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Giants invading the tropics: the oriental vessel fern, *Angiopteris evecta* (Marattiaceae)

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Abstract The Oriental vessel fern, *Angiopteris evecta* (G.Forst.) Hoffm. (Marattiaceae), has its native range in the South Pacific. This species has been introduced into other localities since the 18th century and is now listed as an invasive species in several regions (Jamaica, Hawaii and Costa Rica). The purpose of our study is (1) to trace the distributional history of the species, and (2) to model its potential future range based on climatic conditions. The native range and the history of introduction are based on the existing literature and on 158 specimens from 15 herbaria, together with field observations. As there are taxonomic problems surrounding *A. evecta*, we limited our analysis to samples from the Pacific, most closely resembling the type from Tahiti. We modelled the potential range using GARP species distribution modelling with basic climatic variables, elevation, and location in relation to the coast. Analysis of past records shows that the species is able to colonise new ecosystems with relative ease. The modelling reveals that the species could be cultivated over a much wider range than where it currently is grown. The escape of cultivated plants into nature is probably due to distance from natural areas and is limited by local ecological factors, such as soil conditions or competitors. The predicted distribution in Asia and Madagascar is similar to the native distribution of the entire genus *Angiopteris*. It can therefore be assumed that most *Angiopteris* species have similar climatic preferences, and the absence of *A. evecta* in this predicted region may be due to dispersal limitation. In the Americas there is no native *Angiopteris*, but our climatic model predicts a vast potential habitat in tropical America; an invasion of *A. evecta* should be anticipated here in localities where the species is cultivated. Vessel ferns are known to alter the natural environment, which may reduce local biodiversity. Since *A. evecta* is not yet widely cultivated, it is advisable to restrict the trade and spread of the species and to discourage its cultivation as an ornamental. The global climate data available for modelling is however not detailed enough to predict the spread of *A. evecta* on a local or regional scale.

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Introduction

Species introductions by humans to new areas have become more common due to increased transport, trade, travel, tourism, and the demand for exotic new species for horticulture. All of these provide pathways for organisms to cross biogeographical borders that they would never be able to cross on their own (Vitousek et al. 1996). Some introduced species become invasive and have negative effects on the local biodiversity, economy and even public health (Mack et al. 2000; Forseth and Innis 2004; Reaser et al. 2007). Globally, biological invasion by alien species is a major threat to natural ecosystems and biodiversity. An alien plant becomes invasive if it is able to maintain its population spread and take over suitable habitats from native plants (Williamson 1996).

Exotic plant species have been introduced both intentionally, as garden or crop plants, and unintentionally, with agricultural practices or the moving of soil. The effects of an introduction on the ecosystem are usually irreversible (Wittenberg and Cock 2001). There are various ways in which invasive plants can alter their environment; these are summarised by Reaser et al. (2007). Approximately 39–64% of invasive plant species alter the hydrology and biochemistry of the natural ecosystem (Gordon 1998). These may negatively affect native species, resulting in a lower local biodiversity. In Finland, for instance, vegetational formations invaded by lupine (*Lupinus polyphyllus* Lindl., Fabaceae) were found to have a substantially lower diversity of both plants and butterflies than adjacent vegetations (Valtonen et al. 2006). Valtonen et al. (2006) also showed that invasive plants could affect the diversity of higher trophic levels as well, especially when invading species occur in high densities.

Some invasive species, such as the infamous Japanese knotweed (*Fallopia japonica* (Houtt.) Ronse Decr., Polygonaceae), alter ecosystems by forming dense stands, crowding out native species. This knotweed was introduced into Europe as an ornamental in the 19th century (Christenhusz and Uffelen 2001), and soon became a pest. It has a broad ecological tolerance and invades various habitats. An even more dramatic invasion was the introduction of kudzu (*Pueraria lobata* (Willd.) Ohwi, Fabaceae) to North America to prevent soil erosion. Forseth and

Innis (2004) reported that the ability of this vine to rapidly overtop trees, fix nitrogen and emit isoprene has a highly negative effect on natural nitrogen cycles, forest biodiversity, freshwater eutrophication and local air quality.

The giant hogweed (*Heracleum mantegazzianum* Sommier and Levier, Apiaceae), a species originally from the Caucasian mountains, has spread throughout Europe as a garden plant. According to Pysek and Pysek (1995), this species can invade a variety of vegetation types, although disturbed habitats are more easily invaded. The same study also showed that vegetation invaded by *H. mantegazzianum* has a much lower species diversity than similar adjacent vegetation that has not been invaded; many herbs and shrubs are unable to survive when overshadowed by the large leaves of this *Heracleum*.

In the tropics various alien plants are found as well, which invade natural ecosystems in a similar fashion, altering local ecosystems and reducing biodiversity; an example is *Miconia calvescens* DC. (Melastomataceae), which forms dense stands crowding out the native flora of the Pacific islands (Meyer and Florence 1996). Bamboo (*Bambusa vulgaris* Schrad., Poaceae), the rose apple (*Syzygium jambos* (L.) Alston, Myrtaceae) and the African tulip tree (*Spathodea campanulata* Pal., Bignoniaceae) are well known examples of species invading tropical forests. Their slowly decomposing leaf litter prevents the regeneration of native species, and may change nutrient cycles. The dense thickets formed by bamboo and rose apple prevent the penetration of native species (O'Connor et al. 2000; Bito 2007).

Even though most invasive plants are seed plants, a few alien ferns are also known to be invasive and to present serious problems for conservation. Examples of invasive ferns are *Angiopteris evecta* and *Cyathea cooperi* (F.Muell.) Domin, both from the South Pacific, but now forming major infestations on the Hawaiian Islands, threatening the endemic flora (Wilson 1996). In this article we model the potential distribution of one of these, known variously as 'Oriental vessel fern', 'mule's foot fern', 'giant fern' or 'king fern': *Angiopteris evecta*, a species native to New Guinea, coastal Australia, Melanesia, Micronesia, and Polynesia (Rolleri 2003). This species was brought into cultivation soon after it was discovered (Forster 1786); it is now known to be invasive in

several tropical regions, most notably in Hawaii, Jamaica and Costa Rica (http://plants.usda.gov/ , and http://www.hear.org).

Ferns of the genus *Angiopteris* are of evolutionary interest, because they are eusporangiate and have a fossil history dating back to the Jurassic (Konijnenburg-van Cittert 1975). In addition, the plants are of ornamental value, due to their large rhizomes and gigantic leaves. For these reasons they are commonly cultivated in (botanical) gardens worldwide. The genus consists of some 200 microspecies, occurring throughout (sub-) tropical Asia, the Pacific and Madagascar (Mabberley 1997).

Angiopteris evecta is a species with large, globular rhizomes that can grow up to 1.5 m tall and about 1 m across. The starchy rhizomes are sometimes consumed or used to perfume coconut oil (Mabberley 1997), which may have led to early cultivation in tropical Asia. The enormous bipinnate leaves sprout spirally from the rhizome and can grow up to 6 m long and 3 m wide. At the base of every petiole there are fleshy stipules, which have proliferous buds that can grow into new plants when the stipules break off and find suitable ground (Uffelen 1994; Hoshizaki and Moran 2001). This vegetative reproduction enables the formation of dense stands. The adult leaves are covered in thousands of sporangia, each of which produces 1,440 spores (Sporne 1962). The young plants thrive in both sunny and shady places, allowing the species to spread in dark primary rain- and cloud forest as well as in open secondary vegetation.

Since *Angiopteris evecta* is cultivated throughout the tropics, we may expect it to become more widespread in the near future. We therefore take a closer look at how this species has spread and where it might naturalise. In order to prepare for and prevent further invasion, a better understanding is needed of the taxonomy, ecology, potential distribution, and means and history of introduction to non-native habitats. Here we trace the history of introduction, based on herbarium specimen data and interviews. We then compare the spread of the species by estimating its potential distribution, based on climatic and geographic data. This information will provide an indication of where the naturalisation of Oriental vessel ferns should be anticipated, and where its introduction and cultivation should be restricted.

Material and methods

Data collection

Distribution data for *A. evecta* were obtained from several sources. We have identified 141 specimens of *A. evecta* in 15 herbaria (BISH, CANB, CR, DUKE, H, HVNP, IJ, MO, MT, NSW, NY, P, TUR, UCWI, US; herbarium acronyms according to Holmgren and Holmgren 1998), and this data set was supplemented with 17 field observations. Specimen images and information from the Global Biodiversity Information Facility (http://www.gbif.org/) and the database of the Hawaiian Ecosystems at Risk project (http://www.hear.org/) were evaluated, 35 of whose records were included in our database. A total of 158 records included 128 from Australia, the Cook Islands, Fiji, French Polynesia, Guam, Indonesia (Papua), the Mariana Islands, Micronesia, New Caledonia, Niue, Palau, Papua New Guinea, Samoa, the Solomon Islands, Tonga and Vanuatu, where the species is native, and 30 from Costa Rica, Hawaii, Indonesia (Java, Ambon) and Jamaica, where the species is introduced (Fig. 1). All records were georeferenced using maps, Google Earth (http://www.earth.google.com/), the Alexandria Digital Library Gazetteer (http://www.middleware.alexandria.ucsb.edu/client/gaz/adl/index.jsp), and the Global Gazetteer Version 2.1 (http://www.fallingrain.com/world/). Of the 128 native sites, 95 were spatially unique. Voucher data and sources of all records, with their respective coordinates, are given in Appendix 1.

Taxonomy

The taxonomy of the genus *Angiopteris* is contentious, and species numbers have fluctuated immensely. Mabberley (1997) considered the genus to consist of 200 poorly defined microspecies; Rolleri (2003) reviewed the genus, dealing with a total of only 10. It is evident that additional studies are needed to resolve these taxonomic problems and better define the species morphologically and genetically. To be certain about the identity of our naturalising *Angiopteris*, we identified all the samples included in our study with the key provided by Rolleri (2003). Since it is certain that the species was introduced from Tahiti to both Hawaii and Jamaica,

Fig. 1 Distribution of *Angiopteris evecta* based on 158 herbarium specimens and field observations
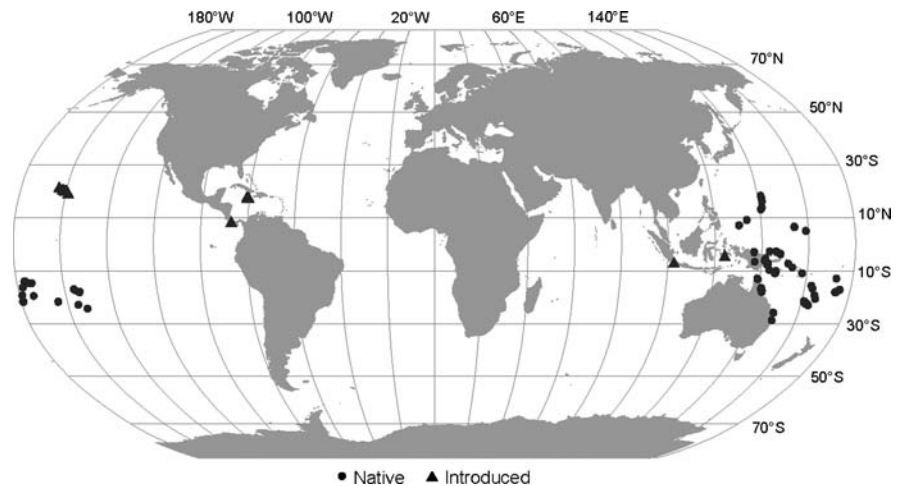
we matched specimens from invasive populations with collections from native populations in the Society Islands, including the type specimen of *A. evecta* (Nicolson and Fosberg 2003).

Modelling potential range

We assessed the potential distribution of the Oriental vessel fern in the Neotropics and Hawaii based on climatic and environmental variables. Macroclimatic and topographic variations have long been considered to be the fundamental factors controlling plant species distributions at global and regional scales (e.g. Holdridge 1967; McArthur 1972).

Three types of explanatory environmental variables were used to predict the potential species range: (1) climatic variables related to temperature and precipitation, (2) an elevational variable representing height above sea level, and (3) a distance variable measuring the Euclidean distance from the nearest sea-coast. The total number of variables was 10, as shown in Table 1.

The climatic variables were selected from high resolution (2.5 arc minutes), interpolated climatic surfaces provided by WorldClim (Hijmans et al. 2005, http://www.worldclim.org). While the spatial resolution of the actual data set is relatively high, weather stations in the tropics are scarce and the data values have been generated for WorldClim with greater interpolation distances than at higher latitudes. Furthermore, on small islands the variability of climate and elevation may vary drastically over short

Table 1 Environmental variables used in GARP modelling

Variable	Range based on *Angiopteris* localities
Annual mean temperature	19.0–27.5°C (Fig. 2a)
Temperature seasonality (coefficient of variation)	107–3,383 (Fig. 2b)
Mean temperature of warmest quarter	19.5–27.8°C (Fig. 2c)
Mean temperature of coldest quarter	15.0–27.3°C (Fig. 2d)
Annual precipitation	1,054–5,447 mm (Fig. 2e)
Precipitation seasonality (coefficient of variation)	14–99 (Fig. 2f)
Precipitation of wettest quarter	386–1,996 mm (Fig. 2g)
Precipitation of driest quarter	37–1,147 mm (Fig. 2h)
Elevation, 2.5 arc minute data with height in meters	3–1,492 m (Fig. 2i)
Euclidean distance from nearest sea-coast	0.042–2.323° (Fig. 2j)

distances; this is not reflected in our climatic data. Distance from the coast was considered relevant, as the native occurrence areas of the species are limited to island habitats and coastal forests, never far from the sea. Distance from the coast thus acts as a surrogate for local climatic differences between the coastal and continental tropics. Distance from the coast was calculated as the Euclidean distance from the shoreline, with 2.5 arc-minute resolution, using ArcGIS and Spatial Analyst extension. Since distance from the coast is not an environmental variable in the usual sense, we tested the effect of this factor on our

model; we therefore ran the GARP model with and without this variable.

In order to better understand the spatial variation of the environmental variables, we first analysed their min–max value ranges in the known localities of *A. evecta* (Table 1) and highlighted these ranges at a global scale (Fig. 2). We then analysed the potential range of *A. evecta* using two alternative approaches: (1) an environmental envelope approach; and (2) the Genetic Algorithm for Rule-set Production (GARP) modelling framework, as described by Peterson (2003).

The environmental envelope approach, following the niche theory of Hutchinson (1957), has been a traditional approach among biogeographers to estimate broad-scale species ranges based on the known environmental conditions of current species occurrences (Walker and Cocks 1991; Guisan and Zimmermann 2000). This method is somewhat mechanistic; at the same time, however, it is very transparent and understandable. We formed the envelopes based on the min–max values of individual environmental variables in the known occurrence localities of *A. evecta*, as shown in Fig. 2. We then searched the intersection of the min–max envelopes of the individual variables to produce an overall environmental envelope of *A. evecta*.

Fig. 2 Theoretical environmental ranges of *Angiopteris evecta*, based on individual variables used in the GARP distribution modelling. Black areas show regions within the value range of known occurrence points of *A. evecta*. White areas fall outside the value range
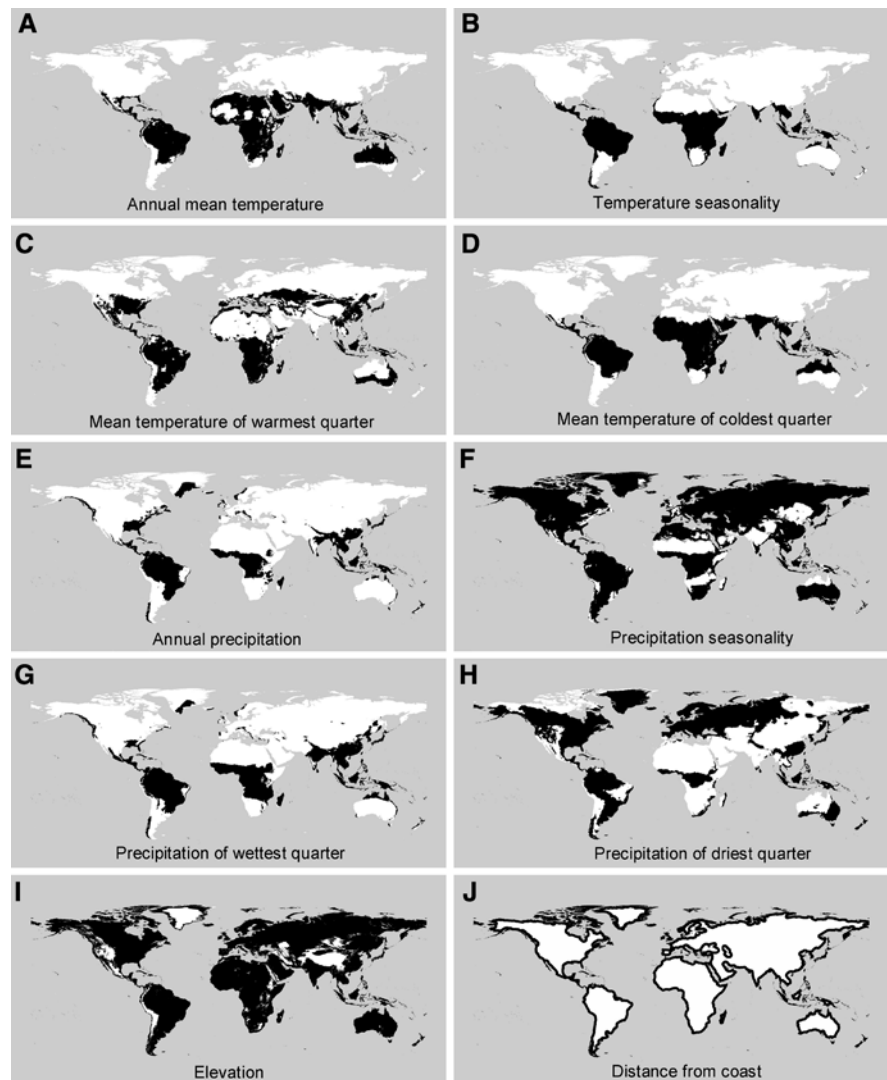
Our other approach, the GARP modelling framework, performs a spatially explicit, iterative climatic niche modelling analysis, to predict the potential distributions of a species based on known records of species occurrence. It is thus a more elaborate version of the bioclimatic envelope approach. GARP modelling has shown to have predictive success in broad scale analyses (Elith et al. 2006). GARP has also been found to have predictive value in cases involving extrapolation to areas without field observations, in comparison to otherwise reliable approaches such as MAXENT (Elith et al. 2006; Peterson et al. 2007).

To model the potential distribution area of *A. evecta*, we used the environmental input variables listed in Table 1. We trained the model using 60% of the above-mentioned georeferenced voucher specimens and observations in the native range. The remaining 40% of the points were used in the internal training of the modeller. We modelled the potential range of *A. evecta* by running the GARP modeller with 40 runs, 1,000 iterations per run and a 0.01 convergence limit. The 10 best predictions were selected by GARP, and these predictive maps were combined with a probability surface, which assigns the highest occurrence probability to areas where occurrence was predicted most often. To test the final modelling result, we used 30 known introduced occurrence points outside the native geographic range of the species.

Historical survey

An expedition to Jamaica in 2004 by the first author yielded many well established populations of *A. evecta* (Fig. 3). Proctor (1985) had already mentioned the occurrence of the species on the island, but its ability to invade and maintain populations in natural forests was unexpected. Discussions with Proctor provided information on the introduction and spread of *A. evecta* to Jamaica. Internet searches provided additional information on the cultivation and invasion of *A. evecta* in Costa Rica, Florida, Hawaii, in various tropical Asian countries, and under glass in temperate countries. More information on the Costa Rican introduction was gathered through correspondence with Luis Diego Gómez and Zak Zahawi. Mónica Palacios-Rios

provided additional data on cultivation of *A. evecta* in Cuba and Mexico. The historical survey was supplemented by data from herbarium specimen labels.

Results

Potential distribution area

With regard to the highest probabilities of occurrence, the two methodologies used to estimate the potential distribution of *A. evecta* resulted in similar overall patterns globally (Fig. 4). The potential range, as predicted by both models, includes the more humid parts of tropical America, Africa and Asia if the species is introduced into these areas. In Asia, Oceania and Madagascar the predicted range of *A. evecta* corresponds roughly to the natural range of the entire genus *Angiopteris*.

The climatic envelope presents a somewhat patchy delineation for the potential distribution area (Fig. 4a). The GARP model resulted in a more diffuse pattern, following the environmental gradients in the area. Comparison to the known localities of introduced *A. evecta* shows that the GARP model performs slightly better: 28 out of 30 test points fall within the area where the model predicts a 90–100% probability for *A. evecta* occurrence in the GARP
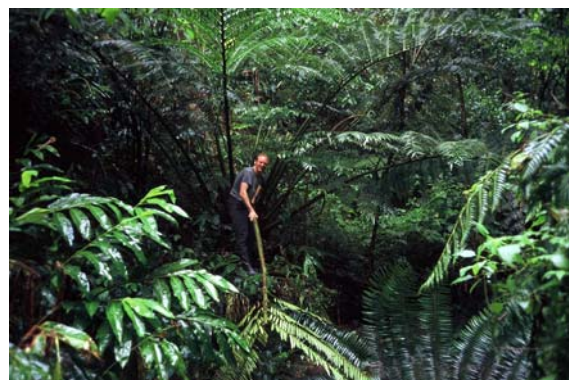

Fig. 3 Maarten Christenhusz collecting *A. evecta* in Hardwar Gap, Jamaica (voucher: *Christenhusz and Tuomisto 2992* (BM, IJ, L ,TI, TUR, UC)). The left foreground shows plants of *Hedychium coccineum* Buch.-Ham. ex Sm. in Rees (Zingiberaceae), another alien invasive from Asia. Photo by Hanna Tuomisto, January 2004

Fig. 4 Comparison of the potential range of *A. evecta* according to the environmental envelope approach (**a**) and GARP modelling (**b**). The areas of highest probability of occurrence are marked in black. These correspond to areas that fall within the min–max envelope of all ten environmental variables in the climatic envelope approach, and that are predicted as occurrence areas in all of the ten best modelling results of the iterative GARP runs
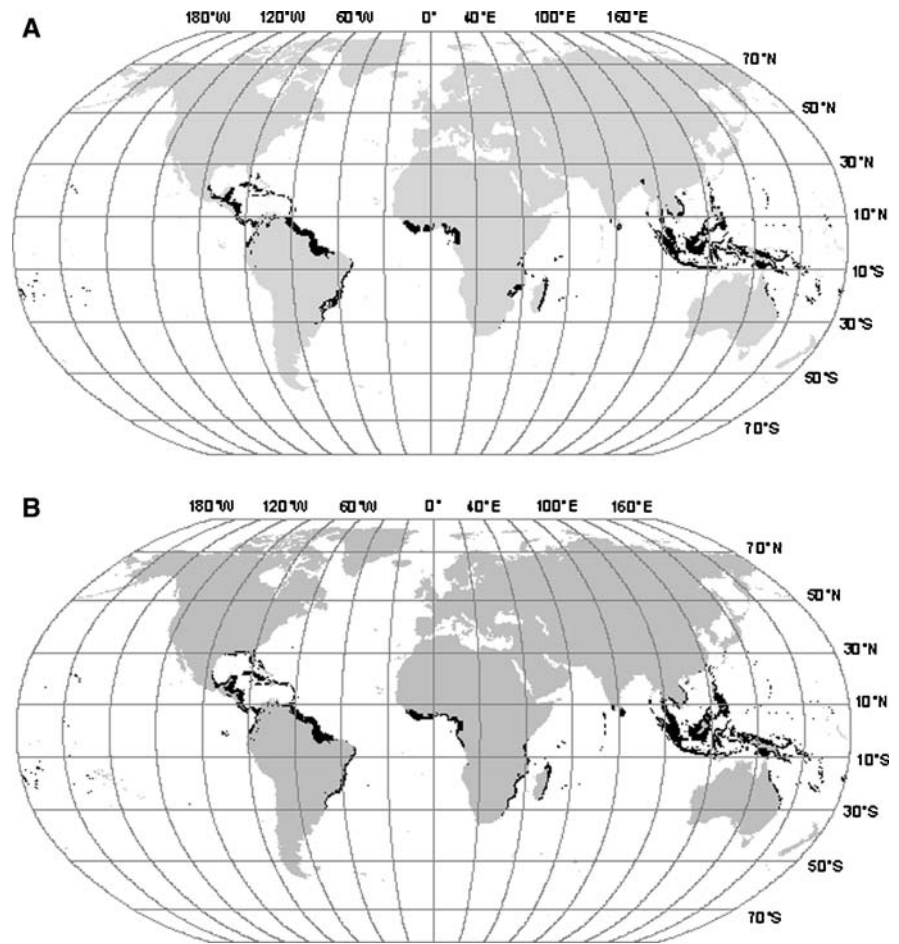
model, whereas only 26 out of 30 test points fall within the environmental envelope created by combining all the min–max variable envelopes of native localities. In the GARP result, the remaining two test points are located within the area of 80–90% predicted probability of occurrence. Thus the GARP model can be considered or greater interest (Fig. 5b). When probabilities above 60% are considered, the potential range becomes very extensive in tropical mainland Africa and South America. The highest probabilities, however, are found in coastal habitats, especially in the Caribbean, Central America, and Hawaii; we also have information from all three areas regarding the history of introduction.

The result of GARP modelling excluding 'distance from the coast' as a variable is presented in Fig. 5a. The main difference from the model where it was included (Fig. 5b) is to be found in continental South America and Africa, where exclusion of this variable

yields a 100% prediction rate for vast inland areas. The model including distance from the coast stretches the northern limit somewhat further. This model (Fig. 5b) predicts the occurrence of *A. evecta* in coastal China and Japan, where another species, *A. lygodiifolia* Rosenst., is found.

History of introduction

Jamaica

Captain William Bligh took command of the *H. M. S. Bounty* in 1787, and sailed to Tahiti to procure breadfruit trees (*Artrocarpus altilis* (Parkinson) Fosberg, Moraceae), after which he planned a course for the West Indies, where breadfruit was needed as an additional food source for slaves (Serle 1949). The *Bounty* never reached its final destination, as mutiny

Fig. 5 Probability of
occurrence of *Angiopteris
evecta* based on GARP
modelling, based on the
best results of the iterative
modelling process. Areas
with the darkest colour were
predicted as occurrence
areas in all of the ten best
modelling results. (**a**)
Distance from the nearest
coast excluded as a
variable. (**b**) Distance from
the nearest coast included as
a variable
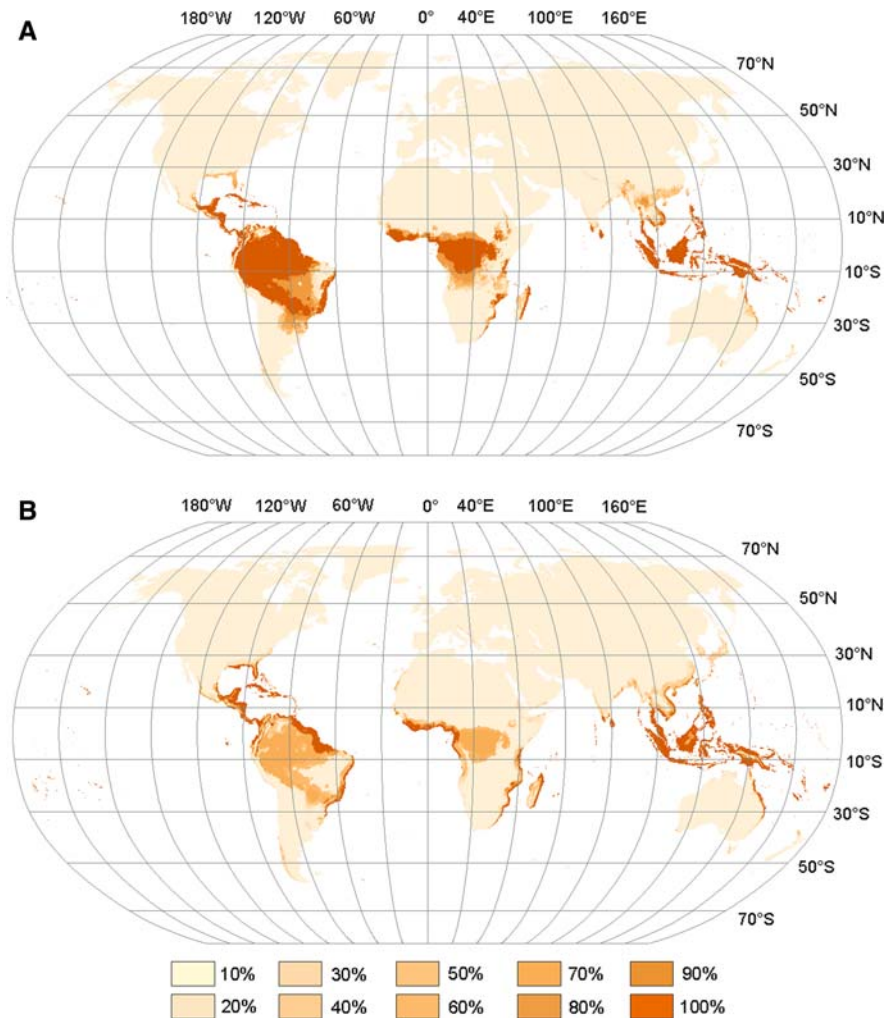
broke out shortly after leaving Tahiti. To carry out his earlier instructions, Bligh sailed again in 1791 and successfully brought several Pacific plants to Jamaica (Serle 1949). *Angiopteris evecta* was probably among the plants introduced from Tahiti to Jamaica. Bligh's plants reached Jamaica in 1793 (Adams 1972), where they were first planted in the Botanic Gardens of Bath (St. Thomas Parish). During the 1860s, cuttings of Bligh's plants were moved to the more sheltered and humid Castleton Gardens in St. Mary's Parish (G. R. Proctor, personal communication, January 2004). According to anonymous voucher specimens at the UCWI herbarium, both *A. evecta* and *A. pruinosa* Kunze were once cultivated in the Castleton Gardens, most likely during the late 19th century under the curatorship of the pteridologist G. Jenman. The oldest dated

collections of *A. evecta* from Castleton were made by *E. T. Robertson 3991* (UCWI) in 1956. *Angiopteris pruinosa* is a native of Java and the Philippines, differing from *A. evecta* in having glaucous leaflets, is not invasive anywhere as far as is known; it is no longer cultivated in Jamaica. *Angiopteris evecta* was first found naturalised at Corn Puss Gap in 1976, *Proctor 36381* (IJ), where it is now extremely common. Currently it has spread throughout the eastern half of Jamaica, where it is commonly found in the Rio Grande Valley and throughout the Blue and John Crow Mountains. It has been found as high as 1,250 m elevation at the Portland Gap, and as far west as Fern Gully. Maarten Christenhusz and Hanna Tuomisto made various collections of these populations during their Jamaican expedition in 2004 (Fig. 3, Appendix 1).

The results of our modelling suggest that the entire island of Jamaica falls within the potential distribution range of *A. evecta* (Fig. 6). However, natural populations were found only in the eastern half of the island. Other ecological factors may restrict the species to the eastern parishes of the island.

Costa Rica

Charles Lankester, owner of an estate in Costa Rica, obtained a young plant of *A. evecta* from Jamaica in the 1950s. Bob Wilson planted a cutting of this plant in his garden around 1965. The original plant in the Wilson Botanical Garden is alive today, and many clones have since been distributed to various gardens in Costa Rica. Since gametophytes and young sporophytes are commonly found in the rainforest surrounding the Wilson Garden and at the nearby Las Cruces Biological Station (L. D. Gómez, personal communication, 7 February 2007), we are certain that the plants produce viable spores. Earlier records of the naturalisation of this species are known. In January 1999, A. R. Smith saw hundreds of thousands of mostly juvenile plants (personal communication).

The first herbarium specimen from a naturalised population that we are aware of was prepared in 2003 by *R. C. Moran 6456* (CR).

The results of our modelling suggest that large parts of Central America (from southern Mexico to Panama and into coastal Colombia) include areas where *A. evecta* could potentially thrive (Fig. 6). The potential range near the known localities of introduced individuals is limited by the mountainous landscape, but all coastal rainforest areas are predicted as suitable for the Oriental vessel fern.

Hawaii

Hawaii has more naturalised fern species than any other state in the USA. Most species have been introduced as garden plants. The introduction and spread of *A. evecta* in Hawaii is surprisingly well documented. It was brought from Tahiti to Oahu in 1927 by H. L. Lyon, who planted it in the upper Manoa Valley close to Honolulu, in what is now the Lyon Arboretum of the University of Hawaii. Within the Lyon Arboretum it soon became a pest, and quickly escaped into adjacent natural areas. Where it grows it poses a threat to the local flora, shading out

Fig. 6 Potential range of *Angiopteris evecta* in Central America and the Caribbean, with known localities of naturalised individuals. In some of the predicted areas (e.g. the Bahamas, Yucatan), the spread of *A. evecta* is unlikely, because most lowland coastal areas in the Caribbean are too dry. The prediction here is most probably due to the crudeness of the climate data, which were probably extrapolated for most of the Caribbean islands
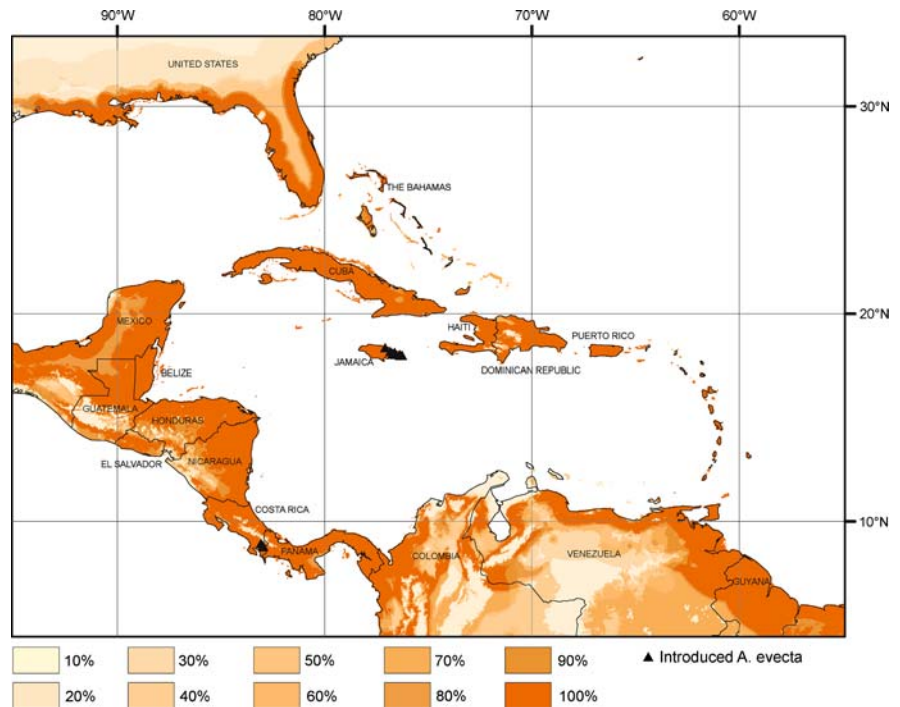
all other vegetation (Wilson 1996). Funk (1987) described its rapid escape into many of Oahu's forested ridges and valleys, but noted that the spread was slow. Nevertheless, Funk reported that in 1968, two populations on either side of Oahu were found within a year from each other. Since the Oahu populations are separated by deep valleys or mountain ranges, Funk (1987) assumed that the species disperses well by wind. She feared that *A. evecta* would soon fill many of the niches formerly occupied by endemic Hawaiian ferns and other plants. In 1994, *A. evecta* was reported to have spread into the lowland wet forest above Hana on the island of Maui, where it probably escaped from cultivation in the nursery at Helani Gardens (Wilson 1996). Likewise on the main island of Hawaii, several large *A. evecta* plants are found outside cultivation on the grounds of the Hawaii Tropical Botanical Garden, where it is also cultivated. It has been found naturalised in the Waiakea Forest Reserve (*Imoto and Bergfeld 03/31/92*, HVNP).

Our predictive model suggests that, apart from the higher elevated areas of Maui and Hawaii, most of the Hawaiian Islands provide good elevational and climatic conditions for *A. evecta* to naturalise (Fig. 7). Nearly the entire islands of Kauai, Lanai and Oahu are predicted to be suitable, and in fact *A. evecta* is naturalised on all three. Of the islands where *A. evecta* has not yet been introduced, Molokai has highest potentiality for supporting the species.

However, large parts of the Hawaiian Islands are much too dry for *Angiopteris*, and this is not reflected in the model. The rainfall data is too crude to say anything about the potential spread within the Hawaiian Islands.

Discussion

The native range of *A. evecta* is geographically rather restricted, and in some areas the conservation of *A. evecta* populations is of great concern. In parts of Australia, for instance, a recovery plan was initiated (NSW National Parks and Wildlife Service 2001). Many *Angiopteris* species are endangered by invasions of other invasive alien species, such as *Lantana camara* L. (Verbenaceae), and herbivory by goats (*Capra hircus* L.). Conservation programmes have been started for instance for the closely related

A. chauliodonta Copel. of Pitcairn Island (Kingston et al. 2004) and for *A. henryi* Hieron. and *A. itoi* (Shieh) J.M.Camus in Taiwan (Chiou et al. 2006). It is interesting that *A. evecta* is endangered in some parts of its native range, requiring conservation, even though it has been shown to be an aggressive invader when introduced into suitable new areas (Funk 1987; Wilson 1996).

There are several other invasive species that have a rather restricted natural range, such as the Himalayan Balsam (*Impatiens glandulifera* Royle, Balsaminaceae), and the already mentioned *Heracleum mantegazzianum*. Both are native in small areas in the Western Himalayas and Caucasus Mountains respectively, but become widespread invaders in many areas once they are helped to cross the dispersal barrier (Williamson 1996). *Heracleum mantegazzianum* does not cause any conservation problems in its natural area, where it coexists with other native flora, and never forms monocultures (observed by Christenhusz in Turkey, 2006). In Europe and North America the species reduces the local biodiversity by overshading other vegetation underneath its dense canopy of large leaves, leaving little else to grow and allowing it to form vast monospecific stands (Pysek and Pysek 1995).

On the island of Moorea (Society Islands), where *A. evecta* is native, it often replaces species of native tree ferns (*Alsophila tahitensis* Brack. and *Cyathea medullaris* (G.Forst.) Sw., Cyatheaceae) in secondary upland forests (Parkes et al. 1992). Wilson (1996) reported that in Hawaii too the natural ecosystems are dramatically altered by dense stands of *A. evecta*, crowding out and outshading native species. It may therefore be a great threat to local plant diversity in the tropics, in a fashion similar to *H. mantegazzianum* in temperate regions. This is especially problematic on islands that house many of endemics, have patchy, relatively disturbed forests; such habitats may resemble the native habitat of *A. evecta*. Tropical island ecosystems are therefore most vulnerable to vessel fern invasion, particularly in the Caribbean, a region known to have a relatively high diversity of tree ferns (Proctor 1985).

Since both *H. mantegazzianum* and *A. evecta* have large leaves, it may be assumed that *A. evecta* affects the ecosystem similarly to *H. mantegazzianum*. However, as a biennial *H. mantegazzianum* reaches the reproductive stage in the second year, whereas it

Fig. 7 Potential range of *Angiopteris evecta* in the Hawaiian Islands, with known localities of naturalised individuals
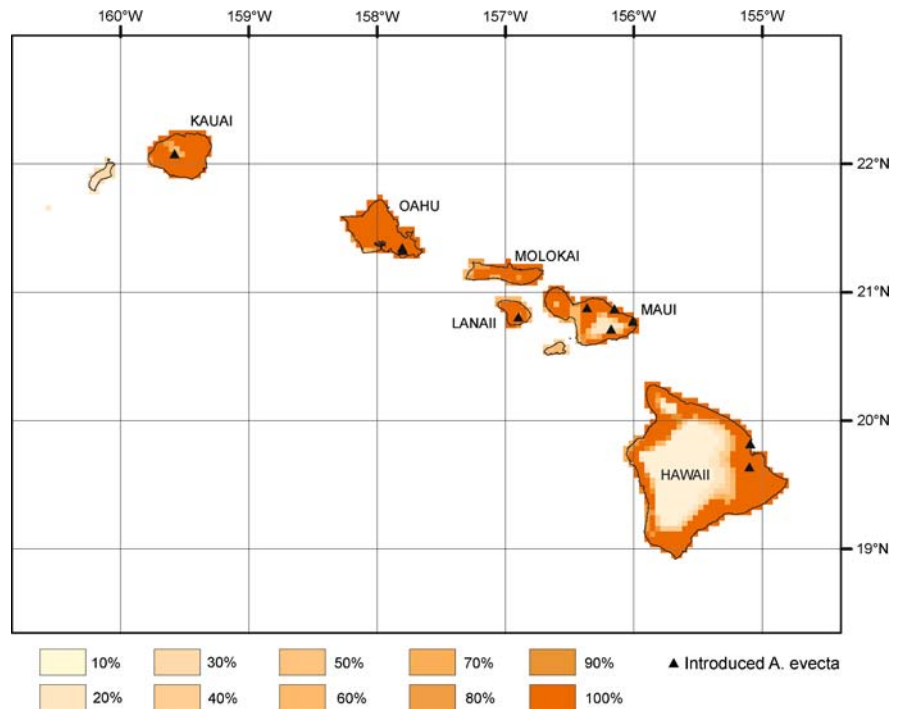
takes *A. evecta* many years before producing spores. In contrast, *A. evecta* is very long-lived, and over its lifetime an individual produces billions of propagules. Invasion by *A. evecta* is therefore slow, and establishment may take several decades after introduction; however, once gametophytes establish, invasion has already occurred and is difficult to stop. The slow pace of the first step of naturalisation makes the invasion insidious.

Our analysis of potential future distribution combines methodologies of environmental modelling and historical examination of distribution patterns. Given our data points, the GARP model provided a good global estimate. For many tropical regions, however, climate data are limited, and a lot of our data were based on extrapolation. Thus our model does not allow assessment of the potential distribution of *A. evecta* on a local scale. Moreover, the distribution pattern of *A. evecta* in Jamaica appears to be impacted by other ecological factors, especially local soil conditions. Unfortunately we were unable to include other ecological factors, due to the lack of sufficiently accurate data at a global scale. In the case of the Caribbean region in particular (Fig. 6), it is evident that the climate data provided by WorldClim are not detailed enough to make any prediction at a

local scale. Low-lying Caribbean islands and cays (such as the Bahamas, Cayman Islands, Virgin Islands and Antigua), for instance, are typically covered by cactus scrub; it is highly unlikely that *Angiopteris* will grow here, even though these areas are predicted by our model. This also pertains to the Galapagos Islands, which are too cool and dry for these giant ferns to grow. The climate data for these areas provided by WorldClim are most probably extrapolated, rather than based on actual measurements from the islands.

Our model does show, however, that the spreading of *Angiopteris evecta* in parts of Florida, Central America, coastal Brazil, the Guianas and large parts of the Caribbean should be anticipated if the species continues to be introduced and cultivated there. From established populations in Jamaica and Costa Rica, the species may slowly but steadily spread into neighbouring regions. *Angiopteris evecta* is additionally cultivated in Santiago de Cuba and Mexico (Shelton and Caluff 1994; Mónica Palacios-Rios, personal communication February 2006), from where it may spread. In southern Florida it is sometimes offered in the garden trade together with other *Angiopteris* species (*A. fokiensis* Hieron., *A. palmiformis* (Cav.) C.Chr. and *A. smithii Racib.;*

http://www.tfeps.org/angiopteris_sp.htm), but here the species has not escaped yet, probably due to occasional cold spells. Our models predict a probable naturalisation in all these areas, even though no escape into the wild has as yet been reported. Therefore we can conclude that the WorldClim climate data is not sufficiently detailed to predict the spread of invasive species on a local scale.

Since *A. evecta* belongs to a taxonomically complex group of closely related microspecies, some of which are endangered, the introduction of *A. evecta* into areas where other *Angiopteris* species occur may be of conservation concern in relation to native vessel ferns. Further research on the taxonomy and spread of *A. evecta* in tropical Asia is needed to determine whether *A. evecta* forms a threat to local *Angiopteris* species by outcompeting or hybridisation.

Reaser et al. (2007) provided guidance and information on technical resources that may help to minimize the effect of *A. evecta* invasion on island ecosystems. Cultivation by nurseries and other gardens, particularly in areas close to native forests, may result in the naturalisation of *A. evecta* in various tropical countries, altering the natural ecosystem and local biodiversity. *Angiopteris evecta*, however, has naturalised only locally, and the spread of these giant ferns can still be prevented in most of the predicted range. Natural resource managers and policy makers should engage local communities in programmes to minimise the impact (Reaser et al. 2007) of the spread of *A. evecta* and other alien invasive species.

Appendix 1

List of specimens studied. Herbarium acronyms follow Holmgren and Holmgren (1998); obs. = observation. GBIF accession numbers are also provided. Latitudes and longitudes, in that order, are given in decimal degrees.

Australia: GBIF-30827 (CANB), −25.367, 153.117; GBIF-191319 (CANB), −12.733, 143.283; GBIF-42523 (CANB), −16.46, 145.31; GBIF-42625 (CANB), −16.33, 145.33; GBIF-42628 (CANB), −17.58, 145.83; GBIF-246999 (NSW) −16, 145.3; GBIF-247014 (NSW), −17.2, 145.9; GBIF-247015 (NSW), −16.7, 145.6; GBIF-247016 (NSW), −16, 145.3; GBIF-247017 (NSW), −28.3, 153.5; GBIF-416480 (NSW), −16.1, 145.3; GBIF-665124 (CANB), −12.46, 142.98; *Kukkonen 10964* (H), −17, 145.7833. **Cook Islands**: *J. C. Space* (obs. 2002), −21.2333, −159.7667; *St. John 15384* (US), −21.25, −159.75. **Costa Rica**: GBIF-237255 (CR) 8.79, −82.96; *R. C. Moran* (obs. 2006), 8.95, −83.0833; *A. R. Smith* (obs. 2006), 8.8333, −82.9667. **Fiji**: *Degener 15488* (MT, US), −17.4, 178.1833; *A. C. Smith 373* (US, P), −16.6667, 179.4167; *A. C. Smith 4368* (US), −17.65, 177.5833; *A. C. Smith 5893* (US), −17.6167, 177.9833; *A. C. Smith s.n.* (US), −17.6167, 178.0167; *St. John 19445* (US), −12.5, 177.0667. **French Polynesia**: *Aubert de la Rue s.n.* (MT), −22.4333, −151.3333; *Copeland 3512* (US), −17.56, −149.59; *De Sloover 146* (P), −17.55, −149.82; *Florence 2096* (US), −17.5833, −149.8167; *Florence 3446* (L, US), −16.8333, −151.4167; *Fosberg 11941* (US), −22.4333, −151.3333; *Fosberg 15841* (US), −23.8667, −147.6833; *Fosberg 61049* (US), −17.5833, −149.8167; *Fosberg 63183* (P), −16.8333, −151.4167; *Moore 362* (US), −16.5, −151.75; *Setchell 7* (US), −17.5167, −149.4167; *St. John 17301* (US), −16.8667, −151.3833; *Tilden 336* (US), −17.65, −149.5667. **Guam**: *Conover 542* (US), 13.44, 144.71; *Grether 3721* (US), 13.44, 144.71; *Tweyey s.n.* (P), 13.4358, 144.7083. **Hawaii**: *Annable 3279* (NY), 21.317, −157.8; *Beck 1218* (NY), 22.07, −159.58; *Funk* (obs.), 20.8714, −156.365; *Funk* (obs.), 19.8099, −155.0943; *Imoto and Bergfeld 03/31/92* (HVNP), 19.63, −155.1; *Lyon* (obs.), 21.337, −157.806; *Medeiros* (obs.), 20.7647, −156.009; *Medeiros* (obs.), 20.8614, −156.1517; *Starr* (obs.), 20.8714, −156.365; (obs.), 20.8714, −156.365; *Wood* (obs. 2006), 20.8, −156.9; http://www.botany.hawaii.edu (obs.), 20.705, −156.177; (obs.), 21.337, −157.806. **Indonesia**: *Barclay s.n.* (K, L, US), −3.7167, 128.2; *Buysman 1726* (P), −6.23, 106.64; *Gibbs 6259* (P), −2.5833, 140.75. **Jamaica**: *Ammann 402* (UCWI), 18.02, −76.37; *Ammann 38* (UCWI), 18.18, −76.84; *Christenhusz 2992* (BM, IJ, L, TI, TUR, UC), 18.08, −76.72; *Christenhusz 3111* (GOET, IJ, L, TI, TUR, U, UC), 18.15, −76.63; *Christenhusz 3166* (IJ, TUR), 18.02,

−76.37; *Christenhusz 3188* (BR, IJ, L, P, TUR, UC), 18, −76.37; *Christenhusz 3292* (IJ, TUR), 18.0466, −76.6143; *Christenhusz* (obs. 2004), 18.37, −77.08; *Proctor 37129* (IJ), 18.035628, −76.391914; *Proctor 51682* (IJ), 18, −76.27; *Proctor 36381* (IJ), 18, −76.37; *Rankin-Hatch s.n.* (DUKE), 18.18, −76.84. **Mariana Islands**: *Evans 2077* (US), 14.14, 145.2; *Evans 2370* (US), 16.7097, 145.7836; *Falanruw 1711* (US), 16.3578, 145.6661; *Falanruw 1931* (US), 17.6017, 145.8383; *Falanruw 6698* (US), 14.14, 145.2; *Fosberg 31623* (US), 18.7675, 145.6672; *Fosberg 31846* (US), 14.14, 145.2; *Fosberg 58269* (US), 14.14, 145.2; *Necker RS25* (US), 14.14, 145.2. **Micronesia**: *Albert 3* (NY), 6.85, 158.29; *Albert 75* (NY), 6.9, 158.27; *Balick 3806* (NY), 6.971, 158.189; *Balick 3960* (NY), 6.877, 158.274; *Balick 3989* (NY), 6.846, 158.303; *Balick 4115* (NY), 6.833, 158.3; *Balick 4179* (NY), 6.95, 158.183; *Dores 174* (NY), 6.915, 158.273; *Ekiek 13* (NY), 6.927, 158.215; *Falanruw 3532* (US), 5.333, 163.0319; *Fosberg 46339* (IJ), 9.4611111, 138.065; *Fosberg 58399* (US), 6.8, 158.2; *Glassman 2310* (US), 6.9756, 158.1869; *Hernandez LR25-462* (US), 5.3675, 162.9764; *Sohn 55* (NY), 6.971, 158.189; *St. John 21440* (US), 5.333, 163.0319; *Trauernicht 95* (NY), 6.9833333, 158.18333; *Wong 420* (US), 9.5406, 138.1344. **New Caledonia**: *Balansa 80* (P), −22.2167, 166.4833; *Balansa 800* (P), −21.4333, 165.6333; *Baumann 10110* (P), −22.0667, 166.35; *Debeaur s.n.* (P), −22.2, 166.5; *Denizot s.n.* (P), −21.0333, 165.2; *Foster 216* (P), −22.183, 166.533; *Franc 20-13* (P), −22.1667, 166.5333; *Franc s.n. ex herb. Rosenstock 120* (L, P, US), −22.1667, 166.5333; *Franc s.n. ex herb. Rosenstock 142* (L, US), −22.2, 166.5; *Franc s.n. ex herb. Rosenstock 142* (P), −22.0667, 166.35; GBIF-1573354 (MO), −22.183, 166.533; *Germain s.n.* (P), −22.6167, 167.5; *McPherson 1683* (MO, TROPICOS), −22.11, 166.32; *Munzinger 1305* (P), −21.6661, 166.2469; *Schlechter 15052* (P), −22.2, 166.5; *Thorne 28296* (P), −21.5667, 165.4667. **Niue**: *Yuncker 9772* (BISH), −19.05, −169.87. **Palau**: *Fosberg 32078* (US), 7.3408, 134.4964; Fosberg (obs., http://www.hear.org), 7.5, 134.5; *Kanehira 550* (US), 7.4506, 134.6017. **Papua New Guinea**: *Brass 23759* (US), −10.3667, 150.5; *Brass 25985* (US), −6.1667, 141.1333; *Brass 27175* (US), −9.55, 150.6167; *Croft 61865* (US), −9.1667, 147.65; GBIF-6954 (NSW), −6.667, 147; GBIF-6955 (NSW), −2.458, 150.125; GBIF-6956 (NSW), −9.158, 147.675; GBIF-6957 (NSW), −4.975, 145.758; GBIF-6958 (NSW), −5.742, 145.325; GBIF-124572 (NSW), −7.25, 146.667; GBIF-124577 (NSW), −10.417, 150.15; GBIF-124580 (NSW), −6.767, 155.55; GBIF-124660 (NSW), −2.45, 150.117; GBIF-124681 (NSW), −9.15, 147.65; GBIF-124685 (NSW), −9.15, 147.667; GBIF-146578 (CANB), −6.76, 155.55; GBIF-358054 (CANB), −10.41, 150.15; GBIF-9005369 (CANB), −3.25, 151.98; *Grether 4040* (P), −2.4167, 147.3667. **Samoa**: *Betsche 1* (P), −13.84, −171.75; *Christophersen 220* (US), −13.9, −171.75; *Garber 579* (http://www.hear.org), −14.23, −169.454; *Godeffroy 452* (P), −14.3, −170.7; *Graeffe 256* (P), −13.612, −172.525; *Safford 941* (US), −14.28, −170.7; *Setchell 38* (US), −14.3, −170.7; *Teraoka-Whitaker 356* (US), −14.2675, −170.5636; *Vaupel 22* (IJ, P), −13.5333, −172.2667; *Vaupel 22* (P), −13.85, −171.75; *Whistler 7560* (US), −13.8, −171.85. **Solomon Islands**: *Braithwaite 4180* (P), −10.5, 162.0167; *Whitmore 1979* (US), −8.2667, 157.5. **Tonga**: *Hürlimann 429* (http://www.hear.org), −15.85, −173.7118; J.S. Space (obs. 2002, http://www.hear.org), −21.1667, −175.1667; Sykes (obs. 1981, http://www.hear.org), −18.8, −174.65; *Yuncker 15331* (http://www.hear.org), −21.63, −174.9344. **Vanuatu**: *Braithwaite 2163* (P), −20.22, 169.8; *Braithwaite 2497* (P), −15.1667, 166.85; *Braithwaite 2591* (P), −16.25, 167.5; *Pattison s.n.* (P), −18.8, 169.1.

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