The introduced flora of Madagascar

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ABSTRACT

We provide the first comprehensive inventory of the non-native plants on Madagascar since Perrier de la Bâthie's effort 80 years ago, and evaluate the characteristics and importance of this biota. Using botanical databases (especially the Tropicos Catalogue of the Vascular Plants of Madagascar), published plant lists, field observation, and relevant literature, we inventory 546 introduced species that have naturalized, as well as 611 other introduced species that only exist in cultivation. We also list 211 species with unclear status, eight native species that have had different genetic stock introduced, and three endemics that have naturalized outside their native range. Of the naturalized species, 101 display invasive behaviour. Highly represented families include *Fabaceae* (224 confirmed introduced species), *Myrtaceae* (143), *Poaceae* (71), *Cactaceae* (52), *Asteraceae* (50), and *Solanaceae*. (33). Humans have been bringing plants to Madagascar since they colonized the island, mainly for their utility. A number of plants with native varieties but which also have long histories of human use and transport are ripe for further historical biogeographical research (including *Eragrostis, Panicum, Sorghum, Dioscorea, Ziziphus,* and *Adansonia*). The introduced flora is similar in composition to other tropical regions; its numerical size appears to confirm that poorer countries experience relatively fewer plant introductions. Madagascar's introduced species deserve more attention, not just through the rubric of invasion biology, but as plants that build new ecologies and that sustain human communities.

Keywords. alien species, fruit trees, forestry species, invasive plants, non-native biodiversity, checklist inventory

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INTRODUCTION

Madagascar's well-known status as a naturalist's paradise has inspired impressive efforts to chronicle the island's diverse and highly endemic native flora and fauna (Goodman and Benstead 2003). Yet policymakers and scientists have given lop-sided attention to the tenth of Madagascar covered by native forests, often ignoring the remaining parts of the island, seen to be non-forest environments poor in biodiversity, degraded, and covered in common pan-tropical and introduced species (Irwin et al. 2010). As a result, there is little recent, comprehensive information available on Madagascar's introduced plants (Binggeli 2003).

Understanding the introduced biota is important for several reasons beyond the threat of biological invasion, a process to which Madagascar is no stranger (Binggeli 2003; Brown et al. 2009; Carrière et al. 2008;). First, in Madagascar as in much of the world, a major proportion of human sustenance and livelihoods is derived from plants and animals not native to the area. Indeed, utility is the predominant motivator for the translocation and diffusion of plants and animals beyond their native areas. In Madagascar, peasant farmers have created productive landscapes over the centuries, almost exclusively through the cultivation of introduced plants and husbandry of introduced animals (Dez 1970; Rakoto Ramiarantsoa 1995; Vérin 1994).

Second, given their anthropogenic origin, introduced plants and animals can provide a window into ancient human movements and livelihoods. The history of plant movements, with evidence from archaeological, botanical, and linguistic techniques, can be used to test and improve ideas about prehistoric trade, agriculture, and migrations around the Indian Ocean basin (Fuller and Boivin 2009; Rangan et al. 2012). For Madagascar in particular, the appearance in sediment cores of *Cannabis* pollen from 2300 BP is consistent with other forms of evidence suggesting that the first humans had arrived by then (Burney et al. 2004). Blench (2007) adds speculative evidence of the presence of *Rattus, Mus,* and *Potamochoerus* to substantiate human arrival before the archaeologically visible records of Austronesian settlement beginning around 1500 BP.

Finally, the introduced biota is important as a component of novel ecosystems and new ecologies that can have both cultural and environmental values (Hobbs et al. 2006). Ecological research increasingly suggests the rejection of idealized ecosystems based on an imagined past, favouring instead an acceptance of the dynamism of the environment, both with and without human influence, and a view towards the future (Choi 2007; Schlaepfer et al. 2011). As a result, anthropogenic landscapes are increasingly seen as interesting for research and relevant for biodiversity and environmental sustainability. Furthermore, some authors eschew the traditional discrimination of alien from native species, calling it mostly irrelevant to analyses of ecological processes, and arguing that it reflects normative values rather than any inherent biological quality (Davis 2009; Warren 2007). Biogeographical origin, for example, is not correlated with a species' appropriateness for any particular ecosystem service (Ewel and Putz 2004).

The introduced biota of Madagascar is poorly documented, yet constitutes a non-negligible portion of overall biodiversity. In **Table 1**, we summarize current estimates of numbers of introduced species. There are circa 60 introduced vertebrates, representing numbers between one and 15 percent of the number of natives, highest for mammals and freshwater fish. For

invertebrates, pathogens, other life forms, and sub-species diversity, insufficient information exists. For plants, as we document in this paper, circa 10 percent of the flora is introduced. This demonstrates that introduced plants and animals constitute a non-negligible portion of the functional and serviceable biodiversity on the island and merit attention.

Convinced of the importance of identifying and quantifying introduced species (c.f. Wu et al. 2004) and of the patchy information on them for Madagascar, we set out to update colonial botanist Perrier de la Bâthie's (1931-32) inventory. We also briefly investigate the history of plant introductions, compare our inventory to those of other tropical flora, and comment on the importance of this biota. Following Richardson et al. (2000), we define introduced species to be those plants (or their propagules) that presumably arrived on the island (hence across a major geographical barrier) due to human actions.

METHODS

Our inventory of introduced plants incorporated the 524 plants listed by Perrier (see discussion of this number at end of inventory found in **Online Resource 1**), and supplemented this list with specialist sources on food crops and other useful plants (Boiteau et al. 1999; Decary 1946; Samyn 2001), on forestry and agroforestry introductions (Chaix and Ramamonjisoa 2001; FOFIFA 1990; Gachet 1966), on fruit trees and cacti (Lefèbvre 1965; Montagnac 1960; Moreuil 1971), on grasses (Bosser 1969), on legumes (Du Puy et al. 2002), on cropfield weeds (Husson et al. 2010) and on introduced and invasive species (Binggeli 2003) as well as with personal observations.

We also incorporated all 376 species categorized as 'naturalized' in the Catalogue of the Vascular Plants of Madagascar (Madagascar Catalogue 2011). This is a component of the Tropicos online database maintained by the Missouri Botanical Garden (hereafter 'Tropicos MadCat'). This catalogue, based purely on herbaria specimen, indicates under the heading 'distribution' one of three possibilities: endemic, naturalized, or indigenous non-endemic (in which case other countries or continents of presence are noted). The determination of this status was based on published opinions in a Flora or taxonomic treatment, re-evaluated based on the collection locations (e.g., relatively undisturbed landscapes vs. anthropogenic landscapes), overseas distribution (e.g., presence in the Mascarenes or East Africa, versus South America), and ecological characteristics ('weediness', seed dispersal mechanisms) of available specimens (P. Phillipson, pers. comm.). In addition to the naturalized taxa, the Tropicos MadCat mentions the presence of 28 cultivars or suspected uncollected species in its 'notes' field (at family, genus, or species level); we also include these in our inventory.

All entries were crosschecked between sources. Correct spelling (Perrier's database contains many typographic faults, for instance), species synonymy and taxonomic status was determined using Tropicos MadCat, the general Tropicos catalogue (www.tropicos.org), GRIN Taxonomy for Plants (USDA - ARS - National Genetic Resources Program 2011), and other databases. Complicated species determinations are commented upon in the 'notes' column of the inventory.

We then categorized each inventoried plant according to its status as naturalized, cultivated, or other (see **Table 2** for definitions). A species was considered naturalized if herbaria records (via Tropicos MadCat) so indicated, or in the absence of mention in Tropicos MadCat, if any of our other sources note the species as spontaneous, self-reproducing. This category includes

both casual and naturalized aliens in the terminology of Wu et al. (2004). The category 'cultivated species' includes all introduced species known to have been planted on the island but not known to be reproducing spontaneously. In addition, we noted whether an inventoried plant displayed invasive behaviour *sensu* Richardson et al. (2000), in that plants produce reproductive offspring at a distance. We included in this definition plants known as pioneers of fallow fields and cropfield weeds. Categorization decisions for species for which data were insufficient or contradictory are described in the 'notes' column in the inventory.

RESULTS

We catalogue 1379 plant species on Madagascar whose presence may be due to intentional or unintentional human transport (see full inventory in **Online Resources 1**). The use of multiple sources allowed us to fill gaps inherent to each (**Figure 1**). For instance, introduced plants are under-represented in Tropicos MadCat. Conspicuous absences, for example, include all *Eucalyptus* L'Hér. spp., *Acacia farnesiana* (L.) Willd., and quite a few food plants. This is explained by the database's reliance on herbaria specimen, which are collected by botanists more likely to be interested in the island's native flora and in its pristine landscapes, and who as a result spend less effort collecting weedy and/or cultivated plants.

Analysis by status

Some 611 plant species in our inventory are known only in cultivation, while 546 have been observed to have become naturalized, at least locally (**Table 2**). The other 222 inventoried plants fall into several other categories described below.

Eight plants were seemingly paradoxically categorized as "indigenous *and* introduced". These species are all considered native by Tropicos MadCat, yet their genetic stock in Madagascar likely includes material introduced from overseas – they are highly useful species that have been cultivated and planted internationally. They include the endemic rosy periwinkle (*Catharanthus roseus* (L.) G. Don) and seven indigenous non-endemic plants: teff (*Eragrostis tef* (Zuccagni) Trotter), common millet (*Panicum miliaceum* L.), robusta coffee (*Coffea canephora* Pierre ex A.Froehner), hyacynth bean (*Lablab purpureus* (L.) Sweet), orchid tree (*Bauhinia monandra* Kurz), an agroforestry albizia (*Albizia gummifera* (J. F. Gmel.) C. A. Sm.), and she-oak or filao (*Casuarina equisetifoli*a L.). The latter plant, to highlight one example, is possibly native to the east coast of Madagascar as part of its native range across the Indian and Pacific Ocean basins, yet it has been planted at forestry stations and reforestation projects around the island, likely with seed stock from overseas.

Three plants in the inventory are endemic. They are included because their Tropicos MadCat record included the word "naturalized". For example, *Gluta tourtour* Marchand and *Kalanchoe delagoensis* Eckl. & Zeyh. are both plants endemic to one part of island yet naturalized elsewhere on the island due to human introductions. There are likely many more plants that have been moved beyond their native range within the island.

Placement in category X (with variants X- and X+) indicates disputed or unconfirmed status. The status of 32 species remained fully unresolved (category X). In many cases, this represents an irreconcilable difference in our sources. One illustration suffices: Tropicos MadCat considers *Ziziphus spina-christi* (L.) Desf. to be native, Chevalier (1948) suggested it

was introduced by Arabs, Sutter (FOFIFA 1990) lists it among recent agroforestry introductions, and Binggeli (2003) lists it as an invasive species with African origins.

Sixteen plants were categorized as "X+". These are cases where we disputed the Tropicos category of "indigenous non-endemic" and consider plants likely to have been introduced. All of these plants are useful to humans, and have a long history of use particularly in the Indian Ocean rim, including for example the apple of sodom (*Calotropis procera* (Aiton) W.T. Aiton), water spinach (*Ipomoea aquatica* Forssk.), bitter melon (*Momordica charantia* L.), tigernuts (*Cyperus esculentus* L.), tossa jute (*Corchorus olitorius* D.), hibiscus tea (*Hibiscus sabdariffa* L.), finger millet (*Eleusine coracana* Gaertn.), and musk mallow (*Abelmoschus moschatus* Medik.). We suggest that *Sporobolus indicus* L. and *Rumex nepalensis* Spreng. are likely introduced given that other sources show their native zone to be far from Madagascar. As far as the sensitive plant (*Mimosa pudica* L.), its presence was already noted in 1638 so Perrier considered it an ancient introduction from the New World.

The inventory includes 163 species with status "X-", which were listed as introduced by Perrier de la Bâthie but which we consider more likely to be indigenous non-endemic, following Tropicos MadCat. Perrier organized his inventory with five categories: (1) cultivated species that never escape; (2) weedy species, whether cultivated or not; (3) ruderal species, i.e. pioneers; (4), 'messicoles', or annual plants growing in cropfields or road edges; and (5), other. This last category included plants found in anthropogenic environments, which Perrier defined more or less as anything other than forest. Recent research demonstrates that a variety of vegetation formations other than closed forest existed prior to human influence (Bond et al. 2008; Burney 2003), so we consider it likely that these species, whose distribution is common to similar savanna landscapes in nearby areas like Africa, are not human introductions.

Analysis by taxa

A total of 122 families are represented in the inventory; the number reduces to 114 if one restricts the analysis to 'near certain' introduced species, i.e., excluding those categorized as E, I&I, X, and X- (**Table 3**).

Fabaceae Lindl. is the family with the most 'near certain' introduced species (224), followed by *Myrtaceae* Juss. (143). Both families are large to begin with, with large numbers of native species in Madagascar (583 for *Fabaceae*, and 82 for *Myrtaceae*, based on counts in Tropicos MadCat). The overwhelming majority of these entries are forestry species (especially *Acacia* Mill. and *Eucalyptus* L'Hér.) introduced by the forest service and agroforestry projects over the last 60 years (Tassin et al. 2009a), and tested in different arboreta, forest stations, and project sites around the country (**Figure 2**). Most remain quite limited in extent, though several genera of *Fabaceae* are known for their naturalization and invasion potential (Richardson et al. 2011). Other families highly represented in forestry introductions are *Pinaceae* Spreng. ex Rudolphi (41), *Cupressaceae* Bartlett (24), and *Meliaceae* Juss. (13). It should be noted, however, that only half of the *Fabaceae* introductions are forestry related; this family would still be the most dominant even if forestry introductions were excluded.

Other dominant families include those with known dispersal ability, such as *Asteraceae* Bercht. & J. Presl (50) and *Poaceae* Barnhart (71), and families of great importance to humans as food and other useful crops, such as *Solanaceae* Juss. (33, including tomatoes, tobacco, capsicum, aubergine), *Rosaceae* Juss. (23, including apples, apricots, raspberries,

almonds, roses), *Rutaceae* Juss. (17, mainly citrus), *Cucurbitaceae* Juss. (14, including melons, gourds, cucumbers), *Anacardiaceae* R. Br. (10, including cashew, mango), and *Cactaceae* Juss. (52, cacti for fruit, fodder, and ornament; see Montagnac 1960).

Certain families are disproportionately represented in the "X-" category of species Perrier considered introduced, but which we consider to be indigenous non-endemic. These include *Asteraceae* Bercht. & J. Presl, *Cyperaceae* Juss., *Fabaceae*, *Malvaceae* Juss., and *Poaceae* Barnhart. *Cyperaceae* introductions are of doubtful status elsewhere (MacKee 1994). *Poaceae* is also notoriously contested, and authors frequently resort to the term 'pantropical' for cosmopolitan species whose native zone is poorly identified (Bosser 1969).

DISCUSSION

A history of introductions

Species have been arriving on Madagascar for millions of years, ever since it split from Gondwana and later from India (Yoder and Nowak 2006). Humans have been introducing plants and animals throughout their history on the island. Multiple lines of evidence suggest human visits to the island starting from 2300 BP (Blench 2007; Burney et al. 2004), likely from Africa, with one piece of tentative evidence – a modified dwarf hippo bone – for the presence of a hunting party 4000 years BP (Gommery et al. 2011). Evidence of settlements and agriculture appears from 1500 BP (Beaujard 2003; Vérin 1994). According to Perrier de la Bâthie (1931-32), the Malagasy have only grown one native species as a major food crop, a type of yam (*Dioscorea seriflora* Jum. & H. Perrier). One can conjecture that this results from human colonization being somewhat recent, and thus the settlers presumably arrived with their techniques, seeds, and cuttings. While the exact nature and timing of prehistoric migrations and trade links between Madagascar, nearby coastal Africa, the Indian Ocean rim, and the distant homeland of Austronesian settlers remains contested (Adelaar 2009; Beaujard 2003, 2011; Blench 2007; Wright and Rakotoarisoa 2003), ample opportunities existed for plant transfers, and these transfers enabled society to flourish on the island. Across the Mozambique Channel came crops such as sorghum (*Sorghum bicolor* (L.) Moench), an African yam (*Dioscorea cayenensis* Lam.), Bambara pea (*Vigna subterranean* (L.) Verdc.), cowpea (*Vigna unguiculata* (L.) Wal), bananas (*Musa* spp.) and taro (*Colocasia esculenta* (L.) Schott) (Beaujard 2011), and, according to Chevalier (1948), about ten fruit species. From across the Indian Ocean, we see, for example, the introduction of rice (*Oryza sativa* L.), coconuts (*Cocos nucifera* L.), sugar cane (*Saccharum officinarum* L.), Pacific yams (*Dioscorea* spp.), saffron/turmeric (*Curcuma longa* L.) and perhaps jackfruit (*Artocarpus heterophyllus* Lam.) (Beaujard 2011).

Contact with Europeans dates to initial Portuguese discovery in 1500. Sporadic French, English, and even pirate settlements were established from the mid-1600s onward, and new sets of plants began to arrive on the island (Chevalier 1948; Flacourt 1658). The dates and introduction pathways for many such species are difficult to establish, such as for manioc *(Manihot esculenta* Crantz) (Raison 1972). In many cases, introduced plants may have first passed through earlier colonial outposts such as Mauritius and Reunion (Chevalier 1948). Once the French conquered the island, the colonial administration (1896-1960) served as a conduit for further plant and animal introductions, largely through formal institutions like the Agricultural Service's experimental stations (Bonneuil and Kleiche 1993), the Forest Service's arboreta (Gachet 1966), and school gardens (Rakoto Ramiarantsoa 1995). These

institutions operated under a spirit conditioned by the 19th Century dominance of Lamarckism in France, exemplified in the *Société d'Acclimatation*, where it was assumed that plants could adapt to new climates and pass on these traits to their offspring (Gade 1987).

The pace of introductions has accelerated over the past centuries, peaking in the late colonial period. This acceleration is best demonstrated by fruit introductions, which are better documented than most (**Figure 3**) but remain speculative for older introductions. Pre-Austronesian settlers from Africa may have brought fruits like oil palm (*Elaeis guineensis* Jacq.), jujube (*Ziziphus mauritiana* Lam.), African baobab (*Adansonia digitata* L.), tamarind (*Tamarindus indica* L.), and marula (*Sclerocarya birrea* (A. Rich.) Hochst.) among others (Chevalier 1948). Austronesians most likely brought coconuts (*Cocos nucifera* L.) and perhaps jackfruit (*Artocarpus heterophyllus* Lam.) (Beaujard 2011). Arab traders may have been responsible for mangos (*Mangifera indica* L.), lemon (*Citrus* spp.), date palm (*Phoenix dactylifera* L.), pomegranate (*Punica granatum* L.) and grapes (*Vitis vinifera* L.) (Montagnac 1960). Early Europeans navigators and settlers introduced more American and Asiatic fruit species. In 1802, the botanist André Michaux created an experimental garden near Toamasina, introducing for instance avocados (*Persea americana* Mill.), guava (*Psidium guajava* L.), litchi (*Litchi chinensis* Sonn.), and breadfruit (*Artocarpus altilis* (Parkinson) Fosberg). In the mid-1800s, Jean Laborde planted a vast orchard in the highlands with plums (*Prunus* spp.), fig (*Ficus carica* L.), apple (*Malus domestica* Borkh.), pear (*Pyrus communis* L.), peach (*Amygdalus persica* L.), and persimmon (*Diospyros kaki* Thunb.). The colonial Agricultural Services continued introductions after 1896, working with the National Museum of Natural History (Paris), home to the Acclimatisation Society, and growing species like sweet chestnut (*Castanea sativa* Mill.), olive (*Olea europaea* L.), and garden strawberries (*Fragaria* ×*ananassa* Duchesne ex Rozier). Fruit introductions have continued at a slower pace since Independence in 1960.

The large number of introduced tree species from a small group of families (*Myrtaceae*, *Fabaceae*, *Pinaceae*, but also *Meliaceae*) is a legacy of the colonial forestry services, doggedly working towards the aim of greening the 'Red Island' through afforestation (François 1924; Olson 1984). Initially focused on propagating a few successful species, in the 1950s, foresters tested a wide variety of trees. Forestry and agricultural institutions continued their efforts after Independence. The 1970s were characterized by deep political and economic crises that disrupted the flow of introductions. More recently, however, introductions continue through a variety of development projects linked to agriculture, forestry, and agroforestry (e.g. Chaix and Ramamonjisoa 2001), as well as via individual gardeners and plant enthusiasts.

The introduced flora in broader comparative context

The consequence of the above history of human migration, trade, and agricultural experimentation is an introduced flora of approximately 1157 to 1376 species, and representing at least 114 families. The species and families with high representation in the list reflect similar inventories of introduced flora elsewhere in the tropics, including West Africa (Alpern 2008), Réunion (Tassin et al. 2006), Polynesia (Whistler 1995), and New Caledonia (MacKee 1994). The main families of forestry species also correspond with those noted elsewhere as common introduced forestry trees, including representatives of *Pinaceae*, *Myrtaceae* and *Fabaceae* (Richardson 1998).

Compared to the native flora, the introduced flora is roughly 10% in number, and the naturalized flora about 5% (**Table 1**). This is small when compared with ratios of numbers of naturalized to native plant species in most island floras, such as the Galapagos islands (46%), New Zealand (66%), Hawaii (90%), and the Mascarenes (100%) (Lavergne et al. 1999; Vitousek et al. 1997; Wu et al. 2004). Madagascar's 5% ratio of naturalized to native flora, like Taiwan's 8.8% ratio (Wu et al. 2004) is more consistent with ratios for continentally-based floras such as 3.1% for Uganda (Vitousek et al. 1997), 3.9% for South Africa's fynbos biome (Wells 1991), 5.7% for Europe and 10.8% for conterminous U.S.A. (Vitousek *et al.* 1997), or 4.4%, 6.6%, and 12.5%, respectively, for southern Africa, the southern cone of South America, and Australia (Rejmanek 2009). Madagascar's ratio is obviously small due to its large native flora (i.e., a large denominator), which, together with the age of the island and its flora, differentiates it from many of the relatively recent oceanic islands listed above. In hosting relatively few naturalized species in proportion to its native flora, the island shows characteristics more typically associated with continental landmasses than with islands (Pyšek and Richardson 2006).

The absolute number of Madagascar's introduced flora (1173), to use the 'near certain' figure from Table 2) is small when compared to combined lists of wild and cultivated plants in New Zealand (~22,000), Hawaii (~10,000), Reunion (~2000), or Tahiti (>1500), and may be correlated in part to lower levels of economic development (Kueffer et al. 2010; Lavergne et al. 1999; Sax and Gaines 2008). On neighbouring Reunion, for instance, ornamentals represent the majority of plant introductions (Tassin et al. 2006), yet in Madagascar, the ornamental sector remains highly embryonic, reflecting the low economic resources and perhaps – at least in the ecotourism sector – a pride in native plants.

While its relative and absolute introduced floras are small, the proportion of Madagascar's introduced plants that display invasive behaviour is high. Based on our counts, 8.9% of introduced plants are invasive in Madagascar, compared to figures of 1.2 to 4.6% for the Mascarenes, Galapagos, Hawaii, and Polynesia (Lavergne and Rameau 1999). This likely reflects more on the character of the introduced flora (relatively small, yet including most common weedy plants and fewer ornamental plants) than any inherent invasibility of the island or latitudinal effect (Pyšek and Richardson 2006; Sax 2001).

Some introduced plants are restricted to very small areas, perhaps to a single cultivated individual in a private garden or experimental station. This can be the case, for example, for forestry species tested in arboreta (Chauvet 1968, **Figure 2**), or cacti and fruits tested in experimental gardens, such as the 'kapoulosan' (no latin name found), a relative of the litchi, with a single specimen planted in 1901 and uprooted in 1950 without having reproduced (Montagnac 1960). In some regions, uptake by Malagasy peasants was slow due to taboos or land tenure conflicts (wherein tree planting constituted a claim on land). Other introductions are widespread, repeated, and sometimes with multiple varieties. Some are spread largely by human agency, such as the mango (*Mangifera indica* L.) or rice (*Oryza sativa* L.); others are spread by natural agents, like *Clidemia hirta* (L.) D. Don.

An analysis of forest species introductions in Malagasy arboreta reveals that introduction pressure is very unequal between species (**Figure 4**). Chauvet (1968) listed 369 forest species planted in these arboreta. Some species, as *Eucalyptus tereticornis* Sm., *E. grandis* W. Hill ex Maiden and *Corymbia citriodora* (Hook.) K.D.Hill and L.A.S. Johnson were introduced in more than 20 of the 31 arboreta; others were extensively propagated beyond arboreta boundaries, in particular *E. robusta* Sm., which currently covers ~180,000 ha and is the

predominant source of wood fuel. On the other hand, 147 (40%) of forest species were introduced in only one arboretum. Widely introduced forest species are usually expected to naturalize and become invasive, but this hypothesis does not seem to be validated in Madagascar (Tassin et al. 2009a). Up-to-date plant collections at introduction sites might reveal as-yet-unrecorded introduced species, ignored for they were never commercialized and have always remained within a very small area.

For a number of fruit introductions, multiple varieties were involved. For instance, in the 1950s the research station in Tulear grew about 150 grape varieties, 97 citrus varieties, 20 figs, and 17 kinds of mango (Montagnac 1960). Likewise, forestry, agroforestry, and agro-pastoral introductions have included multiple subspecies or provenances (Chaix and Ramamonjisoa 2001).

A number of plants, including teff (*Eragrostis tef* (Zuccagni) Trotter), common millet (*Panicum miliaceum* L.), sorghum (*Sorghum bicolor* (L.) Moench), yams (*Dioscorea* spp. L.), and bananas (*Musa* spp. L.) require further research. According to Tropicos Madcat, all have native varieties likely to have been present on the island before human arrival, but each has a long history of human use, domestication, and transport at different points in the past (Beaujard 2011; Burkill and Perrier de la Bâthie 1950). It would be possible, in these cases, to have both native varieties and feral cultivars (cf. Breton et al. 2008). Additional species that present enigmatic histories include those trees that Chevalier (1948) identified as having been introduced very early; a combination of archival, archaeological, and molecular research may be needed to help resolve these cases.

Perspectives on the introduced flora

Attitudes to the introduced flora have changed strikingly over the past century. Perrier de la Bâthie, while a major proponent of nature conservation, did not view introduced plants as threats to native biodiversity (Binggeli 2003). In a visionary paper on 'vegetal pests', Perrier (1928) restricts his focus to plants that impact negatively on human activities. For instance, in this paper he does not mention *Leucaena leucocephala* (Lam.) de Wit, which had naturalized in the northwest by his time but which was seen as useful for farmers. He does, however, state his opposition to introductions for purely ornamental or curiosity purposes. In contrast to Perrier's measured and utility-focused approach, in the past few decades, scientists have come to see species introductions as one of the most important environmental threats globally (Pimentel 2002) as well as – to a lesser extent, perhaps – in Madagascar (Binggeli 2003; Griveaud and Albignac 1972; Holland and Olson 1989).

While some introduced species can transform environments in undesirable ways, we should not lose sight of their importance. Malagasy people living with these plants find some to be problematic, but many others as opportunities (Carrière and Randriambanona 2007; Tassin et al. 2009b). Introduced plants provide people with the raw materials for their lives, from food to construction to medicine (Pernet and Meyer 1957), and add colour, fascination, smells, and sights. They become embedded in memories and emotions, even inspiring songs and folk tales. Introduced plants are incorporated into the language. Many older introductions used in people's homegardens are given the epithet 'gasy' (for Malagasy), such as 'paiso gasy' for peach or 'tongolo gasy' for garlic (Boiteau et al. 1999). The integration of new plants into traditional rural culture demonstrates that the Malagasy are not categorically reluctant towards introduced species.

Environmentally, introduced species have a variety of impacts that may, depending on one's perspective, be evaluated as good or bad. No introduced plant has yet been linked to the extinction of any native plant in Madagascar. In many cases, wildlife adapt to introduced plants, taking advantage of a new food source (e.g., Grassi 2006; Long and Racey 2007; Ralainasolo et al. 2008). Introduced forestry trees may play an urgent role in mitigating the rise in atmospheric carbon (Razakamanarivo et al. 2011). The negative and positive effects of introduced species vary over time and scale, as will the manner in which these effects are perceived by humans (Tassin et al. 2009b).

CONCLUSION

Perrier de la Bâthie's inventory of 524 introduced species to Madagascar, published some 80 years ago, was strikingly thorough and detailed. In the intervening years, new introductions and increased scientific knowledge have only doubled the number of species captured in the inventory, rendering Chevalier's (1948) estimation of 1000 species quite prescient. There are, however, two major differences between these pioneering efforts and our results. The first results from different conceptions of what constitutes non-native species. To Perrier, all plants found outside forests were human introductions (whether direct or indirect), given that he believed that prior to human arrival, no non-forest environments existed. Palaeoecological and biogeographical research has since contradicted this idea, and as a result, many plants Perrier considered introduced are now better seen as native, though often pan-tropical, constituents of pre-human savannas and woodlands. The second difference results from the systematic introduction, particularly in the 1950s and 1960s, but also more recently, of diverse forestry and agroforestry trees. These introductions now constitute more than a quarter of the introduced flora as far as species numbers.

A further difference to Perrier's work is a change in attitudes towards introduced flora. He saw new plants as economic opportunities and/or pests; in recent decades the emphasis has been on invasiveness and threats to native biodiversity. Some introductions, especially crop species, have obviously aided the welfare of the Malagasy people. Other introduced species have become invasive, and have interacted with native species in a variety of ways. Evaluations of such introductions must balance assessments of risks to biodiversity, costs to the economy, and aesthetic considerations against the opportunities the new plants generate and their value in the management of climate change, fire regimes, and soil fertility. Such analyses would need to be contextualized to specific landscape units. In sum, it is perhaps time to rediscover Perrier's fascination with introduced species, and think of them not as categorically negative intruders, but also as plants emblematic of human history, as builders of societies and environments.

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Table 1 Summary of native and introduced species in Madagascar

Class	Number of native species	Number of introduced species	Examples of introduced species	percent of introduced species useful *	Sources
Mammals	101	14	rat, zebu, cat, boar	62%	(Goodman et al. 2003)
Reptiles	346	between 3 and 12	turtles, perhaps crocodile	?	(Raselimanana and Vences 2003; Raxworthy 2003)
Amphibians	at least 230	2	Indian tiger frog	?	(Glaw and Vences 2003; Raselimanana and Vences 2003)
Birds	278	11 (at least 8 domestic)	ostrich, chicken, duck	73%	(Hawkins and Goodman 2003)
Freshwater fish	143	circa 24	tilapia	all?	(Reinthal and Stiassny 1991; Sparks and Stiassny 2003)
Invertebrates	?	?	cochineal	?	
Vascular plants	at least 12,000	between 1157 and 1376 ***(see Tables 2, 3 and Online Resources)***	food crops; fruit trees; forestry; plantation crops; fodder; ornamentals; medicinals; unintentional introductions	at least 70%	(Goodman and Benstead 2003 for native species number; for introduced species see text)

*Usefulness to humans based on known uses, not actual observations of use.

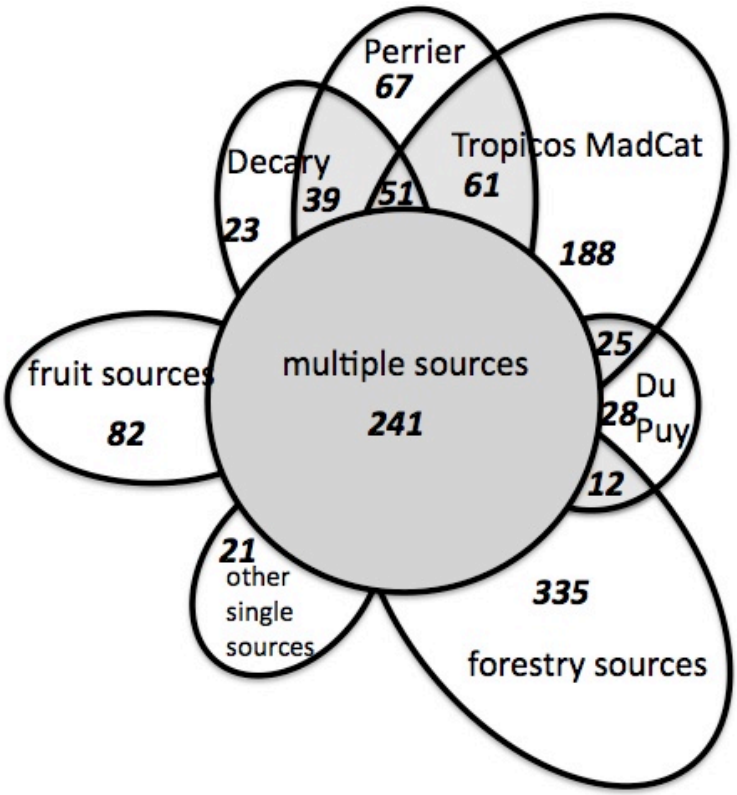
Table 2 Definitions of status and quantification of introduced plants in inventory. Full inventory in Online Resource 1.

Code	Description	Number in inventory	*of which invasive*	Subtotals
N	**Naturalised** (reproduce by themselves)	546	*101*	number of introduced species (low estimate) 1157
C	**Cultivated** (i.e., introduced, but not known to reproduce by itself)	611	*0*	
X+	**Status unconfirmed**, but very likely introduced (in many cases we disagree with Tropicos MadCat's judgment that this plant is indigenous non-endemic)	16	*4*	number of introduced species (near certain status) 1173
X	**Status unconfirmed**	32	*4*	number of introduced species (high estimate) 1376
X-	**Status unconfirmed**, but likely native (in many cases doubtful assumption by Perrier (1931-1932) that non-forest vegetation must be introduced)	163	*23*	
I&I	**Both introduced and indigenous**: Plant is native, but highly likely that cultivars or varieties introduced from elsewhere	8	*1*	
E	**Endemic** plant but noted in Tropicos MadCat as introduced and naturalized outside native range in Madagascar	3	*0*	total in inventory 1379

Table 3 Number of species by category for the 20 most frequent families. Codes explained in Table 2; full analysis by family and full inventory in Online Resources 1 and 2.

Family	C	N	X+	X	X-	I&I	E	near certain introduced (C, N, X+)	total in inventory
	(numbers in parentheses indicate subtotal of category displaying invasive behaviour)								
Fabaceae Lindl.	133	88 (17)	3 (1)	6 (1)	32 (2)	3 (0)		224 (18)	265 (21)
Myrtaceae Juss.	130	13 (6)						143 (6)	143 (6)
Poaceae Barnhart	7	60 (5)	4 (0)	8 (1)	25 (9)	2 (0)		71 (5)	106 (15)
Asteraceae Bercht. & J. Presl	1	49 (16)		1 (0)	21 (3)		1 (0)	50 (16)	73 (19)
Cactaceae Juss.	43	9 (2)						52 (2)	52 (2)
Malvaceae Juss.	15	14 (1)	3 (2)	5 (0)	14 (1)			32 (3)	51 (4)
Pinaceae Spreng. ex Rudolphi	39	2 (2)						41 (2)	41 (2)
Solanaceae Juss.	1	32 (4)			1 (0)			33 (4)	34 (4)
Rubiaceae Juss.	4	13 (3)		2 (0)	5 (1)	1 (0)		17 (3)	25 (4)
Convolvulaceae Juss.	1	16 (1)	1 (0)	2 (0)	4 (0)			18 (1)	24 (1)
Cupressaceae Bartlett	24							24 (0)	24 (0)
Lamiaceae Martinov	8	13 (2)			2 (0)			21 (2)	23 (2)
Rosaceae Juss.	16	7 (3)						23 (3)	23 (3)
Amaranthaceae Juss.	1	18 (2)			3 (0)			19 (2)	22 (2)
Cyperaceae Juss.		2 (0)	1 (1)		19 (3)			3 (1)	22 (4)
Euphorbiaceae Juss.	10	9 (2)			1 (0)			19 (2)	20 (2)
Cucurbitaceae Juss.	6	6 (0)	2 (0)		3 (0)			14 (0)	17 (0)
Polygonaceae Juss.	1	15 (0)	1 (0)					17 (0)	17 (0)
Rutaceae Juss	8	9 (3)						17 (3)	17 (3)
Apocynaceae Juss.	5	7 (0)	1 (0)		1 (0)	1 (1)		13 (0)	15 (1)

Fig. 1 Number of plants inventoried from different documentary sources. Calculated based on those 1173 species entries in inventory (see Online Resource 1) for which introduced status is near certain (categories C, N, and X+).



Total number (out of 1173 species) in key sources

Tropicos MadCat	444
Forestry (Gachet 1966, Chauvet 1968, Sutter 1990, Chaix and Ramamonjisoa 2001)	393
Perrier (1931-1932)	340
Decary (1946)	215
Fruits (Montagnac 1960, Lefèbvre 1965, Moreuil 1971)	141
Du Puy et al. (2002)	113

Fig. 2 Mature eucalyptus plantations at forest stations of Analamazaotra (in the 1950s) and Ialatsara (in 2010). Sources: Aubréville (1953) with permission from CIRAD (left); CK (right)

Fig. 3 Acceleration of introductions: cumulative number of fruit species introduced to Madagascar over time (based on Montagnac 1960)

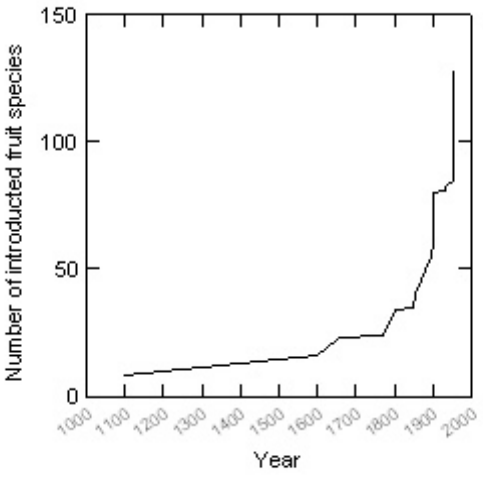


Fig. 4 Large differences in introduction pressure: the number of arboreta to which forestry species were introduced in Madagascar in the 1950s and 1960s (based on Chauvet 1968)