

**THREAT AND WEEDINESS ATTRIBUTES
OF
FICUS (MORACEAE)**

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... the taxonomist should use scrolls to make lengthy and detailed tables of comparison for all species in order to work out their relations. Such tables are the only means of presenting the mass of information in a conspectus, they free the mind, thereby, from the burden of details: it creates as they unroll.

Corner, E. J. H. (1963), p. 1,003

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ABSTRACT

The angiosperm genus *Ficus* (Moraceae) is an ecologically and economically important group of mostly tropical plants. Analyses of some ecological, distributional, human impact, and morphological traits revealed threat and weediness attributes of the 795 *Ficus* species. Threatened *Ficus* species in general tend to be from the South American Kingdom, in the subgenus *Urostigma*, section *Americanae*, are not found in anthropogenic, open habitats, commonly inhabit a single habitat, are monoecious, shorter plants with maximum heights of less than 20 m, and have smaller syconia and shorter leaf lengths compared to the other *Ficus* species. Alternatively, weedy *Ficus* species tend to be from the Indo-Pacific and/or Australian Kingdoms, in the subgenus *Urostigma*, section *Urostigma*, frequently inhabit multiple habitats, including montane and/or lowland evergreen rain forests, anthropogenic open habitats and/or riverine forests, are logged for timber, cultivated, are lithophytes and/or hemi-epiphytes, are taller plants with maximum heights of more than 30 m, have larger syconia and longer leaf lengths compared to the other *Ficus* species. This information is useful for helping to identify priority species for conservation and potential weeds or invasive species unsuitable for introduction to other countries as ornamental plants.

1. INTRODUCTION

The genus *Ficus* (the figs) in the family Moraceae, is one of the largest and most diverse of genera (Corner, 1988). *Ficus* species exhibit so many growth forms (laticiferous trees, shrubs, climbers, lithophytes, epiphytes, hemiepiphytes and/or rheophytes) (Janzen, 1979), that “by themselves the figs could build a forest” (Corner, 1963). *Ficus* species can be identified by the presence of alternate leaves with persistent or deciduous hood-like stipules, and the unique inflorescence, the syconium (Berg and Corner, 2005). The syconium is best described as a “cluster of flowers within a vase” (Corner, 1988).

Ficus species are most famed for an intricate mutualism with their species-specific pollinator fig-wasps (Cook and Rasplus, 2003; Janzen, 1979; Weiblen, 2002). Female fig-wasps carrying pollen enter a syconium through the ostiole, a small opening at the base of the syconium, lay eggs in specialised gall flowers, pollinating the flowers in the process (Ramírez, 1970). After these eggs hatch, the wingless male wasps with the females (Ramírez, 1970). These female wasps then exit the syconium, carrying with them pollen from the anthers, in search of another syconium (Ramírez, 1970). *Ficus* species and fig-wasps are interdependent and generally shown to be strictly species-specific, with each species of *Ficus* species harbouring its own species of fig-wasp (Wiebes, 1979).

Ficus species have a pantropical distribution and comprise approximately 750 species (Berg, 1989). There are approximately 105–110 species in Africa and Madagascar, 500–550 species from Asia, Malesia, the Pacific islands and Australia, and 120–150 species from Central and South America (Berg, 2001; Burrows and Burrows, 2003; van Noort et al., 2007). They are found in a wide spectrum of habitats (coastal,

swamp, riparian, savanna, Mediterranean woodland, limestone karst, lowland and/or montane forest) (Berg & Corner 2005).

Ficus species have been identified as keystone species in tropical forests (Terborgh, 1986), owing to the prominent role they play in tropical forests. They fruit throughout the year, providing invertebrates (Basset et al., 1997; Davis and Sutton, 1997; Laman, 1996) and vertebrates (Felton et al., 2008; Lambert, 1989; McClure, 1964; Shanahan et al., 2001; Tweheyo and Obua, 2001) with a baseline food source even in times of general fruit scarcity (Terborgh 1986). This is an important point as tropical forests are under serious threat from deforestation and other human impacts (Laurance and Peres, 2006; Poorter et al., 2004). If any of these *Ficus* species becomes extinct, many animals dependent on them for survival may starve to death.

Currently, there are 19 threatened *Ficus* species listed by the International Union for the Conservation of Nature (IUCN, 2008) as Critically Endangered, Endangered, Vulnerable or Near Threatened — *Ficus andamanica* and *Ficus angladei* from India; *Ficus bizanae*, *Ficus bojeri*, *Ficus faulkneriana*, *Ficus lateriflora* and *Ficus muelleriana* from Africa; *Ficus mutabilis* from New Caledonia; *Ficus ulmifolia* from the Philippines, and *Ficus aripuanensis*, *Ficus blepharophylla*, *Ficus calyptroceras*, *Ficus lacunata*, *Ficus lapathifolia*, *Ficus meizonochlamys*, *Ficus pakkensis*, *Ficus pulchella*, *Ficus hirsuta* and *Ficus ursina* from the Neotropics.

In contrast, there is a group of *Ficus* species that thrive outside their natural habitats and are weedy, naturalised and/or invasive. Because *Ficus* species fruits are eaten by many frugivores, including urban birds and bats, *Ficus* seeds of such species are frequently dispersed into city centres, where the seedlings and subsequently adult plants, establish (Corlett, 2006; McPherson, 1999).

Weeds are plants (not necessary alien, but often are) that “grow in sites where they are not wanted and which usually have detectable economic or environmental effects (Richardson et al., 2000)”. My classification of weeds include naturalised plants, “alien plants that sustain self-replacing populations for at least 10 years without direct intervention by people (Pyšek et al., 2004)” and invasive plants, “naturalised plants that produce reproductive offspring, often in very large numbers, at considerable distances from parent plants (Richardson et al., 2000)” as naturalised and invasive plants also have economic or environmental impacts (Davis and Thompson, 2000, 2001).

Ficus species weeds can damage urban infrastructure or landscape gardens. Yearly, there is a high cost to remove weedy *Ficus* seedlings from roofs, gutters, stone and brick walls, the vicinity of pools and septic tanks, sidewalks, and expensive landscape trees at risk of strangulation (Nadel et al., 1992). Some *Ficus* species litter the ground with their decomposing syconia making it slippery and dangerous to walk on (Ramírez and Montero, 1988). Besides damaging urban infrastructure, *Ficus benjamina*, a popular ornamental plant and weed, is also a source of allergens that induce rhinitis and asthma (Brehler et al., 1998; Subiza, 1999). *Ficus* species have been reported as weeds in Florida (Nadel et al., 1992), India (Basnet, 2005), Hong Kong (Corlett, 2006), Mexico, Central and South America (Ramírez and Montero, 1988), Australia (McPherson, 1999) and New Zealand (Gardner and Early, 1996).

Ficus species are also a menace to natural ecosystems. *Ficus microphylla*, *Ficus platypoda* and *Ficus microcarpa* are invasive plants in Hawai'i that strangle dominant native canopy trees in the wet and dry forests (Starr et al., 2001). *Ficus carica* and *Ficus microcarpa* are also reported to be invasive in Australia and in many regions of the United States of America (Weber, 2003).

Despite the heavy consequences of *Ficus* species becoming threatened or weedy, not all are well studied. Some are known only from type collections in herbaria, having only been identified once (Berg and Corner, 2005; Ungricht et al., 2005). Many are waiting to be assessed for their threat status while others are cultivated for their beauty and utility before undergoing a thorough evaluation of their potential of becoming weedy. It is only in recent years that more attention has been given to develop assessment tools to predict potentially invasive plants (Daehler et al., 2004; Ou et al., 2008; Pheloung et al., 1999), so as to exclude introducing these plants as ornamentals (Niemiera and Holle, 2009). However such generalisations should be refined for specific groups of plants, such as *Ficus* species. Equally important is the need to identify potentially threatened species to enable prioritising of limited resources for conservation.

Is it possible to determine a set of traits that predispose a species to be threatened or weedy? Many studies have attempted to profile threatened species (Duncan and Young, 2000; Pocock et al., 2006; Quinn et al., 1994; Sodhi et al., 2008), successful invaders (Lloret et al., 2005; Lososova et al., 2008; Pyšek and Richardson, 2007; Staples et al., 2000) and both threatened and invasive species (Bradshaw et al., 2008) or rare to common species (Cadotte and Lovett-Doust, 2002) in order to identify the syndromes of traits that make a plant threatened or weedy. In fact, Bradshaw et al. (2008) have shown that traits of endangerment and invasiveness lie on a continuum. However, there has yet to be any studies specific to the genus *Ficus*.

My study thus aims to uncover the trait syndromes that make a *Ficus* species threatened or weedy. In the process, this study aims to:

1. Compile an up-to-date world *Ficus* species list, including for each species, ecological, distributional, human impact, and morphological attributes that may predict threat or weediness.
2. Identify ecological, distributional, human impact, and morphological attributes that contribute to a species' propensity to threat or weediness.
3. To suggest *Ficus* species in need of conservation, and potentially weedy species that are unsuitable for the horticultural trade.

2. METHODS

2.1 COMPILING THE DATASET

2.1.1 *Ficus* Species

A globally representative database of 795 *Ficus* species was compiled from regional Floras, taxonomic monographs, scientific journal articles, published checklists, online databases and online and print reports. The online database *Figweb* (van Noort and Rasplus, 2009), which contained a global list of *Ficus* species and their updated classification, was particularly useful. Personal observations by experts in the field were also considered in the compilation of the data. This list was subsequently checked against all available taxonomic literature to eliminate synonymy.

2.1.2 Ecological, Distributional and Morphological Attributes

The database included various characteristics for each species (Table 1, Appendix 1 and 2), covering information on ecological, distributional, human impact and morphological attributes.

To determine how widespread a *Ficus* species is, each was assigned to its floristic kingdom using the recently modified system of Cox (2001). The genus *Ficus* that has a tropical and subtropical distribution can be located in these kingdoms: African, Australian, Indo-Pacific and/or South American (Figure 1).

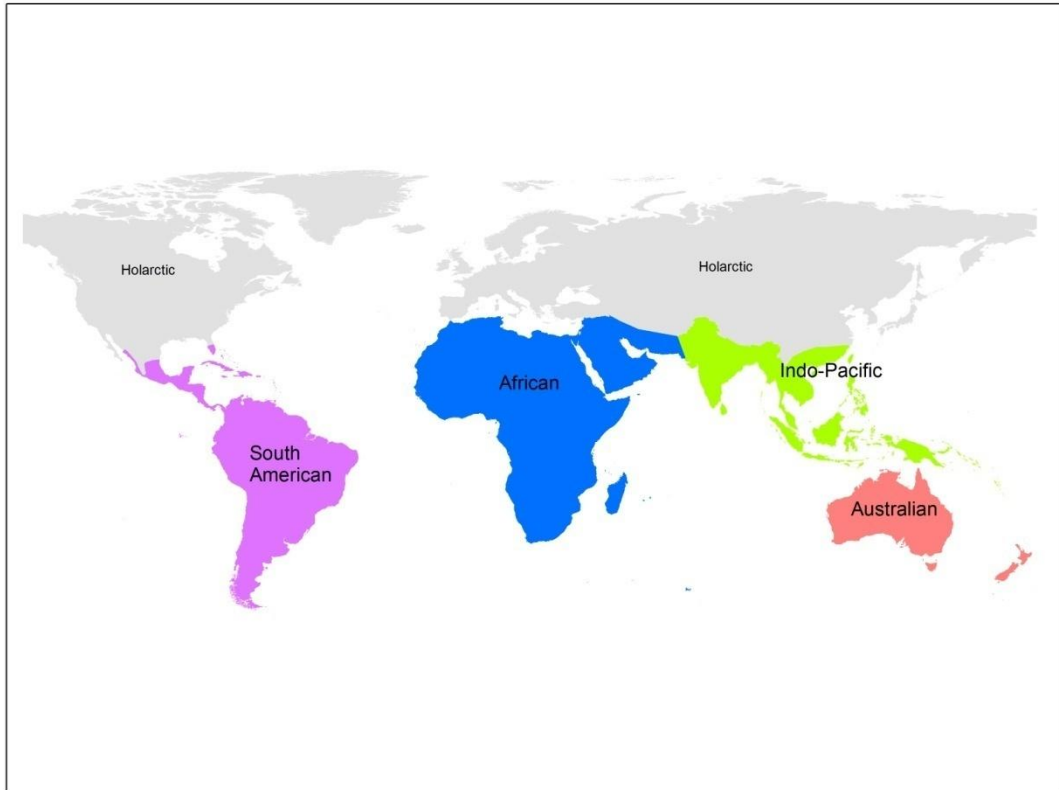


Figure 1.The tropical biogeographic Kingdoms where *Ficus* species are distributed.Map by Alex Yee.

Using all available literature, relevant distributional, ecological, human impact, and morphological data were extracted to create my database. In cases where literature differed, the greatest values were used for the continuous attributes such as maximum height, maximum leaf lamina and petiole length, maximum syconium diameter and largest altitudinal range.

2.1.3 Human Impact Attributes

2.1.3.1 Cultivation history

Many *Ficus* species are popular ornamentals and used as indoor plants, for *bonsai*, garden plants and roadside trees. In Hawaii, *Ficus* species have also been

introduced for reforestation (Staples et al., 2001). Cultivated *Ficus* species were identified from published Floras (Ashton et al., 1997; Berg, 1991; Berg and Corner, 2005; Howard, 1988; Walker, 1976; Zhou and Gilbert, 2003), checklists (Turner, 2000), horticultural books (Australian Plant Study Group, 1980; Boo et al., 2006; Condit, 1969; Elliot and Jones, 1986; Ellison, 1995; Griffiths, 1994; Joffe, 2001; Madulid, 1995), scientific journal articles (Au et al., 2008; Berg, 2004a) and websites (Imada et al., 2005).

2.1.3.2 Logging history

I referred to the Encyclopedia of World Timbers (Boutelje, 1980), logging reports (Lim et al., 2004), and some scientific journal articles (Fredericksen et al., 1999; Nabe-Nielsen et al., 2007) to identify *Ficus* species that were commercially logged. Sometimes, Floras included such information (e.g., Chaudhary, 1999).

2.1.4 Classification Changes

The genus *Ficus*, being one of the largest and more complex of genera, undergoes nomenclatural changes frequently. One reason for this is the differing opinions of *Ficus* systematists on what constitutes a species, subspecies, variety, or form (Dixon, 2001). Despite traditional systematists using morphological traits and distributional ranges to determine a species, very much of the decisions are intuitive and subjective (Burrows and Burrows, 2003). In general, I followed the decisions of the most recent literature, unless the change recommended was not deemed consistent with molecular evidence.

There are also an increasing number of molecular systematists who use genetic markers to determine what constitutes a species and whether the groups assigned by traditional systematists are monophyletic. For example, the results of Rønsted (2008a)

indicated that *Ficus augusta*, *Ficus heteromeka*, *Ficus mafuluensis*, *Ficus sterrocarpa* and *Ficus xylosyca* are separate and distinct species, in contrast to the decision of Berg and Corner(2005)to group them under a single species. The works of these molecular phylogeneticists were also generally accepted.

As my analysis was at the species level, I combined traits from subspecies, varieties and forms for the species to which these subspecific taxa belong.

2.1.5 Classification

The assignation of subgenus, section, subsection and series followed the classification scheme of *Figweb* (van Noort and Rasplus, 2009), a synthesis of various publications (Berg, 2003a, b, c, d, e, 2004b, c; Berg and Corner, 2005; Rønsted et al., 2008a; Rønsted et al., 2005; Rønsted et al., 2008b; Ungricht et al., 2003). It was important to be accurate in this assignation to control for phylogenetic effects where species may be found to be threatened or weedy because of the presence of certain correlated traits owing to their phylogeny.

In my analysis, each *Ficus* species was assigned to its subgenus — *Ficus*, *Pharmacosycea*, *Sycidium*, *Sycomorus*, *Synoecia* or *Urostigma*. Even though there were finer resolutions to the classification such as section, subsection and series, I did not use these ranks for my analysis because not all *Ficus* species have been classified to such resolution and there were disagreements amongst *Ficus* systematists about it.

2.1.6 Threat and Weediness

‘Threatened’ species were identified using The IUCN Red List of Threatened Species 2008 (IUCN, 2008). Based on the IUCN criteria, ‘threatened’ species were categorised as Critically Endangered, Endangered, Vulnerable or Near Threatened.

Since the IUCN Red List was last evaluated for most *Ficus* species in 1998, there had been many taxonomic revisions thereafter. *Ficus cyclophylla* (Miq.) Miq. is now a synonym of *Ficus nymphaeifolia* Mill.; *Ficus aguaraguensis* Vázq. Avila is now a synonym of *Ficus cuatrecasana* Dugand; *Ficus ramiflora* Standl. is now a synonym of *Ficus caballina* Standl. (Berg and Villavicencio, 2003; Vazquez Avila, 1985); *Ficus mexiae* is also a synonym of *Ficus enormis* (Vazquez Avila, 1985). Owing to these changes, the threatened status was no longer assigned to these species, because the species under which these were subsumed are not considered threatened.

‘Weedy’ species were identified using the Global Compendium of Weeds (Randall, 2002), the list compiled by the Institute of Pacific Islands Forestry (Institute of Pacific Islands Forestry, 2009), the compilation of invasive plants by Weber (2003), articles on naturalised *Ficus* species (Gardner and Early, 1996; Nadel et al., 1992), by consultation with field researchers (A. Ng and H.T.W. Tan, personal communication) and through personal observations.

2.2 STATISTICAL ANALYSES

2.2.1 Model Selection and Multimodel Inference

I first used a practical information-theoretic approach called model selection and multimodel inference (Burnham and Anderson, 2002; Johnson and Omland, 2004) that enabled me to control for the confounding effects of shared evolutionary history in cross-species comparison (Bradshaw et al., 2008).

My set of candidate models was first designed based on reasonable hypotheses, to avoid data-dredging and the inclusion of spurious variables and relationships (Burnham and Anderson, 2002). I thus first formulated a set of *a priori* candidate models based on knowledge from the published literature, ecological principles, and personal observations to provide insights into underlying processes leading to a *Ficus* species becoming threatened with extinction or weedy.

Generalised Linear Mixed-Model (GLMM) analyses were conducted using the statistical software, R version 2.7.2 (R Development Core Team, 2008), using the ‘lmer’ function from the ‘lme4’ package. For each GLMM, I coded “threatenedness” or “weediness” as a binomial response variable and each trait as a linear predictor. The usage of the GLMM also enabled many traits to be coded as categorical factors, since the GLMM can model non-normal, response variables.

The random effects error of the GLMM corrects for non-independence of statistical units (species) owing to their common evolutionary history (Felsenstein 1985), and allows for cluster (subgenus)-specific random effects in the linear predictors (Blackburn and Duncan, 2001; Szyszkwicz, 2006). All other variables were coded as fixed effects.

I calculated the percentage deviance explained (%DE) as a measure of goodness-of-fit or how good the data are fitted by the model. The %DE tells me the total variance

accounted for in the response by the independent variables (Bradshaw et al., 2007). This was obtained through dividing the deviance of a model by the deviance of a null model with no fixed effects but retaining the cluster-specific random effect (Bradshaw et al., 2008).

I used an estimate of Kullback-Leibler information (K-L distance) loss, Akaike's Information Criterion (AIC) corrected for small sample sizes (AICc), to assign relative strengths of evidence to the different competing models (Burnham and Anderson, 2002). Models were first ranked by second-order AICc differences (Δ_i), whereby the model estimated to be the best has $\Delta_i = 0$ and those with $\Delta_i > 10$ have essentially no support or fail to explain some substantial explainable variation in the data (Burnham & Anderson 2002). The relative likelihood of each model was then estimated with AICc weights (wAICc). The wAICc value for each model varies from 0 (no support) to 1 (complete support) relative to the entire model set (Burnham and Anderson, 2002). In most cases, the sample size for each model was reduced because of missing data in the hypothesised correlates (updated sample sizes given in the *Results and Discussion* section).

2.2.2 Null Hypothesis Testing

One-way analysis of variance (ANOVA) was used to test whether there were any differences between binomial variables for the threatened, status-less (representation of general *Ficus* population) and weedy groups. This was followed by the post-hoc Scheffe's multiple-comparison procedure to find group differences.

For the continuous data, I performed the nonparametric, one-way, Kruskal-Wallis Test as model checking revealed that the continuous data was nonparametric (non-normal with unequal variances). After which, box-plots were plotted for variables

which Kruskal-Wallis Test revealed as having differences between groups to gauge the magnitude of the differences.

ANOVA, Scheffe's Test and Kruskal Wallis test were performed using the statistical software package SPSS Release 16.0.1 (SPSS for Windows, 2008) at a 5% level of significance.

3. RESULTS AND DISCUSSION

3.1 MODEL SELECTION RESULTS

3.1.1 Description of threatened and weedy species

From my study, the total *Ficus* species count stands at 795 species from six subgenera (Table 1). Of these, 19 species are threatened with extinction (2.39%) and 28 species are considered weeds at least in one part of the world (3.52%) (See Appendix 1 and 2).

Table 1. Species attribute summary for the 795 sampled threatened (Thr), no status (NS) and Weedy (Wd) *Ficus* species examined. Note that not all attribute level sample sizes sum up to 795 because of missing data.

Taxonomy/ status	No. of spp./gp	Attribute	Level	No. of spp.	No. ofThr	Proportion of Thr	No. ofNtr	Proporti on of NS	No. of Wd	Proportion of Wd
<i>Ficus</i>	74	Altitudinal range	Lowland (<1200m)	300	10	0.033	285	0.950	5	0.017
<i>Pharmacosycea</i>	89		Montane (>1200m)	46	1	0.022	43	0.935	2	0.043
<i>Sycidium</i>	112		Mixed (both)	286	2	0.007	265	0.927	19	0.066
<i>Sycomorus</i>	140	Kingdom	1 kingdom	759	19	0.025	721	0.950	19	0.025
<i>Synoecia</i>	74		>1 kingdom	36	0	0.000	27	0.750	9	0.250
<i>Urostigma</i>	306	Habitat flexibility	Closed forest or open	552	14	0.025	528	0.957	10	0.018
			Both	210	4	0.019	188	0.895	18	0.086
'threatened'	19	Hemiepiphytic habit	Absent	565	14	0.025	537	0.950	14	0.025
'no status'	748		Present	209	3	0.014	188	0.900	14	0.067
'weedy'	28	Cauliflory-type habit	Absent	421	12	0.029	395	0.938	14	0.033
			Present	347	4	0.012	329	0.948	14	0.040
		Clustering of syconia	Absent	134	1	0.007	128	0.955	5	0.037
			Present	596	15	0.025	559	0.938	22	0.037
		Cultivation	Not cultivated	654	17	0.026	637	0.974	0	0.000
			Cultivated	141	2	0.014	111	0.787	28	0.199
		Timber	Not harvested	756	19	0.025	719	0.951	18	0.024

	Harvested	39	0	0.000	29	0.744	10	0.256
Maximum syconium diameter	scalar	-	-	-	-	-	-	-
Maximum height	scalar	-	-	-	-	-	-	-

Table 2. The five most parsimonious generalised linear mixed-effects models investigating correlates of threat risk for *Ficus* (full data set, n = 795 species, 19 'threatened') according to Akaike's Information Criterion corrected for small sample size (AICc). Terms shown are maxheight = maximum height, alt = altitude range, hemiepi = hemiepiphytic habit, timber = used for timber, kingdom = number of Kingdoms species is found in, flex = exhibit habitat flexibility (found both in closed and open habitats) or not (only found either in closed or open habitats). Also shown are the maximum log-likelihood (*LL*), the number of parameters (*k*), the number of species involved (*n*), the difference in AICc for each model from the most parsimonious model (Δ AICc), AICc weight, and the percent deviance explained (%DE) in the response variable by the model under consideration.

Model	<i>LL</i>	<i>k</i>	AICc	Δ AICc	wAICc	Evidence ratio	%DE
AICc-ranked							
~ maxheight + alt + hemiepi	-47.949	6	108.054	0.000	0.138	1.000	45.74
~ timber + maxheight + alt + hemiepi	-47.451	7	109.110	1.056	0.082	1.696	46.30
~ maxheight + kingdom + alt + hemiepi	-47.510	7	109.230	1.175	0.077	1.800	46.24
~ maxheight + alt + flex + hemiepi	-47.692	7	109.594	1.540	0.064	2.159	46.03
~ maxheight + alt	-49.778	5	109.667	1.613	0.062	2.240	43.67

Table 3. The five most parsimonious generalised linear mixed-effects models investigating correlates of weediness for *Ficus* (full data set, n = 795 species, 28 "weedy") according to Akaike's Information Criterion corrected for small sample size (AICc). Terms shown are cult = cultivation, maxheight = maximum height, kingdom = number of Kingdoms species is found in, alt = altitude range, cluster = clustering of syconia, cauli = cauliflorous habit, maxfig = maximum syconium diameter. Also shown are the maximum log-likelihood (*LL*), the number of parameters (*k*), the number of species involved (*n*), the difference in AICc for each model from the most parsimonious model (Δ AICc), AICc weight, and the percent deviance explained (%DE) in the response variable by the model under consideration.

Model	<i>LL</i>	<i>k</i>	AICc	Δ AICc	<i>w</i> AICc	Evidence ratio	%DE
AICc-ranked							
~ cult + maxheight + alt + cluster	-54.339	7	122.897	0.000	0.372	1.000	55.09
~ cult + maxheight + kingdom + alt + cluster	-53.327	8	122.937	0.040	0.364	1.020	55.93
~ cult + maxheight + kingdom + alt + cauli + cluster + maxfig	-52.764	10	125.971	3.074	0.080	4.650	56.39
~ cult + maxheight + alt + cauli + cluster + maxfig	-53.894	9	126.148	3.251	0.073	5.082	55.46
~ cult + maxheight + kingdom + alt	-57.312	7	128.833	5.936	0.019	19.454	52.63

3.1.2 Threat as a Binary Response

Using threat as a binary response (i.e., ‘threatened’ or ‘not’, where the ‘not’ category is inclusive of all ‘no status’ and ‘weedy’ species; $n = 795$), the five most highly supported models had very low Akaike weights (< 0.9) (Table 2). The probability that these models are the best approximating model given the data at hand and the initial model set is very low. This can be clearly seen in the low evidence ratio for all five models. This relatively weak support for the best model means there is relatively little evidence in favour of the best model.

Generally, variables such as maximum height and altitudinal range that appear in all models are roughly responsible for threat. However, there is no strong support for any model in particular.

3.1.3 Weediness as a Binary Response

Using weediness as a binary response (i.e., ‘weediness’ or ‘not’, where the ‘not’ is inclusive of all ‘no status’ and ‘threatened’ species; $n = 795$), the five most parsimonious models, as ranked by the AIC, also have very low Akaike weights, though the signal for weediness, as seen by the higher weight of 0.372 for the best model (Table 3), is stronger than the signal for threat, as seen by the lower weight of 0.138 for the best model (Table 2), likely owing to the higher percentage of weedy species compared to threatened species. This is reflected in the evidence ratios for the top five models. The evidence ratio for the 4th and 5th ranking models are approximately 5 and 6 and gives relatively stronger support for the best model compared to the top five models for threat which had evidence ratios of below 3. However, we are still unable to distinguish between the first three models.

In general, cultivation and maximum height that appear in all models are roughly responsible for weediness, being present in each of the top five models. However, there is no strong support for any model in particular.

3.1.4 Poor Support for *a priori* Models

There are two likely reasons for the low weights and hence low probability of the models being the best model, given that one of the models in the candidate model set is the best model and able to explain the data.

One reason is the low number of threatened (2.39 %) and weedy species (3.52%) recorded relative to the total number of *Ficus* species in the world. Only 48 out of 795 species (6.04%) in the world have been assessed by IUCN (www.iucnredlist.org, accessed on 3 April 2009). Of these, only 19 have been assigned a threat status. In fact, many species that have been mentioned in the grey literature to be endangered and species listed in the 1997 IUCN Red List of Threatened Plants have not been assessed. Species such as *Ficus iidaiana*, *Ficus nishimurae*, *Ficus pseudopalma*, *Ficus reflexa* subsp. *aldabrensis*, *Ficus reflexa* subsp. *seychellensis* which were mentioned as threatened in the 1997 IUCN Red List of Threatened Plants (Walter and Gillett, 1998) and *Ficus cotinifolia* var. *hondurensis* from The World List of Threatened Trees (Oldfield et al., 1998) have not been assessed. *Ficus cupulata*, a species known to be endemic to India and threatened (Khanna and Kumar, 2002) has likewise not been assessed.

The low level of assessment for threat is not unique to *Ficus* species, but for all known plant species. Only 3.2% of the total population of plant species have been assessed as yet (Paton et al., 2008). Reasons why so few plants have been assessed have

been attributed to the lack of experts, conflicting systems of assessment and lack of recent Floras or checklists for most regions of the world (Brummitt et al., 2008).

Likewise, the number of weedy species could be an underestimate as evidence suggests a strong geographical bias, with Africa and Asia understudied in invasion ecology (Pysek et al., 2008). Considering that Africa and Asia form some of the largest landmasses on the globe, such a bias, would undoubtedly give a false impression on the true number of weedy species.

Coupled with poor systematics, such as those mentioned in the *Methods* section, the true number of threatened and weedy species is confounded and uncertain and is likely to be higher than is reported in my study. This is also one of my assumptions that the current threatened and species counts are accurate at this point of time.

Another possible reason for the low support is the wrong choice of attributes that affect threat and weediness. Pollination data such as the number of fig-wasps and non-pollinating (parasitic) fig-wasps are likely to be major factors determining threat and weediness, owing to the 87 million years old mutualistic relationship (Machado et al., 2001) between each *Ficus* species and their corresponding pollinator fig-wasps and the competition fig-wasps have with non-pollinating wasps (Machado et al., 1996). It has been found that some *Ficus* species have in fact, more than one pollinator (Kerdelhué et al., 1999; Lopez-Vaamonde et al., 2002) and the number of non-pollinators or parasites often vary widely between species (Burrows and Burrows, 2003).

Female pollinator fig-wasps are known to collect pollen either passively or actively by filling their thoracic pollen pockets (Kjellberg et al., 2001). This might possibly predict for threat or weediness as well, as active pollination of *Ficus* florets is known to increase pollen dispersion in a syconium, resulting in better gall formation and survival of fig-wasps (Jousselin et al., 2003). However, at the moment, fig-wasps

are still understudied, especially for the *Ficus* species of the Indo-Pacific and South American Kingdoms and pollination data are often difficult to obtain.

Besides pollination data, phenological (phenology is the study of periodic events in the life cycles of plants, as influenced by the environment) data could also be very important, especially for monoecious *Ficus* species. In order to sustain pollinator populations, *Ficus* species have evolved to have intra-tree synchrony and inter-tree asynchrony (McKey, 1989). The interval between successive crops of an individual tree has been shown to be an important determination of the critical population size (CPS) or the minimum number of *Ficus* plants required to maintain a population of the pollinator fig-wasps (Bronstein et al., 1990). This is directly related to a species' propensity to be threatened, as given a fixed population of *Ficus* species, a species with a smaller CPS would be less affected by habitat destruction and less easily becomes ecologically extinct, compared to a species with a larger CPS, which is more sensitive to reductions and subdivisions to its population size. A species with a smaller CPS would also more likely be weedy, as it is easier for such species to support their pollinator fig-wasps. Currently, phenological studies have only been conducted for a handful of species (e.g., Bronstein and Patel, 1992; Corlett, 1987; Corlett, 1993; Milton et al., 1982; Ragusa-Netto, 2002; Spencer et al., 1996; Windsor et al., 1989), while the CPS data are even rarer as their calculation from simulation studies requires phenological data (e.g., Anstett et al., 1995; Bronstein et al., 1990; Mawdsley et al., 1998).

I believe that these attributes are likely drivers of extinction and weediness. I urge field ecologists to include such data in their observations of *Ficus* species and subsequent publications, especially in Floras and manuals to aid in our understanding of extinction and weediness proneness in *Ficus* species.

3.2 SIGNIFICANT VARIABLES FROM NULL HYPOTHESIS TESTING

3.2.1. Subgenus

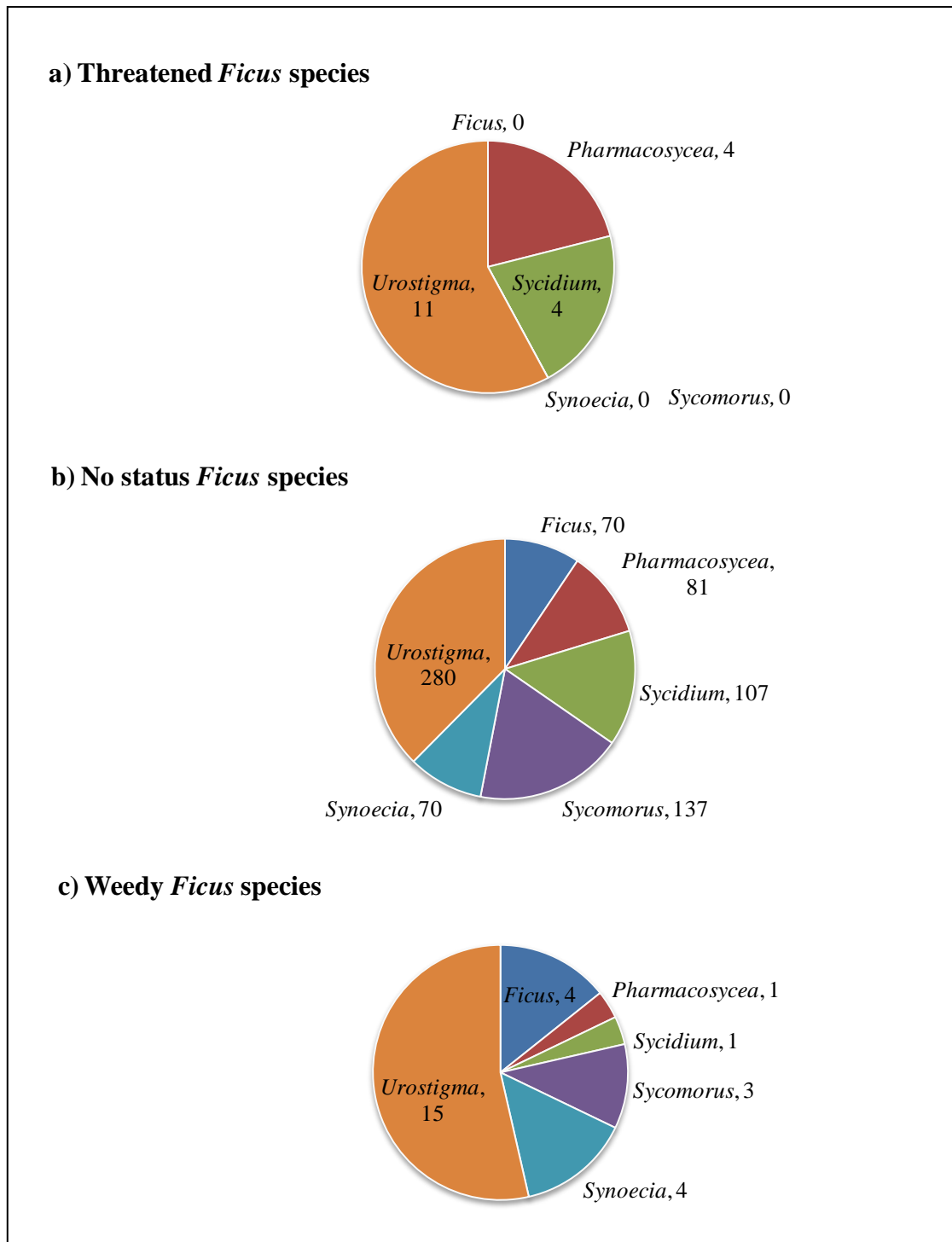


Figure 2. Pie-charts of the distribution of *Ficus* subgenera in threatened, status-free and weedy groups.

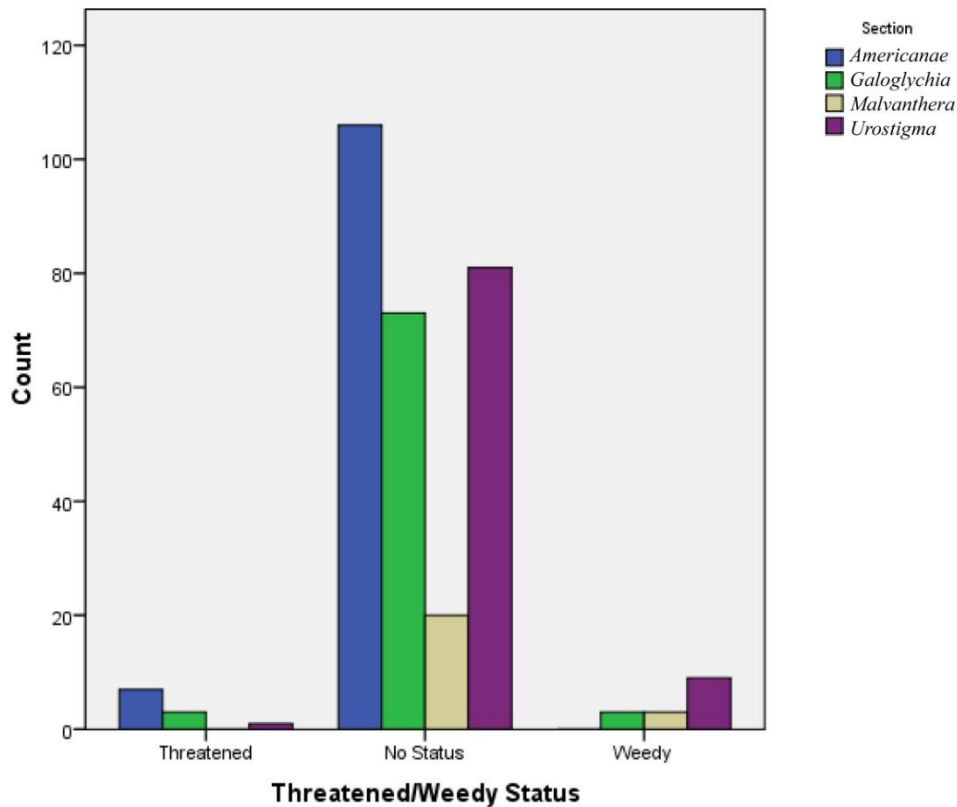


Figure 3. Distribution of *Ficus* species in threatened, status-free and weedy groups in subgenus *Urostigma*.

Both threatened and weedy *Ficus* species tend to be from the *Urostigma* subgenus (Figure 2). *Ficus* species from the *Urostigma* subgenus are monoecious trees, with aerial adventitious roots, mostly hemi-epiphytes (beginning its life-cycle above ground level like an epiphyte, but grows its roots down into the soil), stranglers (forming root-baskets around trunks of host-trees), sometimes lithophytic, and rarely climbers (Berg and Corner, 2005). Their syconia are mostly axillary, either solitary or in pairs, sometimes they are ramiflorous and cauliflorous with syconia clustered on short spurs. This subgenus is divided into four subdivisions— section *Americanae* (American), section *Galoglychia* (African), section *Malvanthera* (mainly Australian) and section *Urostigma* (mainly Indo-Pacific) and comprises 306 species (Berg and Corner, 2005).

A further analysis of the threatened and invasive species that lie in subgenus *Urostigma* reveals that *Ficus* species from section *Americanae* tend to be threatened while those from section *Urostigma* tend to be weedy (Figure 3). This is unexpected as *Ficus* species from section *Americanae* are essentially similar to *Ficus* species from section *Urostigma* and the main differentiating character is that *Ficus* species from section *Americanae* have two basal bracts on the syconium instead of three (Berg and Corner, 2005). Another difference between the two groups is their geographical distribution. *Ficus* species of section *Americanae* are from the South American kingdom, while *Ficus* species from section *Urostigma* ranges from West Africa to the Pacific (Berg and Corner, 2005).

The main reason why *Ficus* species from subgenus *Urostigma* section *Americanae* appear to be over-represented in the list of threatened species (namely *Ficus blepharophylla*, *Ficus calyptroceras*, *Ficus hirsuta*, *Ficus meizonochlamys*, *Ficus pakkensis* and *Ficus ursina*) is that *Ficus* species from the South American Kingdom are more assessed for threat status than *Ficus* species from any other Kingdom. Out of the 795 species of *Ficus* species, 48 have been assessed for threat status. Of the 48 assessed, 39 are from the South American Kingdom (81.25%) though South American *Ficus* species only form 17.11% (136 species) of the total *Ficus* population. On the other hand, only nine (namely *Ficus bizanae*, *Ficus bojeri*, *Ficus carica*, *Ficus faulkneriana* and *Ficus muelleriana* from the African Kingdom and *Ficus andamanica*, *Ficus angladei*, *Ficus carica* (also in the African Kingdom), *Ficus mutabilis* and *Ficus ulmifolia* from the Indo-Pacific Kingdom) out of 48 (18.75%) species of *Ficus* from the African, Australian and Indo-Pacific Kingdoms have been assessed, though they form 82.89% (659 species) of the *Ficus* population. This unreasonable and surprising bias

could have led to the false impression that *Ficus* from the South American Kingdom are more likely to be threatened than elsewhere.

Conversely, from Figure 3, *Ficus* species from the Australian and Indo-Pacific Kingdoms appear to be weedier than others. I postulate that this trend for Australian *Ficus* species tending to be weedier is the higher likelihood of Australian *Ficus* species being cultivated compared to those of other Kingdoms. The link between cultivation and weediness will be further elaborated upon in *Section 3.2.5.2*. Even though there are only 45 species of *Ficus* in the Australian Kingdom, 25 are cultivated (55.5%). This means *Ficus* species from the Australian Kingdom are more likely to be cultivated than any other Kingdom (African Kingdom: 29.2%; Indo-Pacific Kingdom: 16.4%; South American Kingdom: 10.3%). Though the absolute number of *Ficus* species cultivated from the Australian Kingdom is lower than that of the African (33) and Indo-Pacific (88) Kingdoms, the high percentage of cultivated Australian *Ficus* could possibly reflect the successful quarantine controls that the Australian government implements in order to “control pests” and for the “protection of native flora and fauna” (Nairn et al., 1996). These restrictions on the number and type of exotic plants that can be imported into Australia, which forms most of the Australian Kingdom, could have led to native Australian plants being more widely propagated and encouraged within the country (ANPSA, 2009). This might explain why Australian *Ficus* species have a greater probability to be cultivated than others and consequently, a greater chance of being weedy.

Besides being the largest group of *Ficus* species in the world (535 out of 795) and the most likely to be cultivated (88 out of 137), Indo-Pacific *Ficus* species on the other hand are also more likely to be more weedy because they share many weedy species in common with both the African and Australian Kingdoms. In other words, weedy Indo-

Pacific *Ficus* species are commonly also found naturally distributed in the African and Australian Kingdoms. For example, *Ficus carica*, *Ficus exasperata* and *Ficus palmata* are found both in the African and Indo-Pacific Kingdoms; while *Ficus benghalensis*, *Ficus benjamina*, *Ficus carica*, *Ficus drupacea* and *Ficus macrophylla* are found in the Australian and Indo-Pacific Kingdoms. This means their distribution is naturally more widespread. Bradshaw et al. (2008) have shown that legumes that naturally span multiple floristic kingdoms are more likely to become invasive. A study conducted by Pemberton and Liu (2009) also showed that cultivated plants with large native ranges were more likely to be naturalised. These findings can be explained on the basis that widespread species are better able to tolerate new environments as they have already encountered diverse climatic and habitat conditions in their evolutionary history and have the variation required to produce combinations of traits needed to become established in many habitats (Sax and Brown, 2000). Therefore, owing to higher number in cultivation and wider natural distribution, Indo-Pacific species tend to be weedier.

Table 4. Percentages and ratios of status-less, threatened and weedy *Ficus* species for character states which ANOVA revealed as different between the three groups (see Appendix 3). In grey are the proportions in which Scheffe's multiple comparison test revealed as significant (see Appendix 4), i.e. weedy species are more likely than no status and no status more likely than weedy to be used for timber.

Character	Character State	No status		Threatened		Weedy	
		%	Ratio	%	Ratio	%	Ratio
Economic Value	Timber	4.58	35/764	0.00	0/19	35.71	10/28
Use in Cultivation	Cultivated	16.18	123/760	10.53	2/19	100.00	28/28
	Montane forest	68.43	505/738	42.11	8/19	78.57	22/28
Habitat Type	Lowland evergreen rain forest	45.93	339/738	52.63	10/19	82.14	23/28
	Anthropogenic open habitats	13.55	100/738	0.00	0/19	42.86	12/28
	Riverine forest	28.3	208/735	21.05	4/19	60.71	17/28
Life Form	Lithophyte (grow on rocks/cliffs)	15.65	115/735	21.05	4/19	39.29	11/28
	Hemi-epiphyte	26.44	197/745	17.65	3/17	50.00	14/28
Breeding System	Monoecious	50.92	387/760	83.33	15/18	60.71	17/28
	Indo-Pacific Kingdom	68.19	521/764	21.05	4/19	71.43	20/28
Biogeographic Kingdom	Australian Kingdom	5.24	40/764	0.00	0/19	32.14	9/28
	South America Kingdom	16.49	126/764	52.63	10/19	3.57	1/28

3.2.2 Biogeographic Regions

Threatened *Ficus* species are more likely to be from the South American Kingdom, while weedy *Ficus* species are more likely to be from the Indo-Pacific and Australian Kingdoms (Table 4). This result has been explained in *Section 3.2.1*.

3.2.3 Monoecious Sexual System

The genus *Ficus* has two breeding systems: approximately half are monoecious and the rest are functionally dioecious (Kjellberg et al., 1987). Monoecy is the condition of having both the staminate and carpellate flowers in the same syconium, while dioecy is the condition where the male and female functions are separated into different trees, called the seed and gall *Ficus* trees. Gall *Ficus* trees are functionally male as they produce pollen and rear the pollination fig-wasps in the gall flowers, while seed *Ficus* trees are functionally female because fig-wasp larvae purely pollinate the carpellate flowers, without preying on the seeds (Dumont et al., 2004).

Threatened *Ficus* species tend to be monoecious (Table 4). Monoecy has been shown to be ancestral in *Ficus* (Weiblen, 2000). This has led to many speculations as to the evolution of dioecy in *Ficus*. One of them being that dioecy appeared under the selective pressure of non-pollinating fig-wasps (Kerdelhué and Rasplus, 1996a). Besides its mutualistic partners, *Ficus* species are also associated with a great diversity of non-pollinating (parasitic) chalcid wasps which compete with fig-wasps for sites to oviposit their young yet do not pollinate the host plants (Bronstein, 1991; Janzen, 1979; Kerdelhué and Rasplus, 1996b). Kerdelhué and Rasplus (1996a) have argued that dioecious *Ficus* species have fewer parasitic fig-wasp species because they have fewer flower layers compared to monoecious *Ficus* species, hence reducing the number of

niches available for the parasitic wasps. Therefore, the state of monoecy could be comparatively less fit than the state of dioecy.

3.2.4 Habit

Weedy *Ficus* species tend to be lithophytes and/or hemi-epiphytes.

3.2.4.1 Hemi-epiphytism

There are nearly 300 species of hemi-epiphytic (banyans or strangling figs) *Ficus* species in the world (Berg and Corner, 2005). It is the life-form characteristic of subgenus *Urostigma* but also found in a few species in subgenus *Sycidium* such as *Ficus tinctoria* and *Ficus virgata* (Berg and Corner, 2005).

Hemi-epiphytic species begin life as an epiphyte, germinating at about 20–25 m above the forest-floor, where they fix their roots in a crevice or hole (Berg and Corner, 2005) and then send their roots down to the soil surface as they grow, becoming independent, or almost independent (Richards, 1966). This habit means that seedlings do not have to compete with the ground dwelling species for light to become established, increasing its ability to survive in dense rainforests where little light reaches the forest floor (Laman, 1995).

Their dependence on phorophytes (plants that structurally support epiphytes), however means that their survival is also dependant on the survival of large, old trees in the forests, making them vulnerable to forest loss and disturbances (Turner et al., 1994).

Many *Ficus* species appear to overcome this predicament by colonizing empty urban niches (Corlett, 2006; McKey and Kaufmann, 1988). Hemi-epiphytic *Ficus* are able to establish on structural features that accumulate organic matter which develop into humic soil (McPherson, 1999). In the forest, the forks of trunks and branches are

popular sites of establishment for *Ficus* (Clark and Clark, 1990; Daniels and Lawton, 1991). In urban areas, the equivalent of such establishment sites would be the trunks of landscape trees and cracks on walls and buildings (Corlett, 2006).

3.2.4.2 Lithophytism

Closely linked to hemi-epiphytism is lithophytism. Many species that are hemi-epiphytic are also known to be epi-lithophytes or lithophytes (Berg and Corner, 2005). Lithophytic *Ficus* species are possibly more weedy due to the ability to take advantage of vacant rock or cliff-like niches in the urban environment (Jim, 1998). Jim (1998) showed that rooting habit is important in determining whether trees were able to colonise walls and attain mature sizes. *Ficus* species which are cliff-hangers, with the ability to grip tightly onto other trees or stone faces are able to occupy the manmade surfaces of the city (Jim, 1998).

The invasive *Ficus microcarpa*, alone occupies 50% of the population of trees growing on the stone walls of Hong Kong (Jim, 1998), again proving the superior ability of some weedy *Ficus* species to take advantage of urban environments. A possible reason enabling lithophytes such as *Ficus microcarpa* to thrive in urban environments is their ability to tolerate drought. Obligate cliff-hangers are known to be more drought resistant than their non-obligate associates (Coates and Kirkpatrick, 1992). For example, *Ficus rubiginosa*, a weedy *Ficus* species of Australia, is able to withstand drought for short periods of time (Gilman and Watson, 1993).

3.2.5 Human Impact Attributes

Weedy *Ficus* species are more likely to be timber species and cultivated compared to threatened *Ficus* species.

3.2.5.1 Use for timber

Thirty-nine *Ficus* species are commercially logged for timber. Of these 39 species, 10 are weedy species (*Ficus benghalensis*, *Ficus benjamina*, *Ficus drupacea*, *Ficus exasperata*, *Ficus insipida*, *Ficus microcarpa*, *Ficus platypoda*, *Ficus retusa*, *Ficus sur* and *Ficus thonningii*) and none are threatened. *Ficus* species, or more commonly known as “ara” in the logging industry, might seem unlikely candidates for commercial timber because of their sticky white latex, but many are commercial timber species. *Ficus* wood are suitable for uses in which strength is not critical such as veneer and plywood, disposable chopstick, packing cases and wall panelling (Lim et al., 2004). Owing to the presence of thick layers of wood parenchyma, flat-sawn materials of *Ficus* timbers are decorative and popular for decorative sliced-veneer and wall panelling (Lim et al., 2004).

Despite the threat that commercial logging poses on forest species (Chazdon, 1998; Hubbell et al., 2008), threatened *Ficus* species are not known to be commercially logged, instead, weedy *Ficus* are more likely to be popular timber species. A possible reason for this is that threatened *Ficus* species are already rare in the wild and it does not make commercial sense to target them, whereas weedy *Ficus* species are common and naturally targets for logging. The fact that many commercially timbered *Ficus* species are weedy, tells us that these species are established in the wild.

3.2.5.2 Cultivation

Ficus species are cultivated for various purposes, mainly for their ornamental value and economic utility such as for timber (Fredericksen et al., 1999; Gautier, 1996; Lim et al., 2004), edibility, livestock fodder (Jokthan et al., 2003), medicine (Lansky et al., 2008), latex, paper, cloth (Condit, 1969; Ipulet, 2007) and also for reforestation

(Woodcock, 2003). Over 60 species have been introduced into southern Florida alone as ornamentals (Barrett, 1946, 1948, 1951; Nadel et al., 1992).

Owing to the mutualistic relationship of *Ficus* species with their pollinators, *Ficus* species when unaccompanied by their fig-wasps are theoretically sterile and considered ‘safe’ introductions (Lyon, 1929). However, when pollinators are intentionally or accidentally introduced with the *Ficus* species, they can become weedy. One example is *Ficus microcarpa*, together with its imported fig-wasps, which had been deliberately introduced into Hawai’i to reforest the watershed areas and restore ecological systems (Woodcock, 2003). *Ficus microcarpa* is currently an invader in Hawai’i, favouring disturbed urban sites to degraded forests (Starr et al., 2001, 2003).

Cultivated *Ficus* species are more likely to be weedy for various reasons. Unlike non-cultivated *Ficus* species, cultivated *Ficus* species have the opportunity to be human-dispersed to localities out of their natural ranges, and besides increased global movement and increased propagule pressure (Lockwood et al., 2005), they are also given special care to ensure their survival and propagation (Mack, 2000).

Many studies have shown that naturalised flora is largely the product of deliberate introductions (Mack and Erneberg, 2002; Reichard and White, 2001). Many invasive plants are also of horticultural origin (Bell et al., 2003). In fact, in Australia, 65% of the invasive plants that have naturalised over the past 25 years were ornamentals (Groves, 1997) and more than 60% of the most invasive plants in California were purposefully cultivated (Bossard et al., 2000). We have found the same for *Ficus* species in our results. Published papers on naturalization of *Ficus* species also indicate that cultivated species are often the culprits of naturalization (Gardner and Early, 1996; Nadel et al., 1992; Ramírez and Montero, 1988).

Most alien plants are sensitive to environmental stochasticity or factors external to the population such as weather, disease, competition and predation (Mack, 2000). Most are extirpated, few naturalised and only an exceedingly small fraction grow into invasive species (Mack, 2000). Mack (2000) proposed that cultivation (e.g., protection from predators, parasites, drought, frost and seed harvest and storage) shields small alien populations from the extreme expressions of environmental stochasticity, hence fostering plant naturalization.

The most famous example of a cultivated *Ficus* species, which is also invasive, is *Ficus carica* or the edible fig. The woody cuttings of *Ficus carica* root so readily that no other method of propagation is used commercially (Condit, 1969). Unsurprisingly, *Ficus carica* is an invasive species (Weber, 2003).

3.2.6 Habitat Preference

Threatened *Ficus* species are less likely to inhabit montane forests, anthropogenic open habitats and riverine forests compared to weedy *Ficus* species.

3.2.6.1 Montane forest

Weedy *Ficus* species are more likely to be found in montane forests than threatened *Ficus* species (Table 4). Montane forest includes cloud forests, mossy forests, lower, upper and sub-montane forests and upland forests, essentially habitats above 750m (Whitmore, 1990). Initially, this sounds counter-intuitive, as montane habitats are unique ecosystems where only plants that have specialised adaptations can thrive (Billings, 1974). However, on further examination of the data set (see Appendix 2), all 28 weedy species found in montane forests also inhabit a second type of lowland habitat such as the lowland evergreen rain forests, savannas, dry forests or coastal

vegetation. Therefore, weediness can be attributed to habitat breadth or wider ecological amplitudes, being able to thrive in high and low altitudes.

Threatened *Ficus* species on the other hand, have a lower likelihood of being montane species. This is reasonable as montane habitats are relatively scarcer and development almost always occurs at lower altitudes first. This means that lowland species would normally be the first to be threatened with extinction, with widespread deforestation. Threatened species having a more limited habitat breadth, are often first eliminated with lowland development, while weedy *Ficus* species, though might be wiped out in the lowlands with development, can continue to thrive in the uplands, before recolonising the lowlands again.

However, with the imminent threat of global warming, attention should be paid to *Ficus* species that only grow in montane forests. While *Ficus* species adapted to both montane and lowland habitats are able to retreat, montane specialists, often endemics, do not have this option. Montane species are dependent upon regular cloud immersion for their survival (Foster, 2001). With global climate change, there is a risk that the narrow altitude range cloud forests might be replaced by lower altitude ecosystems (Foster, 2001). If this were to occur, obligate montane *Ficus* species would certainly risk extinction. Besides facing the threat of climate change, montane forests are also rapidly being cleared for land for development (van der Hammen, 1995). The vulnerability of montane habitats and the risk posed to montane *Ficus* species should be seriously considered in threat assessment, as up to 120 species has been identified in my list as montane specialists.

3.2.6.2 Lowland evergreen rain forest

Weedy species are more likely to reside in lowland evergreen rain forests than threatened species. As mentioned earlier, species adapted to lowland evergreen rain forest habitats are both more easily eliminated and yet also better adapted to invade anthropogenic habitats that are mainly located at lower altitudes. Hence, the important question to ask in predicting threat and weediness is not whether a species is a lowland species or upland species, rather whether a species resides only in only one or both types of habitats. Having a distributional range limited to only lowlands or only highlands would mean a higher chance of being threatened, whereas species exhibiting habitat flexibility are more likely to thrive and be weedy.

3.2.6.3 Bright open areas

Weedy *Ficus* species are less likely to be found in anthropogenic open habitats and riverine forests than threatened *Ficus* species.

Anthropogenic open habitats include wastelands, forest clearings, plantations, villages, and trails and are basically habitats that have been cleared or disturbed as a consequence of human development. Riverine (riparian) forests include gallery forests. What these two kinds of habitat share in common is that they are bright and open areas. Many *Ficus* species such as *Ficus pertusa* and *Ficus trigonata* from the South American Kingdom have relatively high light demands and do not grow where canopy cover exceeds 60% (Putz and Holbrook, 1989).

Ficus insipida, a weed from the South American Kingdom, was also found to exhibit the highest photosynthetic rates both in low light and higher irradiances compared to some other tree species (Strauss-DeBenedetti and Bazzaz, 1991). This suggested that *Ficus insipida* has a broad habitat preference (Strauss-DeBenedetti and

Bazzaz, 1991), consistent with my data that this species can both be found in closed lowland evergreen rain forests and open anthropogenic habitats. Such ecological breadth and ability to grow fast and well in high light intensities would also give *Ficus insipida* an advantage as a weed in disturbed forests and urban environments.

Ficus grossularioides, a native weed from the Indo-Pacific Kingdom, also responds well to bright condition. It is common in secondary forests, and only fruits in medium-sized and large canopy gaps or edges in primary forests (Metcalf and Grubb, 1997). *Ficus grossularioides* seedlings were found to grow much faster when grown in 7.5% daylight compared to 1% daylight. This is in stark contrast to *Ficus chartacea*, a shade-loving species, which almost never grows in secondary forest (Kochummen, 1978). *Ficus chartacea* grew only modestly larger in 7.5% daylight compared to 1% daylight where they grew more vigorously (Metcalf and Grubb, 1997). This experiment clearly shows us that *Ficus* species are differentially adapted to various light intensities. With urbanisation and loss of shadier closed-forest habitats, *Ficus* species that prefer open habitats have a higher chance of surviving and becoming weedy.

Besides having a high light requirement, another reason for such a trend is that closed-forest specialists tend to be more affected by habitat loss than species that live in open or forest-edge habitats (Brook et al., 2003). Therefore, with the removal of forest habitats, forest specialists that are dependent on such habitats would die, whereas species that are able to tolerate environmental perturbations associated with open and forest-edge habitats, such as high wind speed and sunlight, and low relative humidity, can continue to thrive in disturbed and urban environments (Sodhi et al., 2008).

Most hemi-epiphytic *Ficus* species also require high light for seed germination and seedling establishment (Laman, 1995; Titus et al., 1990). Such a requirement is met in the disturbed and urbanised habitat and this might perpetuate the propensity to be

weedy, as hemi-epiphytes already have the tendency and advantage over others to be weedy.

Therefore, *Ficus* species are seen to vary in their responses to disturbances and light requirement and this preadapts some *Ficus* species to be prone to being threatened, and others weedy.

3.2.7 Morphology

3.2.7.1 Maximum height

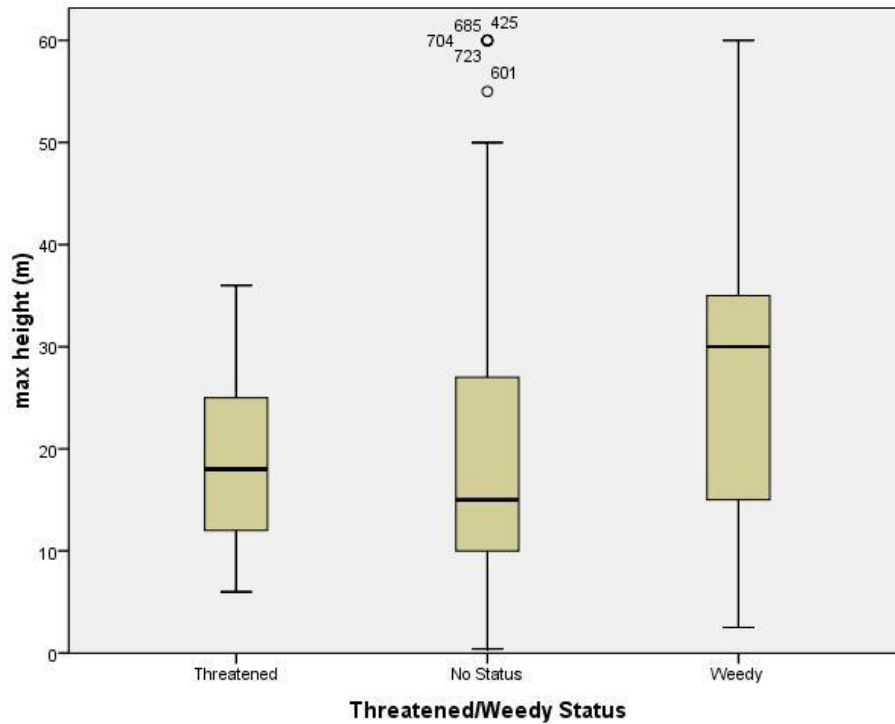


Figure 4. Boxplots showing maximum heights of threatened, status-free and weedy groups (See Appendix 5 for Kruskal-Wallis Test results).

The threatened *Ficus* species tend to be shorter at maturity than the weedy *Ficus* species (Figure 4). Being taller might confer advantages to plants, as on average they can receive more sunlight and are generally longer-lived. Other studies have shown similar results (Duncan and Young, 2000; Hedge and Ellstrand, 1999; Walker and Preston, 2006). Since plant height is closely linked to life-form, as shrubs tend to be shorter than trees and the height of climbers are normally not recorded, this result could be owed to taller species having a longer lifespan than their shorter counterparts (Turner et al., 1996). Even if all species become non-viable at the same time, for example, the

fig-wasps becoming extinct, taller species would out-live shorter species (Duncan and Young, 2000).

3.2.7.2 Maximum dry syconium diameter

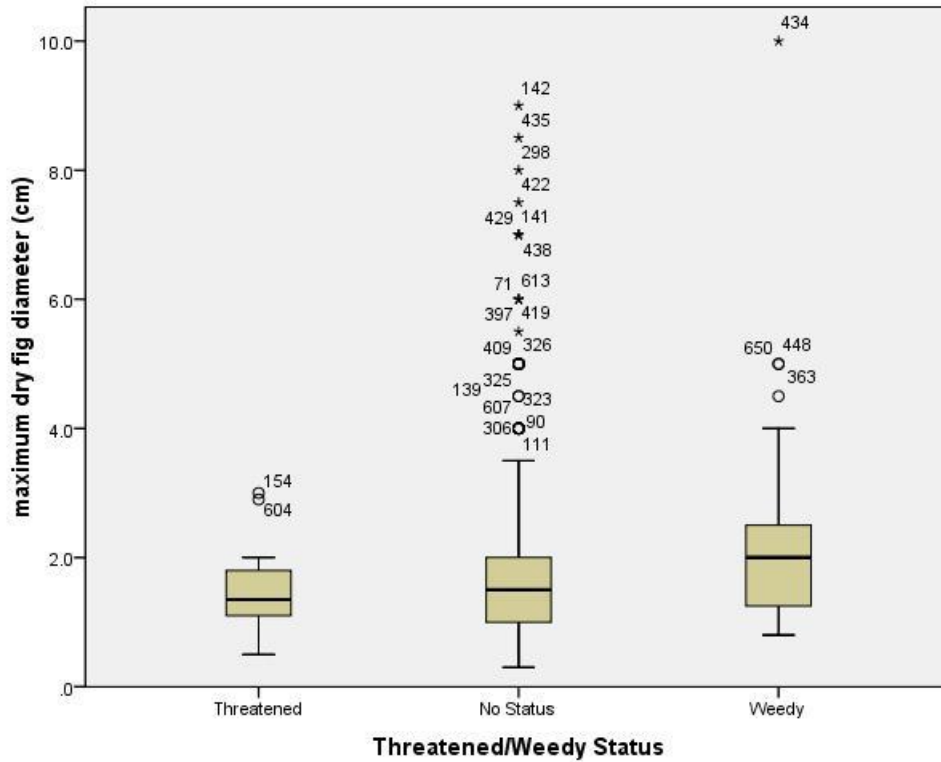


Figure 4. Boxplots showing maximum dry syconium diameter of threatened, status-free and weedy groups. Outlier values refer to index number of the species.

Unlike what is intuitively expected, my results show that weedy *Ficus* species tend to have larger syconia than threatened *Ficus* species.

Most oriental birds swallow fruits whole, hence fruit consumption and dispersal is mainly limited by their maximum gape widths (Corlett, 1998). The smallest fruits are therefore accessible to all such birds, though it is less economical for larger species to eat them (Corlett, 2002). Research has pointed to the existence of discrete guilds of *Ficus* species that differentially attract subsets of sympatric frugivore communities

(Shanahan et al., 2001), with larger birds preferring larger syconia and smaller birds preferring smaller syconia (Lambert, 1989). Knowing that larger fauna are often the first to become extinct in degraded forests (Corlett, 2002), I had expected weedy *Ficus*, which are more likely to be dispersed to have smaller syconia, reflected by the smaller syconia diameter.

A possible reason for threatened species having smaller syconia than weedy species is that there are many outliers for the unassessed or status-less *Ficus* species with very large syconia that are unaccounted for (Figure 4). Perhaps with more comprehensive threat assessment in the future, it can be ascertained whether these outlier species are truly threatened, status-less or weedy.

Other reasons for these results are that mammals and Neotropical frugivorous birds are also consumers of larger sized fruits (Corlett, 2002; Levey et al., 1994; Shanahan et al., 2001), and they are known to have a greater ability to acquire larger fruits and process them, instead of swallowing them whole (Levey et al., 1994). This would enable them to be able to consume syconia of larger sizes. Though these larger species are commonly the first fauna to go extinct in forest (Corlett, 2002), compared to smaller birds, at this point of time, they might still be offering dispersal services to for *Ficus* species with larger syconia.

The differences between the medians of the syconium diameter of threatened, status-less and weedy *Ficus* species differ by a sizeable 3–4 mm. Another possible reason for the tendency of weedy *Ficus* species to be larger than threatened species could be that having larger syconia is advantageous, as they are more visible and offer a greater reward for dispersers (Foster, 2008). Given that the median for the maximum syconium diameter of weedy *Ficus* species of 2 cm is still consumable by many small-sized passerine birds such as bulbuls (maximum gape of 13–15mm), laughing thrushes

(maximum gape of 20 mm) and non-passerines such as the Asian koel (maximum gape of > 20 mm), larger syconia still offer larger rewards than smaller syconia (Corlett, 2002).

3.2.7.3 Maximum leaf length

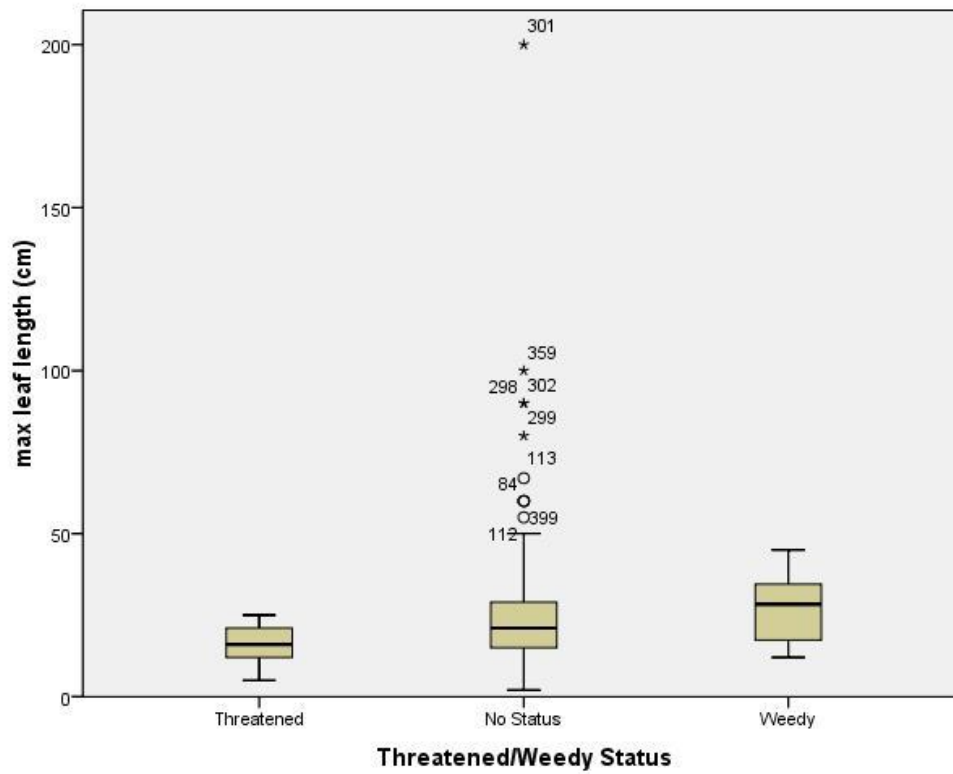


Figure 5. Boxplots showing maximum leaf lamina lengths of threatened, status-free and weedy groups.

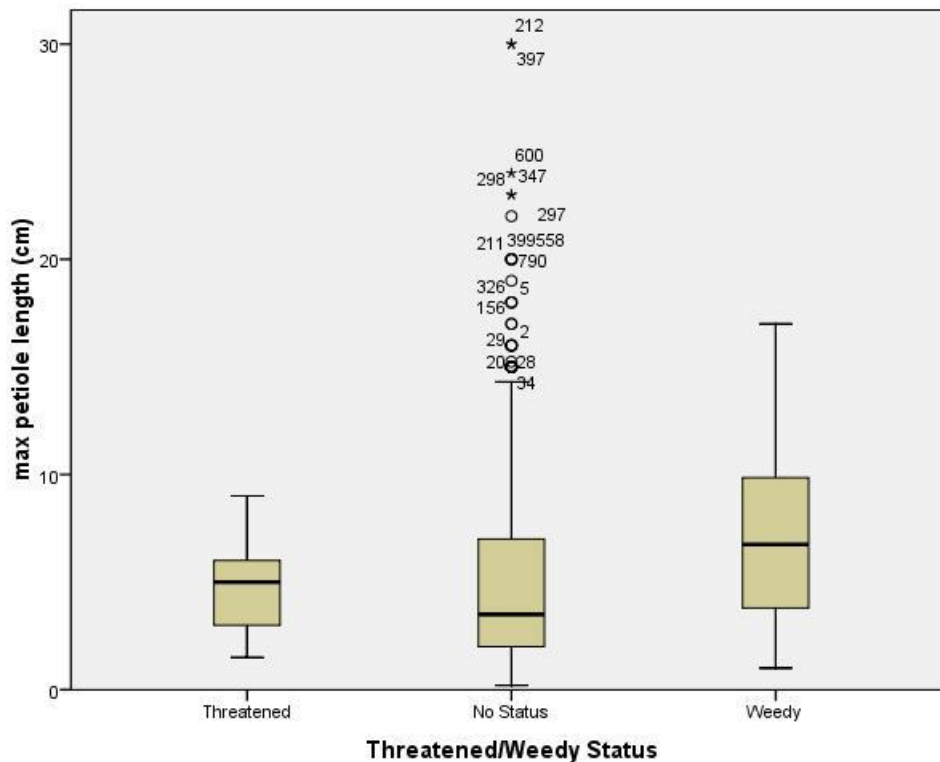


Figure 6. Boxplots showing maximum petiole lengths of threatened, status-free and weedy groups.

Weedy *Ficus* species are shown to have longer median leaf (lamina and petiole) lengths than threatened *Ficus* species (Figure 5 and 6). Leaf length was used to approximate leaf mass which correlates to leaf life span and photosynthetic rate (Royer et al., 2007). A study by Lake and Leishman (2004) found that specific leaf area of invasive species was consistently higher than non-invasive species. Since leaf area is an approximate of leaf mass (Roderick and Cochrane, 2002), my results show a similar trend. Species with a larger specific leaf area have a shorter investment return rate and higher potential for faster growth (Lake and Leishman, 2004). The reverse can be implied for threatened plants. There is also evidence that longer petiole lengths may confer advantageous to invasive plants by reducing self-shading (Kitajima et al., 2006).

4. CONCLUSIONS

Threatened species were identified to have this syndrome of traits: possess a maximum height of less than 20 m, syconium diameter of less than 2 cm, leaf lamina length of less than 20 cm, are not cultivated, not commercially exploited for timber, not hemi-epiphytic or lithophytic, not found in anthropogenic, open habitats, are often restricted to a single habitat type, have a monoecious breeding system and are from the subgenus *Urostigma*, section *Americanae*.

Weedy species were identified to have this syndrome of traits: possess a maximum height more than 30 m, syconium diameter greater than 2 cm, leaf lamina length of greater than 20 cm, are cultivated, are commercially exploited for timber, inhabit more than one habitat such as anthropogenic, open habitats, and lowland and/or montane forests, have either the hemi-epiphytic and/or lithophytic life forms and are from the subgenus *Urostigma*, section *Urostigma*.

Based on the traits identified for threatened and weedy species, I have identified a list of potentially threatened and potentially weedy *Ficus* species to aid both conservationists and invasion ecologists in their assessments.

Putative threatened species, with the threat traits listed above, include *Ficus bahiensis*, *Ficus caatingae*, *Ficus duartei*, *Ficus francoae*, *Ficus laureola*, *Ficus ovalis*, *Ficus quichuana*, *Ficus rimacana*, *Ficus valaria* from the South American Kingdom; *Ficus densifolia*, *Ficus kamerunensis*, *Ficus madagascariensis* and *Ficus marmorata* from the African Kingdom; *Ficus costata*, *Ficus patellata*, and *Ficus orthoneura* from the Indo-Pacific Kingdom.

Putative weedy species, based on the syndrome of weedy traits, include *Ficus watkinsiana* from the Australian Kingdom and *Ficus sundaica* from the Indo-Pacific Kingdom.

In making my judgment, I did not consider the kingdom distributions of the *Ficus* species as I have earlier shown in my discussion that the relationship between threat and invasive status and kingdom distribution were often biased due to uneven geographical assessments.

One major limitation of this assessment is that, this prediction is only as accurate as the data collected at this point of time and with increased and improved knowledge on species through ecological or systematic studies, the traits that predict for threat and weediness might change, hence changing the potentially threatened and weedy species specified in my list.

In view of the heavy ecological consequences of *Ficus* species becoming threatened or weedy, or worse, invasive, it is important to know what ecological, distributional, human impact, and morphological attributes make one species prone to becoming weedy while another threatened with extinction. Knowing the principle hallmarks of threatened and weedy *Ficus* species would hand conservationists, horticulturalists, landowners and government authorities the tools to identify species that deserve more attention in conservation and species that should not be cultivated for the ornamental trade to avoid future invasions.

5. References

- ANPSA (2009). Australian Native Plants Society (Australia) URL: <http://asgap.org.au/>. Downloaded on 16th March 2009.
- Anstett, M.-C., Michaloud, G., and Kjellberg, F. (1995). Critical population size for fig/wasp mutualism in a seasonal environment: effect and evolution of the duration of female receptivity. *Oecologia* 103, 453-461.
- Ashton, M.S., Gunatilleke, S., De Zoysa, N., Wijesundera, S., Dassanayake, M.D., and Gunatilleke, N. (1997). A field guide to the common trees and shrubs of Sri Lanka, 1 edn (Colombo, WHT Publications).
- Au, D.T., Wu, J., Jiang, Z., Chen, H., Lu, G., and Zhao, Z. (2008). Ethnobotanical study of medicinal plants used by Hakka in Guangdong, China. *Journal of Ethnopharmacology* 117, 41-50.
- Australian Plant Study Group (1980). *Grow what where*, 1 edn (Melbourne, Thomas Nelson).
- Barrett, M.F. (1946). *Ficus* in Florida I. Australian species. *American Midland Naturalist* 36, 412-430.
- Barrett, M.F. (1948). *Ficus* in Florida. II. African species. *American Midland Naturalist* 39, 188-219.
- Barrett, M.F. (1951). *Ficus* in Florida. III. Asiatic species. *American Midland Naturalist* 45, 118-183.
- Basnet, D.B. (2005). Some common weed flora in forest plantation of Darjeeling Hill, West Bengal, India. In *Biodiversity and Conservation*, A. Kumar, ed. (New Delhi, APH Publishing Corporation).
- Basset, Y., Novotny, V., and Weiblen, G.D. (1997). *Ficus*: a resource for arthropods in the Tropics, with particular reference to New Guinea. In *Forests and Insects*, A.D. Watt, N.E. Stork, and M.D. Hunter, eds. (London, Chapman & Hall).
- Bell, C.E., Wilen, C.A., and Stanton, A.E. (2003). Invasive plants of horticultural origin. *HortScience* 38, 14-16.
- Berg, C.C. (1989). Classification and distribution of *Ficus*. *Experientia* 45, 605-611.
- Berg, C.C. (1991). Moraceae. In *Flora Zambesiaca*, E. Launert, and G.V. Pope, eds. (London, Flora Zambesiaca Managing Committee).
- Berg, C.C. (2001). Moreae, Artocarpeae, and *Dorstenia* (Moraceae) with introductions to the family and *Ficus* and with additions and corrections to *Flora Neotropica Monograph* 7. *Flora Neotropica Monograph* 83, 289-292.

- Berg, C.C. (2003a). Flora Malesiana precursor for the treatment of Moraceae 1: The main subdivision of *Ficus*: the subgenera. *Blumea* 48, 167-178.
- Berg, C.C. (2003b). Flora Malesiana precursor for the treatment of Moraceae 2: *Ficus* subgenus *Pharmacosycea* section *Oreosycea*. *Blumea* 48, 289-301.
- Berg, C.C. (2003c). Flora Malesiana precursor for the treatment of Moraceae 3: *Ficus* subgenus *Ficus*. *Blumea* 48, 529-550.
- Berg, C.C. (2003d). Flora Malesiana precursor for the treatment of Moraceae 4: *Ficus* subgenus *Synoecia*. *Blumea* 48, 551-571.
- Berg, C.C. (2003e). Flora Malesiana precursor for the treatment of Moraceae 5: *Ficus* subgenus *Sycidium*. *Blumea* 48, 573-597.
- Berg, C.C. (2004a). A new species of *Ficus* (Moraceae) of uncertain provenance. *Brittonia* 56, 54-57.
- Berg, C.C. (2004b). Flora Malesiana precursor for the treatment of Moraceae 6: *Ficus* subgenus *Sycomorus*. *Blumea* 49, 155-200.
- Berg, C.C. (2004c). Flora Malesiana precursor for the treatment of Moraceae 7: *Ficus* subgenus *Urostigma*. *Blumea* 49, 463-480.
- Berg, C.C., and Corner, E.J.H. (2005). Flora Malesiana. Series I, Seed Plants Vol 17 Part 2 (Leiden, Nationaal Herbarium Nederland).
- Berg, C.C., and Villavicencio, X. (2003). A new species of *Ficus* and a new species of *Pseudolmedia* (Moraceae) from Bolivia. *Revista de la Sociedad Boliviana de Botánica* 4, 75-79.
- Billings, W.D. (1974). Adaptations and origins of alpine plants. *Arctic and Alpine Research* 6, 129-142.
- Blackburn, T.M., and Duncan, R.P. (2001). Determinants of establishment success in introduced birds. *Nature* 414, 195-197.
- Boo, C.M., Omar-Hor, K., and Ou-Yang, C.L. (2006). 1001 Garden plants in Singapore, 2 edn (Singapore, National Parks Board).
- Bossard, C.C., Randall, R.P., and Horshovsky, M.C. (2000). Invasive plants of California's wildlands (Berkeley, Los Angeles, University of California Press).
- Boutelje, J.B. (1980). Encyclopedia of world timbers : names and technical literature (Stockholm, Swedish Forest Products Research Laboratory).
- Bradshaw, C.J.A., Giam, X.L., Tan, H.T.W., Brook, B.W., and Sodhi, N.S. (2008). Threat or invasive status in legumes is related to opposite extremes of the same ecological and life-history attributes. *Journal of Ecology* 96, 869-883.

- Bradshaw, C.J.A., Sodhi, N.S., Peh, K.S.-H., and Brook, B.W. (2007). Global evidence that deforestation amplifies flood risk and severity in the developing world. *Global Change Biology* 13, 2379-2395.
- Brehler, R., Abrams, E., and Sedlmayr, S. (1998). Cross-reactivity between *Ficus benjamina* (weeping fig) and natural rubber latex. *Allergy* 33, 402-406.
- Bronstein, J.L. (1991). The nonpollinating wasp fauna of *Ficus pertusa*: exploitation of a mutualism? *Oikos* 61, 175-186.
- Bronstein, J.L., Gouyon, P.-H., Gliddon, C., Kjellberg, F., and Michaloud, G. (1990). The ecological consequences of flowering asynchrony in monoecious figs: a simulation study. *Ecology* 71, 2145-2156.
- Bronstein, J.L., and Patel, A. (1992). Causes and consequences of within-tree phenological patterns in the Florida strangling fig, *Ficus aurea* (Moraceae). *American Journal of Botany* 79, 41-48.
- Brook, B.W., Sodhi, N.S., and Ng, P.K.L. (2003). Catastrophic extinctions follow deforestation in Singapore. *Nature* 424, 420-426.
- Brummitt, N., Bachman, S.P., and Moat, J. (2008). Applications of the IUCN Red List: towards a global barometer for plant diversity. *Endangered Species Research* 6, 127-135.
- Burnham, K.P., and Anderson, D.R. (2002). *Model selection and multimodel inference : a practical information-theoretic approach*, 2nd edn (New York, Springer).
- Burrows, J., and Burrows, S. (2003). *Figs of Sourthern and South-Central Africa*, 1 edn (Hatfield, Umdaus Press).
- Cadotte, M.W., and Lovett-Doust, J. (2002). Ecological and taxonomic differences between rare and common plants of southwestern Ontario. *Ecoscience* 9, 397-406.
- Chaudhary, S.A. (1999). Moraceae. In *Flora of the Kingdom of Saudi Arabia*, S.A. Chaudhary, ed. (Riyadh, Ministry of Agriculture & Water), pp. 105-116.
- Chazdon, R.L. (1998). Tropical forests - log 'em or leave 'em? *Science* 281, 1295-1296.
- Clark, D.B., and Clark, D.A. (1990). Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. *Journal of Tropical Ecology* 6, 321-331.
- Coates, F., and Kirkpatrick, J.B. (1992). Environmental relations and ecological responses of some higher plant species on rock cliffs in northern Tasmania. *Austral Ecology* 17, 441-449.
- Condit, I.J. (1969). *Ficus the exotic species*, Vol 1 (Berkeley, Agricultural Publications).

- Cook, J.M., and Rasplus, J.Y. (2003). Mutualists with attitude: coevolving fig wasps and figs. *Trends in Ecology & Evolution* 18, 241-248.
- Corlett, R.T. (1987). The phenology of *Ficus fistulosa* in Singapore. *Biotropica* 19, 122-124.
- Corlett, R.T. (1993). Sexual dimorphism in the reproductive phenology of *Ficus grossularioides* Burm. f. in Singapore. *Malayan Nature Journal* 46, 149-155.
- Corlett, R.T. (1998). Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews* 73, 413-448.
- Corlett, R.T. (2002). Frugivory and seed dispersal in degraded tropical East Asian landscapes. In *Seed dispersal and frugivory: Ecology, evolution and conservation*, D.J. Levey, W.R. Silva, and M. Galetti, eds. (Wallingford, UK, CAB International), pp. 451-465.
- Corlett, R.T. (2006). Figs (*Ficus*, Moraceae) in Urban Hong Kong, South China. *Biotropica* 38, 116-121.
- Corner, E.J.H. (1963). Why *Ficus*, why Moraceae? *Flora Malesiana Bulletin* 18, 1000-1004.
- Corner, E.J.H. (1988). *Wayside trees of Malaya*, 3rd edn (Kuala Lumpur, Malayan Nature Society).
- Cox, C.B. (2001). The biogeographic regions reconsidered. *Journal of Biogeography* 28, 511-523.
- Daehler, C.C., Denslow, J.S., Ansari, S., and Kuo, H.-C. (2004). A risk-assessment system for screening out invasive pest plants from Hawaii and other Pacific Islands. *Conservation Biology* 18, 360-368.
- Daniels, J.D., and Lawton, R.O. (1991). Habitat and host preferences of *Ficus crassiuscula*, a Neotropical strangling fig of the lower-montane rain forest. *The Journal of Ecology* 79, 129-141.
- Davis, A.J., and Sutton, S.L. (1997). A dung beetle that feeds on fig: implications for the measurement of species rarity. *Journal of Tropical Ecology* 13, 759-766.
- Davis, M.A., and Thompson, K. (2000). Eight ways to be a colonizer: two ways to be an invader. *Bulletin of the Ecological Society of America* 81, 226-230.
- Davis, M.A., and Thompson, K. (2001). Invasion terminology: should ecologists define their terms differently than others? No, not if we want to be of any help! *Bulletin of the Ecological Society of America* 82, 206.
- Dixon, D.J. (2001). Figs, wasps and species concepts: a re-evaluation of the infraspecific taxa of *Ficus macrophylla* (Moraceae: *Urostigma* sect. *Malvanthera*). *Australian Systematic Botany* 14, 125-132.

- Dumont, E.R., Weiblen, G.D., and Winkelmann, J.R. (2004). Preferences of fig wasps and fruit bats for figs of functionally dioecious *Ficus pungens*. *Journal of Tropical Ecology* 20, 233-238.
- Duncan, R.P., and Young, J.R. (2000). Determinants of plant extinction and rarity 145 years after European settlement of Auckland, New Zealand. *Ecology* 81, 3048-3061.
- Elliot, W.R., and Jones, D.L. (1986). *Encyclopaedia of Australian plants suitable for cultivation*. Volume 4 (Victoria, Lothian Publishing Company Pty. Ltd).
- Ellison, D. (1995). *Cultivated Plants of the World*, 1 edn (Brisbane, Flora Publications International Pty Ltd).
- Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist* 125, 1-15
- Felton, A.M., Felton, A., Wood, J.T., and Lindenmayer, D.B. (2008). Diet and feeding ecology of *Ateles chamek* in a Bolivian semihumid forest: the importance of *Ficus* as a staple food resource. *International Journal of Primatology* 29, 379-403.
- Foster, M.S. (2008). Freeze-frame fruit selection by birds. *The Wilson Journal of Ornithology* 120, 901-905.
- Foster, P. (2001). The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Science Reviews* 55, 73-106.
- Fredericksen, T., Rumiz, D., Bravo, M.J.J., and Abacay, R.A. (1999). Harvesting free-standing fig trees for timber in Bolivia: potential implications for forest management. *Forest Ecology and Management* 116, 151-161.
- Gardner, R.O., and Early, J.W. (1996). The naturalisation of banyan figs (*Ficus* spp., Moraceae) and their pollinating wasps (Hymenoptera: *Agaonidae*) in New Zealand. *New Zealand Journal of Botany* 34, 103-110.
- Gautier, D. (1996). *Ficus* (Moraceae) as part of agrarian systems in the Bamileke region (Cameroon). *Economic Botany* 50, 318-326.
- Gilman, E.F., and Watson, D.G. (1993). *Ficus rubiginosa*. In Fact Sheet ST-257 (University of Florida).
- Griffiths, M. (1994). *Index of Garden Plants*, 1 edn (Portland, Timber Press).
- Groves, R. (1997). Recent incursions of weeds to Australia, 1971-1995. Technical Series No. 3, Cooperative Research for Weed Management Systems, Cooperative Research Centre for Weed Management Systems, Glen Osmond, SA.
- Hedge, S.G., and Ellstrand, N.C. (1999). Life history differences between rare and common flowering plant species of California and the British Isles. *International Journal of Plant Sciences* 160, 1083-1091.

- Howard, R.A. (1988). Flora of the Lesser Antilles (Leeward and Windward Islands), Vol 4. Dicotyledoneae- Part 1 (Jamaica Plain, Arnold Arboretum, Harvard University).
- Hubbell, S.P., He, F., Condit, R., Borda-de-Água, L., Kellner, J., and ter Steege, H. (2008). How many tree species are there in the Amazon and how many of them will go extinct? *Proceedings of the National Academy of Sciences* *105*, 11498-11504.
- Imada, C.T., Staples, G.W., and Herbst, D.R. (2005). Annotated checklist of cultivated plants of Hawai‘i.
- Institute of Pacific Islands Forestry (2009). US Forest Service, Pacific Island Ecosystems at Risk (PIER).
- Ipulet, P. (2007). Uses of genus *Ficus* (Moraceae) in Buganda region, central Uganda. *African Journal of Ecology* *45*, 44-47.
- IUCN (2008). IUCN Red List of Threatened Species. <www.iucnredlist.org> Downloaded on 8th March 2009.
- Janzen, D.H. (1979). How to be a fig. *Annual Review of Ecology and Systematics* *10*, 13-51.
- Jim, C.Y. (1998). Old stone walls as an ecological habitat for urban trees in Hong Kong. *Landscape and Urban Planning* *42*, 29-43.
- Joffe, P. (2001). Creative gardening with indigenous plants, a South African guide (Pretoria, Briza Publications).
- Johnson, J.B., and Omland, K.S. (2004). Model selection in ecology and evolution. *Trends in Ecology & Evolution* *19*, 101-108.
- Jokthan, G.E., Afikwu, E.V., and Olugbemi, T.S. (2003). The utilization of fig (*Ficus thonningii*) and Mango (*Mangifera indica*) leaves by rabbits. *Pakistan Journal of Nutrition* *2*, 264-266.
- Jousselin, E., Hossaert-McKey, M., Herre, E.A., and Kjellberg, F. (2003). Why do fig wasps actively pollinate monoecious figs? *Oecologia* *134*, 381-387.
- Kerdelhué, C., Le Clainche, I., and Rasplus, J.-Y. (1999). Molecular phylogeny of the *Ceratosolen* species pollinating *Ficus* of the subgenus *Sycomorus* sensu stricto: biogeographical history and origins of the species-specificity breakdown cases. *Molecular Phylogenetics and Evolution* *11*, 401-414.
- Kerdelhué, C., and Rasplus, J.-Y. (1996a). The evolution of dioecy among *Ficus* (Moraceae): an alternative hypothesis involving non-pollinating fig wasp pressure on the fig-pollinator mutualism. *Oikos* *77*, 163-166.
- Kerdelhué, C., and Rasplus, J.Y. (1996b). Non-pollinating Afrotropical fig wasps affect the fig-pollinator mutualism in *Ficus* within the subgenus *Sycomorus*. *Oikos* *75*, 3-14.

- Khanna, K.K., and Kumar, A. (2002). Recollection of an endemic plant, *Ficus cupulata* Haines from type locality (Pachmarhi Biosphere Reserve). *Bulletin of the Botanical Survey of India* 44, 145-146.
- Kitajima, K., Fox, A., Sato, T., and Nagamatsu, D. (2006). Cultivar selection prior to introduction may increase invasiveness: evidence from *Ardisia crenata*. *Biological Invasions* 8, 1471-1482.
- Kjellberg, F., Gouyon, P.-H., Ibrahim, M., Raymond, M., and Valdeyron, G. (1987). The stability of the symbiosis between dioecious figs and their pollinators: a study of *Ficus carica* L. and *Blastophaga psenes* L. *Evolution* 41, 693-704.
- Kjellberg, F., Joussetin, E., Bronstein, J.L., Patel, A., Yokoyama, J., and Rasplus, J.-Y. (2001). Pollination mode in fig wasps: the predictive power of correlated traits. *Proceedings: Biological Sciences* 268, 1113-1121.
- Kochummen, K.M. (1978). Moraceae. In *Tree Flora of Malaya*, F.S.P. Ng, ed. (Kuala Lumpur, Longman), pp. 119-168.
- Lake, J.C., and Leishman, M.R. (2004). Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biological Conservation* 117, 215-226.
- Laman, T.G. (1995). *Ficus stupenda* germination and seedling establishment in a Bornean rain forest canopy. *Ecology* 76, 2617-2626.
- Laman, T.G. (1996). The impact of seed harvesting ants (*Pheidole* sp. nov.) on *Ficus* establishment in the canopy. *Biotropica* 28, 777-781.
- Lambert, F. (1989). Fig-eating by birds in a Malaysian lowland rain forest. *Journal of Tropical Ecology* 5, 401-412.
- Lansky, E.P., Paavilainen, H.M., Pawlus, A.D., and Newman, R.A. (2008). *Ficus* spp. (fig): Ethnobotany and potential as anticancer and anti-inflammatory agents. *Journal of Ethnopharmacology* 119, 195-213.
- Laurance, W.F., and Peres, C.A. (2006). *Emerging threats to tropical forests* (Chicago, University of Chicago Press).
- Levey, D.J., Moermond, T.C., and Denslow, J.S. (1994). Frugivory: an overview. In *La Selva: Ecology and Natural History of a Neotropical Rain Forest*, L.A. McDade, K.S. Bawa, H.A. Hespenheide, and G.S. Hartshorn, eds. (Chicago, University of Chicago Press), pp. 287-294.
- Lim, S.C., Gan, K.S., and Choo, K.T. (2004). Identification and utilisation of lesser-known commercial timbers in Peninsular Malaysia 1: Ara, Bangkal, Bebusok and Bekoi. *Timber Technology Bulletin*, 1-8.

- Lloret, F., Medail, F., Brundu, G., Camarda, I., Moragues, E., Rita, J., Lambdon, P., and Hulme, P.E. (2005). Species attributes and invasion success by alien plants on Mediterranean islands. *Journal of Ecology* 93, 512-520.
- Lockwood, J.L., Cassey, P., and Blackburn, T. (2005). The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution* 20, 223-228.
- Lopez-Vaamonde, C., Dixon, D.J., Cook, J.M., and Rasplus, J.Y. (2002). Revision of the Australian species of *Pleistodontes* (Hymenoptera: *Agaonidae*) fig-pollinating wasps and their host-plant associations. *Zoological Journal of the Linnean Society* 136, 637-683.
- Lososova, Z., Chytry, M., and Kuehn, I. (2008). Plant attributes determining the regional abundance of weeds on central European arable land. *Journal of Biogeography* 35, 177-187.
- Lyon, H.L. (1929). Figs in the Hawaiian forestry. *Hawaiian Planters' Record* 33, 83-97.
- Machado, C.A., Herre, E.A., McCafferty, S., and Bermingham, E. (1996). Molecular phylogenies of fig pollinating and non-pollinating wasps and the implications for the origin and evolution of the fig-fig wasp mutualism. *Journal of Biogeography* 23, 531-542.
- Machado, C.A., Jouselin, E., Kjellberg, F., Compton, S.G., and Herre, E.A. (2001). Phylogenetic relationships, historical biogeography and character evolution of fig-pollinating wasps. *Proceedings: Biological Sciences* 268, 685-694.
- Mack, R. (2000). Cultivation fosters plant naturalization by reducing environmental stochasticity. *Biological Invasions* 2, 111-122.
- Mack, R.N., and Erneberg, M. (2002). The United States naturalized flora: largely the product of deliberate introductions. *Annals of the Missouri Botanical Garden* 89, 176-189.
- Madulid, D.A. (1995). A pictorial cyclopedia of Philipphine ornamental plants, 1 edn (Manila, Bookmark, Inc.).
- Mawdsley, N.A., Compton, S.G., and Whittaker, R.J. (1998). Population persistence, pollination mutualisms, and figs in fragmented tropical landscapes. *Conservation Biology* 12, 1416-1420.
- McClure, H.E. (1964). Some observation of primates in climax diptocarp forest near Kuala Lumpur, Malaya. *Primates* 5, 39-58.
- McKey, D.B. (1989). Population biology of figs: applications for conservation. *Experientia* 45, 661-673.
- McKey, D.B., and Kaufmann, S.C. (1988). Naturalization of exotic *Ficus* species (Moraceae) in south Florida. Paper presented at: Proceedings of the Symposium on Exotic Pest Plants, Miami, Florida.

McPherson, J.R. (1999). Studies in urban ecology: strangler figs in the urban parklands of Brisbane, Queensland, Australia. *Australian Geographical Studies* 37, 214-229.

Metcalf, D.J., and Grubb, P.J. (1997). The responses to shade of seedlings of very small-seeded tree and shrub species from tropical rain forest in Singapore. *Functional Ecology* 11, 215-221.

Milton, K., Windsor, D.M., Morrison, D.W., and Estribi, M.A. (1982). Fruiting phenologies of two Neotropical *Ficus* species. *Ecology* 63, 752-762.

Nabe-Nielsen, J., Severiche, W., Fredericksen, T., and Nabe-Nielsen, L.I. (2007). Timber tree regeneration along abandoned logging roads in a tropical Bolivian forest. *New Forests* 34, 1573-5095.

Nadel, H., Frank, J.H., and Knight Jr, R.J. (1992). Escapees and accomplices: The naturalisation of exotic *Ficus* and their associated faunas in Florida. *The Florida Entomologist* 75, 29-38.

Nairn, M.E., Allen, P.G., Inglis, A.R., and Tanner, C. (1996). *Australian Quarantine: A Shared Responsibility* (Canberra, Department of Primary Industries and Energy).

Niemiera, A.X., and Holle, B.V. (2009). Invasive plant species and the ornamental horticulture industry. In *Management of Invasive Weeds*, pp. 167-187.

Oldfield, S., Lusty, C., and MacKinven, A. (1998). *The world list of threatened trees* (Cambridge, UK, World Conservation Press).

Ou, J., Lu, C., and O'Toole, D.K. (2008). A risk assessment system for alien plant bio-invasion in Xiamen, China. *Journal of Environmental Sciences* 20, 989-997.

Paton, A.J., Brummitt, N., Govaerts, R., Harman, K., Hinchcliffe, S., Allkin, B., and Lughadha, E.N. (2008). Towards target 1 of the global strategy for plant conservation: a working list of all known plant species - progress and prospects. *Taxon* 57, 602-611.

Pemberton, R.W., and Liu, H. (2009). Marketing time predicts naturalization of horticultural plants. *Ecology* 90, 69-80.

Pheloung, P.C., Williams, P.A., and Halloy, S.R. (1999). A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *Journal of Environmental Management* 57, 239-251.

Pocock, M.J.O., Hartley, S., Telfer, M.G., Preston, C.D., and Kunin, W.E. (2006). Ecological correlates of range structure in rare and scarce British plants. *Journal of Ecology* 94, 581-596.

Poorter, L., Bongers, F., Kouamé, F.N., and Hawthorne, W.D. (2004). *Biodiversity of west African forests : an ecological atlas of woody plant species* (Massachusetts, CABI Publishing).

- Putz, F.E., and Holbrook, N.M. (1989). Strangler fig rooting habits and nutrient relations in the Llanos of Venezuela. *American Journal of Botany* 76, 781-788.
- Pyšek, P., and Richardson, D.M. (2007). Traits associated with invasiveness in alien plants: where do we stand? In *Biological Invasions*, pp. 97-125.
- Pyšek, P., Richardson, D.M., Pergl, J., Jarosík, V., Sixtová, Z., and Weber, E. (2008). Geographical and taxonomic biases in invasion ecology. *Trends in Ecology & Evolution* 23, 237-244.
- Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G.L., Williamson, M., and Kirschner, J. (2004). Alien plants in checklists and Floras: towards better communication between taxonomists and ecologists. *Taxon* 53, 131-143.
- Quinn, R.M., Lawton, J.H., Eversham, B.C., and Wood, S.N. (1994). The biogeography of scarce vascular plants in Britain with respect to habitat preference, dispersal ability and reproductive biology. *Biological Conservation* 70, 149-157.
- R Development Core Team (2008). R: A language and environment for statistical computing (Vienna, Austria, R Foundation for Statistical Computing).
- Ragusa-Netto, J. (2002). Fruiting phenology and consumption by birds in *Ficus calyptroceras* (Miq.) Miq. (Moraceae). *Brazilian Journal of Biology* 62, 339-346.
- Ramírez, W.B. (1970). Host specificity of fig wasps (*Agaonidae*). *Evolution* 24, 680-691.
- Ramírez, W.B., and Montero, J.S. (1988). *Ficus microcarpa* L., *F. benjamina* L. and other species introduced in the New World, their pollinators (*Agaonidae*) and other fig wasps. *Revista de Biología Tropical* 36, 441-446.
- Randall, R.P. (2002). *A Global Compendium of Weeds*, 1 edn (Melbourne, R. G. and F. J. Richardson).
- Reichard, S.H., and White, P. (2001). Horticulture as a pathway of invasive plant introductions in the United States. *BioScience* 51, 103-113.
- Richards, P.W. (1966). *The tropical rain forest : an ecological study*, 2nd edn (Cambridge, New York, Cambridge University Press).
- Richardson, D.M., Pyšek, P., Rejmanek, M., Barbour, M.G., Panetta, F.D., and West, C.J. (2000). Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6, 93-107.
- Roderick, M.L., and Cochrane, M.J. (2002). On the conservative nature of the leaf mass-area relationship. *Annals of Botany* 89, 537-542.
- Rønsted, N., Weiblen, G.D., Clement, W.L., Zerega, N.J.C., and Savolainen, V. (2008a). Reconstructing the phylogeny of figs (*Ficus*, Moraceae) to reveal the history of the fig pollination mutualism. *Symbiosis* 45, 45-55.

- Rønsted, N., Weiblen, G.D., Cook, J.M., Salamin, N., Machado, C.A., and Savolainen, V. (2005). 60 Million years of co-divergence in the fig-wasp symbiosis. *Proceedings of the Royal Society B: Biological Sciences* 272, 2593-2599.
- Rønsted, N., Weiblen, G.D., Savolainen, V., and Cook, J.M. (2008b). Phylogeny, biogeography, and ecology of *Ficus* section *Malvanthera* (Moraceae). *Molecular Phylogenetics and Evolution* 48, 12-22.
- Royer, D.L., Sack, L., Wilf, P., Lusk, C.H., Jordan, G.J., Niinemets, U., Wright, I.J., Westoby, M., Cariglino, B., Coley, P.D., *et al.* (2007). Fossil leaf economics quantified: calibration, Eocene case study, and implications *Paleobiology* 33, 574-589.
- Sax, D.F., and Brown, J.H. (2000). The paradox of invasion. *Global Ecology and Biogeography* 9, 363-371.
- Shanahan, M., Samson, S., Compton, S.G., and Corlett, R. (2001). Fig-eating by vertebrate frugivores: a global review. *Biological Reviews* 76, 529-572.
- Sodhi, N.S., Koh, L.P., Tan, H.T.W., Chazdon, R.L., Corlett, R.T., Tien, M.L., Colwell, R.K., Brook, B.W., Sekercioglu, C.H., and Bradshaw, C.J.A. (2008). Correlates of extinction proneness in tropical angiosperms. *Diversity and Distributions* 14, 1-10.
- Spencer, H., Weiblen, G., and Flick, B. (1996). Phenology of *Ficus variegata* in a seasonal wet tropical forest at Cape Tribulation, Australia. *Journal of Biogeography* 23, 467-475.
- SPSS for Windows (2008). Release 16.0.1 (March 11, 2008) (Chicago, SPSS Inc).
- Staples, G., Cowie, R.H., and Hawaii Biological Survey. (2001). Hawaii's invasive species : a guide to invasive plants and animals in the Hawaiian Islands (Honolulu, Hawaii, Mutual Publishing).
- Staples, G.W., Herbst, D.R., and Imada, C.T. (2000). Survey of invasive or potentially invasive cultivated plants in Hawai'i Bishop Museum Occasional Papers.
- Starr, F., Starr, K., and Loope, L. (2001). Invasion of Maui, Hawaii, by three species of *Ficus* (Moraceae): biotic interactions and consequences. In Hawaii Conservation Conference (Hilo, Hawaii).
- Starr, F., Starr, K., and Loope, L. (2003). *Ficus microcarpa*. In United States Geological Survey - Biological Resources Division (Maui, Hawai'i, Haleakala Field Station).
- Strauss-Debenedetti, S., and Bazzaz, F.A. (1991). Plasticity and acclimation to light in tropical Moraceae of different successional positions. *Oecologia* 87, 377-387.
- Subiza, J. (1999). *Ficus benjamina*, a new source of household environmental allergens. *Alergología e Inmunología Clínica* 14, 203-208.

- Szyszkowicz, M. (2006). Use of generalized linear mixed models to examine the association between air pollution and health outcomes. *International Journal of Occupational Medicine and Environmental Health* 19, 224-227.
- Terborgh, J. (1986). Keystone plant resources in the tropical forest. In *Conservation biology : the science of scarcity and diversity*, M.E. Soule, ed. (Sunderland, Massachusetts, Sinauer Associates), 584 p.
- Titus, J.H., Holbrook, N.M., and Putz, F.E. (1990). Seed germination and seedling distribution of *Ficus pertusa* and *F. tuerckheimii*: are strangler figs autotoxic? *Biotropica* 22, 425-428.
- Turner, I.M. (2000). *The plants of the Singapore Botanic Gardens* (Singapore, National Parks Board).
- Turner, I.M., Chua, K.S., Ong, J.S.Y., Soong, B.C., and Tan, H.T.W. (1996). A century of plant species loss from an isolated fragment of lowland tropical rain forest. *Conservation Biology* 10, 1229-1244.
- Turner, I.M., Tan, H.T.W., Wee, Y.C., Ibrahim, A.B., Chew, P.T., and Corlett, R.T. (1994). A study of plant species extinction in Singapore: lessons for the conservation of tropical biodiversity. *Conservation Biology* 8, 705-712.
- Tweheyo, M., and Obua, J. (2001). Feeding habits of chimpanzees (*Pan troglodytes*), red-tail monkeys (*Ceropithecus ascanius schmidti*) and blue monkeys (*Cercopithecus mitis stuhmannii*) on figs in Budongo Forest Reserve, Uganda. *African Journal of Ecology* 39, 133-139.
- Ungricht, S., Rasplus, J.-Y., and Kjellberg, F. (2003). Nomenclature of the Endemic Monoecious Fig Trees (Moraceae: *Ficus* L.) of New Caledonia and Vanuatu (Pacific Ocean). *Taxon* 52, 319-325.
- Ungricht, S., Rasplus, J.Y., and Kjellberg, F. (2005). Extinction threat evaluation of endemic fig trees of New Caledonia: priority assessment for taxonomy and conservation with herbarium collections. *Biodiversity and Conservation* 14, 205-232.
- van der Hammen, T. (1995). Global change, biodiversity, and conservation of Neotropical montane forests. In *Biodiversity and Conservation of Neotropical Montane Forests*, S.P. Churchill, H. Balslev, E. Forero, and J.L. Luteyn, eds., pp. 603-607.
- van Noort, S., Gardiner, A.J., and Tolley, K.A. (2007). New records of *Ficus* (Moraceae) species emphasize the conservation significance of inselbergs in Mozambique. *South African Journal of Botany* 73, 642-649.
- van Noort, S., and Rasplus, J.Y. (2009). Figweb URL: <http://www.figweb.org/> (Cape Town, Iziko Museums of Cape Town).
- Vazquez Avila, M.D. (1985). *Ficus luschnathiana* (Miq.) Miq., nombre correcto para *Ficus monckii* Hassler. *Darwiniana* 26, 381-382.

- Walker, E.H. (1976). *Flora of Okinawa and the southern Ryukyu Islands* (Washington, D. C., Smithsonian Institution Press).
- Walker, K., and Preston, C. (2006). Ecological predictors of extinction risk in the Flora of lowland England, UK. *Biodiversity and Conservation* 15, 1913-1942.
- Walter, K.S., and Gillett, H.J. (1998). 1997 IUCN red list of threatened plants (Gland, Switzerland; Cambridge, UK, International Union for Conservation of Nature and Natural Resources), pp. v.
- Weber, E. (2003). *Invasive plant species of the world : a reference guide to environmental weeds* (Wallingford, Oxon, UK ; Cambridge, MA, USA, CABI Pub.).
- Weiblen, G.D. (2000). Phylogenetic relationships of functionally dioecious *Ficus* (Moraceae) based on ribosomal DNA sequences and morphology. *American Journal of Botany* 87, 1342-1357.
- Weiblen, G.D. (2002). How to be a fig wasp. *Annual Review of Entomology* 47, 299-330.
- Whitmore, T.C. (1990). *An introduction to tropical rain forests*, 1 edn (Oxford, Clarendon Press).
- Wiebes, J.T. (1979). Co-evolution of figs and their insect pollinators. *Annual Review of Ecology and Systematics* 10, 1-12.
- Windsor, D.M., Morrison, D.W., Estribi, M.A., and de Leon, B. (1989). Phenology of fruit and leaf production by 'strangler' figs on Barro Colorado Island, Panamá. *Cellular and Molecular Life Sciences (CMLS)* 45, 647-653.
- Woodcock, D. (2003). To restore the watersheds: early twentieth-century tree planting in Hawai'i. *Annals of the Association of American Geographers* 93, 624-635.
- Zhou, Z., and Gilbert, M.G. (2003). Moraceae. In *Flora of China*, Z. Wu, P.H. Raven, and D. Hong, eds. (Beijing, St. Louis, Science Press (Beijing), Missouri Botanical Garden Press (St. Louis), pp. 21-73.

6. APPENDICES

Appendix 1. List of threatened species with their distributional, ecological, human impact and morphological attributes.

S/No.	Species	Author(s)	Subgenus	Section	Timber	Cultivated	Mediterranean woodland	Limestone habitat	Montane forest	Lowland evergreen rain forest	Dry forest	Secondary forest	Coastal vegetation	Forest Fringes	Open forest	Anthropogenic open habitats	Semi-desert	Savannas	Shrub/bushlands and thickets	Mangrove forest	Herbaceous swamps (Marsh)	Peat swamp forest	Freshwater swamp forest	Riverine forest	Rheophyte (grow on river beds)	Lithophyte (grow on rocks/cliffs)	Climber/creep	Shrub	Tree/shrub	Hemi-epiphytic lifeform	Position of syconia - axil	Syconia on older wood (1+2+3+4)	Previous season's growth (1)	Ramiflory (2)	Cauliflory (3)	Flagelliflory/geocarp (4)	Solitary	Paired	Clusters (three or more hunched)	Maximum height (m)	Maximum leaf length (cm)	Maximum petiole length (cm)	Sexual system	number of known pollinators	number of known parasites	minimum altitude (m)	maximum altitude (m)	Maximum dry fig diameter (cm)	Sessile/subsessile	Maximum petuncle length (cm)	Maximum ostiole diameter (mm)	African Kingdom	Indo-Pacific Kingdom	Australian Kingdom	South America Kingdom				
1	<i>F. mutabilis</i>	Bureau	<i>Pharmacosycea</i>	<i>Oreosycea</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0	0	0	0	10.0	16.0	4.0	1	-	-	0	600	1.2	0	0.20	2.0	0	1	0	0			
2	<i>F. lapathifolia</i>	(Liebm.) Miquel	<i>Pharmacosycea</i>	<i>Pharmacosycea</i>	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	-	25.0	3.0	1	-	-	0	1,200	2.0	1	0.90	-	0	0	0	1			
3	<i>F. lacunata</i>	Kvitvik	<i>Pharmacosycea</i>	<i>Pharmacosycea</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	25.0	21.0	3.0	1	-	-	1,500	2,500	2.9	0	1.10	-	0	0	0	1				
4	<i>F. pulchella</i>	Schott	<i>Pharmacosycea</i>	<i>Pharmacosycea</i>	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	-	-	-	-	-	-	-	-	-	36.0	13.0	1.8	1	-	-	-	-	-	-	-	-	0	0	0	1				
5	<i>F. andamanica</i>	Corner	<i>Sycidium</i>	<i>Sycidium</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	0	1	0	0				
6	<i>F. bojeri</i>	Baker	<i>Sycidium</i>	<i>Sycidium</i>	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	1	1	0	12.0	24.0	5.0	2	-	-	0	750	1.2	1	1.50	-	1	0	0	0			
7	<i>F. lateriflora</i>	Vahl	<i>Sycidium</i>	<i>Sycidium</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	1	0	0	1	1	0	12.0	21.0	7.0	2	1	1	0	1,400	1.5	0	1.50	-	1	0	0	0				
8	<i>F. ulmifolia</i>	Lamarck	<i>Sycidium</i>	<i>Sycidium</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1	1	0	6.0	23.0	3.0	2	-	-	0	750	1.3	0	1.50	-	0	1	0	0				
9	<i>F. aripuanensis</i>	C. C. Berg & F. Kooy	<i>Urostigma</i>	<i>Americanae</i>	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	25.0	14.0	3.5	1	-	-	0	1,000	1.0	0	0.70	-	0	0	0	1				
10	<i>F. blepharophylla</i>	Vazquez Avila	<i>Urostigma</i>	<i>Americanae</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	20.0	5.0	5.0	1	-	-	-	-	-	-	0.5	1	-	-	0	0	0	1			
11	<i>F. calyptroceras</i>	(Miquel) Miquel	<i>Urostigma</i>	<i>Americanae</i>	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	18.0	20.0	9.0	1	-	-	0	600	1.5	1	0.30	-	0	0	0	1				
12	<i>F. hirsuta</i>	Schott	<i>Urostigma</i>	<i>Americanae</i>	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	9.0	7.7	4.0	1	-	-	250	950	1.0	-	-	-	0	0	0	1				
13	<i>F. meizonochlamys</i>	Rosberg	<i>Urostigma</i>	<i>Americanae</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	1	-	-	-	-	-	-	-	-	0	0	0	1					
14	<i>F. pakkensis</i>	Standley	<i>Urostigma</i>	<i>Americanae</i>	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	25.0	21.0	6.0	1	-	-	100	800	2.0	-	1.20	-	0	0	0	1					
15	<i>F. ursina</i>	Standley	<i>Urostigma</i>	<i>Americanae</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	15.0	19.0	5.0	1	-	-	0	500	1.4	1	-	-	0	0	0	1					
16	<i>F. bizanae</i>	Hutchison & Burt-Davy	<i>Urostigma</i>	<i>Galoglychia</i>	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1	0	0	1	1	0	1	0	1	1	0	0	1	1	1	18.0	13.0	8.5	1	1	0	0	750	3.0	0	2.50	-	1	0	0	0					
17	<i>F. faulkneriana</i>	C. C. Berg	<i>Urostigma</i>	<i>Galoglychia</i>	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0	0	1	1	0	30.0	7.0	1.5	1	-	-	0	450	1.2	0	1.50	-	1	0	0	0				
18	<i>F. muelleriana</i>	C. C. Berg	<i>Urostigma</i>	<i>Galoglychia</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	1	0	-	-	-	-	-	-	10.0	6.0	1	-	-	-	570	0.5	1	-	-	1	0	0	0
19	<i>F. angladet</i>	Fischer	<i>Urostigma</i>	<i>Urostigma</i>	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	-	-	-	12.0	8.5	1	-	-	300	1,800	1.6	0	1.60	-	0	1	0	0			

Appendix 3. One-way ANOVA results for comparison of attributes (habitat – yellow, habit – orange, human impact – green, distributional – blue) between threaten, weedy and no status categories (* indicates p-value < 0.05).

		Sum of Squares	df	Mean Square	F	Sig.
Mediterranean woodland	Between Groups	.034	2	.017	13.669	.000
	Within Groups	.964	766	.001		
	Total	.999	768			
Limestone habitat	Between Groups	.004	2	.002	.038	.963
	Within Groups	44.123	766	.058		
	Total	44.127	768			
Heath forest	Between Groups	.000	2	.000	.032	.968
	Within Groups	.999	766	.001		
	Total	.999	768			
Montane forest	Between Groups	1.593	2	.796	3.681	.026
	Within Groups	165.713	766	.216		
	Total	167.306	768			
Lowland evergreen rainforest	Between Groups	3.757	2	1.879	7.669	.001
	Within Groups	187.647	766	.245		
	Total	191.404	768			
Dry forest	Between Groups	.685	2	.343	2.508	.082
	Within Groups	104.670	766	.137		
	Total	105.355	768			
Secondary forest	Between Groups	.426	2	.213	1.885	.152
	Within Groups	86.570	766	.113		
	Total	86.996	768			
Coastal vegetation	Between Groups	.067	2	.033	.332	.718
	Within Groups	77.091	766	.101		
	Total	77.157	768			
Forest Fringes	Between Groups	.019	2	.010	.397	.673
	Within Groups	18.511	766	.024		
	Total	18.531	768			
Open forest	Between Groups	.004	2	.002	.229	.795
	Within Groups	6.932	766	.009		
	Total	6.936	768			
Anthropogenic open habitats	Between Groups	2.801	2	1.400	12.311	.000
	Within Groups	87.134	766	.114		
	Total	89.935	768			
Semidesert	Between Groups	.001	2	.000	.098	.907
	Within Groups	2.988	766	.004		
	Total	2.988	768			
Savannas	Between Groups	.431	2	.215	2.832	.060
	Within Groups	58.243	766	.076		
	Total	58.674	768			
Shrub/bushlands and thickets	Between Groups	.309	2	.155	2.188	.113
	Within Groups	54.164	766	.071		
	Total	54.473	768			
Mangrove forest	Between Groups	.004	2	.002	.229	.795
	Within Groups					
	Total					

	Within Groups	6.932	766	.009		
	Total	6.936	768			
Herbaceous swamps (Marsh)	Between Groups	.027	2	.014	2.653	.071
	Within Groups	3.952	766	.005		
	Total	3.979	768			
Peat swamp forest	Between Groups	.019	2	.010	.497	.609
	Within Groups	14.688	766	.019		
	Total	14.707	768			
Freshwater swamp forest	Between Groups	.087	2	.044	2.452	.087
	Within Groups	13.658	766	.018		
	Total	13.745	768			
Riverine forest	Between Groups	3.098	2	1.549	7.732	.000
	Within Groups	152.860	763	.200		
	Total	155.958	765			
Rheophyte	Between Groups	.053	2	.027	.843	.431
	Within Groups	24.131	763	.032		
	Total	24.184	765			
Lithophyte (grow on rocks/cliffs)	Between Groups	1.574	2	.787	5.790	.003
	Within Groups	103.700	763	.136		
	Total	105.274	765			
Climber/Creeper	Between Groups	.268	2	.134	.941	.391
	Within Groups	109.937	773	.142		
	Total	110.205	775			
Shrub	Between Groups	.023	2	.012	.054	.948
	Within Groups	165.462	770	.215		
	Total	165.485	772			
Tree/Treelet	Between Groups	.163	2	.082	.624	.536
	Within Groups	100.494	769	.131		
	Total	100.657	771			
Hemiepiphytism	Between Groups	1.636	2	.818	4.153	.016
	Within Groups	151.844	771	.197		
	Total	153.479	773			
Buttress	Between Groups	.414	2	.207	2.350	.096
	Within Groups	68.142	773	.088		
	Total	68.557	775			
Stilt/Prop roots	Between Groups	.016	2	.008	.513	.599
	Within Groups	11.799	773	.015		
	Total	11.814	775			
Position of syconia (axillary)	Between Groups	.301	2	.151	1.191	.304
	Within Groups	96.777	765	.127		
	Total	97.078	767			
Syconia on older wood (previous+rami+cauli+flagi)	Between Groups	.722	2	.361	1.457	.234
	Within Groups	189.496	765	.248		
	Total	190.217	767			
Found just below leaves, in previous season's growth	Between Groups	.663	2	.332	1.782	.169
	Within Groups	142.332	765	.186		
	Total	142.995	767			

Ramiflory	Between Groups	.110	2	.055	.583	.558
	Within Groups	72.347	765	.095		
	Total	72.457	767			
Cauliflory	Between Groups	.514	2	.257	1.806	.165
	Within Groups	108.799	765	.142		
	Total	109.313	767			
Flagelliflory/Geocarpic	Between Groups	.061	2	.030	.585	.557
	Within Groups	39.642	765	.052		
	Total	39.703	767			
Solitary	Between Groups	.428	2	.214	.885	.413
	Within Groups	175.221	725	.242		
	Total	175.648	727			
Paired	Between Groups	.947	2	.473	2.325	.099
	Within Groups	147.625	725	.204		
	Total	148.571	727			
Clusters (three or more bunched)	Between Groups	.268	2	.134	.792	.453
	Within Groups	122.920	726	.169		
	Total	123.188	728			
Sexual system	Between Groups	2.063	2	1.032	4.161	.016
	Within Groups	195.113	787	.248		
	Total	197.176	789			
Sessile/Subsessile	Between Groups	1.079	2	.539	2.201	.111
	Within Groups	176.230	719	.245		
	Total	177.309	721			
Timber	Between Groups	2.783	2	1.391	32.121	.000
	Within Groups	34.304	792	.043		
	Total	37.087	794			
Cultivated	Between Groups	19.908	2	9.954	84.331	.000
	Within Groups	93.483	792	.118		
	Total	113.391	794			
African Kingdom	Between Groups	.642	2	.321	2.639	.072
	Within Groups	96.297	792	.122		
	Total	96.938	794			
IndoPacific Kingdom	Between Groups	4.189	2	2.094	9.712	.000
	Within Groups	170.780	792	.216		
	Total	174.969	794			
Australian Kingdom	Between Groups	2.045	2	1.022	19.198	.000
	Within Groups	42.177	792	.053		
	Total	44.221	794			
South America Kingdom	Between Groups	2.923	2	1.461	10.539	.000
	Within Groups	109.812	792	.139		
	Total	112.735	794			

Appendix 4. Scheffe's Multiple Comparison Test results comparing significant attributes from ANOVA (habitat – yellow, habit – orange, human impact – green, distributional – blue) between threaten, weedy and no status categories.

Dependent Variable	(I) Threatened/Weedy Status	(J) Threatened/Weedy Status	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
						Lower Bound	Upper Bound
Montane forest	No Status	Threatened	.262	.108	.054	.00	.53
		Weedy	-.103	.090	.517	-.32	.12
	Threatened	No Status	-.262	.108	.054	-.53	.00
		Weedy	-.365*	.138	.031	-.70	-.03
	Weedy	No Status	.103	.090	.517	-.12	.32
		Threatened	.365*	.138	.031	.03	.70
Lowland evergreen rainforest	No Status	Threatened	-.075	.115	.810	-.36	.21
		Weedy	-.370*	.095	.001	-.60	-.14
	Threatened	No Status	.075	.115	.810	-.21	.36
		Weedy	-.295	.147	.134	-.66	.07
	Weedy	No Status	.370*	.095	.001	.14	.60
		Threatened	.295	.147	.134	-.07	.66
Anthropogenic open habitats	No Status	Threatened	.127	.078	.267	-.06	.32
		Weedy	-.301*	.065	.000	-.46	-.14
	Threatened	No Status	-.127	.078	.267	-.32	.06
		Weedy	-.429*	.100	.000	-.67	-.18
	Weedy	No Status	.301*	.065	.000	.14	.46
		Threatened	.429*	.100	.000	.18	.67
Riverine forest	No Status	Threatened	.063	.104	.830	-.19	.32
		Weedy	-.333*	.086	.001	-.54	-.12
	Threatened	No Status	-.063	.104	.830	-.32	.19
		Weedy	-.397*	.133	.012	-.72	-.07
	Weedy	No Status	.333*	.086	.001	.12	.54
		Threatened	.397*	.133	.012	.07	.72
Lithophyte (grow on rocks/cliffs)	No Status	Threatened	-.056	.086	.807	-.27	.15
		Weedy	-.238*	.071	.004	-.41	-.06
	Threatened	No Status	.056	.086	.807	-.15	.27
		Weedy	-.182	.110	.251	-.45	.09
	Weedy	No Status	.238*	.071	.004	.06	.41
		Threatened	.182	.110	.251	-.09	.45
Hemiepiphyte	No Status	Threatened	.090	.109	.713	-.18	.36
		Weedy	-.234*	.085	.024	-.44	-.02
	Threatened	No Status	-.090	.109	.713	-.36	.18
		Weedy	-.324	.136	.061	-.66	.01
	Weedy	No Status	.234*	.085	.024	.02	.44
		Threatened	.324	.136	.061	-.01	.66
Sexual system	No Status	Threatened	.324*	.119	.025	.03	.62
		Weedy	.098	.096	.595	-.14	.33
	Threatened	No Status	-.324*	.119	.025	-.62	-.03
		Weedy	-.226	.150	.323	-.60	.14

	Weedy	No Status	-.098	.096	.595	-.33	.14
		Threatened	.226	.150	.323	-.14	.60
Timber	No Status	Threatened	.039	.048	.725	-.08	.16
		Weedy	-.318*	.040	.000	-.42	-.22
	Threatened	No Status	-.039	.048	.725	-.16	.08
		Weedy	-.357*	.062	.000	-.51	-.21
Weedy	No Status	.318*	.040	.000	.22	.42	
	Threatened	.357*	.062	.000	.21	.51	
Cultivated	No Status	Threatened	.038	.080	.894	-.16	.23
		Weedy	-.857*	.066	.000	-1.02	-.69
	Threatened	No Status	-.038	.080	.894	-.23	.16
		Weedy	-.895*	.102	.000	-1.15	-.64
	Weedy	No Status	.857*	.066	.000	.69	1.02
		Threatened	.895*	.102	.000	.64	1.15
Indo-Pacific Kingdom	No Status	Threatened	.473*	.108	.000	.21	.74
		Weedy	-.031	.089	.941	-.25	.19
	Threatened	No Status	-.473*	.108	.000	-.74	-.21
		Weedy	-.504*	.138	.001	-.84	-.17
Weedy	No Status	.031	.089	.941	-.19	.25	
	Threatened	.504*	.138	.001	.17	.84	
Australian Kingdom	No Status	Threatened	.051	.054	.638	-.08	.18
		Weedy	-.271*	.044	.000	-.38	-.16
	Threatened	No Status	-.051	.054	.638	-.18	.08
		Weedy	-.321*	.069	.000	-.49	-.15
Weedy	No Status	.271*	.044	.000	.16	.38	
	Threatened	.321*	.069	.000	.15	.49	
South America Kingdom	No Status	Threatened	-.359*	.087	.000	-.57	-.15
		Weedy	.131	.072	.187	-.04	.31
	Threatened	No Status	.359*	.087	.000	.15	.57
		Weedy	.491*	.111	.000	.22	.76
Weedy	No Status	-.131	.072	.187	-.31	.04	
	Threatened	-.491*	.111	.000	-.76	-.22	

*. The mean difference is significant at the 0.05 level.

Appendix 5. Nonparametric Kruskal-Wallis Test results for continuous variables comparing between threaten, weedy and no status categories.

Test Statistics^a

	max height (m)	max leaf length (cm)	max petiole length (cm)	max basal bract length (mm)	max dry fig diameter (cm)	max fresh fig diameter (cm)	max peduncle length (cm)	max stem diameter (mm)
Chi-Square	8.157	11.044	12.395	5.871	6.619	.344	2.838	1.102
df	2	2	2	2	2	2	2	2
Asymp. Sig.	.017	.004	.002	.053	.037	.842	.242	.576

a. Grouping Variable: Threatened/Weedy Status