Research

Wider spectrum of fruit traits in invasive than native floras may increase the vulnerability of oceanic islands to plant invasions

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Plant–animal mutualisms such as seed dispersal can play an important role in enabling some species to become invasive. For example, an introduced species could become invasive because birds prefer its fruits to those of native plants. To investigate this possibility, we compared various measures of fruit quality of 22 of the most common native and invasive woody species on the oceanic island Mahé (Seychelles, Indian Ocean).

Individual measures of food quality tended to vary much more amongst invasive species than amongst native species; thus, whereas for particular traits the fruits of some invasive species had higher values than any native species, others had relatively low values. However, invasive species consistently produced fruits with a lower water content, resulting in a higher relative yield (i.e. dry pulp weight to total wet fruit weight ratio), and a higher energy content. The fruits of the most abundant invasive tree *Cinnamomum verum* (Lauraceae) were of particularly high nutritional quality, with individual berries containing 3.5 more protein and 55 times more lipid than the median values of the native species.

We suggest that our results may reflect a general tendency for island plants to produce fruits of low energy content, perhaps reflecting reduced competition for dispersal agents on isolated islands. In addition, we argue that inconsistent results on the relevance of fruit quality for plant invasions reported in the literature may be resolved by comparing the widths of trait spectra for native and alien floras rather than average values. Gaps in the native fruit trait spectrum may provide opportunities for particular invasive species, and weaken the resistance of regional floras to invasions. Such empty niche opportunities may occur for several reasons, including generally broader trait spectra in globally assembled alien than regional native floras (especially on oceanic islands), or the loss of native species due to human activities. More generally, a focus on trait variation rather than average trends may help to advance generalisation in invasion biology.

Invasions of alien plant species pose major threats to biodiversity and ecosystem functioning (Millennium Ecosystem Assessment 2003), particularly on oceanic islands (Denslow 2003). Increasingly, the importance of plant–animal mutualisms such as pollination and seed dispersal in plant invasions has been recognized (Richardson et al. 2000). However, although many of the most problematic invasive plants are frugivore-dispersed (Buckley et al. 2006) – especially among tropical woody species (Binggeli 1996, Kueffer et al. 2004) – there have been few studies of how frugivores influence plant invasions (Gosper et al. 2005, Buckley et al. 2006).

It has been suggested that some invasive plants are successful because native frugivores prefer their fruits to those of native plants (Vila and D'Antonio 1998, Gosper et al. 2005, Buckley et al. 2006), and they therefore gain an advantage in dispersal. Effective dispersal by frugivores could facilitate an invasion by increasing the rate of spread – even enabling propagules to reach remote areas – and by weakening the resistance of habitats to invasion through increased propagule pressure at a site (Von Holle and Simberloff 2005). Furthermore, the presence of invasive plants could attract dispersers away from native plants,

thereby negatively affecting the mutualisms between native plants and their frugivores (Traveset and Richardson 2006). If such effects are common, fruit traits may help in predicting the invasiveness of alien plants (Buckley et al. 2006). It is therefore important to understand whether fruiting traits of invasive plants – at the level of both the single fruit, e.g. size and nutritional content, and the whole plant, e.g. phenology and size of the fruit crop – tend to make them more attractive to birds than native species.

Several studies have shown that invasive plants often produce larger fruit crops or have longer fruiting periods than native species, but few have considered the traits of the fruits themselves, and no clear and consistent picture has emerged of differences between native and invasive species (Buckley et al. 2006). In particular, we are unaware of any study comparing the fruit characteristics of a set of common native and invasive plants in one region.

We compared the fruit characteristics of bird-dispersed native and invasive woody plants on the oceanic island Mahé in the Seychelles (Indian Ocean) to test the hypothesis that native plants of oceanic islands produce fruits of lower nutritional value than introduced aliens. It has been said that isolated islands are particularly vulnerable

to invasions because the native plants are thought to be less competitive than mainland species (Denslow 2003). This idea has so far mainly been tested for competition for growth-related resources (Denslow 2003, Schumacher et al. 2008, 2009), and we extended it to include competition for seed dispersers. There are a number of reasons why oceanic island plants may be less competitive than mainland species. In communities that owe their origin to long-distance dispersal, particular niches are commonly filled by taxonomic groups that are not necessarily well suited to this role (disharmony, e.g. woodiness of typically herbaceous genera), and ecologically very plastic generalists typically dominate habitats across broad environmental gradients (e.g. *Metrosideros polymorpha* in Hawaii, or *Northea hornei* in Seychelles) (Carlquist 1965, Whittaker 1998, Denslow 2003). Thus, more specialized mainland species may be stronger competitors under particular environmental conditions. And in the case of competition for seed dispersers, high dispersability may be less important for plant fitness on islands than on the mainland (Carlquist 1965, Whittaker 1998).

The island of Mahé offered a convenient study system for our purposes because the diversity of both plants and dispersers is small, and the dispersal systems are highly generalized (Stoddart 1984, Kueffer 2006). Thus, about 20 native and 10 invasive woody plants dominate these forests, and the majority of these produce small fruits (less than about 15 mm in diameter) that are dispersed by three common frugivorous birds (Stoddart 1984, Kueffer 2006) – an endemic bulbul *Hypsipetes crassirostris*, an endemic fruit pigeon *Alectroenas pulcherrima*, and an introduced Mynah *Acridotheres tristis*. In addition to birds, one endemic fruit bat species *Pteropus seychellensis* is also an important seed disperser.

To test the hypothesis that invasive species produce fruits of higher nutritional quality than native species, we compared various measures of fruit quality of 22 common native and invasive woody species.

Methods

Study system

The study was carried out on Mahé, the main inner island of the Republic of Seychelles (4°S, 55°E, total area 154 km², 0–900 m a.s.l.). The island has a humid tropical climate, with a mean annual rainfall of 1600–3500 mm depending on altitude. Although there is no pronounced seasonality in rainfall, the period from June through September is generally drier (mean monthly rainfall: 80–150 mm at sea level) than from November through February (300–450 mm) (Schumacher et al. 2008). The forest vegetation of Mahé was heavily affected by human activities until the 1970s, and is mostly secondary and dominated by alien trees, especially *Cinnamomum verum* (Kueffer and Vos 2004).

The original frugivore fauna of the inner Seychelles islands consisted mainly of various lizards (*Mabuya* and *Phelsuma* spp.), a giant tortoise (now extinct), an endemic fruit bat *Pteropus seychellensis seychellensis*, and six bird species. The latter included two mainly insectivorous white-eyes *Zosterops modestus*, (of which only ca 300 individuals are left on one small island); *Z. semiflava* (extinct), two fruit predatory parrots *Coracopsis nigra barklyi* (ca 300 individuals left on one island); *Psittacula eupatria wardi* (extinct), a bulbul *Hypsipetes crassirostris* (length: 24–25 cm), and a fruit pigeon *Alectroenas pulcherrima* (a genus related to the *Ptilinopus–Ducula* fruit pigeons, length: 23–25 cm). Today, an introduced mynah *Acridotheres tristis* (length: 25–26 cm) is also an important seed disperser. The largest fruits known to be swallowed by the common native bird species are of 10–15 mm diameter (depending on firmness) for *Hypsipetes* and 20 mm diameter for *Alectroena* (Kueffer 2006).

Plant material

The plant species used in the study included 14 native and 8 invasive woody species (Table 1); the species range from shrubs to large trees and include members of 12 plant families. The native plants selected are all common in inland habitats in the Seychelles (Friedmann 1994), and include 11 species endemic to the Seychelles, and three (*Aphloia theiformis, Canthium bibracteatum* and *Dracaena reflexa*) that also occur on other Indian Ocean islands. Most of the invasive species are common in semi-natural to natural mid-altitude habitats in the Seychelles, though *Litsea glutinosa* is mainly restricted to lowland areas (Kueffer and Vos 2004). Two of the invasive (*Chrysobalanus icaco, Syzygium jambos*) and one native species (*Syzygium wrightii*) have larger fruits that are only dispersed by fruit bats, although they are eaten by birds (Kueffer 2006). Fruits of *Psidium cattleianum* are dispersed in parts by birds and as whole fruits by fruit bats. The species studied include most of the widespread fleshy-fruited native and invasive woody species of inland habitats in Seychelles, the main omissions being the invasive *Lantana camara*, and the natives *Deckenia nobilis, Ludia mauritiana, Pouteria obovata*, and two *Ficus* species (Fleischmann 1997, Kueffer and Vos 2004, Kueffer 2006).

Samples for chemical analysis were collected on the island of Mahé between February to September 2004. The fruits were taken from several individuals and two to four sites per species in secondary forests and inselberg (rocky outcrop) vegetation, except for those of *Litsea glutinosa*, which were collected from gardens, and those of *Phoenicophorium borsigianum*, which were collected from the botanic garden in Victoria. Each species sample consisted of 25 to several 100 ripe fruits, or 10–15 fruits in the case of *Gastonia crassa, Memecylon caeruleum* and *Syzygium wrightii*.

Fruit quality

Pulp and seeds were separated and weighed. They were then dried at 40–50°C for four days and weighed again to determine the water content and dry mass per fruit. One pooled sample per species was stored in plastic bags with silica gel before being analysed at the Swiss Federal Res. Inst. for Farm Animals and Dairy Farming (ALP) in Posieux, Switzerland. For the chemical analyses, the dried pulp was ground in a laboratory mill with a one millimetre sieve. A constant dry matter content was determined with a

Table 1. The characteristics of the studied woody native and invasive plant species and the measured parameters. The wet fruit weight is given in mg and the fruit diameter in mm. For asymmetric fruits the minimum diameter is given. A small tree is <10 m. Nomenclature and maximal stem height was taken from Friedmann (1994).

Species	Family	Height	Fruit weight	Fruit diameter
Native species				
*Aphloia theiformis**	Flacourtiaceae	small tree	431	10
Canthium bibracteatum	Rubiaceae	small tree	167	5.5
Dillenia ferruginea	Dilleniaceae	tree	932	9.5
Dracaena reflexa	Liliaceae	shrub	1857	11.5
Erythroxylum sechellarum	Erythroxylaceae	small tree	290	6
Gastonia crassa	Araliaceae	small tree	954	10
Memecylon eleagni	Melastomataceae	small tree	424	8.5
Nephrosperma vanhoutteana	Palmae	tree	2303	12.5
Paragenipa wrightii	Rubiaceae	small tree	867	9.5
Phoenicophorium borsigianum	Palmae	tree	324	8
Psychotria pervillei	Rubiaceae	shrub	104	6
Roscheria melanochaetes	Palmae	small tree	187	6.5
Syzygium wrightii	Myrtaceae	tree	5124	18
Timonius sechellensis	Rubiaceae	small tree	891	9.5
Invasive species				
Ardisia crenata	Myrsinaceae	shrub	220	9
Chrysobalanus icaco	Chrysobalanaceae	small tree	16137	32.5
Cinnamomum verum	Lauraceae	tree	723	9
Clidemia hirta	Melastomataceae	shrub	230	7.5
Litsea glutinosa	Lauraceae	small tree	621	5.5
Memecylon caeruleum	Melastomataceae	shrub	625	9
Psidium cattleianum	Myrtaceae	small tree	21380	35
Syzygium jambos	Myrtaceae	tree	6884	24.5

*subspec. *madagascariensis* var. *seychellensis*.

thermographic system (at 105°C for 2 h 40 min). The following minimum quantities of dry fruit were used for the various analyses: 5 g for lipid determinations, 5 g for sugar and fibre and 0.5 g for protein. There was insufficient fruit material of some species to perform all these analyses (Table 1).

Crude fibre as determined by the Weende method (von Lengerken 2004) represents the content of organic structural material such as cellulose or lignin that is not soluble in a weak acid or alkali solution (similar to the conditions in animal digestion). The plant material was dissolved in sulphuric acid (1.25% H_2SO_4 solution, 1 h at 95°C) and potassium hydroxide base (1.25% KOH solution, 1 h at 95°C). The insoluble residue was then washed with water and acetone, dried (1 h at 130°C), weighed and ignited at 530°C for 1 h. The loss in weight on ignition was identified as crude fibre.

To determine total sugar content, the sample was shaken with 80% ethyl alcohol at 80°C for 1 h. After filtration, total sugar content was quantified colorimetrically based on a reaction with 1 g 3,5-dihydroxyltoluol (Orcin) in 1 l 70% sulphuric acid (H_2SO_4) (calibrated with sucrose).

Crude protein was determined using the DUMAS method (von Lengerken 2004). Nitrogen content was determined with a nitrogen analyzer after complete oxidation of the plant material at ca 1100°C. From these results, crude protein content was calculated as total nitrogen content multiplied by 6.25.

Crude total lipid content was determined with a Soxhlet system. The plant material was hydrolysed in boiling 10% HCl solution for 1 h (Berntrop method), and then extracted with petrol ether at 40–60°C in the Soxhlet system.

Calculations and statistical analyses

Mean fruit characteristics per species were used in the data analyses. The energy content of the pulp was calculated based on the following conversion factors: 5.2 kcal g^{-1} (protein), 9.3 kcal g^{-1} (lipid), and 4.0 kcal g^{-1} (sugar) (Watt and Muriel 1963). The following derived factors were calculated: relative yield (ratio of dry pulp to total wet fruit weight including seeds), seed burden (seed to total wet fruit weight ratio), overall profitability (nutritional contents per total wet fruit weight), and single fruit profitability (nutritional contents per single fruit). The differences in fruit characteristics between native and invasive species were tested with a Wilcoxon–Mann–Whitney-test. All statistical analyses were performed with R ver. 2.7.0 (R Development Core Team 2008).

Results

The fruits of invasive species had a lower average water content than those of native species (p = 0.003), resulting in a 50% higher relative yield (p = 0.01), i.e. ratio of dry pulp to total wet fruit weight including seeds (Fig. 1, Table 2). However, the seed burden, i.e. the seed to total fruit weight ratio, did not differ between the two groups (p = 0.2, Fig. 1).

There were no significant differences between native and invasive fruits in the average values of fibre, protein, lipid and sugar contents (p ≥ 0.5). However, the highest values of these traits – which ranged from around twice the median value of native species for fibre, protein and sugar, to 30
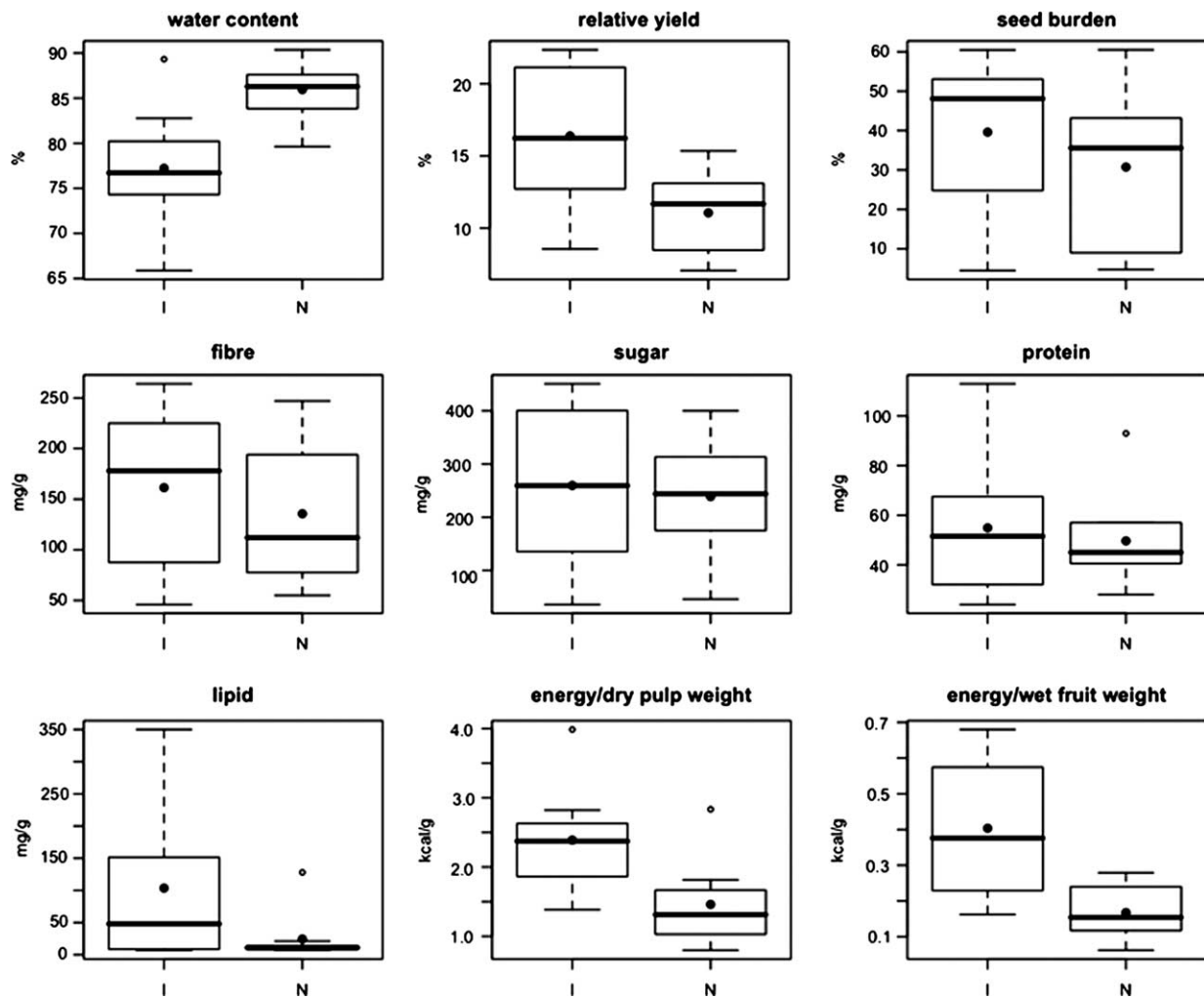
Figure 1. The water content of the pulp (%), relative yield (dry pulp weight: total wet fruit weight,%), seed burden (wet seed: total fruit weight,%), and the chemical composition in mg or kcal (energy content) per g dry pulp of 14 native (N) and 8 invasive (I) woody species. The overall profitability (OP) is calculated based on the relative yield and the content per dry pulp as the energy content per g of total wet fruit weight. The box–whisker-plots indicate the median (line), mean (filled circle), first and third quartiles (box), and the range of the data, with outliers indicated by open circles and defined as being more than 1.5 times the interquartile range above/below the first/third quartile.

times as high for lipid content – were always found in fruits of invasive species (Fig. 1). The average energy value of invasive fruits (calculated from the protein, sugar and lipid contents) was 1.6 times higher than that of native fruits, and the overall profitability (i.e. energy content per total wet fruit weight) was 2.4 times higher, both of these differences being significant (p = 0.02 and 0.01, respectively; Fig. 1). The variances in the trait values were mostly lower for native species than for invasive species (Fig. 1), with the differences being especially marked for water and lipid contents (ratios of variances of 0.18 and 0.08, respectively).

Across all species, the protein content of pulp was positively correlated with the lipid content (r = 0.6, p = 0.01) and negatively with the sugar content (r = −0.7, p = 0.002). Lipid and sugar contents were negatively correlated (r = −0.5, p = 0.05). The water content was negatively correlated with the lipid and energy contents (r = −0.6, p = 0.02).

Discussion

A trend for low energy content among native woody plants on an oceanic island?

We found that native species on the tropical oceanic island of Mahé tended to produce fruits of lower energy content than invasive species (Fig. 1, Table 2). The reason for the difference was the higher water (resulting in a lower relative yield) and lower energy contents per dry pulp of fruits of native species. These trends were also supported in the two intra-generic comparisons (*Memecylon eleagni* vs *M. caeruleum*, *Syzygium wrightii* vs *S. jambos*). Among the invasive species studied, *Litsea glutinosa* is restricted to some lowland areas, but exclusion of this species from the analysis did not substantially alter the results.

The mean water content of the invasive fruits (77.2%) was similar to values reported for bird-dispersed fleshy fruits

Table 2. Water content of the pulp (%), relative yield (%), and nutritional composition in mg or kcal (energy content) per g dry pulp of the studied native and invasive woody species from the Seychelles.

Species	Water content	Relative yield	Fibre	Protein	Sugar	Lipid	Energy
Native species							
Aphloia theiformis	87	12	80	57	162		
Canthium bibracteatum	80	15	112	40	351	7	1.7
Dillenia ferruginea	86	13	59	57	276	10	1.5
Dracaena reflexa	86	11					
Erythroxylum sechellarum	88	8	55	46	351	128	2.8
Gastonia crassa	86	13	75	41	270		
Memecylon eleagni	84	15	133	28	400	8	1.8
Nephrosperma vanhoutteana	90	7	231	57	131	13	0.9
Paragenipa wrightii	87	12	217	43	208	21	1.3
Phoenicophorium borsigianum	88	8	112	93	46	14	0.8
Psychotria pervillei	90	7					
Roscheria melanochaetes	84	10					
Syzygium wrightii	87	9	171	45	244	11	1.3
Timonius sechellensis	82	13	247	39	188	8	1.0
Invasive species							
Ardisia crenata	83	11	180	51	232		
Chrysobalanus icaco	89	9	81	28	421	7	1.9
Cinnamomum verum	66	22	264	62	39	252	2.8
Clidemia hirta	76	22	210	73	380	51	2.4
Litsea glutinosa	74	17	46	113	36	350	4.0
Memecylon caeruleum	78	15	94	36	451	48	2.4
Psidium cattleianum	74	20	240	24	264	7	1.8
Syzygium jambos	77	15	176	52	255	10	1.4

in the global angiosperm flora (71.8%, Jordano 1995), and fleshy fruits of the native flora of Hong Kong (78%, Corlett 1996), and alien plants in Hong Kong, Australia and New Zealand (76–78%, n = 12–15 species per region, Williams and Karl 1996, Corlett 2005, Gosper et al. 2006), while the native species had a considerably higher water content (86%). Methodological differences make it difficult to compare our data on energy with those from other studies, but Jordano (1995) reported an inverse relationship between water and energy contents for the global angiosperm flora, and the same trend was also evident in our study. Although a high water content can contribute to fruit quality during the dry season in areas with a seasonal climate (Herrera 1982), such an effect is unlikely to be relevant in the Seychelles, with its humid tropical climate. In view of these comparisons, we conclude that fruits of native species tend to be poor in energy, rather than those of the invasive species being particularly energy-rich. Indeed, it may be hypothesised that, compared to mainland species, plants on oceanic islands have evolved under conditions of less severe competition for seed dispersal agents, and therefore do not invest as much in attracting frugivores (Kueffer 2006). This could be partly because of the lower plant and frugivore species richness on islands, and partly because high dispersability is less important for plant fitness (Carlquist 1965, Whittaker 1998). We are unaware of any comparative data that could be used to support this hypothesis apart from a single observation that fruits of the island endemic *Arbutus canariensis* have a substantially lower energy content than those of the continental congener *A. unedo* (A. G. Fernandez de Castro pers. comm.). More research is needed to test the hypothesis that fruits from island plants have generally a lower energy content than those of continental species.

Higher variation of fruit traits among invasive than native species

A second pattern in our data was that the variation of fruit traits was generally considerably higher among invasive than native species (Fig. 1). In particular, the highest contents of sugar, protein and lipids were consistently found among the invasive species. The most common invasive tree in the Seychelles, *Cinnamomum verum*, had particularly high protein and lipid contents, so that the single fruit profitability (i.e. protein or lipid intake per fruit) was 3.5 times higher than the median values of native species for protein, and 55 times higher for energy. Given that searching and feeding on fruits are costly in terms of both time and energy, these differences may significantly affect fruit choices by birds.

In the case of the native species, the scarcity of fruits with high contents of particular nutrients may reflect a paucity of specialised fruits in the flora of a small oceanic island. Fruits that are particularly rich in either lipids, protein or particular types of sugars are often interpreted as being adapted to dispersal by specialist frugivores (Snow 1981, Corlett 1998, Witmer and Van Soest 1998, Jordano 2000, Levey and Martinez del Rio 2001). In particular, relatively large fruits of high nutritional quality are typically dispersed by specialised frugivorous birds such as fruit pigeons (Snow 1981, Corlett 1998, Meehan et al. 2002). However, few if any plants on the Seychelles depend only upon the endemic fruit pigeon *Alectroenas pulcherrima* for fruit dispersal (Kueffer 2006); and, except for the palms, no native species belong to families producing specialised lipid- or protein-rich fruits (e.g. Burseraceae, Lauraceae, Meliaceae, Myristicaceae, Rutaceae, Solanaceae, Jordano 1995, Corlett 1996, 1998). Rather, the Seychelles fruit pigeon may depend on a more opportunistic diet composed mainly of smaller fruits

that are also dispersed by other frugivorous birds. According to our data, some of the smaller fruits do, indeed, have relatively high lipid and/or protein contents, e.g. *Phoenicophorium borsigianum* and *Erythroxylum seychellarum*; the same may also apply to some of the species that we did not study, such as *Trema orientalis* and *Rapanea* spp. (Snow 1981). Further research is needed to determine if and why specialised fruits are missing from small oceanic islands.

There are other possible explanations for the lower variation of fruit traits among native species that also deserve to be mentioned. For example, human activities could have reduced the abundance of species with lipid or protein-rich fruits disproportionately (e.g. the now rare *Trema orientalis* or *Rapanea* spp.), though it is not clear why this should have happened. Or trait variation in the invasive flora may be broader than that in the local flora, simply because the invasive species have been sampled' from a much wider spectrum of biogeographic and ecological contexts.

Do fruit traits help to predict the invasiveness of alien species?

Effective dispersal is often important for an alien species to become invasive. Debussche and Isenmann (1990) suggested that competition for dispersal by a diverse native community of fleshy-fruited plants may have hindered the invasion of fleshy-fruited alien species in the Mediterranean. In contrast, several studies have shown that invasive species may profit from preferential dispersal of their fruits by the local frugivore community (Buckley et al. 2006).

However, apart from the importance of producing a fruit of a comparable size to some native fruits (Richardson et al. 2000, Renne et al. 2002, Gosper et al. 2005), rather little is known about which fruit traits contribute to the invasiveness of an alien species (Buckley et al. 2006). Previous studies comparing pairs of native and invasive or alien species have produced contradictory results, so that no general conclusions can be drawn about the importance of fruit quality: in some cases, fruits of invasive or alien species were found to be larger (Sallabanks 1993, Corlett 2005) or to have a lower seed load (Corlett 2005), a higher lipid content (Gosper et al. 2006) or a higher energy content (Vila and D'Antonio 1998), but in other cases the native species produced fruits with a higher energy (White and Stiles 1992, Drummond 2005) or mineral (calcium, iron and sodium) content (Nelson et al. 2000), or there were no differences in fruit quality (Gosper 2004). Our study appears to be the first to compare the fruit characteristics of a broad set of common native and invasive plants in a given region, but our results seem to add further to this incoherent pattern. Invasive species in Seychelles produce fruits with a wide range of properties: some have particularly high nutrient contents, especially protein or lipids, but others are of lower quality than most or all native species studied.

However, there is good evidence that some of the invasive species in Seychelles that produce fruits with particularly high contents of some nutrients profit from an efficient dispersal. Following heavy deforestation at around 1800, *Cinnamomum verum* (true cinnamon), a species that produces fruits of particularly high protein and lipid contents, rapidly colonized large areas (Sauer 1967, Stoddart 1984). Today *C. verum* is by far the most abundant species on Mahé, accounting for >80% of the canopy trees in most inland habitats. In a food preference experiment in which captive birds were offered the fruits of several native and alien species, Seychelles bulbuls *Hypsipetes crassirostris* – the most common frugivorous bird – preferred fruits of *C. verum* to those of all other species except the endemic *Dillenia ferruginea* (Kueffer 2006). *Clidemia hirta*, which produces fruits with 1.6 times more sugar and protein than the median of the native species, has recently spread rapidly on Mahé; within four years of it being first recorded in the late 1990s, it had spread into natural areas throughout the island (Kueffer and Zemp 2004).

The relevance of variation rather than general trends for comparing traits of native and invasive floras

We suggest that the inconsistent conclusions about the relevance of fruit quality for plant invasions reported in the literature may be resolved by comparing the width of trait spectra between native and alien floras rather than average values. General differences in fruit traits between the means for native and invasive species groups may not be expected for several reasons. First, only some invasive species may depend on efficient dispersal or on high fruit quality for efficient dispersal, while others rely on some other advantage for reproduction or dispersal (e.g. fruiting phenology, asexual reproduction). For instance, the species that produced the fruits with the lowest energy content among the invasive species, *Syzygium jambos*, has a patchy distribution in the form of dense, monospecific clumps, indicating low dispersability (Kueffer pers. obs.). Second, because of tradeoffs in fruit specialisation, fruits tend to have either high sugar or lipid and protein contents (Snow 1981, Corlett 1998, Witmer and Van Soest 1998, Jordano 2000, Levey and Martinez del Rio 2001). In fact, in our dataset sugar content was negatively correlated with lipid and protein contents. Thus, invasive species may profit from opposing specialisations, which has recently also been emphasised for growth-related traits (Daehler 2003, Schumacher et al. 2008, 2009). Thus, rather than comparing native and invasive floras in terms of the average values of particular traits, it may be more informative to compare their ranges of variation, so as to identify gaps in the native trait spectrum that could be exploited by an alien species (Moles et al. 2008).

This study has shown that gaps in the native fruit quality spectrum, especially the lack of lipid-rich fruits, may provide opportunities for invasive species with such fruits, and weaken the resistance of an oceanic island flora to invasions. On continents, empty niche opportunities for lipid-rich fruits may also occur, for example when anthropogenic disturbances affect plants with specialised fruits more than those with generalised fruits. Or, as discussed above, a sampling effect may generally lead to broader trait spectra within invasive than native floras. Several other cases have been reported of invasive species with particularly lipid-rich fruits becoming problematic because of efficient bird-assisted seed dispersal (e.g. *Cinnamomum camphora*,

Litsea glutinosa, Ochna serrulata, Mandon-Dalger et al. 2004, Vos 2004, Gosper et al. 2006, Neilan et al. 2006).

We conclude that a focus upon trait variation rather than on average differences between native and invasive floras may help to resolve inconsistencies in conclusions about the relevance of fruit quality for plant invasions. Even if there is no general tendency for lower nutritional quality among native species, empty niche opportunities might make oceanic islands more vulnerable to invasions by some alien species with particular fruit traits. More generally, a focus on trait variation rather than general trends may help to overcome inconclusive results on the invasiveness of alien plants, and advance generalisation in invasion biology.

References

Binggeli, P. 1996. A taxonomic, biogeographical and ecological overview of invasive woody plants. – J. Veg. Sci. 7: 121–124.

Buckley, Y. M. et al. 2006. Management of plant invasions mediated by frugivore interactions. – J. Appl. Ecol. 43: 848–857.

Carlquist, S. 1965. Island life. – Natural History Press.

Corlett, R. T. 1996. Characteristics of vertebrate-dispersed fruits in Hong Kong. – J. Trop. Ecol. 12: 819–833.

Corlett, R. T. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) region. – Biol. Rev. 73: 413–448.

Corlett, R. T. 2005. Interactions between birds, fruit bats and exotic plants in urban Hong Kong, south China. – Urban Ecosyst. 8: 275–283.

Daehler, C. C. 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. – Annu. Rev. Ecol. Syst. 34: 183–211.

Debussche, M. and Isenmann, P. 1990. Introduced and cultivated fleshy-fruited plants: consequences of a mutualistic Mediterranean plant–bird system. – In: Di Castri, F. et al. (eds), Biological invasions in Europe and the Mediterranean basin. Kluwer, pp. 399–416.

Denslow, J. S. 2003. Weeds in paradise: thoughts on the invasibility of tropical islands. – Ann. Miss. Bot. Gard. 90: 119–127.

Drummond, B. A. 2005. The selection of native and invasive plants by frugivorous birds in Maine. – Northeastern Nat. 12: 33–44.

Fleischmann, K. 1997. Invasion of alien woody plants on the islands of Mahé and Silhouette, Seychelles. – J. Veg. Sci. 8: 5–12.

Friedmann, F. 1994. Flore des Seychelles. – Orstom.

Gosper, C. R. 2004. Fruit characteristics of invasive bitou bush, *Chrysanthemoides monilifera* (Asteraceae), and a comparison with co-occuring native plant species. – Aust. J. Bot. 52: 223–230.

Gosper, C. R. et al. 2005. Seed dispersal of fleshy-fruited invasive plants by birds: contributing factors and management options. – Div. Distr. 11: 549–558.

Gosper, C. R. et al. 2006. Reproductive ecology of invasive *Ochna serrulata* (Ochnaceae) in southeastern Queensland. – Aust. J. Bot. 54: 43–52.

Herrera, C. M. 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. – Ecology 63: 773–785.

Jordano, P. 1995. Angiosperm fleshy fruits and seed disperser: a comparative analysis of adaptation and constraints in plant–animal interactions. – Am. Nat. 145: 163–191.

Jordano, P. 2000. Fruits and frugivory. – In: Fenner, M. (ed.), Seeds: the ecology of regeneration in plant communities (2nd ed.). CAB Int., pp. 125–165.

Kueffer, C. 2006. Impacts of woody invasive species on tropical forests of the Seychelles. ETH Diss., no. 16602, Dept of Environ. Sci. – ETH Zurich.

Kueffer, C. and Vos, P. 2004. Case studies on the status of invasive woody plant species in the western Indian Ocean: 5. Seychelles. – For. Dept, FAO, UN.

Kueffer, C. and Zemp, S. 2004. *Clidemia hirta* (Fo Watouk): a factsheet. – Kapisen 1: 11–13. <www.plantecology.ethz.ch/ publications/books/kapisen>

Kueffer, C. et al. 2004. Case studies on the status of invasive woody plant species in the western Indian Ocean. 1. Synthesis. – For. Dept, FAO, UN.

Levey, D. J. and Martinez del Rio, C. 2001. It takes guts (and more) to eat fruit: lessons from avian nutritional ecology. – Auk 118: 819–831.

Mandon-Dalger, I. et al. 2004. Relationships between alien plants and an alien bird species on Reunion Island. – J. Trop. Ecol. 20: 635–642.

Meehan, H. J. et al. 2002. Potential disruptions to seed dispersal mutualisms in Tonga, western Polynesia. – J. Biogeogr. 29: 695–712.

Millennium Ecosystem Assessment. 2003. Ecosystems and human well-being: a framework for assessment. – Island Press.

Moles, A. T. et al. 2008. A new framework for predicting invasive plant species. – J. Ecol. 96: 13–17.

Neilan, W. et al. 2006. Do frugivorous birds assist rainforest succession in weed dominated oldfield regrowth of subtropical Australia? – Biol. Conserv. 129: 393–407.

Nelson, S. L. et al. 2000. Nutritional consequences of a change in diet from native to agricultural fruits for the Samoan fruit bat. – Ecography 23: 393–401.

Renne, I. J. et al. 2002. Generalized avian dispersal syndrome contributes to Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasiveness. – Div. Distr. 8: 285–295.

Richardson, D. M. et al. 2000. Plant invasions – the role of mutualisms. – Biol. Rev. 75: 65–93.

Sallabanks, R. 1993. Fruiting plant attractiveness to avian seed dispersers: native vs invasive *Crataegus* in western Oregon. – Madrono 40: 108–116.

Sauer, J. D. 1967. Plants and man on the Seychelles coast. A study in historical biogeography. – Univ. of Wisconsin Press.

Schumacher, E. et al. 2008. Influence of drought and shade on seedling growth of native and invasive trees in the Seychelles. – Biotropica 40: 543–549.

Schumacher, E. et al. 2009. Influence of light and nutrient conditions on seedling growth of native and invasive trees in the Seychelles. – Biol. Invas. Doi: 10.1007/s10530-008-9371-6.

Snow, D. W. 1981. Tropical frugivorous birds and their food plants: a world survey. – Biotropica 13: 1–14.

Stoddart, D. R. (ed.) 1984. Biogeography and ecology of the Seychelles Islands. – Junk Publishers.

Traveset, A. and Richardson, D. M. 2006. Biological invasions as disruptors of plant reproductive mutualisms. – Trends Ecol. Evol. 21: 208–216.

Vila, M. and D'Antonio, C. M. 1998. Fruit choice and seed dispersal of invasive vs. noninvasive *Carpobrotus* (Aizoaceae) in coastal California. – Ecology 79: 1053–1060.

Von Holle, B. and Simberloff, D. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. – Ecology 86: 3212–3218.

von Lengerken, J. 2004. Qualität und Qualitätskontrolle bei Futtermitteln. – Deutscher Fachverein.

Vos, P. 2004. Case studies on the status of invasive woody plant species in the western Indian Ocean: 2. The Comoros archipelago (Union of the Comoros and Mayotte). – For. Dept, FAO, UN.

Watt, B. K. and Muriel, A. L. 1963. Composition of foods. – US Dept Agriculture.

White, D. W. and Stiles, E. W. 1992. Bird dispersal of fruits introduced to eastern North America. – Can. J. Bot. 70: 1689–1696.

Whittaker, R. J. 1998. Island biogeography. Ecology, evolution and conservation. – Oxford Univ. Press.

Williams, P. A. and Karl, B. J. 1996. Fleshy fruits of indigenous and adventive plants in the diet of birds in forest remnants, Nelson, New Zealand. – N. Z. J. Ecol. 20: 127–145.

Witmer, M. C. and Van Soest, P. J. 1998. Contrasting digestive strategies of fruit-eating birds. – Funct. Ecol. 12: 728–741.