mauritius central plateau, in the Black River Gorges National Park (Fig.1). This National Park has the largest remnants of native forests on Mauritius (Florens, 2013). The studied plots are located at 560-600 m asl and receive ca 2400 mm of mean annual rainfall (Tab.1). The forest at MAU-BF is classified as a tropical rainforest (Lorence and Sussman, 1986). Trees can reach 18 m high and canopy is about 12-15 m. MAU-BF has 1000-1600 stems >10 cm dbh per hectare but lower basal area than REU-ML (Tab.1). The area has been weeded of alien plant species since 1996 (Baider and Florens, 2011) .

Sampling

Monitoring of permanent plots began in the 1990s (at REU-ML), but we used the data sampled between 2010 and 2014 to avoid temporal bias. We used saplings reaching 1 cm diameter at breast high (dbh, measured at 1.3 m), as this was the threshold for measurements at REU-ML. We calculated an equivalent dbh for plants that had multiple stems.

Growth forms

We categorized the growth form of each woody species as either tree, shrub or climber according to the description in the *Flore des Mascareignes* (Bosser et al., 1976–ongoing) or newer publication, and expert knowledge of the local floras. Shrubs could reach up to 15 cm dbh, while trees reached a maximum of 94 cm at MAU-BF and 148.8 cm dbh at REU-ML.

Diameter cohorts

We excluded climbers and species without secondary growth (e.g. Monocots, fern trees) from the analyses and defined “young”, “intermediate” and “adult” cohorts as stems with dbh of [1; 3[cm, [3; 10] cm and >10 cm, respectively for trees, and [1; 1.5[cm, [1.5; 3] cm and >3 cm, respectively for shrubs (Fig.2). For each site, we extracted the number of young, intermediate and adult cohorts for each species.

Dispersal traits

We categorized the fruit type of each woody species as either fleshy (FF) or dry (DF), using the *Flore des Mascareignes* (Bosser et al., 1976-ongoing), and expert knowledge of the local floras when information was missing or incomplete. Fruits were classified as fleshy if they had noticeable fleshy pericarps or fleshy appendages when mature. In the Mascarenes, most DF plants rely on abiotic agents for their dispersal.

We used seed length as a proxy for seed size as this trait was known for all species, based on the *Flore des Mascareignes* (Bosser et al., 1976-onwards) and authors’ field measurements. At MAU-BF and REU-ML, seed length of woody species ranged from 0.06 cm (*Weinmannia tinctoria*, Cunoniaceae) to 5.3 cm (*Elaeocarpus integrifolius*, Elaeocarpaceae), which represented an order of magnitude of 10^6 in seed mass. We assigned seed length to three size classes (Appendix Fig.A1): small-seeded plants [0.06; 0.6] cm, medium-seeded plants [0.6; 1.5] cm and large-seeded plants [1.5; 5.3] cm (following Corlett and Primack, 2006; Costa et al., 2012). Large seeds cannot be swallowed by the extant frugivores in the Mascarenes, but can be dispersed by flying foxes over short distances at MAU-BF (Florens et al., 2017a). Because there were no large-seeded and few medium-seeded DF species, we combined both classes to create a “dispersal trait” factor with four classes: (1) all DF species; and FF species that were (2) small-seeded, (3) medium-seeded, and (4) large-seeded.

Analyses

Dominance-diversity across diameter cohorts

To analyze changes in woody species dominance-diversity across diameter cohorts (i.e. from adults to youngs), we used a rank-abundance distribution approach. Rank-abundance distributions display log-transformed species abundance ranked in declining order of species abundance. This approach, recommended by Matthews and Whittaker (2015), allows to describe the full distribution of commonness and rarity for the whole woody community and according dispersal traits at each site.

Diversity indices across diameter cohorts

We first used the Shannon diversity index ($I_{shannon}$) to synthetically characterize changes in diversity highlighted with rank-log abundance plots. We then assessed changes in phylogenetic diversity using the function *pla* (R package 'adiv') that generalizes PD index of Faith (1992) to account for species abundance (Pavoine, 2020). In this respect, we constructed phylogenetic trees for woody plant communities based on the phylogeny from Zanne et al. (2013) (R package 'brranching').

Phylogenetic decoupling can show whether changes in diversity affect particular lineages. Phylogenetic decoupling was calculated as $(pI_{a=1,\ adult} / pI_{a=1,\ young}) / (I_{shannon,\ adult} / I_{shannon,\ young})$ and $(pI_{a=1,\ adult} / pI_{a=1,\ int.}) / (I_{shannon,\ adult} / I_{shannon,\ int.})$ for “adult vs young cohorts” and “adult vs intermediate cohorts” respectively. We assume values >1.1 and <0.9 would reveal stronger and weaker changes in phylogenetic diversity than in Shannon diversity, respectively.

Demographic status assessment

The demographic status of a tree population can be assessed via the ratio of juveniles to adults (Condit et al., 1998), hereafter called recruitment index. We therefore calculated the recruitment index of each woody species: $n_{young} / (n_{young} + n_{adult})$ for youngs and $n_{int} / (n_{int} + n_{int})$ for intermediate cohorts, including rare species, e.g. a single canopy tree without any conspecific individual in the understory. Finally, we estimated, at each site, the distribution of the recruitment index within classes of dispersal traits and growth forms (shrubs vs. trees). Analyses were done in R ver. 4.0.2 (R Core Team).

RESULTS

Total woody species richness was higher at Brise Fer (MAU-BF, 100 species: 65 trees, 35 shrubs) than at Mare Longue (REU-ML, 51 species: 42 trees, 9 shrubs). Woody plants were overwhelmingly fleshy-fruited (FF) (91% at MAU-BF; 88% at REU-ML). MAU-BF and REU-ML shared only 20 of the 130 species studied in total, but shared 35 genera (51% of those at MAU-BF and 81% at REU-ML; Tab.A2). Eight other genera present at REU-ML, but absent at MAU-BF do exist on Mauritius. Among the 31 genera present at MAU-BF but absent at REU-ML, 19 were present on Réunion (often in subhumid habitats, e.g. *Pleurostylia, Pyrostria, Securinega, Scutia*) and 12 only occurred on Mauritius (Tab.A2). MAU-BF showed 1.47 species per genus on average against 1.16 species per genus at REU-ML, as a result of the existence of various radiated plant species at MAU-BF.

Dominance-diversity across diameter cohorts

Across diameter cohorts (from adults, to intermediate cohorts and youngs), woody species richness strongly decreased from 47, to 40 and 35 species at REU-ML, whereas it slightly decreased at MAU-BF from 87, to 84 and 80 species (Fig.3). We detected a strong increase in the steepness of the dominance-diversity curves of woody species overall at REU-ML. Some species excessively dominated young cohorts, and rare species were more numerous among intermediate and young cohorts despite depauperate richness. On the contrary, we detected no increase in steepness in the dominance-diversity curves at MAU-BF, but a tailing-off of rare species (Fig.3).

Considering dispersal traits (DF plants, FF small-, medium- and large-seeded plants), all groups were negatively impacted at REU-ML, seen by a noticeable decline in species richness across diameter cohorts (Fig.3). The increase in steepness curves of FF plants was related to one or several species becoming more dominant, e.g. the shrub *Chassalia corallioides* (Rubiaceae) and the tree *Labourdonnaisia calophylloides* (Sapotaceae) among medium-seeded and large-seeded plants, respectively. Actually, most ranks among young cohorts at REU-ML showed a strong deficit of abundance in comparison to adults, whatever dispersal traits (Fig.3).

At MAU-BF, FF small- and medium-seeded plants showed stability and a slight increase of species richness across diameter cohorts, respectively. Both groups had higher juvenile abundance on most ranks (Fig.3). Conversely, the strong increase in the steepness of dominance-diversity curve of FF large-seeded plants was accompanied by an important decline in species richness (-8 species; Fig.3). Large-seeded species were diverse in the canopy of MAU-BF with five species exceeding 100 stems (surprisingly, only one species at REU-ML), but their stem proportion strongly decreased across diameter cohorts from 0.37 to 0.21. Hence, the tailing-off of the overall dominance-diversity curve at MAU-BF was mainly due to diversity loss of large-seeded plants.

Dry-fruited plants showed low species richness at both REU-ML and MAU-BF, but they were nevertheless fairly well represented in the canopies of both forests (Fig.3). While dominance-diversity curves were relatively similar across diameter cohorts at MAU-BF, dry-fruited plants were rare among juveniles at REU-ML. This shows that these plants could not be involved in any replacement in the understory at both sites and, therefore, were not studied further below.

Diversity indices across diameter cohorts of fleshy-fruited plants

Similarly to dominance-diversity curves, Shannon indices of small and medium-seeded plants strongly decreased across diameter cohorts at REU-ML, while they increased at MAU-BF (Fig.4). The Shannon index of large-seeded plants, which was already low for adults at REU-ML, declined further, and steadily decreased at MAU-BF. Phylogenetic diversity showed broadly similar trends across diameter cohorts for most dispersal traits at both sites. However, phylogenetic decoupling, i.e. values > 1.1 and < 0.9 (Fig.4), was observed for medium-seeded plants at REU-ML and large-seeded plants at MAU-BF. At MAU-BF, the lower decrease in phylogenetic diversity of large-seeded plants was actually associated with the decline among youngs of several radiated large-seeded species within *Eugenia* / *Syzygium* (Myrtaceae), *Labourdonnaisia* (Sapotaceae) and *Diospyros* (Ebenaceae; Fig.A2). Conversely, the higher decrease in phylogenetic diversity of medium-seeded plants at REU-ML came from the high dominance of few medium-seeded Rubiaceae among youngs and from species of *Ocotea* (Lauraceae), *Xylopia* (Annonaceae) and *Tambourissa* (Monimiaceae) showing very few individuals, leading to low occurrence of Magnoliidae in the understory.

Demographic status assessment of fleshy-fruited plants

The median recruitment index of small- and medium-seeded FF trees was between three and five times higher at MAU-BF (between 0.7 & 0.8, Fig.5) than at REU-ML (between 0.15 & 0.26). In other words, half of small- and medium-seeded tree species had at least three times as many adults as juveniles at REU-ML and at least three juveniles for every adult at MAU-BF. For large-seeded FF trees, the median recruitment index was low at both sites (between 0.11 & 0.43), and the situation was paradoxically better at REU-ML than at MAU-BF for youngs. If this result has to be tempered by the low diversity of large-seeded trees at REU-ML, the collapse of the recruitment index observed in this group at MAU-BF was particularly striking.

The median recruitment index of small- and medium-seeded FF shrubs was relatively similar at MAU-BF and REU-ML (between 0.57 & 0.69 and between 0.45 & 0.58 for youngs and intermediate cohorts, respectively, Fig.5). The median recruitment index of shrubs at REU-ML was thus four times higher than that of trees with the same dispersal traits, despite the low number of shrub species. Conversely, although not low at MAU-BF, the median recruitment index of small- and medium-seeded shrubs was slightly lower than for juvenile trees. The few large-seeded shrubs in this study were only encountered at MAU-BF and showed a particularly low median recruitment index (< 0.09). For details of the results for each woody species, please report to the dataset (available at http://dx.doi.org/10.17632/r3x9hxt98s.1#file-2e500bfd-9b67-4bee-adac-e21e2d55f06c).

DISCUSSION

Comparing three one-hectare plots of Mare Longue on Réunion (REU-ML) and Brise Fer on Mauritius (MAU-BF), famous for being the land of the Dodo, is a unique opportunity to explore the consequences of frugivores extinctions on the maintenance of diversity within tropical forests, as initiated by Terborgh et al. (2008) in Peru. On Réunion, all large-bodied native frugivores went extinct 200 years ago and the largest extant frugivore, the bulbul *Hypsipetes borbonicus*, weighs just over 50 g (Cheke and Hume, 2008). On Mauritius, all frugivores above 600 g (including the Dodo), are also extinct, but MAU-BF still hosts a sister species of bulbul, but also a parakeet and more importantly a population of flying foxes (*Pteropus niger*) which weighs up to 540 g (Fig.1 & Tab.A1). Our results support three assumed differences between REU-ML considered as treatment (defaunated forest) and MAU-BF as pseudocontrol: (1) diversity is better preserved at MAU-BF than at REU-ML; (2) number of juveniles relative to adults is larger at MAU-BF than at REU-ML, indicating stronger forest regeneration at MAU-BF; (3) large-seeded plants have difficulties in regenerating in the understory at both sites. Our results therefore indicate that the loss of frugivores likely has a severe impact on the regeneration of lowland tropical forests in the Mascarenes. Hence, even protected forests on oceanic islands would be just as much at risk as tropical forests in Neotropics (Terborgh et al., 2008), in Central Africa (Effiom et al., 2013; Trolliet et al., 2019) and in Borneo (Harrison et al., 2013).

Concern about strong diversity loss at REU-ML, encouraging situation at MAU-BF

Overall woody species richness is about twice as high at MAU-BF than at REU-ML, and if the associated factors are beyond the scope of this study, the maintenance of diversity across diameter cohorts (from adult to young) at MAU-BF compared to REU-ML is noteworthy. Over a third (ca 35%) of woody species do not have even a single sapling in the understory at REU-ML, compared to less than a fifth (ca 18%) at MAU-BF, especially large-seeded FF plants. In accordance, the recruitment is notably higher at MAU-BF than at REU-ML, except for large-seeded FF species, for which it is low at both sites. Although REU-ML forest is considered as the best preserved tropical rainforest in Mascarene islands (Strasberg, 1996), the extent of diversity loss in the understory and the poor recruitment of saplings for most species, questions the long-term sustainability of native forests on Réunion (Albert et al., 2020b). On the contrary, the important regeneration of numerous species at MAU-BF shows that weeding of invasive alien plants since the mid-1990s (Lorence and Sussman, 1986; Monty et al., 2013), has allowed this today promising recruitment (Fig.A3). Moreover, these observed differences between sites are remarkable as invasive alien mammals as pigs, deer or macaques are present at MAU-BF and absent at REU-ML (Florens, 2013). However, while the situation is encouraging at MAU-BF, our results indicate that when immediate threats are removed, there are still ongoing problems, as most large-seeded plants cannot recover despite conservation actions (Krivek et al., 2020). Therefore, it is likely that MAU-BF forest will probably experience a shift in composition in the future with considerably less large-seeded plants present in the canopy, as predicted elsewhere (Effiom et al., 2013; Harrison et al., 2013; Terborgh et al., 2008). This would be all the more problematic as this loss would affect structural tree species derived from the largest radiations, e.g. within *Eugenia, Syzygium* or *Diospyros* genera.

One might argue that we did not study community dynamics, and that caution must be taken about the demographic status of plants, as few juveniles at a given time would not necessarily translate in a population decline (Condit et al., 1998). Indeed, the non left-skewed diametric distribution might reflect the normal depletion in the understory of a fast-growing species sampled at an unfavourable time window. However, fast-growing species are very rare in the Mascarene flora (Cadet, 1977; Florens et al., 2017b), and the lack of recruitment of numerous large-seeded plants that are theoretically adapted to deeply shaded understory with strong competition (Leishman et al., 2000) suggests that anomalies in static diameter distribution truly derive from failure in forest regeneration because of strong dispersal limitation. Taking into account all dbh (and not only >1 cm) at MAU-BF shows, for example, that the recruitment of large-seeded plants remains very low, contrary to small- and medium-seeded FF plants which show a (very) large number of saplings with dbh < 1cm (Fig.A4). The difficulty now lies in disentangling the mechanisms underlying this pattern of diversity, particularly since factors other than the availability in frugivores, such as vegetation structure or other post-dispersal limitations, fluctuate between the two sites.

The likely crucial role of flying foxes in woody plant dispersal on Mauritius

Diversity loss at both sites primarily involves FF plants that make the bulk of woody plants at both sites. The disparities observed in the results between REU-ML and MAU-BF may be strongly influenced by a more or less significant alteration of mutualism networks at archipelago scale (Schleuning et al., 2014). Such a discrepancy in diversity maintenance and sapling recruitment of FF plants, except for large-seeded ones, may be mainly due to the persistence of an important population of flying foxes on Mauritius. Indeed, this bat is today the most important keystone species at MAU-BF due to the extinction of all other large-bodied frugivores. Flying foxes are known to feed upon numerous native species on Mauritius (Florens et al., 2017a; Nyhagen et al., 2005) and the role of Pteropodidae as effective seed dispersers of small- and medium-seeded plants is well-known throughout the Paleotropics (Bollen and Elsacker, 2002; McConkey and Drake, 2006; Muscarella and Fleming, 2007; Oleksy et al., 2017; van Toor et al., 2019). Flying foxes probably ensure island-scale mobility for numerous small-seeded native species that are sometimes absent from MAU-BF canopies (Oleksy et al., 2019), ultimately allowing maintenance of local diversity. At REU-ML, the largest frugivore is the Réunion bulbul, which occurs at a relative small density since the beginning of the 20th century (Cheke and Hume, 2008), and might not ensure effective dispersal of many plant species even though it can theoretically swallow their fruits (McConkey and O'Farrill, 2016). In fact, the good recruitment of FF shrubs that the Réunion bulbul preferentially disperse (Albert, 2020) suggests that it still plays an important role in the understory of old-growth forests. Similarly, the high increase in density of several FF shrubs after weeding at MAU-BF (Baider and Florens, 2011) might be explained by consumption of their fruits by the Mauritius bulbul. The population levels of this bird nevertheless remain relatively low (< 600 individuals, Cheke and Hume, 2008).

Unlike other FF woody plants, large-seeded plants do not regenerate any better at MAU-BF than they do at REU-ML on average. The weak increase of large-seeded tree recruitment at REU-ML relative to smaller-seeded plants might be counterintuitive because of the extinction of all large native frugivores since 1800, but it might also be an artifact. Indeed, several endangered large-fruited trees might have already died out within permanent plots, e.g. *Sideroxylon majus* (Sapotaceae), *Hernandia mascarense* (Hernandiaceae), *Scolopia heterophylla* (Salicaceae). This would explain why there is so low diversity among adults, and this would also lead to the overestimation of median recruitment of extant species. Isolated large-seeded trees that still survive near the plots, hardly regenerate and might go locally extinct, thus further impoverishing local diversity, and at the same time, increasing beta diversity at larger spatial scale (Wandrag et al., 2017). Exceptions exist, as the large-seeded *Labourdonnaisia calophylloides* that dominates plots at REU-ML and regenerates well, because invasive rats may act as secondary seed dispersers (Shiels and Drake, 2011). However, while rats could occasionally move large fruits, they are poor effective dispersers because their potential dispersal distance is limited, but more importantly, they do destroy most seeds, and those hoarded are usually clumped inside trees. Another possible contribution to this species regeneration are bird poachers that, for centuries, have made glue from the fruit flesh (Cheke and Hume, 2008), reproducing to some extent the behavior of extinct frugivores. Indeed, flesh persistence has a strong negative impact on the regeneration of this species (Albert, 2020), as already demonstrated elsewhere in the Sapotaceae family (Levi and Peres, 2013).

At MAU-BF, flying foxes feed upon large-seeded plants (Florens et al., 2017a), but fail to recruit in the understory. Despite their relative large body mass allowing them to move large fruits, flying foxes cannot swallow large seeds. This incapacity has two major implications as already demonstrated at MAU-BF for the endangered endemic shrub *Syzygium mamillatum* (Myrtaceae): (1) seeds are dispersed close from parents trees resulting in increased Janzen-Connell effects on seedlings and saplings; (2) seeds are not cleaned properly, leading to the persistence of potential dormancy-inducing or pathogen-attracting compounds, or increased attraction of introduced mammals (Hansen et al., 2008). Anyhow, the effectiveness of large-seeded plant dispersal by extinct large-bodied frugivores was probably much higher in the past. Entire lineages that had likely complementary functional roles in frugivory went extinct at both sites: fruit pigeons including the dodo (Meehan et al., 2002; Whittaker and Jones, 1994; Wotton and Kelly, 2011, 2012), parrots with the exception of the extant endangered parakeet (Sebastián-González et al., 2019; Tella et al., 2020), skinks (Zuël et al., 2012) or giant tortoises (Hansen et al., 2008). Their absence probably plays a major role in recruitment failure of numerous large-seeded plants at both sites.

Potential post-dispersal factors: seed predation, herbivory and light availability

Recruitment failure in some large-seeded species may also be due to seed predation, such as in the large tree *Canarium paniculatum* (Burseraceae) of which seeds are often predated by introduced rats at MAU-BF (Auchoybur and Florens, 2005). However, seed predation by invasive mammals may be a secondary cause of recruitment failure as already shown at MAU-BF (Hansen et al., 2008), on Réunion (Albert, 2020) or in New Zealand (Wotton and Kelly, 2011). Furthermore, seedlings and saplings are impacted by invasive herbivores, such as macaques or deers, as already reported by Thompson in the late 19th century (Cheke and Hume, 2008). Large-seeded plants such as Sapotaceae or *Diospyros* spp. may have specific vegetative traits which would make them more palatable than other plants (Cheke and Hume, 2008). Again, herbivory might be a secondary limitation on large-seeded plants that would primarily have difficulty establishing because of strong dispersal limitation.

One may argue that some species are shade-intolerant and have major difficulties in regenerating under closed canopy where competition for light is strong. This is especially true for most DF trees that include the smaller-seeded woody plants in the Mascarenes, as elsewhere (Leishman et al., 2000). The fact that saplings of anemochorous long-lived pioneer species such as *Agarista salicifolia* (Ericaceae), *Homalium paniculatum* (Salicaceae) or *Nuxia verticillata* (Stilbaceae) are absent or very rare at REU-ML reinforces this hypothesis (Cadet, 1977; Strasberg, 1996), and contributes to the observed decline in diversity. This influence of light availability is shown at MAU-BF where DF plants such as *Homalium integrifolium* or *N. verticillata*, only regenerate well where canopy cover is the lowest (Fig.A5). Canopy tree species with large, wind-dispersed seeds are absent in the Mascarenes, a common feature of oceanic islands (Whittaker et al., 1997). Therefore, a gradual replacement of large-seeded FF plants in the understory, as shown in continental tropical forests (Harrison et al., 2013; Terborgh et al., 2008), is not possible.

Finally, native large-fruited light-demanding trees are usually absent in gaps at REU-ML because they are not dispersed to such areas (Wandrag et al., 2017) and most native tree species do not have a seedling/sapling bank prior to disturbance. These gaps are often occupied by alien FF small-seeded plants that benefit from high levels of dispersal by small frugivores (Albert, 2020; Baret et al., 2008; Mandon-Dalger et al., 2004), indicating the importance of seed dispersal in forest dynamics.

RECOMMENDATIONS FOR CONSERVATION

The protected tropical rainforest of REU-ML shows insufficient regeneration of most of its species because of large-bodied frugivore loss, while that of MAU-BF shows an important recruitment of FF plants, indicating their capacity of being effectively dispersed. There is consequently an urgent need to protect flying foxes that face repeated mass culling on Mauritius (Florens and Baider, 2019) and to promote the recolonization of larger forested areas by this species, which has now only a small population on Réunion, after over 200 years of absence. While the ideal would be to rewild ecosystems with large-gape frugivores as already undertaken in several South-West Indian Ocean islands (Griffiths et al., 2011; Pedrono et al., 2013), direct sowing actions of large-seeded species should nevertheless be considered to support their recruitment. Ultimately, we provide additional evidence of a bleak future for diverse tropical rainforest if seed dispersal networks are not restored wherever necessary.

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DATA ACCESSIBILITY

Data associated with this study will be archived in the *Mendeley Data*. DOI: http://dx.doi.org/10.17632/r3x9hxt98s.1#file-2e500bfd-9b67-4bee-adac-e21e2d55f06c

FIGURES & TABLE

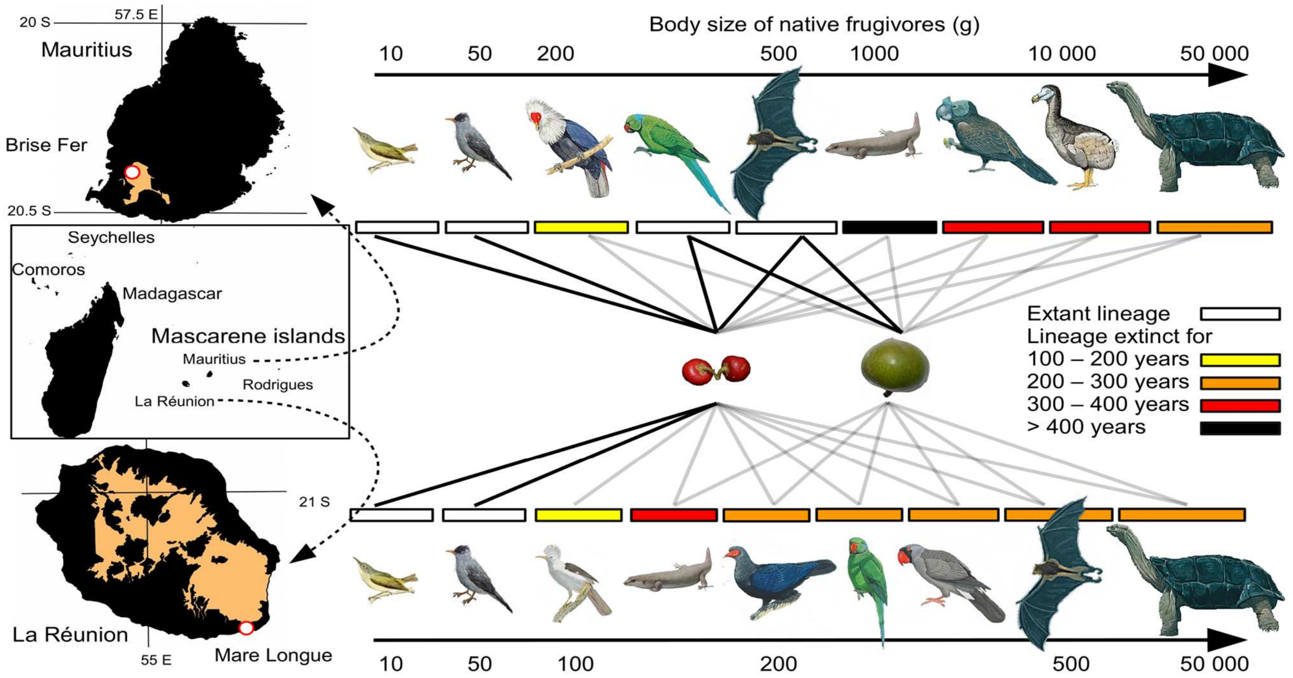

Fig.1 *Overview of native frugivore guild at study sites. Réunion and Mauritius are the two main islands of the Mascarenes. Permanent plots of Mare Longue and Brise Fer (red circles) are located in the National Parks of Réunion and Mauritius, respectively (in orange). Réunion and Mauritius hosted a diverse and plethoric fauna of frugivores until the 17th century (from right to left, in descending order of body size): giant tortoises, dodo (Mauritius only), broad-billed parrot (Mauritius only), giant skink (Mauritius only), flying foxes, Mascarin parrot (Réunion only), parakeets, fruit pigeons, skinks, starlings (Réunion only), bulbuls and white-eyes. The extinction period of frugivore lineages is indicated by the rectangle colour. Extant and extinct frugivory interactions are given by black and grey lines, respectively. The red and green berries symbolize several hundred woody species with small and large fleshy fruits, large fleshy-fruited plants being theoretically not dispersible by small frugivores. Actually, the Mascarenes initially showed highly asymmetric dispersal networks with relatively few species of frugivores compared to the diversity of plants (see Schleuning et al., 2014). Illustrations: giant tortoises, dodo, flying foxes, parrots, fruit pigeons, starling by J. Hume; white-eyes by J.G. Keulemans; skinks by J. Noseworthy; bulbuls by D. Strasberg. For more details, see Appendix Tab.A1.*

Tab.1 *Descriptors of permanent plots at MAU-BF and REU-ML. Main environmental factors are shown: elevation (“asl”: above sea level) and annual precipitation (“Precip.”). Basal area and number of stems are also displayed depending on diameter cohorts. Basal area and number of stems account for all woody species.*

Site	Plot	Elevation (m asl)	Precip. (mm)	Sampling year	Basal area dbh>1 cm (m².ha^{-1})	Basal area dbh>10 cm (m².ha^{-1})	Number of stems with dbh>1 cm	Number of stems with dbh>10 cm
Mauritius	BF1	560-600	2400	2011	41.6	34.8	6369	1026
	BF2	560-600	2400	2011	58.9	48.7	8003	1631
	BF3	560-600	2400	2010	65.2	58.4	5799	1463
Réunion	ML1	310-320	4540	2012	74.6	69.6	5807	984
	ML2	300-310	4520	2012	80.1	76.7	4580	935
	ML3	140-150	4375	2014	60.8	57.9	3098	814

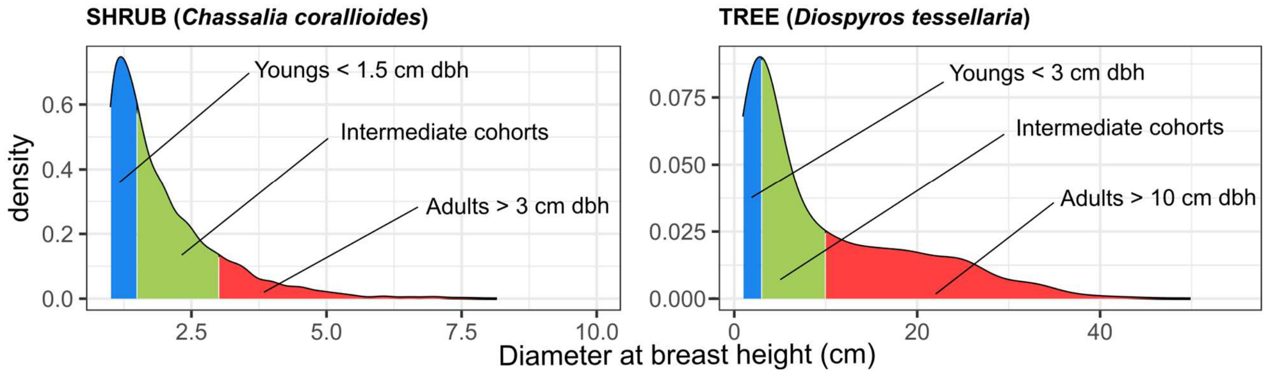

Fig.2 *Definition of diameter cohorts according to growth forms. Young cohorts of shrubs and trees show a diameter at breast height (dbh) of [1; 1.5[cm and [1; 3[cm (blue), respectively. Intermediate cohorts of shrubs and trees have a dbh of [1.5; 3[cm and [3; 10[cm (green), respectively. Adult cohorts of shrubs and trees have a dbh>3 cm and >10 cm (red), respectively. Two species with a left-skewed diametric distribution illustrate the assignment.*

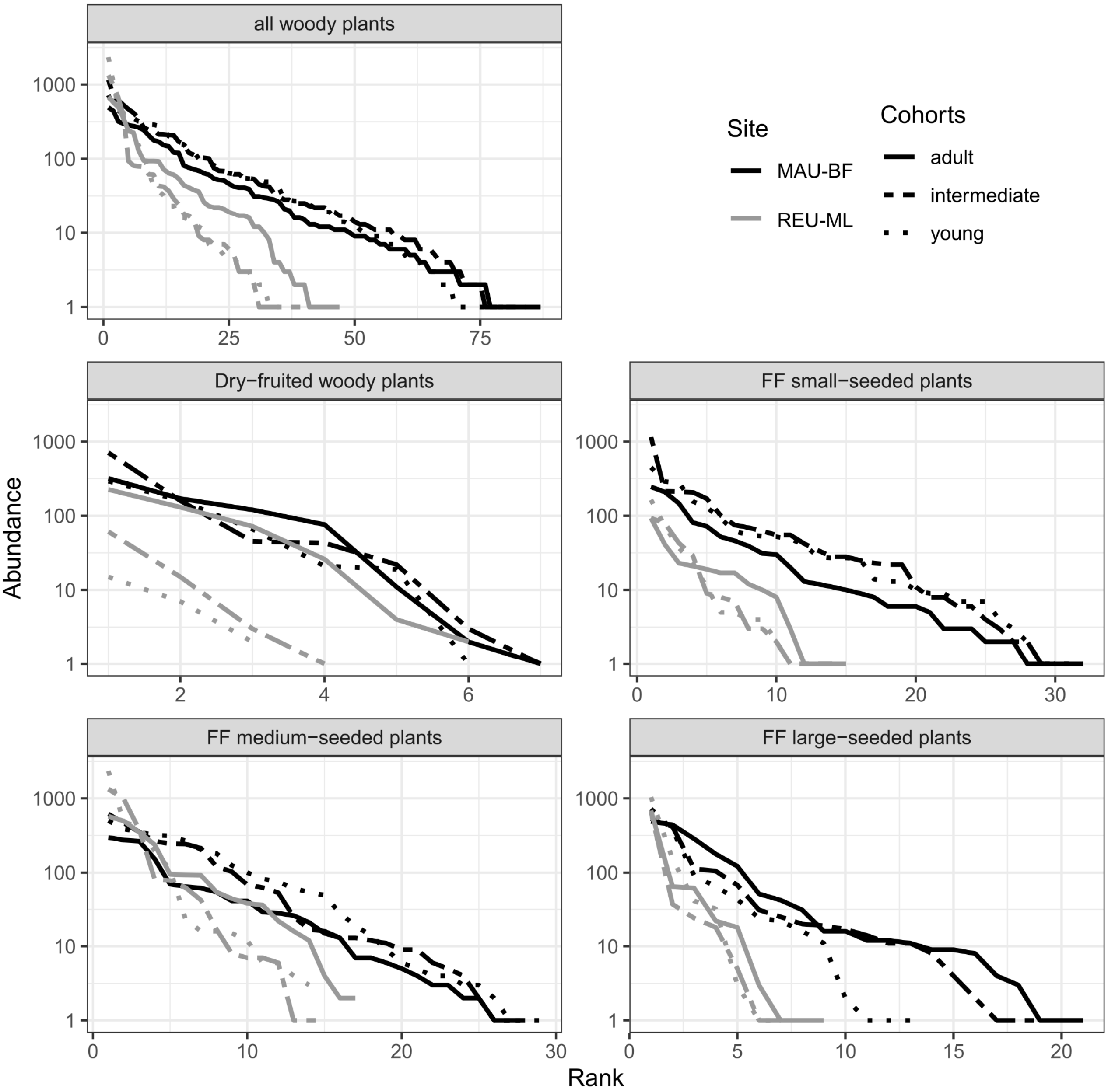

Fig.3 *Rank-abundance diagrams at MAU-BF (black) and REU-ML (grey) for woody species overall and according dispersal traits: dry-fruited plants that were mainly anemochorous at both sites and fleshy-fruited (FF) small-seeded, medium-seeded and large-seeded plants of which mean seed length was [0.06; 0.6[, [0.6; 1.5[and [1.5; 5.3] cm, respectively. Solid, dashed-dotted and dotted lines respectively displayed adult, intermediate and young cohorts. Note the different scale for the x-axis.*

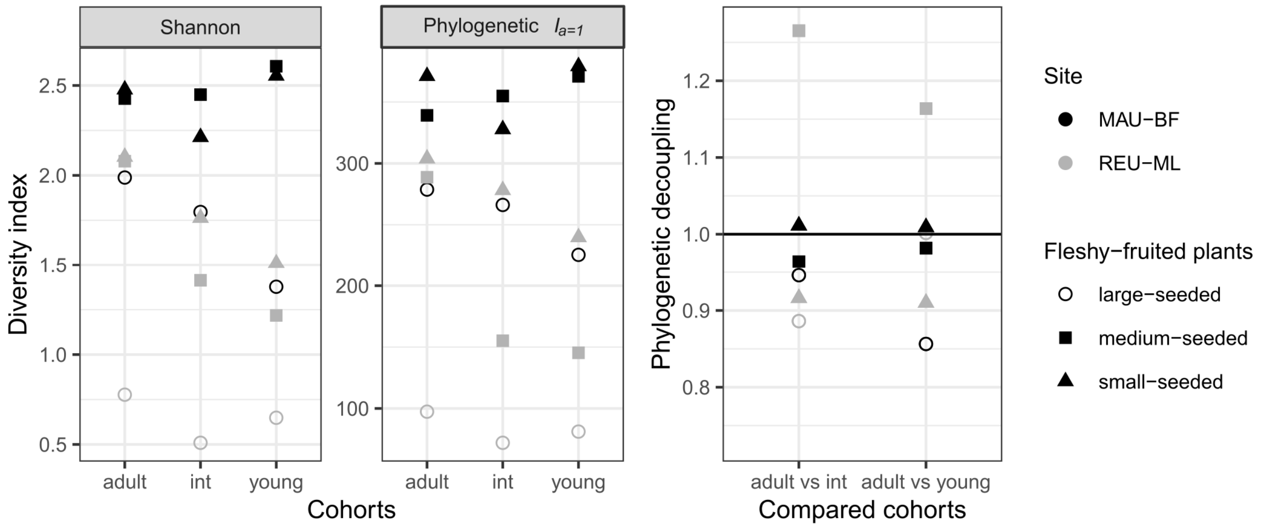

Fig.4 *Changes in diversity indices of fleshy-fruited plant assemblages across diameter cohorts at MAU-BF (black) and REU-ML (grey). Left, Shannon diversity index; Center, phylogenetic diversity index* $pI_{a=1}$ *of Pavoine (2020); Right, phylogenetic decoupling, e.g. for “adult vs young”* $(pI_{a=1,\ adult} / pI_{a=1,\ young}) / (I_{shannon,\ adult} / I_{shannon,\ young})$*. Values of phylogenetic decoupling > 1 and < 1 indicated stronger and lower changes in phylogenetic diversity than in Shannon diversity across diameter cohorts, respectively. Circles, squares and triangles displayed large-, medium- and small-seeded fleshy-fruited plants, respectively. Note the different scale for the y-axis.*

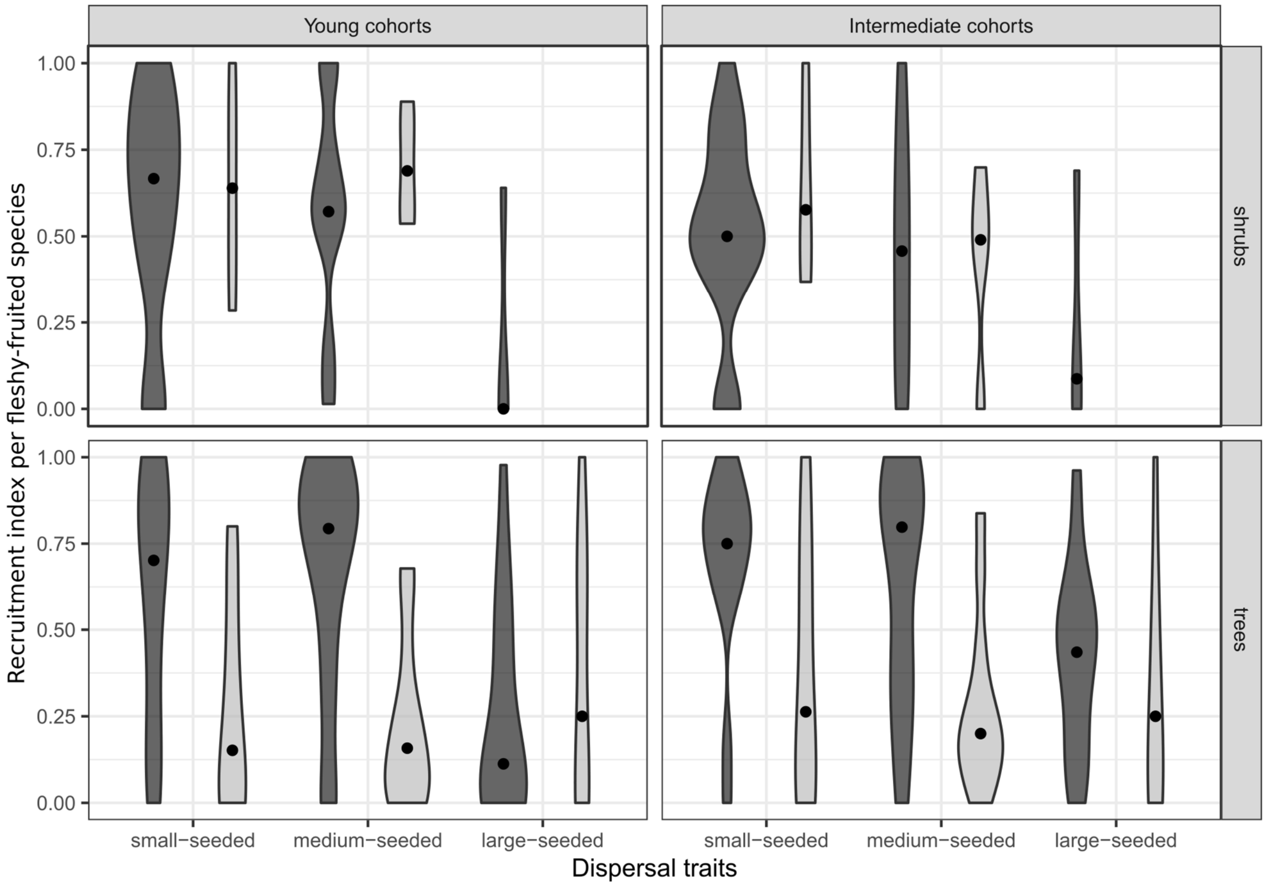

Fig.5 *Violin plots of recruitment index of fleshy-fruited plants calculated as* $n_{young}/(n_{young}+n_{adult})$ *and* $n_{int.}/(n_{int}+n_{adult})$ *per species at MAU-BF (black) and REU-ML (grey) in relation to dispersal traits and growth forms. A value of 0.5 and 0.25 for young cohorts means that a species has as many youngs as adults and three times as many adults as youngs, respectively. Black dots display the median of observed distributions. Note that areas of violins are scaled proportionally to the number of species.*